

R1 EARLY SEED PLANTS

Key Notes

Pteridosperms

The first true seed plants had leaves that resembled ferns. Abundant fossils are known from Devonian to Permian times. Some had one vascular bundle, some several and most had secondary thickening. The female gametophyte resembled that of heterosporous ferns and lycopsids.

Bennettitales and Caytoniales

These groups were common from Triassic to Cretaceous times and resembled the pteridosperms from which they probably descended. The Bennettitales had flower-like reproductive structures, the Caytoniales a cupule surrounding the ovules.

Other fossil seed plants

The Cordaitales, mainly from the Carboniferous period, resemble living conifers of today and may be ancestral to them. They were large trees with strap-like leaves and clustered reproductive structures. There were other seed plant groups without clear affinity.

Related topics

Evolution of the seed (Q4) Cycads, Ginkgo and Gnetales (R3)
Conifers (R2) Evolution of flowering plants (R4)

Pteridosperms

The **pteridosperms**, or ‘seed ferns’, were the earliest seed plants (Topic Q4). They first appear in Devonian rocks and there are abundant fossils from the Carboniferous and Permian periods. They must have been among the dominant plants. Their leaves were large and pinnate like those of ferns. They were trees or climbers, some large, and their stems were varied, some possessing a single vascular strand, others with many vascular strands but, unlike ferns, they had secondary thickening giving rise to tapered trunks. Many details of their anatomy are known and they are divided into several families.

Like all seed plants they were heterosporous retaining the megasporangia (each with one spore) on the leaves. The female gametophyte was multicellular with archegonia similar to those of heterosporous ferns and clubmosses (Topics Q2 and Q3). The integument was variable (Topic Q4). The pollen grains were probably trapped by a drop of fluid by the gap in the integument, as seen in living cycads (Topic R3).

Fossil evidence suggests that their descendants include the extinct Caytoniales and Bennettitales and the living group, the cycads (Topic R2).

Bennettitales and Caytoniales

The Bennettitales had an unbranched or sparingly branched trunk and large pinnate, fern-like leaves like the pteridosperms. They resembled living **cycads** (Topic R2) but differed in details of leaf anatomy. They are abundantly represented in the fossil record from the Triassic to the Cretaceous period. Their reproductive structures were borne on very short separate stems on the trunks, with the ovules towards the tip. The ovules were surrounded by modified leaves bearing the microsporangia (anthers), and these anthers were surrounded

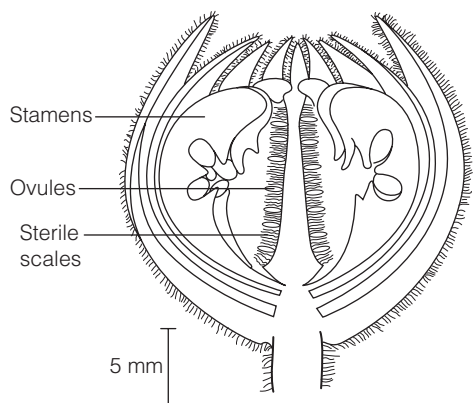


Fig. 1. The hermaphrodite flower-like reproductive structure of fossil *Bennettitales*.

by bracts making the whole structure look remarkably like a flower (Fig. 1). It is likely that some, at least, were insect-pollinated, but this structure probably arose independently from the flowers of the angiosperms.

Another fossil group, the Caytoniales, may be ancestral to the flowering plants, since the ovules, and later the seeds, were surrounded by cup-like outgrowths, known as cupules (Fig. 2), resembling the ovary of flowering plants.

Other fossil seed plants

One of the most abundant fossil seed plant groups in the Carboniferous period was the **Cordaitales**. They were massive trees to 30 m high with simple strap-shaped leaves, often quite large but with simple traces in the vascular system. Their vegetative parts strongly resembled those of some living conifers such as the monkey-puzzle, *Araucaria*, and they may be ancestral to conifers. Male and female reproductive structures were separated onto different shoots, perhaps on the same tree. Shoots of both sexes had overlapping bracts (modified leaves)

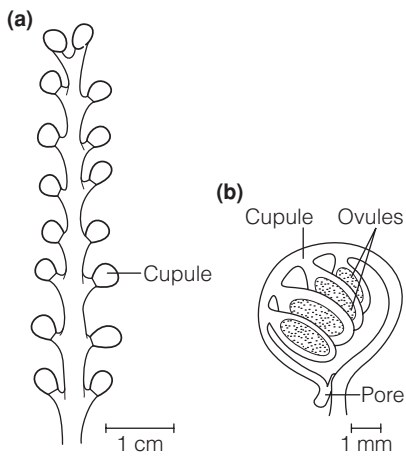


Fig. 2. The female reproductive structure of fossil *Caytoniales* showing cupule surrounding the ovule.

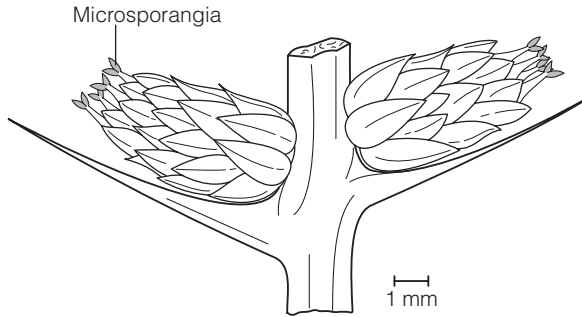


Fig. 3. Cone-like male reproductive structure of the Cordaitales.

with sporangia at their tips (Fig. 3). Their relationships are obscure, perhaps with the pteridosperms, but their leaves resemble microphylls such as possibly those of progymnosperms (Topic Q4). If they are related to the progymnosperms it suggests that Cordaitales and conifers may have developed the seed habit independently from pteridosperms and other groups.

There were several other groups of seed plants found only as fossils that had died out by the end of the Cretaceous period. Five groups of seed plants survive. Of these, the conifers have a fossil history extending right back to the Carboniferous, the cycads to the Triassic and the Ginkgoales as far as the Permian period. The Gnetales and the angiosperms are more recent, probably appearing first in the Jurassic period.

R2 CONIFERS

Key Notes

Ecology and human uses

The conifers comprise about 560 species of woody plants, mainly occurring in temperate and boreal regions. They form extensive forests and include the tallest, oldest and most massive of trees. They are important as sources of timber and wood pulp. Leaves decay slowly and accumulate on the ground forming an acid litter; periodic fires may be characteristic of conifer forests. The fossil record extends to the Carboniferous period.

Stems and roots

The stems resemble those of angiosperms except that the xylem has only tracheids and the phloem only one specialized type of cell, the sieve element. The tracheids have bordered pits in lines. The roots of most have ectomycorrhiza associated with them.

Leaves

The leaves are mostly needle-like or scale-like with a single central vein resembling microphylls but have a vascular trace in the stem. A few are broader and fossil leaves are forked. Resin canals are often present.

Male reproductive structures

Anthers are borne in pairs on the underside of scales forming male cones. The pollen grains usually have air bladders mainly involved with orientation at the micropyle for fertilization. All are wind-pollinated and pollen is produced in enormous quantities. In most conifers, the male gametophyte consists of four cells contained within the pollen grain.

Female reproductive structures

Ovules (megasporangia) are borne on ovule scales in female cones, except for yews that bear seeds individually. The female gametophyte initially has a free nuclear stage before forming cells and archegonia. A drop of fluid is secreted by the micropyle to trap pollen when it is mature.

