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An introduction to plant morphology

Plants are such a familiar part of the landscape that we commonly take them for granted. Of course, we know their importance to us as sources of food, materials and medicines, but we often do not appreciate just how fundamental plants are to life on Earth. Through the process of photosynthesis, they trap energy from sunlight and use that energy to convert carbon dioxide and water into organic molecules. When plants are eaten by other organisms, this carbon and energy is incorporated into their bodies. And it is not just through the production of carbon and energy that plants are useful; with their roots firmly embedded in the soil, they take up virtually all the minerals that enter the biosphere. Through this intimate contact with sunlight, air and soil, plants provide the link between the living and non-living components of the Earth's system.

Plants have not always been part of Earth's terrestrial environment. However, their colonization of the land over the past 400 million years has been the game changer that allowed animals to follow them out of the water, and eventually led to the complex biotas we see today. This chapter introduces plants – what they are, where they came from, how we describe their structure and the different types of plants – and sets the scene for exploring them in greater detail through the rest of the book.

What is a plant?

Plants are multicellular photosynthetic organisms that have adapted to life on land. Their cells are specialized and arranged to form tissues and organs, they have an outer protective cover of cutin, and they have reproductive organs with an outer layer of vegetative cells to protect their sex cells. After the egg cell is fertilized during sexual reproduction, the embryo into which it develops is retained on the parent plant, where it continues to be nourished; this feature gives land plants their formal scientific name, the Embryophyta, or embryophytes.

(↗) Horsetail; Equisetum; arvense to the approximate length shown here please supply this caption, thanks. Caption here.

(↓) Marchantia here please write accordingly to the approximate length shown here please Caption here please write accordingly.

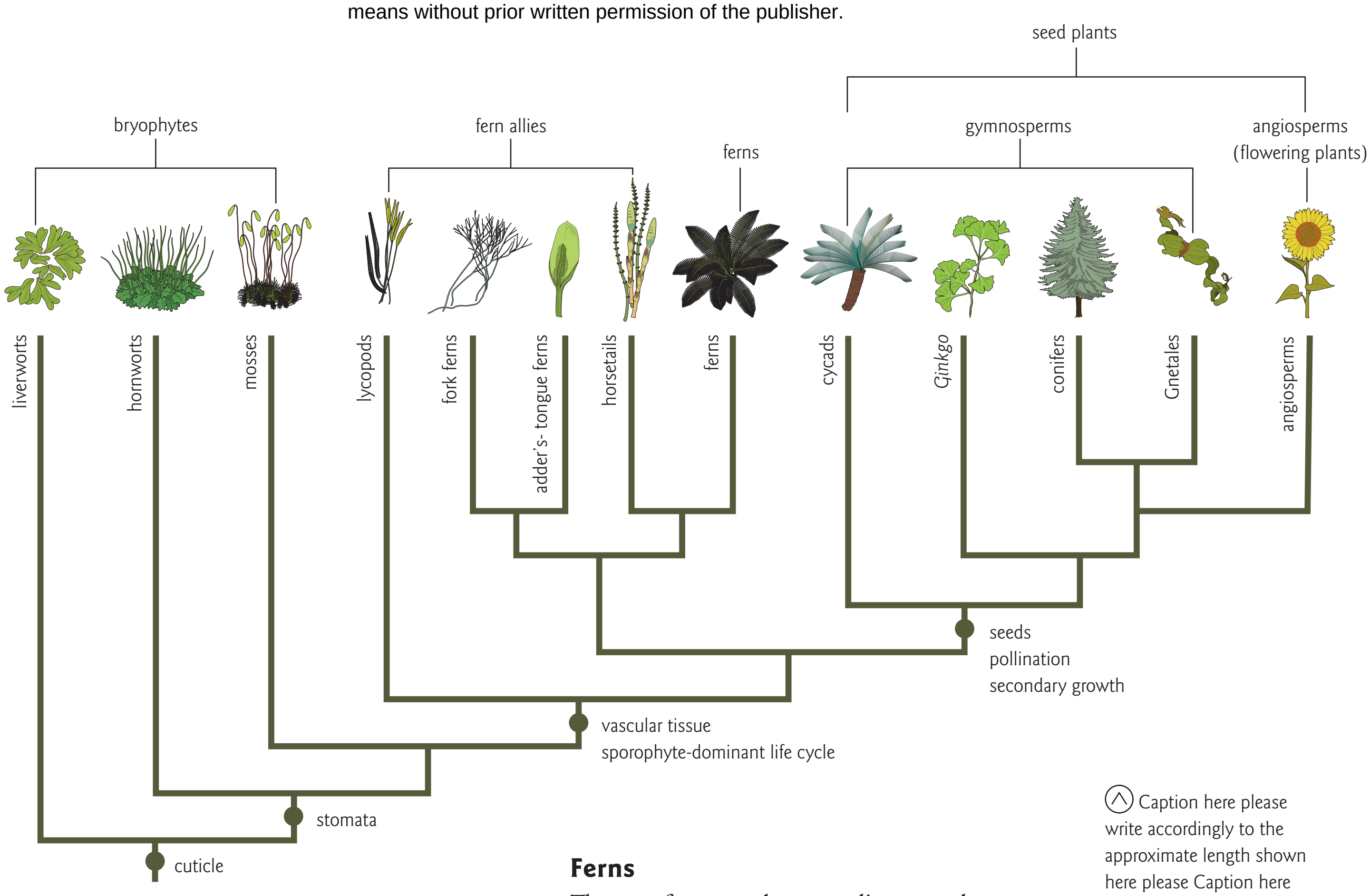
Bryophytes

The most primitive plants are the liverworts, hornworts and mosses, together informally called the bryophytes. These plants lack water-conducting tissue and hence are also often referred to as non-vascular land plants. They are usually found in wet or damp environments, and are small and grow close to the substrate, allowing them to absorb water readily. Bryophytes reproduce by dispersing small spores into the environment.

Some liverworts, like common garden weeds in the genera *Marchantia* and *Lunularia*, are simple flattened plants that are anchored to the soil by a mat of hair-like rhizoids; other liverworts are small and leafy. Hornworts are superficially like the flattened liverworts. In contrast, all mosses are leafy, and although they lack specialized strengthening and supporting tissue and are generally small in stature, some species are quite stiff and robust: the largest species, tall dawsonia (*Dawsonia superba*), reaches up to 40 cm (16 in) in height in southeastern Australian eucalypt forests.

Fern allies

Another group of plants that disperse their spores freely, but do conduct water throughout their tissues and so can grow to be larger and more complex, are known as the fern allies. The lycopods, which include clubmosses, quillworts and spikemosses, have a fossil record extending back about 400 million years, making them the most ancient lineage of living plants. Whisk or fork ferns (Psilotales) and adder's-tongue ferns (Ophioglossales) are also ancient lineages,



although they play a relatively minor role in modern flora. The horsetails (*Equisetum* spp.), another group of fern allies, are frequently encountered in the northern hemisphere and have a fossil record extending back about 300 million years. Together with the true ferns, these plants are informally called the pteridophytes.

Ferns

The true ferns are the most diverse and most conspicuous spore-producing plants. They are widely distributed around the world, and are locally common in rainforests and moist, shaded environments. They range in size from tree ferns, with trunks up to 20 m (65 ft) tall and a massive crown of fronds, to small, creeping plants with fronds just a few centimetres long. Aside from being common in the wild, ferns are popular garden ornamentals.

Ⓐ Caption here please write accordingly to the approximate length shown here please Caption here please write accordingly. Caption here please write accordingly.

Ⓛ Ferns here please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here.

Gymnosperms

Plants that produce seeds are called spermatophytes and are split into two main groups, the gymnosperms (meaning 'naked seeds') and the angiosperms, or flowering plants. The gymnopserms include the cycads, ginkgo (*Ginkgo biloba*), the gnetophytes and the conifers.

Cycads, numbering about 70 species in three extant families, look superficially like small palm trees, but they represent the remnants of a group that reached its greatest importance in the Mesozoic period, 252–66 million years ago – the age of the dinosaurs. The genus *Ginkgo*, with just one surviving species, is another relict – its relatives were also prominent in vegetation of the Mesozoic, but it is now restricted to a small region of China. Its alternative common name, maidenhair tree, refers to its delicate and ornamental foliage, and it has long been prized as a horticultural specimen tree. The gnetophytes also arose in the Mesozoic, and today they comprise three genera: *Gnetum*, *Welwitschia* (with just one species) and *Ephedra*.

The conifers, numbering around 630 species, are the most familiar of the non-flowering seed plants and mainly produce their seeds in woody cones. Pines (*Pinus* spp.), spruces (*Picea* spp.), firs (*Abies* spp.) and larches (*Larix* spp.) dominate large areas of boreal forests, and other conifers are represented in most vegetation types of the world, from rainforests to arid areas. The giant redwood (*Sequoiadendron giganteum*) of California is the tallest of all plants, some individuals comfortably exceeding 100 m (330 ft) in height. The Great Basin bristlecone pine (*Pinus longaeva*), also from California, and additionally Nevada and Utah, are the longest-lived of all plants – tree ring counts have determined some individuals to be around 5,000 years old. Conifers are an important forestry resource, providing softwoods for timber and paper.

Ⓥ Pine trees here please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly to the approximate length shown here please Caption here please write accordingly to the approximate length.

Angiosperms

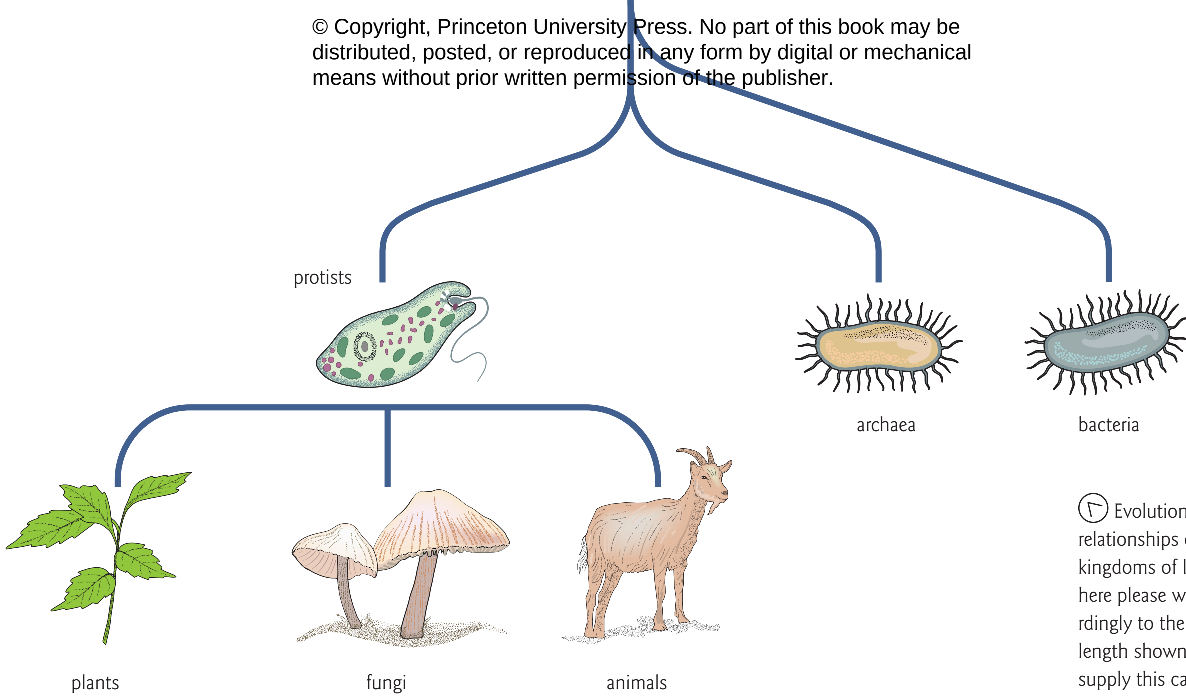
Flowering plants, or angiosperms, are the most diverse and abundant group of land plants. Including more than 250,000 species, the group comprises the most prominent and most dominant components of the world's vegetation. They range from tiny herbs through to woody shrubs and the tallest trees – a mountain ash (*Eucalyptus regnans*) in Tasmania, Australia, is 99.8 m (327.4 ft) in height, just shy of the giant redwood conifers. With such an enormous diversity, the angiosperms have managed to occupy most habitats worldwide, including the seagrasses in marine environments. Their reproductive strategies include pollination and seed dispersal by wind, water and a range of interactions with animals, the latter including bizarre examples of reward and deception.