Fertilization and the seed

Pollen tubes penetrate the archegonium and the largest gamete fertilizes the egg. Several embryos may be formed initially but one occupies the mature seed. It has several cotyledons. Seeds are released by the cone scales separating, and some are an important food source for animals.

Related topics

Meristems and primary tissues (C1) Evolution of the seed (Q4)
Woody stems and secondary growth (C4) Early seed plants (R1)

Ecology and human uses

Conifers, the Pinopsida, are the largest and most important seed plant class except for the flowering plants. Most conifers are trees, a few are shrubs; all are woody. They are found throughout the world but achieve their greatest abundance as the dominant growth form of the boreal forests of the northern hemisphere (Topic K1) with high diversity mainly in western North America

and east Asia. They also cover extensive areas in temperate parts of the southern hemisphere. They are much less common in the tropics with only a few tropical genera, mainly in the mountains. In total there are seven living families and about 560 species. They are the tallest and most massive of trees, at least three species reaching to well over 100 m, all taller than any angiosperm. They can live to a great age and are among the oldest known organisms, with the bristlecone pines of California over 4000 years old and the huon pine of Tasmania possibly reaching $\geq 10\,000$ years of age. Most have specialist reproductive structures, the familiar cones that give the class its name. A few, such as the yew, bear seeds individually. They are an ancient group with fossil conifers first appearing in Carboniferous rocks (see Topic Q1, Table 1).

Conifers are enormously important economically since their wood is widely used for furniture and other constructions and they are one of the main sources of pulp for paper. They have been planted extensively throughout the temperate world, particularly on poor soils, and huge part-managed coniferous forests occur in Eurasia and north America. They are extensively used for ornaments and many are resinous, with the resins widely used in gums and varnishes. Turpentine is derived from pine resin.

The decay of many conifer leaves is slower than their production by the tree, leading to an accumulation of fallen leaves in a conifer forest that can acidify the ground and provide a fire hazard. Periodic fires are characteristic of many conifer woodlands and one of the main ways in which the accumulation of fallen leaves can be removed.

Stems and roots

The stems of conifers are all woody and have xylem made of **tracheids** with no vessels (Topics C1 and C4). There is extensive **secondary thickening** and the secondary tracheids form regular ranks. In temperate species, tracheids that are formed in the spring are wider than later ones resulting in clear annual rings. The tracheids have lines of large circular pits with conspicuous borders in their cell walls. The xylem is interlaced with rays containing living parenchyma cells and sometimes **resin** cells (Topic C4). There are differences in xylem structure between different conifers that are well preserved in fossils, e.g. wood similar to that of the living *Araucaria* (monkey-puzzle and its relatives) first appeared in the Carboniferous; pine-like wood did not appear until the Cretaceous period. The phloem has a simpler structure than that of flowering plants with only one specialized type of cell, an elongated **sieve element** (Topic C1), with parenchyma cells rich in starch and mitochondria next to them. A pith is present in the young stages of stem growth.

Many conifers have a single straight stem with much smaller side branches, giving rise to the characteristic narrow pyramidal shape. The straightness of the stem has greatly helped foresters use the timber. Others, such as most pines, have a much more rounded crown with more even branching, and a few, such as the junipers, are shrubs with gnarled stems or several stems arising from the base.

The roots of conifers resemble those of angiosperms (except that the xylem has only tracheids). **Ectomycorrhizae** (Topic M1) are associated with all except the southern hemisphere families Podocarpaceae and Araucariaceae, and the fungi aid in the decay of the leaf litter. Araucariaceae have endomycorrhizae with a similar function and Podocarpaceae have nodules in their roots like those of legumes (Topic M2).

Leaves

The leaves of living conifers are all simple and most are shaped like **needles**, sometimes long, or **scales**, semicircular or flattened in cross-section. A few southern hemisphere conifers in the Araucariaceae and Podocarpaceae families have larger, broader leaves, up to 5 cm wide; a few fossils show forked leaves. The great majority of conifers retain their leaves throughout the year, each leaf living for 2 years or more, and up to 15 years in *Araucaria*. A few have deciduous leaves, such as the larches (*Larix*) and swamp cypress (*Taxodium*). Leaves are borne either directly on branches or on small pegs or scales and sometimes in bundles or whorls. Some species have two different forms of leaf growing together, needle-like and scale-like (e.g. pines), and some cypresses have needle-like leaves in juvenile stages, with the scale leaves appearing later. In the pines, the coast redwood (*Sequoia*) and some others, the small leaf-bearing lateral branches are shed with the leaves.

The leaf structure resembles that of flowering plants (Topic C5) with a thick cuticle, palisade and spongy mesophyll, but all conifers have simple leaf venation, either with one central vein or a few parallel veins. In this they resemble **microphylls** (Topics Q1 and R1), although the traces in the stem vascular tissue are not similar to those of clubmosses and other microphyll-bearing plants, and their origin remains anomalous. Most conifers have **resin** canals throughout the mesophyll, this resin consisting of acidic phenols, terpenes and other complex molecules. It can be present in large quantities and may protect the leaves from insect attack and make the leaves resistant to decay. A few conifers have other aromatic oils in their leaves, e.g. *Thuja*, giving characteristic scents, often species-specific, when the leaves are crushed.

Male reproductive structures

The **microsporangia**, or anthers, are borne on the underside of specialized fertile leaves in short strobili (**cones**) (Fig. 1). These leaves often have expanded tips to which the anthers are attached. There are two anthers per fertile leaf in many

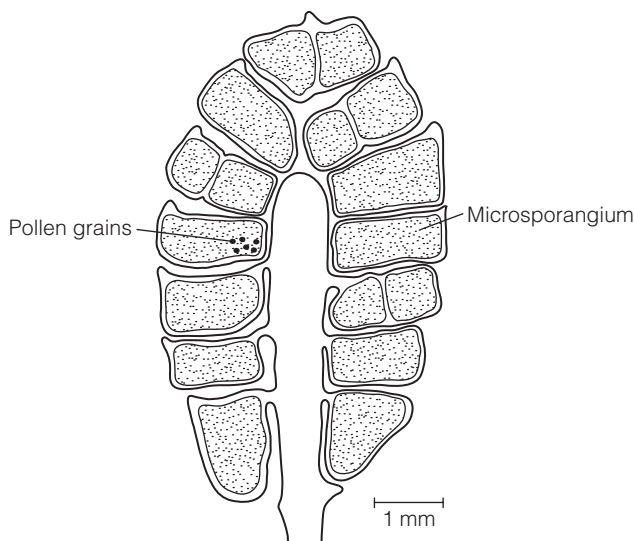


Fig. 1. Cross section of a male cone of a pine, *Pinus*.

conifers but in some there are more. The cones themselves are produced in the axils of scale-leaves in pines, or at the tips of lateral shoots in other families.

The anthers have a thin wall, of one or a few cell layers. The outer cells have uneven thickening, in rings or a reticulate pattern, which are involved in dehiscence. They take about a year to develop to maturity and to release the pollen. The pollen grains resemble those of flowering plants except that pines and some other conifers have characteristic air bladders formed from an extension of the outer pollen wall giving a most distinctive appearance (Fig. 2). These bladders may aid with wind dispersal but are mainly involved with the orientation of the pollen as it fertilizes the ovules. All conifers are wind-pollinated and pollen can be produced in enormous quantities, frequently coming off in visible clouds when the cones are mature. By lakes they can form yellowish lines in the water or 'tide-lines' as the water recedes.