Ⓛ Amborella trichopoda, write caption here please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly.

Ⓡ Mountain ash (Eucalyptus regnans) write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly. Caption here please write accordingly. Caption here please write accordingly.

REASSESSING RELATIONSHIPS

The traditional method of determining the relationships between plants, and classifying them, has relied on morphological characters that can be readily observed, such as stomata, vascular tissue, woody tissues and flowers. However, since the 1990s there has been an ever-increasing emphasis on DNA sequence data, to the extent that most systematic studies now rely on this. DNA (deoxyribonucleic acid) is the genetic material in cells, and in plant cells there are three sets of DNA, one each in the nucleus, chloroplast and mitochondria; all three can be used to assess the degree of similarity between different plant groups. DNA data has led to some significant reassessments of plant relationships over the past two decades, including the recognition of lycophytes as the most primitive vascular plants, the grouping of Psilotales with ferns, the affinities of gnetophytes with conifers, and the clarification that *Amborella trichopoda* from New Caledonia is the most primitive flowering plant.



Evolutionary relationships of the six kingdoms of life. Caption here please write acco rdingly to the approx imate length shown here please supply this caption, thanks.

Where did plants come from?

Plants are such a ubiquitous part of our environment that it is difficult to imagine a world without them. But there was a time when there were no plants. Prior to the end of the Cambrian period, about 485 million years ago, life on Earth was much simpler, and it was mostly found in the sea, or at least in water. Animals had already begun their evolutionary journey, and were rapidly expanding the variety of their body forms in the sea. But plants were late starters, lagging several hundred million years behind their animal cousins.

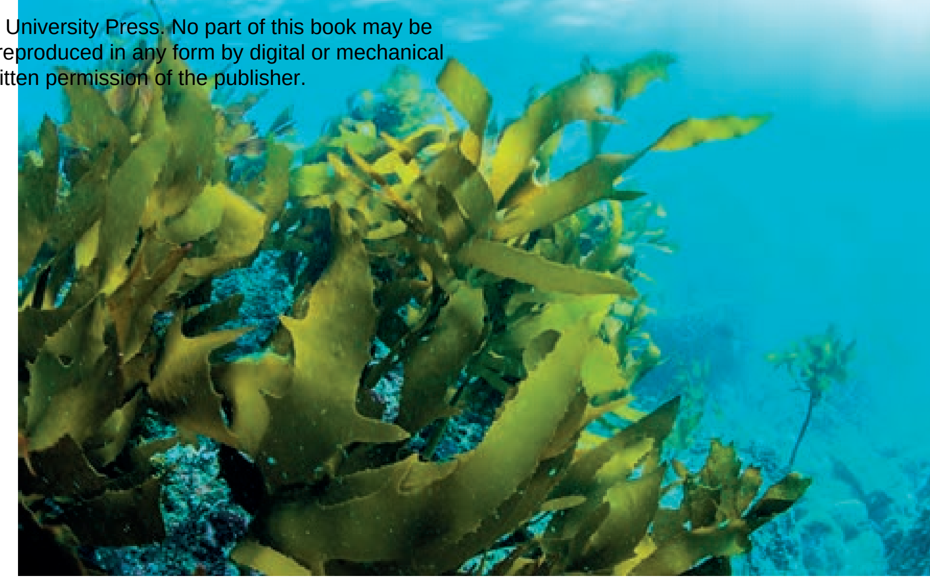
Six kingdoms

All living organisms are arranged into a classification of six kingdoms. A major division is between the two prokaryote kingdoms (bacteria and archaea) and the eukaryote kingdoms (protists, plants, fungi and animals). The prokaryotes are simple cells lacking a well-defined nucleus, whereas the eukaryotes have more complex cells with a membrane-bound nucleus and intricate intracellular structures. A significant feature of all eukaryote cells is the presence of mitochondria. These specialized organelles harvest energy from food molecules, and were themselves once bacteria that became incorporated into eukaryotic cells in a process known as endosymbiosis.

The protists

The simplest of the eukaryotes are the protists, a heterogeneous assemblage of mostly single-celled organisms. They are primarily organisms of aquatic or damp environments, but they also include some of our most significant disease-causing parasites, and they may be either photosynthetic and non-photosynthetic (colourless). Diatoms and dinoflagellates are photosynthetic protists, and between them account for a major proportion of the sun's energy captured in the biosphere. Dinoflagellates are responsible for toxic red tides, and their close relatives the apicomplexans are a group of parasites that cause diseases such as malaria and toxoplasma.

The colourless protists include amoebae, ciliates and flagellates, some of which are also responsible for human disease. Because most protists are single-celled organisms, and microscopic, they are usually observed only as slime in ponds or in damp places. Only the large multicellular seaweeds, species of brown, red and green algae, can be readily observed with the naked eye.



Higher organisms

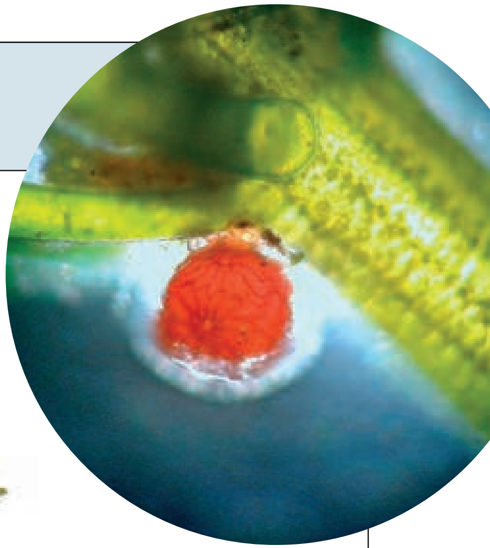
The remaining three eukaryote kingdoms, the fungi, animals and plants, arose independently from within the protists, and are notable for their evolution as complex, multicellular organisms. Animals and fungi originated close to one another, which is evinced by some similar features such as cell walls made of chitin.