The male gametophyte is much reduced and formed within the outer wall of the pollen grain. The largest male gametophytes are found in *Agathis*, the southern hemisphere white pines of the Araucariaceae family that have a male prothallus with up to 40 cells. In pines there are four cells by the time the pollen is shed, two vegetative prothallus cells, the pollen tube nucleus and the generative cell. The generative cell gives rise to a sterile cell and two unequal sized sperm cells (after another division). In the cypresses there are no vegetative cells at all, only the generative cell and tube nucleus. In all conifers the sperms have no flagellum and are not motile.

Female reproductive structures

The female reproductive branch is the familiar pine or fir cone (Fig. 3). It has two ovules attached to each fertile scale leaf, but the cone differs markedly from the male in that each fertile scale has a bract underneath it, in some partially fused with the ovule scale. This, and evidence from fossil conifers, suggests that the cone is a compound structure with each fertile scale derived from a whole shoot. The cone can take 2 years to mature. A few conifers, notably the **yew** and its relatives, Taxaceae, do not have cones and the ovule is solitary, borne at the tip of a minute shoot in the leaf axils.

The megasporangium (Topic R1) has a single integument, and four megaspores are produced, though only one is functional. The megaspore starts to divide to produce the megagametophyte at an early stage, and in northern species there is usually a dormant period in the first winter. Eventually many free nuclei are produced and cell walls form once there are around 2000 nuclei. Between one and six archegonia are produced next to the **micropyle** (Topic D1) and, in these, the egg is surrounded by neck cells and a canal cell as in other vascular plants and bryophytes (Topic P4).

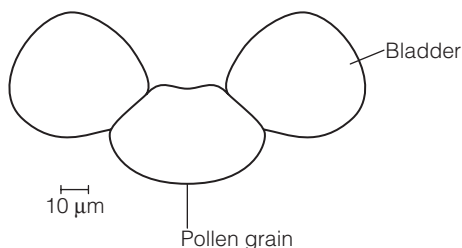


Fig. 2. Pollen grain of a pine, showing bladders.

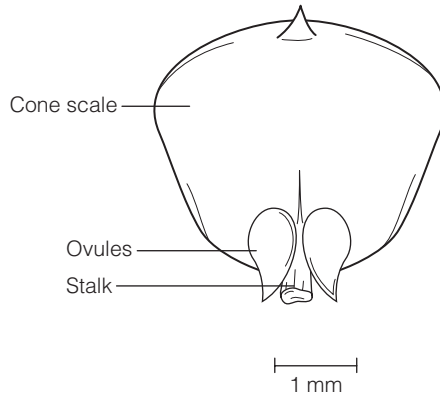


Fig. 3. Surface view of a scale from the female cone of a pine, showing two ovules at its base.

When the ovule is receptive, the cone scales open apart slightly and a drop of sticky liquid is exuded from the micropyle. Pollen grains are caught in this drop which is then reabsorbed, and after pollination the cone scales may close up again. The air bladders on the pollen grains serve to orient the pollen grain as it approaches the micropyle.

Fertilization and the seed

Once a pollen grain has reached the micropyle, the two male **gametes** are formed and the pollen tube grows actively through the nucellus to reach the archegonia. The male gametes are discharged into the egg along with the tube nucleus and the sterile nucleus. Fertilization is achieved by the fusion of the larger of the male gametes with the egg nucleus, the other three male nuclei degenerating.

If more than one archegonium has been fertilized several **embryos** may be formed, and each fertilized egg may divide to form several embryos, so competition can occur. Eventually, one embryo outcompetes the others and absorbs the nutrients from the female gametophyte, filling the seed when it is mature. The embryo has several **cotyledons** (the food stores and first leaves; Topic D3). In most conifers the seeds are released when the cone scales separate at maturity. The seeds may be nutritious and can be a major food for some birds, such as crossbills, and small mammals. Some species have a resistant integument that allows the seed to lie dormant, and a few only germinate after a fire has passed over them. The **yew** has a fleshy outgrowth from the integument which is attractive to birds.

In comparison with most flowering plants the stages of reproduction are slow, taking about a year from female cones being receptive to the mature seed, but in pines fertilization does not occur until a year after the female cones become receptive and the cycle takes 2 years.

R3 CYCADS, GINKGO AND GNETALES

Key Notes

Cycads

There are about 76 species of cycads of the tropics and subtropics, the nearest living relatives of the pteridosperms. They have stout trunks with a pith and little secondary thickening, usually unbranched, and long pinnate leaves, interspersed with scale leaves.

Reproduction in cycads

All are dioecious, bearing either male or female fertile leaves, usually in cones. The sporangia are in pairs or groups. Pollen grains have three cells when released and produce two enormous flagellate sperm after they have reached the pollination drop by the ovules. The female gametophyte has many cells and archegonia. Fertilization can take 5 months from pollination.

Ginkgo

One species, *Ginkgo biloba*, is the survivor of an ancient group. It is a tall ornamental tree with unique fan-shaped leaves and secondary thickening in the trunk.

Reproduction in ginkgo

Ginkgo is dioecious with male sporangia in catkin-like cones and ovules in pairs. The pollen has four nuclei on dispersal, and, at fertilization, produces two flagellate sperms. Fertilization takes 5 months.

Gnetales

Two genera of trees shrubs and climbers, *Gnetum*, *Ephedra* and the unique desert plant *Welwitschia* make up the group. They have vessel-like xylem cells and phloem resembling that of angiosperms.

Reproduction in the Gnetales

They are dioecious or monoecious and the sporangia are borne in pairs or whorls. Pollen grains have two to five cells and produce two non-flagellate sperms when they reach the pollination drop. This drop may attract insects for pollination. Two eggs are fertilized, paralleling the double fertilization in angiosperms, although one embryo aborts.

Related topics

Pollen and ovules (D2)
Early seed plants (R1)

Conifers (R2)
Evolution of flowering plants (R4)

Cycads

The cycads, Cycadales, are a group of palm-like plants that are the nearest living relatives to the pteridosperms. Their current distribution ranges from southern North America to Chile (about 36 species), South Africa (15 spp.) and eastern Asia to Australia (25 spp.), but fossils are much more widespread, and between the Triassic and Cretaceous periods they were more abundant and varied. All are woody, slow-growing plants with large pinnate leaves in a cluster at the tip, occupying understorey positions in plant communities, though common in

places. The trunks are thick, normally unbranched, and typically to about 2 m tall, though a few grow to 15 m and a few have branched horizontal stems with leaf rosettes at ground level. They have a large central pith, restricted secondary thickening and a cortex. Scale leaves occur interspersed with the foliage leaves and can cover part of the trunk. Age can be inferred from the leaf scars and they can live to 1000 years or more. They have a deep tap root and surface roots often associating with cyanobacteria and fungi which probably aid in nutrition (Topics M1 and M2). The starchy central pith is eaten in some places as sago (the main sago plants are palms) and some species are grown as ornamentals.

Reproduction in cycads

All cycads are dioecious and most produce reproductive structures on specialized leaves in terminal or lateral **cones** (Fig. 1). These cones can be enormous, weighing up to 40 kg. The anthers are borne on the underside of thick, scale-like leaves. The male gametophyte grows first within the wall of the pollen grain. The pollen is released when the gametophyte has three cells. The pollen grain bursts once it has reached a drop of fluid by the micropyle of an ovule, and the cells divide to give rise to two or more sperms (one genus, *Microcycas*, has up to 16 sperms). The sperms are like those of ferns in that they have numerous flagella and swim actively to fertilize the ovules, but they are about 1000 times the size of fern sperms.