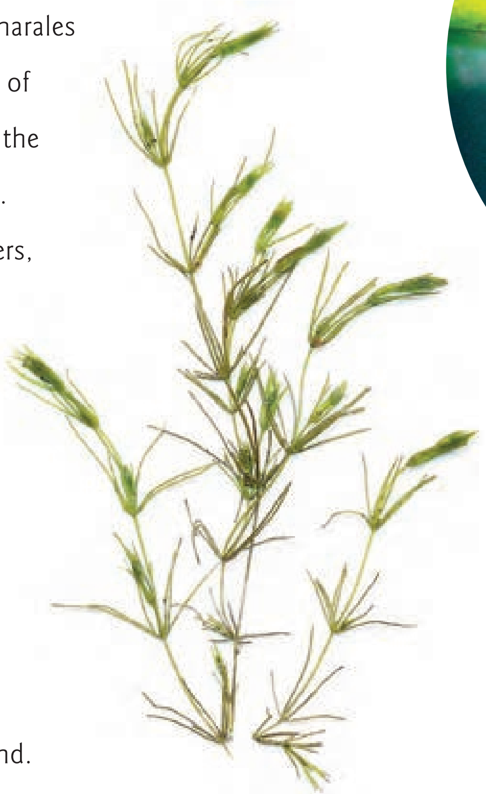
Plants arose from the lineage of protists that comprises the red and green algae. This lineage is referred to as the primary photosynthetic group, and it represents the descendants of the organisms that captured the original chloroplast around 900 million years ago (see page 00=Ch4). Green algae share a number of features with land plants, such as the photosynthetic pigments chlorophyll *a* and *b*, the same storage carbohydrate (starch), and cell walls made of cellulose.

Ⓐ Green Seaweed please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write acco rdingly to the approximate length shown here.

DISTANT RELATIVES

The freshwater green algae of the orders Charales and Coleochaetales (in particular members of the genus *Coleochaete*), are thought to be the closest modern-day relatives of land plants. They share a number of important characters, including a particular type of cell division that is not seen in most other algae, similarly shaped sperm cells, and some similar enzymes. The study of *Coleochaete* DNA sequences confirms this close relationship. Because Charales and Coleochaetales species are aquatic, it is thought that their divergence from plants occurred well before colonization of the land.



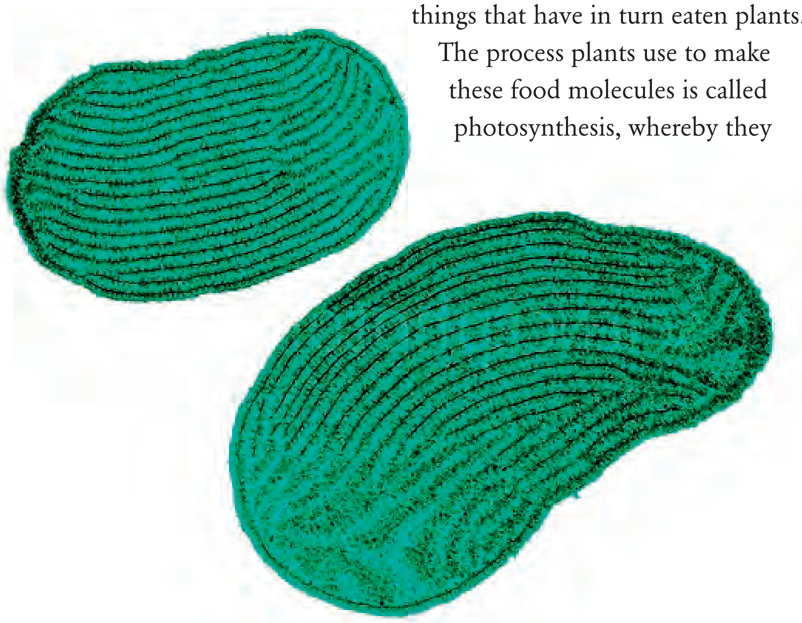


Ⓐ Charales here please write caption here please write accordingly to the approximate length shown here please supply this caption, write accordingly.

Ⓒ The stoneworts alga Chara globularis (Syn.: Chara fragilis; Characeae). length shown here please supply this caption, write accordingly.

Why are plants green?

Perhaps the most obvious feature of plants, and the vegetation they compose, is their consistent colour. While there is some variation in the hue, from the deep green of forests to the bright green of grassy fields and the grey-green of desert vegetation, the overwhelming colour of plants is green. Curiously, this greenness we perceive as so important is visible to us because the colour green is of no importance to plants.



(V) Chloroplasts here please write accordingly to the approximate length shown here please Caption here please write accordingly to the approximate length shown here please Caption here please write.

Reflecting on colour

Plants are fundamentally different to animals because they make their own food molecules – the sugars that all cells use as an energy source. Animals, including humans, get their food molecules by eating plants, or eating things that have in turn eaten plants. The process plants use to make these food molecules is called photosynthesis, whereby they capture the energy from sunlight and use that energy to convert carbon dioxide from the air, along with water, into sugars.

Plants contain a number of different pigment molecules that capture the sunlight and harvest its energy. The most important of these pigments, and the one that captures the vast majority of light, is chlorophyll.

The overall colour of sunlight is white, but this visible spectrum is actually a combination of many different wavelengths, each with its own colour. These different wavelengths can be separated, as when sunlight shines through raindrops to create a rainbow. Red, orange and yellow are at the long wavelength end; blue, indigo and violet are at the short wavelength end; and green is in between. Chlorophyll pigments are choosy when it comes to light. They absorb light at the reddish and bluish regions of the spectrum, but not in the middle. As green light is not collected by the plant, it is reflected back, which is why plants appear green.