The ovules vary from 6 mm to 6 cm in diameter and are borne in pairs, or as six or eight together, on large scale-leaves. The female gametophyte, developing entirely within the ovule wall, first has free nuclear divisions and later forms cell walls when there are 1000 or more nuclei. Archegonia are formed by the micropyle with a single ventral canal cell above an egg that is the largest among land plants, up to 3 mm in diameter. A pollination drop is secreted by the

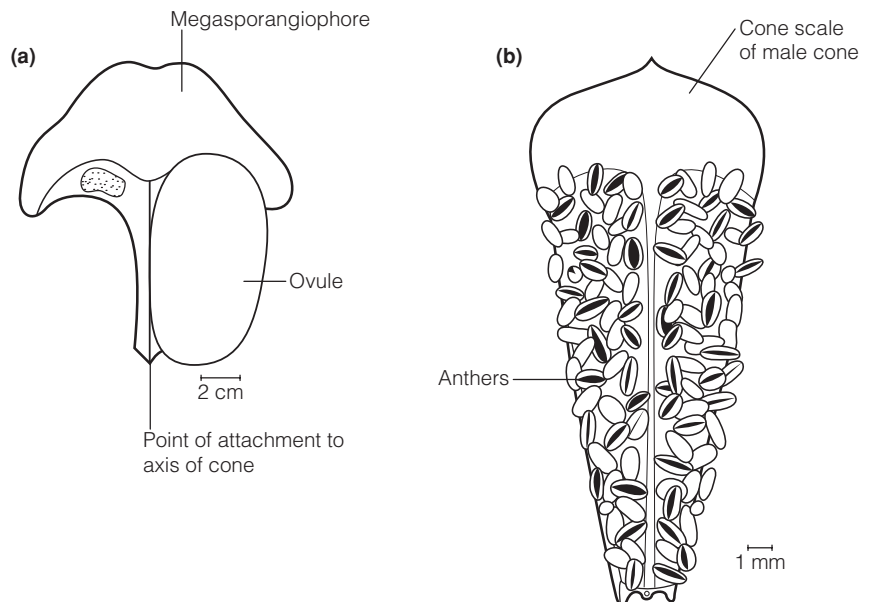


Fig. 1. Cone scales of cycads: (a) female scale; (b) male scale with anthers. (Redrawn from Bell PR and Hemsley AR (2000). Green Plants, 2nd edn. Cambridge University Press.)

micropyle containing sugars and amino acids, and the pollen is trapped in this. Some cycads are pollinated by insects, mainly weevils, so the drop is an attractant as well as a pollen trap; others may be wind-pollinated. The whole process of fertilization in cycads takes about 5 months. Once fertilized, the ovule grows quickly, again with a period of free nuclear divisions first, absorbing the female gametophyte tissue. One, two or three cotyledons are formed and the seed germinates as soon as there are favorable conditions.

Ginkgo

The ginkgo or maidenhair tree, *Ginkgo biloba*, is the sole living member of the Ginkgoales and is a truly astonishing survivor. It is native of China but only survives in cultivation and has now been planted throughout the temperate world, particularly in towns where it is resistant to pollution and insect attack. The seeds are eaten in Japan and China. It resembles conifers in its vegetative structure and cycads in its reproduction, but it has several unique features. It is a tall, elegant, deciduous tree with a unique leaf shaped like a notched fan which turns bright yellow in autumn. Similar leaves are found in Jurassic deposits from many sites and even Triassic deposits from about 200 million years ago. The trunk has secondary thickening and the tracheids have bordered pits in a single row (Topic C4); in this it resembles conifers. Characteristically, it has long shoots with numerous leaves and short shoots bearing leaf whorls and the reproductive structures.

Reproduction in ginkgo

Ginkgo is dioecious. The male cones resemble small catkins and are made up of scale leaves, each of which bears two anthers on its underside. Each pollen grain contains four cells of the male gametophyte by the time it is shed. It is dispersed by the wind until caught in the pollination drop of a female plant, which then retracts the drop drawing the pollen into the ovule. There the pollen grain bursts, pollen tubes are produced and two more cell divisions of one of the four cells give rise to two sperms. These have many flagella, like those of cycads although the cells are smaller, and swim to the egg cell.

The ovules are borne in pairs on stalks from the leaf axils on short shoots (Fig. 2). The female gametophyte, like cycads, has a free nuclear stage which forms cell walls once several thousand nuclei are present. There are chloroplasts in the

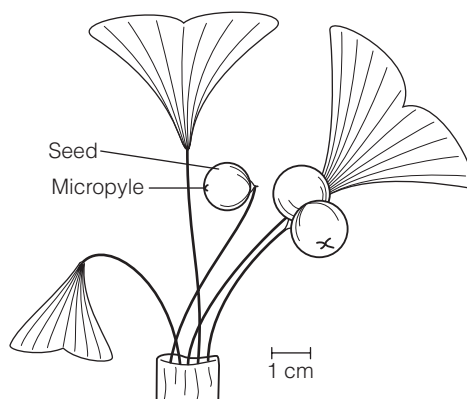


Fig. 2. Shoot of a female ginkgo, showing developing seeds.

female gametophyte. Two archegonia are formed, each with a neck of four cells, a canal cell and an egg. By the time the pollination drop is retracted into the ovule there is a small chamber for the male gametophyte to grow. As in cycads, the time from pollination to fertilization can take about 5 months. After fertilization, one of the pair of ovules usually grows to about 2 cm in diameter and the outer part of the integument becomes fleshy and smells of rancid butter. The embryo, as in cycads, develops a free nuclear stage before cell walls develop and two cotyledons are produced.

Gnetales

The Gnetales comprise three rather disparate genera, *Gnetum*, *Ephedra* and *Welwitschia*. *Gnetum* comprises about 40 species of climbers and small trees in tropical rainforests of South America, Africa and south-east Asia. They closely resemble angiosperms except in their reproductive structures, and their leaves are almost identical to those of a dicotyledonous angiosperm. One species is cultivated for its edible seeds in Asia. *Ephedra* has 40 species of much-branched shrubs, with a few small trees and climbers, in arid warm temperate parts of Eurasia, north Africa and North and South America. They have photosynthetic stems with whorls of scale leaves. *Ephedra* provides the important drug ephedrin. *Welwitschia* has a single extraordinary species confined to the deserts of south-western Africa. It is unlike any other plant in that it produces a woody central crown at the top of a mainly underground stem, from which two leaves grow continuously, fraying at the ends and splitting. In mature plants, which can live for more than 1000 years, these can reach 3 m or more long and 1 m wide.

The Gnetales, unlike any other seed plants except angiosperms, have xylem with cells with such large pits that they can be described as vessels, and phloem with cells associated with sieve elements resembling companion cells. On morphological grounds they have been considered to be closely related to the angiosperms, but molecular studies suggest that they are closer to conifers and other gymnosperms and that the similarities in anatomy have arisen independently.

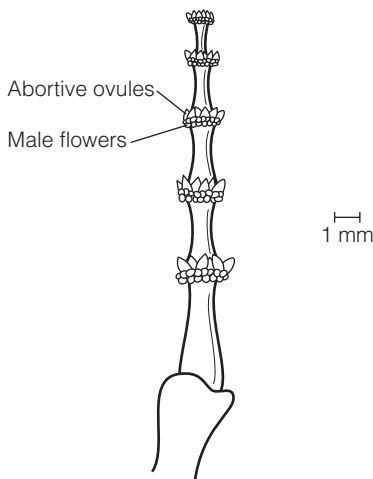


Fig. 3. Male cone of *Gnetum*.

Reproduction in the Gnetales

Male and female organs are borne in separate cone-like structures (Fig. 3), usually on separate plants, although a few species are monoecious. The anthers are borne in pairs or small groups on stalks in the axils of scale-like leaves (bracts). Sterile ovules may occur in these male cones but fertile ones are in separate cones, again in pairs or whorls.

The pollen grains contain two (*Welwitschia*), three (*Gnetum*) or five cells (*Ephedra*) of the male gametophyte by the time they are shed. The female gametophyte has a free nuclear stage as in other gymnosperms. In *Ephedra*, two archegonia are formed with many neck cells, but these are not differentiated in *Gnetum* or *Welwitschia*. The ovules, including sterile ones in the male cones, secrete a sugary pollination drop by the micropyle attractive to insects and the pollen is dispersed by insects or wind, to be caught in this fluid. There the pollen grains burst and one of the cells divides into two non-motile sperms to fertilize the egg. By the time the pollen reaches the egg in *Ephedra* (and perhaps others) the egg has also divided and each sperm fertilizes an egg, but one of the eggs aborts. The interval between pollination and fertilization is only about 1 day, in marked contrast to cycads and ginkgo. The double fertilization of Gnetales has parallels with that in angiosperms and may suggest how that originated (Topics D2 and R4).

In the developing embryo, only *Ephedra* has free nuclear divisions, the other two genera developing cells immediately. Many embryos may be formed initially but only one with two cotyledons is present in the ripe seed. Mature seeds may have a fleshy integument or surrounding bracts or develop wings for dispersal by wind.

R4 EVOLUTION OF FLOWERING PLANTS

Key Notes

Origin of the flower

The fertile parts of a flower are a further reduction from those of other seed plants. The anther is simple and the male gametophyte consists of a pollen tube nucleus and two sperm nuclei. The ovule is enclosed by a carpel and the female gametophyte is reduced to an embryo sac. Fertilization of the endosperm is unique to angiosperms.

The earliest flowering plants

The earliest known fossils come from the early Cretaceous and resemble pollen grains of living Chloranthaceae. DNA evidence suggests that a shrub, *Amborella*, and water-lilies diverged first in angiosperm evolution. These plants share features and it is likely that the primitive flowers were mainly small but variable in size with few but indefinite numbers of fertile parts, some hermaphrodite, other unisexual. Some had a bract. A range of large and small flowers appeared soon after.

Early evolution

The sepals derive from a whorl of leaves around the fertile parts. Some petals derived from sterile stamens, others from a second whorl of sepals. There were two main lines of evolution, one to large flowers and specialist insect pollination, mainly by beetles, the other to small flowers in inflorescences pollinated by wind. Subsequent developments led to smaller flowers with floral parts in fives or threes.

Later evolution

In the late Cretaceous/early Tertiary period, flowering plants radiated to dominate the world, in conjunction with specialist flower-feeding insects. Innovations included fused petals, carpels inserted below the petals and bilateral symmetry. Some had inflorescences. Wind-pollination evolved many times. Most modern plant families appeared.

Specialization in flowers

A few plants are specialized to one or a few pollinator species. The orchids may attract just one species of bee and figs can only be visited by one group of wasps with which they have a close interdependent relationship. Generalization in pollination is much more common.

Evolution of vegetative structure

Flowering plants are enormously variable in vegetative structure, but the earliest were probably shrubs from which developed trees and herbaceous plants. Vessels appeared early but a few families have none. Dicot leaves are mainly net-veined, many monocot leaves parallel veined, but there are exceptions and some variable families.

Evolution of fruits and seeds

Primitive fruits are likely to have been fleshy and seeds filled with endosperm. Many fruit and seed types have evolved in parallel in different families. Major trends have been towards reduction in size of fruit and seed number, and towards seeds with a large embryo and little or no endosperm at maturity.

Classification	The distinctions between plant families are based mainly on flower form but there are often associated fruit and vegetative characters. Some large families vary little; some, particularly those with primitive features, vary more. The two main divisions, monocots and dicots, are confirmed by molecular evidence, except for those families that branched off early in evolution, now known as primitive dicots.	
Three families of plants	As examples of features on which the classification is based, the daisies, grasses and orchids are all large important families each with many unifying features.	
Related topics	The flower (D1) Fruits (D4) Ecology of flowering and pollination (L1)	Cycads, ginkgo and gnetales (R3) Mechanisms of evolution (R5)

Origin of the flower

The flower of an angiosperm (Topic D1) represents a further reduction and specialization of the heterosporous form discussed in relation to the other seed plants. The anther is simpler than that of the Bennettitales or Gnetales (Topics R1 and R3); the ‘fertile leaf’ is, in most, a simple stalk or **filament**. The male gametophyte is always reduced to a total of three cells (Topic D2). The origin of the carpel surrounding the ovules is obscure but it may be a modified leaf, or a cupule as in the Caytoniales (Topic R1). In nearly all angiosperms the ovary completely encloses the ovules. The carpel also has a stigma and usually a style joining this to the ovary. The carpel may have evolved in response to insect visitation of the flowers, perhaps as protection for the vulnerable and nutritious ovule. Insects could transfer pollen to other flowers and **insect pollination** is thought to be the primitive pollination type in angiosperms.

The female gametophyte that develops within the ovule, known as the **embryo sac**, is much reduced compared with other seed plants (Topic D2). No archegonia are produced and, in many, nuclei are formed without cell walls. From pollination to fertilization in angiosperms takes a few hours and, in contrast to all other seed plants, the **double fertilization** leads to growth of the endosperm as the seed’s food store. This means that the food store only grows in fertilized seeds, potentially saving resources. In all other seed plants the female gametophyte provides the food store.

The earliest flowering plants

The earliest evidence of flowering plants is fossil pollen grains and fragmentary flowers and fruits from lower **Cretaceous** rocks, about 110 million years old (some 130 million year old fragments may be angiosperms), suggesting that flowering plants evolved some time in the **Jurassic**, perhaps 150 million years ago, long after the other seed plant groups (see Topic Q1, Table 1). The fossil record is always fragmentary and the conditions for preservation such that only certain plants are likely to be preserved, e.g. those living by water or acid peat. Small or isolated plant populations, which are likely to be particularly significant in evolution (Topic R5) are not likely to be well preserved.