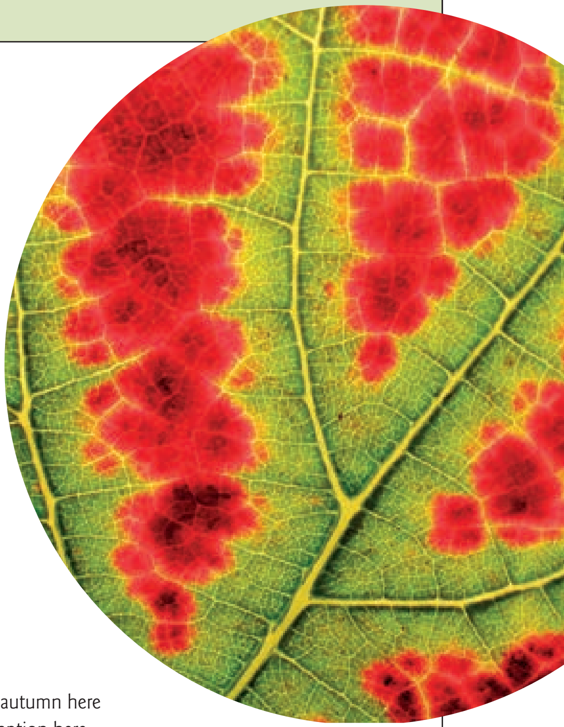
CONTRASTING CHLOROPLASTS

The chloroplasts of red algae have a similar structure and pigments to those in a cyanobacterial cell. The knobbly appearance of the membrane system, which is the location of specialized red and blue light-capturing pigments called phycobilins, is indicative of both the link between cyanobacteria and chloroplasts and the primitive condition of the chloroplast in red algae. Chloroplasts of green algae and plants differ from those found red algae, in that their membranes are folded into pancake-like stacks and are dominated by the green light-capturing pigment chlorophyll.

DIFFERENT GREENS

There are two types of chlorophyll in plants, designated chlorophyll *a* and chlorophyll *b*, which absorb slightly different wavelengths of light. Plants in low light environments have more chlorophyll *b* than *a*, and appear dark green; plants in brighter environments are just the opposite – they have more chlorophyll *a* and appear brighter green. Plants of drier environments appear greyish green because their thick, waxy cuticle affects the way light is reflected.

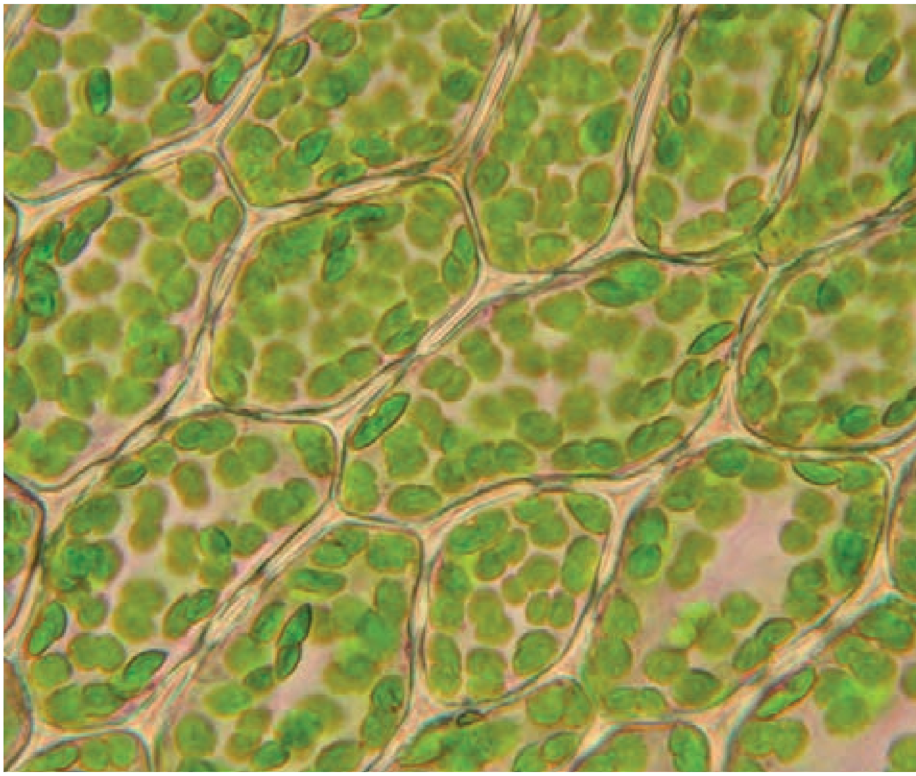
Chlorophylls dominate the pigment composition of healthy leaves, so these structures almost invariably appear some shade of green. But there are other pigments in leaves that reflect different colours – the yellow xanthophylls, orange carotenoids and purple anthocyanins. As leaves of deciduous leaves cease function in autumn, the chlorophyll breaks down and the colours of the other pigments are revealed.



Vine leaf autumn here please write caption here please write accordingly to the approximate length shown here please supply this caption, write accordingly.

The origins of photosynthesis

Plants did not invent photosynthesis; the process occurred in cyanobacteria more than 2.5 billion years ago. In one of the most important events in life's history, which took place almost a billion years ago, a cyanobacterium was engulfed by another cell and incorporated as a specialized organelle, a chloroplast. This created a new lineage of photosynthetic organisms that has led to red algae, green algae and plants, all of which inherited their chloroplasts from the same common ancestor.



Plagiomnium affine, Chloroplasts here please write accordingly to the approximate length shown here please supply this caption, write accordingly.

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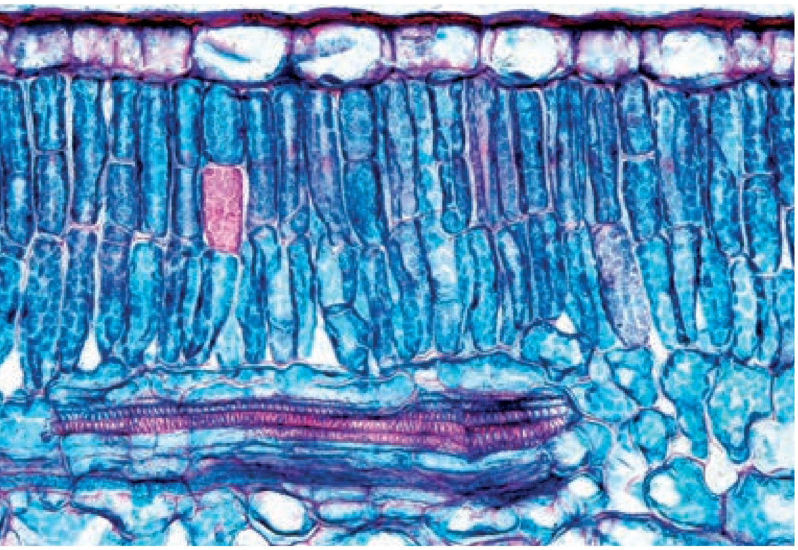
Living on land versus living in water

Plants are terrestrial organisms, living on land. However, we know from their evolutionary origins among the green algae that they started off in the water. Living on land is very different to living in water, and the move to a terrestrial way of life presented plants with a number of challenges. These essentially relate to four major functions: water balance and transport, structural support, gas exchange, and reproduction.