The pollen and form of the flower of the earliest fossils are similar to those of living members of the **Chloranthaceae**, a small family from tropical America, east Asia and New Zealand. The flowers of these plants are simple and tiny, up

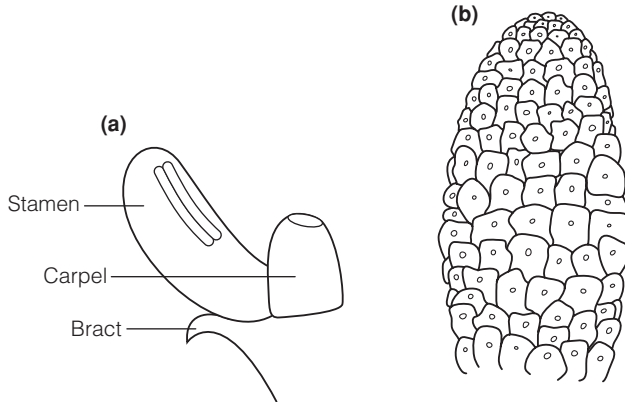


Fig. 1. Flowers of living members of the Chloranthaceae. (a) Hermaphrodite flower of *Sarcandra*, (b) inflorescence of male flowers of *Hedysosmum* (from Endress P, (1994) *Diversity and Evolutionary Biology of Tropical Flowers*, Cambridge University Press).

to 3 mm long, some genera bearing hermaphrodite flowers, others unisexual, borne in inflorescences (Fig. 1). Each flower contains one or three stamens and/or one carpel and some have a bract (small modified leaf) under them. They have no petals or sepals. Hermaphrodite species are pollinated by unspecialized insects; unisexual species by the wind. Several other living plant families are represented as fossils in slightly younger rocks, with a wide range of flower structure from large-flowered magnolias to catkin-bearing trees such as the planes. In some of these the flower structure is not rigidly set, and they have variable numbers of stamens and carpels surrounded by a **perianth**, i.e. modified leaves or bracts not clearly sepals or petals.

Over the last few years, **DNA** from genes in the nucleus, plasmids and mitochondria of many angiosperms has been analyzed. Putting all the molecular evidence together it appears that a shrub, *Amborella*, from New Caledonia that bears unisexual flowers, and the **water-lilies**, which are herbaceous aquatics bearing large hermaphrodite flowers, diverged from the other angiosperms earlier than any other group. Both of these have numerous stamens and an indefinite number of perianth segments. The Chloranthaceae and its relatives are, on this evidence, closer to other families.

Whatever the most primitive plant is, it is likely that the earliest flowers had certain features since these are shared by all the plants mentioned above and are consistent with the fossil record. There was a **variable number** of stamens and carpels, each separate and inserted above the perianth where this was present. **Unisexual** and **hermaphrodite** forms appeared early, and some had a perianth or bracts underneath the fertile parts but no well-defined petals or sepals. They are likely to have been visited and pollinated by unspecialized beetles, flies and wasps, though wind-pollination probably arose early on. They were small **shrubs** and perhaps herbs among dominant gymnosperms.

Early evolution

Adaptive radiation of flowering plants, i.e. their spread and diversification, occurred through the Cretaceous period in parallel with other seed plant groups and some living families appeared. Outer whorls of the flower became differentiated early on, the outermost layer, referred to as sepals even if there is only

one whorl, probably evolving from bracts. When there are two different whorls, the inner whorl is referred to as the petals, but some probably evolved from a second whorl of sepals, others from stamens losing their anthers and becoming organs purely for attracting insects. Some water lilies have intermediate organs, stamens with flattened colored filaments, between the fertile stamens and larger entirely sterile petals. Cultivated ‘double’ flowers such as roses have some stamens replaced by petals (Topic N4). One main early line of evolution was towards a fixed number in each whorl, often five in the dicots and three in the monocots, making the flowers radially symmetrical (**actinomorphic**).

There was specialization for pollination, by beetles along one line of evolution including the magnolias, and by wind along another leading to the catkin-bearing trees. The insect-pollinated group had hermaphrodite flowers of, at first, increasing size and complexity, though later insect-pollinated flowers are smaller. By the end of the Cretaceous period, many families with actinomorphic insect-pollinated flowers had appeared, such as buttercups, pinks and heathers. The wind-pollinated group retained small unisexual flowers, with few parts borne in inflorescences, usually with male and female on the same plant. This **monoecious** breeding system (Topic H2) includes less than 5% of living species but several of these are dominants such as the oaks and beeches, birches, hazels and planes.

Later evolution

At the end of the Cretaceous and beginning of the **Tertiary** period, between 75 and 50 million years ago, there was a second and much larger adaptive radiation which saw the increasing dominance of the angiosperms and the appearance of the majority of modern plant families. This was closely associated with the adaptive radiation of specialist insect pollinators and leaf feeders, the butterflies and moths, long-tongued flies and bees. Innovations included the fusion of the lower part of the petals and/or the sepals into a tube and the fusion of the carpels. Bilaterally symmetrical, or **zygomorphic**, flowers appeared, usually facing sideways rather than upwards and with the lower petal(s) forming a lip as a landing platform for insects. Some flowers such as members of the thyme family have fused petals and zygomorphic flowers (Fig. 2). These were adaptations for specialist insect pollination and at least in part serve to exclude other visitors. Adaptations for pollination by birds or bats appeared later, mainly derived from specialist insect-pollinated flowers. The main trends are outlined in Table 1.

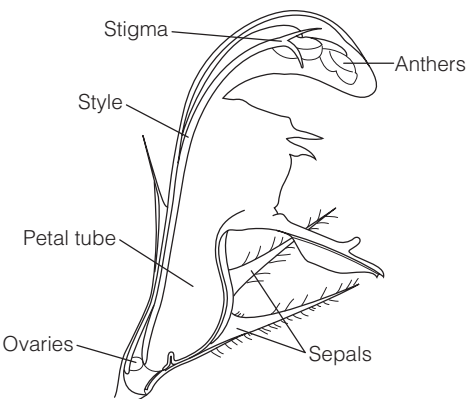


Fig. 2. Flower of dead-nettle, *Lamium* (Lamiaceae), showing zygomorphy and fused petals.

Table 1. Evolutionary trends in flowers from the end of the Cretaceous to the early Tertiary period

Radial symmetry → bilateral symmetry
Separate petals → fused petals
Large numbers of floral parts → fixed small numbers of parts
Large flowers → small flowers
Carpels inserted above the petals → carpels inserted below the petals
Carpels free → carpels fused
Flowers with pollen as food reward → flowers with nectar as food reward
Pollination by unspecialized insects → pollination by specialized bees; butterflies/moths; long-tongued flies; birds or bats
In insect-pollinated species, hermaphrodite flowers → unisexual flowers
Insect-pollinated species → wind-pollinated species

Many trends occurred in parallel in different families; some also happened in reverse.

Aggregation of flowers into **inflorescences** is an adaptive trend in many plant families. It is taken to extreme specialization in the daisy family in which there are often two different forms of flower in each inflorescence, the whole aggregation, sometimes of more than 100 flowers, resembling a single flower (Fig. 3).

Specialization for wind-pollination has nearly always involved a reduction in size and numbers of floral parts. Some families are nearly all wind-pollinated, e.g. grasses, but wind-pollinated species occur in numerous mainly insect-pollinated families and have evolved many times. Evolution in the reverse direction, from wind to insect-pollination has rarely occurred.

Specialization in flowers

A few flowers show extremes of specialization in their pollination. In many orchids, each flower needs a single visit for the successful pollination of hundreds of seeds, so they can become highly selective in the species that they use. Some tropical species have a long spur growing out of the back of the flower with nectar at its base, which only moths with extremely long thin

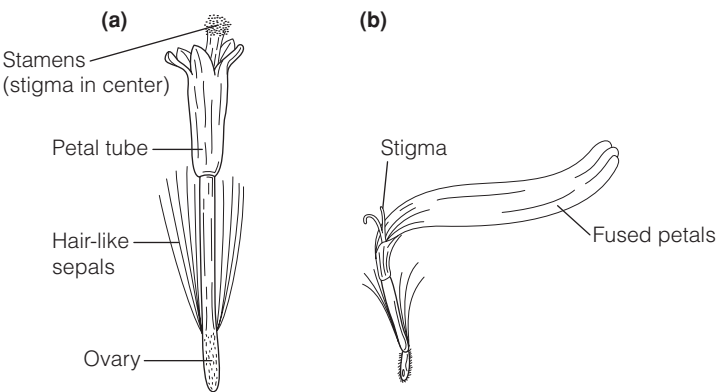


Fig. 3. Florets from the composite inflorescence of a daisy: (a) hermaphrodite disc floret; (b) female ray floret.