Cuticle on plant surface accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly to the approximate length shown here please

Xylem tissue of sunflower accordingly to the approximate length shown here please Caption here please write accordingly to the approximate. Caption here please write accordingly to the approximate length shown here please Caption here please write accordingly to the approximate.

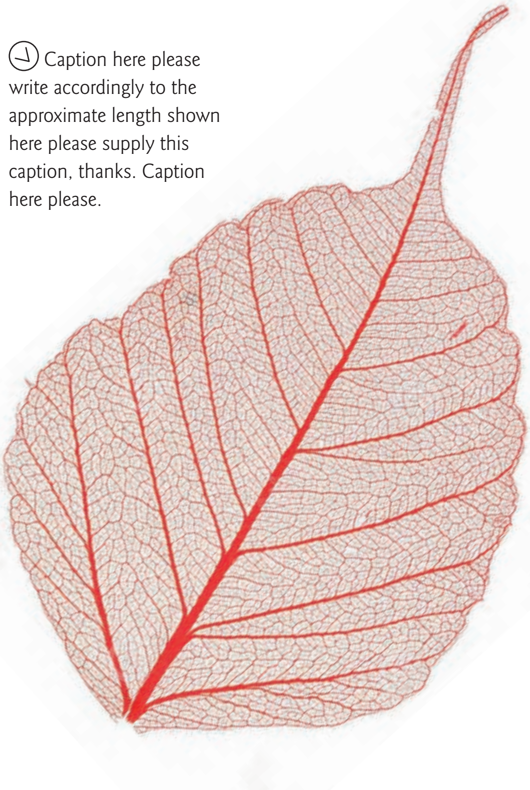
Water balance and transport

Aquatic seaweeds, such as green algae, are surrounded by water. Consequently, they have no need for special water-absorbing structures, tissues to move water internally or mechanisms to prevent them drying out. In contrast, land plants inhabit an environment where water is scarce, and usually confined to the soil in which they grow. They require specialized organs – roots – to extract water from the soil, they need complex tissue to transport this water to above-ground parts of the plant, and they need a protective, water-resistant coating to minimize water loss to the atmosphere. The degree to which these features are developed in a plant largely determines its growth form and ecological tolerance.

Xylem is the conducting tissue that transports water throughout the plant, forming a continuous plumbing system of elongated, hollow cells. The walls of these cells are conspicuously reinforced by a rigid framework of lignin, which prevents them from collapsing as water is sucked through them. Because of the need to supply water to every part of the plant, the size of a plant is limited by its vascular system.

Structural support

Aquatic plants get their structural support from their buoyancy. For example, the giant kelp (*Macrocystis pyrifera*) forests of the American Pacific coast can grow up to 50 m (160 ft) in height, but if the water were removed, they would collapse onto the sea



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floor. In a terrestrial environment, if plants want to gain height to compete for sunlight with their neighbours, they must therefore provide their own support. Lignin, the rigid compound that reinforces the walls of water-conducting cells, is also used to strengthen other tissues in the stem. In shrubs and trees, the old wood that is no longer needed for water transport provides the structural support for trunks and branches.

Reproduction

Algae reproduce in the water, many releasing their male sex cells into the water, where they must swim around to locate an egg cell. In a terrestrial environment, relying on free water for reproduction is risky. Primitive land plants such as liverworts, mosses and ferns do just this, and as a consequence they are restricted to environments where moisture is regularly available. Seed plants have overcome this need for watery reproduction by developing the process of pollination. The sperm cells are produced by germinated pollen grains, but only after these have been transported to the location of the egg cell. The pollen tube grows directly to the egg cell and deposits the sperm cells in precisely the right place.

AQUATIC ABOUT-TURN

A number of flowering plants are aquatic, but all of these have evolved from terrestrial ancestors that have subsequently returned to the water. Most have colonized freshwater habitats, but a few, such as the seagrasses, are found in the sea. Aquatic plants have had to revisit the challenges of living in water with a suite of characters that were adapted for life on land. For the large part, they have simply reverted: submerged plants do not produce a cuticle or stomata, their water-conducting tissue is reduced, and structural support is provided by buoyancy rather than strengthening tissue. However, one area in which they have had to innovate is reproduction. Constrained by flowers and pollination, which are apparently too hard (or too good) to be undone, they bloom at or above the surface of the water and achieve pollination in a conventional manner.

Pollination in seagrass Enhalus write caption here please write accordingly to the appro ximate length shown here please supply this caption, thanks. Caption here. Cap tion here. Caption here. Caption here. Caption here.

The evolution of plants on land

The increase in the complexity and specialization of plant vegetative and reproductive features that occurred with their colonization of the land is the key to understanding the remarkable diversity of plant life on Earth. This is best explored in the context of the plant life cycle.

Male gametophyte of Moerckia flotoviana to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly to the approximate length shown here please

Snake liverwort, Snakeskin liverwort (Conocephalum conicum), with capsules, length shown here please Caption here please write accordingly to the approximate. Caption here please write accordingly to the approximate length shown here please Caption here please write accordingly to the approximate.

The life cycle of a land plant

The land plant life cycle describes the process of sexual reproduction. This involves a specialized cell division that halves the chromosome number (meiosis) on one side of the cycle, followed by the production and fusion of sex cells (syngamy) to return to the original chromosome number on the other side.

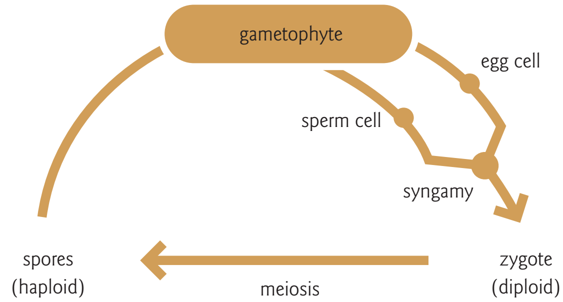
There are two discrete stages in the life cycle of land plants, which are referred to as separate generations. This is a uniform feature from liverworts and mosses to flowering plants, and is the foundation for any comparative study of plant diversity. The gametophyte generation is haploid (one set of chromosomes per cell) and produces two types of sex cells (gametes). One type of gamete (conventionally referred to as the male gamete, or sperm cell) is shed, while the other gamete (the female gamete, or egg cell) is retained. Male and female gametes then fuse, doubling the chromosome number. This new cell is called the zygote, and it divides and grows into the multicellular sporophyte generation, which is diploid (two sets of chromosomes per cell).