Evolution of vegetative structure

tongues can reach. The European bee orchid group, and a few other groups of orchids in other parts of the world, have flowers that resemble the female bee, both in looks and in scent, each orchid species resembling a different bee; they are visited and successfully pollinated by the males of that bee species.

The figs, a large and important group of tropical trees and ‘stranglers’ (Topic K2) have flowers in an inverted inflorescence with flowers opening into a central cavity, surrounded by a solid mass (Fig. 4). The inflorescences can only be penetrated by small wasps through a hole at the tip. The wasps lay their eggs, grow and mate in the inflorescences before collecting pollen and dispersing to another fig. Plant and wasp are totally interdependent. There is a similar interdependence between yuccas and moths, but otherwise such specialization is rare.

More generalist flowers are much more common than the specialists, particularly among the dominant vegetation, which are usually pollinated either by wind or by a range of insects and sometimes birds as well. Pollinating insects (and other animals) can vary manyfold in numbers from year to year and place to place, so specialization to one or a few species can be risky.

There is a great range of vegetative form from tall long-lived trees (although none grows as tall or lives as long as certain conifers) to short-lived plants (Topic K2). They may float in fresh water without attachment to any soil or spread by underground rhizomes to cover a large area. Their leaves range from minute duckweeds measuring around 1 mm in diameter, to some palm leaves that can exceed 15 m in length, or they may be reduced to spines or absent. Most woody plants are dicots and have secondary thickening (Topic C4). Palms, bamboos and some other monocots have numerous separate vascular bundles and most only start to produce a trunk when the bud has grown broad at ground level; their trunk often tapers only slightly or not at all. In a few monocot trees, the vascular bundles line up and they have some secondary thickening. Evidence for the direction of evolution in these plants is thin, and vegetative form is flexible, many families containing a wide variety of form and leaf shape. The earliest flowering plants and their living representatives are mainly shrubs or trees and all living gymnosperms are woody. It is likely that herbaceous plants are derived from woody forms originally, but some woody

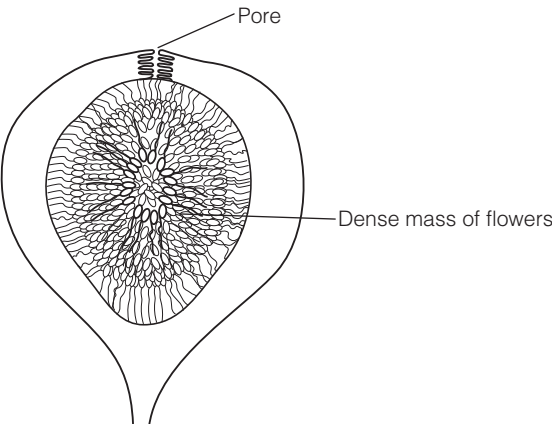


Fig. 4. Inverted inflorescence of a fig.

plants, including monocot trees, may be secondarily evolved from herbaceous plants. Short-lived plants are the end-points of the reduction.

Xylem vessels evolved early on, but a few angiosperms including *Amborella* and the Winteraceae, a family with flowers retaining many primitive features, have none and in water-lilies the xylem cells are somewhat intermediate between tracheids and vessels.

Dicot leaves are mostly net-veined, the veins joining together in many places. Among monocots there is great variation, although many have spear-shaped leaves with parallel veins. Some monocot families, especially the arum family, have enormous variation in leaf shape, with net venation like the dicots and some even developing holes in the leaf such as the 'swiss-cheese plant', *Monstera*, popular as a house plant.

Evolution of fruits and seeds

There is some dispute over which fruit type is primitive; fossil evidence gives few clues, but it is likely that the early fruits were fleshy as many of the representatives of primitive groups have fleshy fruits, sometimes with outgrowths from the seed (an **aril**). Trends in the evolution of fruits have gone in many directions, towards larger or smaller fruits or seeds, and towards dry dehiscent fruits, but one main trend appears to have been for a reduction in size and in number of seeds per fruit. There has been a **parallel evolution** of fruit types in many plant families, i.e. evolution along similar paths in unrelated groups.

Primitive seeds are likely to have been fairly large and rich in endosperm, features retained in some specialized large-seeded plants such as the coconuts. The small seeds, mainly filled by the embryo, that are seen in many families are likely to be derived. Some of the most successful families such as the grass and daisy families have one-seeded fruits, but another large family, the orchids, have many hundreds or thousands of tiny seeds per pod.

Classification

Classification of flowering plants is mainly based on the form of the flower, as this is regarded as a **conservative** character (one that does not change fast in evolution; often a suite of connected characters). Frequently it is correlated with the structure of fruits and vegetative form. Many plant families are defined by the shape and orientation of the flowers, and some large families have remarkably uniform flowers and growth form. Some families, particularly those with primitive features, are more varied but classified together because of a suite of characters, e.g. the buttercup family. Some of the relationships between families are obscure, particularly among those with primitive features.

Flowering plants have long been classified as two main divisions based on morphological characters: **dicots**, comprising about 70% of angiosperms, and **monocots** comprising the other 30%. The groupings are largely supported by molecular studies into their relationships, except for the group of families that retain primitive features, comprising about 5% of angiosperm species including water-lilies, magnolias and Chloranthaceae. These form a disparate group of more or less related families that diverged from the main angiosperm line earlier than the monocot/dicot split. They are now known as **primitive dicots**.

Three families of plants

To illustrate the unifying features that are used to place plants in different families, examples of three large and important families are given.

Daisy family (Asteraceae or Compositae)

The daisy family has over 20 000 species, all with specialized inflorescences of tiny flowers (Fig. 3) each maturing one seed. They are unspecialized in their pollination but many are extremely attractive to bees, butterflies and other flower visitors. Fruits are dry and small and many are effectively dispersed by the wind using a cottony sail. They are mostly herbaceous with very few small trees, perhaps primitive in the family. They are associated particularly with dry regions and many have a deep tap root, but they flourish everywhere.

Grass family (Poaceae or Gramineae)

The grass family has about 9000 species and dominates large areas of the world. Grasses are entirely wind-pollinated except for one or two secondarily adapted to insect pollination. The fruit is one-seeded and dry, dispersed by wind or sticking to animals. All are herbaceous except for the bamboo group which have a most unusual woody form. Growth is not from the stem tip but from nodes on the stem allowing particular tolerance of grazing and fire (Topic K2).

Orchid family (Orchidaceae)

The orchid family has over 25 000 species. Their flowers have three sepals and three petals, one looking different from the others forming a lip. Their pollen is dispersed in aggregations (pollinia), and many species are adapted to one or a few insect species, usually bees. Many provide unusual food rewards such as oil or scent, or no food reward, deceiving their pollinators. The fruit is a pod with huge numbers of microscopic seeds deriving from one or few pollinations. All are herbaceous with specialist mycorrhizal infection in their roots and many are epiphytic (Topic K2).

R5 MECHANISMS OF EVOLUTION

Key Notes

Isolating mechanisms	Plants become isolated geographically or ecologically and can diverge. In any one place physiological barriers, barriers to pollination or chromosomal changes, especially polyploidy, can lead to isolation. The different forms may be known as varieties, subspecies or species depending on the degree of difference and the distribution.	
Breakdown of isolating mechanisms	Environmental change or a second colonization can lead to reconnection and a breakdown of any distinction. Many plants can hybridize with related species, the hybrids sometimes being sterile or partially sterile and often less well adapted than their parent species. Natural selection normally favors a physiological breeding barrier between species.	
Polyploidy	If the chromosomes divide but the cell does not it becomes tetraploid. If this happens in the reproductive cells the plant will be tetraploid and may become reproductively isolated from its parent diploid species. This has happened many times after hybridization and it can restore fertility. A majority of flowering plants are polyploid and it occurs in all other land plant groups.	
Patterns of speciation	Plants are more diverse in the tropics than the temperate, partly owing to the period of isolation. Trees and wind-pollinated plants have fewer species than herbaceous or insect-pollinated plants. The most specialized insect-pollinated plants, orchids, have a large number of species, many of them rare.	
Related topics	Plant communities (K2) Ecology of flowering and pollination (L1)	Polymorphisms and population genetics (L4) Evolution of flowering plants (R4)

Isolating mechanisms

Most plant species live in populations in which the individuals are capable of interbreeding (Topic K3). If one population becomes isolated from the others and does not interbreed with them, new varieties or species may form. Plants may become isolated through being physically separated. If seeds are transported to an isolated island by freak weather or via a bird, they may become isolated **geographically** by an area of unfavorable habitat. This may be an oceanic island surrounded by sea, or an island of suitable habitat such as a mountain peak surrounded by lowland. A population can become at least partially isolated **ecologically** within the distribution of the parent species if it colonizes a habitat with different soil conditions or dominant vegetation type requiring markedly different adaptations.

A reproductive barrier to other members of population may develop in one location. This can be a **physiological** barrier between two plants, perhaps

associated with a self-incompatibility system (Topic H3). Flowers may open at different times of the year and not overlap in their flowering seasons, or they may become adapted to different pollinating insects, especially if the flowers are highly specialized to one or a small group of insect species. Plants may be isolated by chromosome number through **polyploidy** since this is flexible and variable in plants and those with different numbers may be incapable of reproducing together. If a species is capable of self-fertilization or asexual reproduction (Topic H2), a single isolated individual can found a new population. Once a group of individuals becomes reproductively isolated it can diverge from the parent population either in its morphology or in its physiology, or both. A small isolated population may be subject to genetic drift (Topic L4) or to different selection pressures, particularly if it is in a new area or habitat.

Where recognizably different populations are geographically isolated, they are regarded as **species** if the differences are marked, but **races** or **subspecies** if they are minor; there is no absolute distinction between a species and a race. For populations in different ecological conditions, the term **ecotype** is used (Topic L4). Subspecies, or more generally **variety**, is also used for different chromosome types or morphological types that coexist, if distinct consistent forms can be recognized. A physiological reproductive barrier, used as a definition of a species in the 'biological species concept', is useful in some plant groups, but many plants can hybridize and, with a range of different breeding systems (Topic H2), the definition cannot be used consistently. No one definition of species works for all plants.

Breakdown of isolating mechanisms

If environmental conditions change, what was previously a geographical barrier may cease to be one, e.g. with the expansion and retreat of glaciers in the northern hemisphere during the last million years, or where two previously isolated plant species have met following their introduction by humans. Geographically isolated populations can reconnect with the parental population through a second colonization or a return to the place of origin and the two populations may interbreed and become one species.

Many plant species are capable of hybridizing with related species. These **hybrids** may be sterile (like the horse/donkey hybrid, the mule), and the reproductive barrier between the species is maintained, but frequently the sterility is partial, and some fertile pollen (rarely ovules) is produced. In some plants the hybrids are fully fertile with their parents. Some hybrids are capable of interbreeding with one parental species but not the other, and in these circumstances, the interbreeding parent may become highly variable in those sites where there is hybridization. In some plants, hybrid swarms between species are fairly common and the species barrier has locally broken down completely.

Hybrids are frequently rare and confined to disturbed or intermediate habitats between those of its parent species. They are likely to be less well adapted than either parent and hybridization may break up any collections of genes that allow the plant to be well adapted to its habitat. Under these circumstances, natural selection will favor or reinforce a physiological or other barrier to interbreeding, often coupled with a divergence in flowering time, pollinator type or pollen placement.

Polyploidy

Plants have many cells that contain more than one set of chromosomes (Topic B6). These appear to derive from a division of the chromosomes not being followed by a cell division. If this happens at some point in the reproductive

cycle, around or during meiosis or just after fertilization, the basic number for the plant can be doubled. This has occurred frequently and can happen spontaneously within a species, when it is known as **autopolyploidy**. Some individuals of the species will then be **tetraploid** and have four (or more) sets of chromosomes alongside the diploids with two. Morphologically, the diploid and tetraploid plants are often identical or nearly so, but they may be completely isolated from each other reproductively and have different distributions. Some authors regard these as separate species but most, for practical reasons, regard them as chromosomal varieties. Some are not completely isolated from each other and can reproduce successfully across the ploidy levels, though there may be abnormalities at meiosis leading to partial sterility.

Following hybridization polyploidy can restore fertility. If a hybrid is partially or completely sterile, this is normally due to the inability of the chromosomes of the two parents to pair correctly at meiosis (Topic B6) because they are too different. If the chromosomes double without cell division, then at meiosis there will be an exact copy of each chromosome, so pairing at meiosis will be possible and fertility restored. This has happened numerous times in plants, many tetraploids being the product of a hybridization followed by a doubling of chromosomes. This is known as **allopolyploidy**. The new polyploid is likely to be reproductively isolated from both parents immediately, so, in effect, forms a new species in a single generation. Polyploids are frequently self-compatible even if the parents have a self-incompatibility mechanism (Topic H3) so one plant is often viable as the founder of a new species.

A small majority of flowering plant species are probably derived by polyploidy at some stage in their ancestry since they have a high number of chromosomes (50 or more). It occurs in numerous angiosperm families and is also common among all other land plants, the highest chromosome number known (over 1000) being found in an adderstongue fern (Topic Q3).

Patterns of speciation

The number of species is highly variable between families and between genera and these can be related to climate, mode of growth and reproduction. There are more species in the tropics and in certain places like the Cape region (Topic K1) than in the northern temperate region. Although there are many reasons for this, one of them must be the period of isolation. Where the climate has forced large-scale plant migrations, many species are widespread but where the migrations have been less owing to less severe climatic fluctuation they have been more isolated and more species have formed as a result. This will promote γ diversity (Topic K4), and, in the most species-rich regions, each species has a more restricted distribution than in the less diverse regions.

In general, trees are less diverse than herbaceous plants and wind-pollinated plants are less diverse than insect-pollinated plants. Trees and wind-pollinated plants disperse their pollen greater distances and more generally than herbaceous plants (most insect-pollinated trees can be pollinated by a range of insects), thereby connecting populations over a large area. Among insect-pollinated families the most specialized to particular insects are the most species-rich. The extreme example is the orchids, in which each species has become specialized to one or a few insect species as pollinators. This has allowed numerous species to form (Topic R4), most of which are rare members of the plant communities in which they grow. Many are capable of hybridization with related species producing fertile offspring, but they do not normally hybridize because the insect species remain constant.