Sporophytes undergo the reduction division of meiosis to produce spores (now haploid again), which in turn germinate into new gametophytes. Because sporophyte and gametophyte generations in turn give rise to the other, they are said to alternate in the life cycle – called the alternation of generations (see box on page 00). Taking a liverwort, the most primitive land plant, as an example, the persistent green plants are the gametophyte generation in its life cycle, with the sporophyte is the white stalk with a spherical black capsule on the end. Spores are produced by meiosis in the capsule, which splits open for spore dispersal. The gametes and the organs that produce them can be observed only with a microscope.

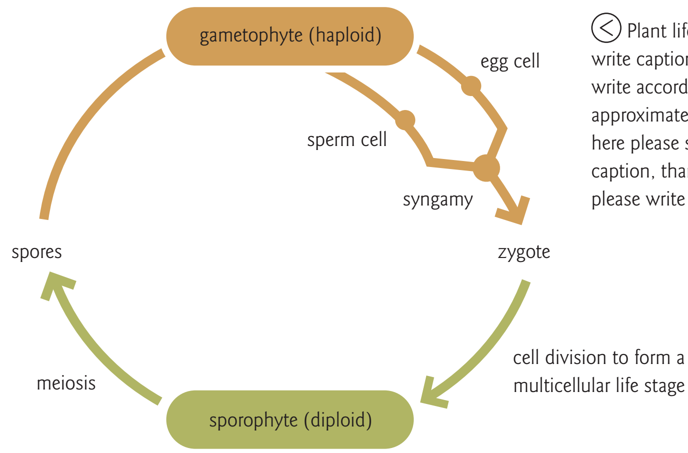
Evolution of the plant life cycle

To explore the evolution of the life cycle of land plants, we must take a comparative approach, and the obvious comparison is with the closest relative within the green algae, *Coleochaete*. *Coleochaete* is a small disc-shaped, multicellular green alga that grows in fresh water. It is haploid, and it produces egg cells that are retained and sperm cells that are dispersed to locate and fertilize an egg cell. The fusion product of this fertilization event is a diploid zygote. So far, so good. But in *Coleochaete*, the zygote does not develop into a multicellular sporophyte. Instead, it immediately undergoes meiosis to form four haploid spores, which in turn regenerate the gametophyte generation.

Assuming that the *Coleochaete* life cycle is a primitive condition from which the land plant life cycle has evolved, we interpret the multicellular sporophyte generation as unique to land plants; a developmental stage that has been inserted into the life cycle between the zygote and meiosis. So why is this significant? At the most advanced levels of land plant evolution, for example the giant redwood confers or the mighty mountain ash eucalypts, the plants that we observe are the sporophyte generation. These massive trees are the direct life-cycle equivalent of the tiny stalk and capsule of a liverwort. All of the structure and complexity associated with the success of plants on land, and which is encompassed in the diversity of conifers and flowering plants, has occurred in the sporophyte generation, and that sporophyte generation is unique to land plants.



Coleochaete life cycle charts write caption here please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly.



Plant life cycle charts write caption here please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly.

Giant Sequoias write caption here please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly. Caption here please write accordingly.

Evolutionary adaptations to life on land

There are number of major plant features that were critical to the success of plants on land. Some of these, such as a water-resistant cuticle and specialized water-conducting cells, have already been mentioned. These features did not all appear at once – they evolved gradually over several hundred million years, each building on the success of those that had come before them. Curiously, some of these features were tried out by different plants several times, only for them to stagnate or disappear, while others survived and succeeded to the present day.

Successful specializations

Cuticle is a feature of all plants, and was the first of the key features to appear. In liverworts and mosses the cuticle is very thin, but plants cannot survive exposed to the air without it. Stomata, the specialized pores that allow carbon dioxide to enter the plant, followed a little later; they are absent in liverworts, and first occurred in moss and hornwort sporophytes. Specialized conducting or vascular tissue first appears in lycophytes. This is also the stage of plant evolution at which we see the sporophyte becoming the prominent generation in the life cycle, and where it becomes branched and more complex in its anatomy and morphology. It is also in the lycophytes, and more noticeably in the ferns, that we see the differentiation of the plant into specialized organs such as stems, roots and leaves.

With increased complexity and an accompanying increase in size came a demand for more conducting tissues than were available. This problem was solved by the evolution of a special growing region in the stem called the vascular cambium, which produces wood, leading to the formation of shrubs and trees.

Lycopodium clavatum L. Common Name: Running Club-Moss shown here please supply this caption, thanks. Caption here please write accordingly to the approximate length shown here please Caption here please write accordingly to the approximate length shown here please

Reproductive remodelling

All plants from liverworts to ferns shed their spores directly, leaving them to fend for themselves. But in plants from the cycads up – in other words, all seed plants – the spores are surrounded by a protective covering and are retained on the parent plant. Here, the spore develops into the gametophyte, produces an egg cell, is fertilized, and forms the embryo that will become the seedling of the next sporophyte generation, all the while being nourished by its parent sporophyte – until it is shed as a seed. Seed plants also developed pollination, which delivers the sperm cells directly to the egg, removing the requirement of free water for reproduction.

KINGS OF THE CARBONIFEROUS

Ⓐ A fossil tree bole (Sigillaria) in a churchyard please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly.

Lycophytes were the first vascular plants, and although they now form only a minor part of the world's flora, they were once one of the most successful and certainly one of the most innovative groups. Just as history is written by the victors, the seed plants get most of the credit as the modern pinnacle of plant evolution. But lycophytes had done much of it much earlier.

The lycophyte sporophyte is branched and complex, and the shoot is differentiated into stems and leaves. These are not the same as the true leaves of other plants, which developed independently, but they have successfully served the function of photosynthetic organs for more than 400 million years.

Lycophytes were also the first plants to have roots. Around 300 million years ago, during the Carboniferous period, they even developed a type of woody tissue from their own specialized vascular cambium, which allowed them to grow as tall trees with thick woody trunks. Forests of these lycophyte trees dominated swampy environments, and they contributed to the formation of extensive coal deposits across Europe and North America.

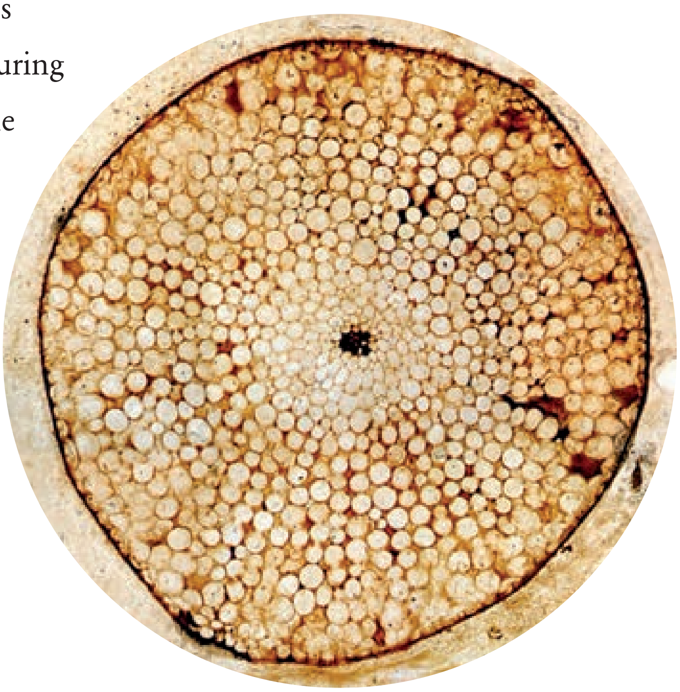
Sadly for lycophytes, and despite their early success, they were still constrained by a free-sporing reproductive biology that needed water for fertilization. In an unforgiving terrestrial realm, these kings of the Carboniferous were ultimately displaced by newcomers that had solved that problem.

Ⓥ Carboniferous lycopods write caption here please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly.

Palaeobotany and the plant fossil record

Transverse section of a stem of Rhynia Gwynne-vaughanii, Lower Devonian Rhynie chert supply this caption, thanks. Caption here please write.

The fossil record of plants is extensive, and tells a complex story from the time plants appeared during the Silurian more than 400 million years go to the present day. Although we can infer much about the evolution of plants by looking at those that are living today, the fossil record provides a unique window into the past. It tells us about groups of plants that are now extinct, about the ages of different plant groups and when key features appeared, and about geographic distributions that are very different to those we see today.



A polished piece of Rhynie chert showing many cross-sections of Rhynia stems (axes). supply this caption, thanks. Caption here please write accor dingly to the approximate length shown here please

First fossils

The first fossil evidence of land plants is dispersed spores, but we do not know anything about the plants that produced them. Owing to the delicate nature of primitive plants at the bryophyte level, their preservation as fossils is unlikely, and indeed the earliest fossils we find are of vascular plants, which are more robust.

One of the most impressive fossil beds is the Rhynie Chert, located near the village of Rhynie in Scotland. Here, about 410 million years ago, plants that were growing in the margins of a spring were embedded in rock that crystallized around them from the mineral-rich water. When these rocks are

Rhynia sp. here please write accordingly to the appro ximate length shown here please supply this caption, thanks. Caption here please write accord ingly to the approximate length shown here.

ONE AND THE SAME

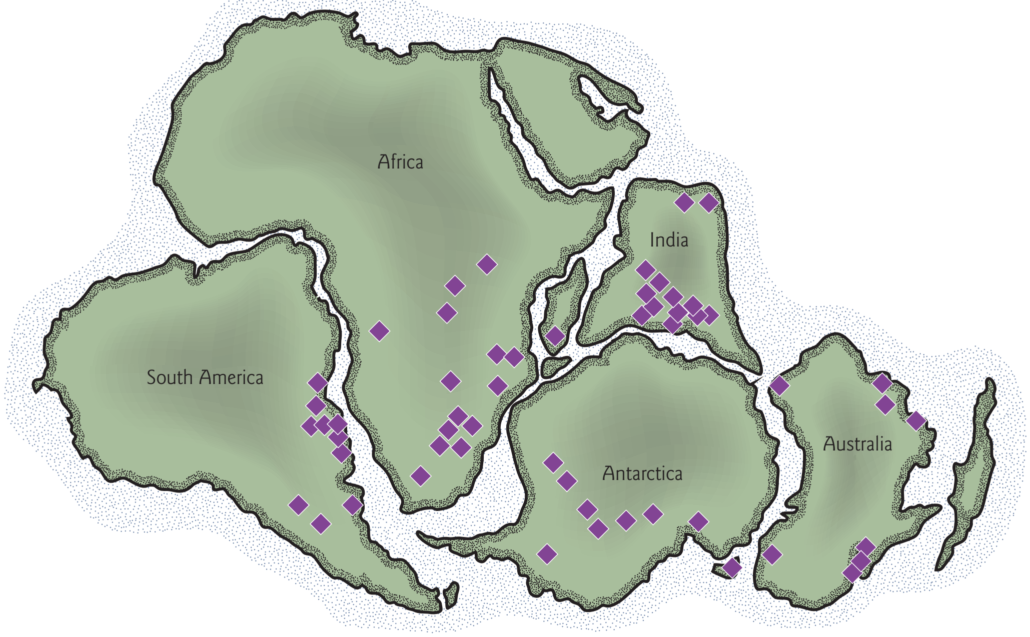
In many locations worldwide, plants in the genus *Archaeopteris* are found as fossils in Late Devonian deposits dating back around 380 million years. They have large frond-like leaves, and were originally thought to be ferns because they have unprotected sporangia that split open and shed their spores. Also found in deposits of the same era are pieces of fossilized wood known as *Callixylon*. This wood is superficially conifer-like, and was clearly produced by a stem that had a vascular cambium. In the 1960s, some particularly well-preserved *Archaeopteris* fronds were discovered, and the stalks of these fronds contained *Callixylon* wood. It turned out that the two different fossils were indeed parts of the same plant. All living plants that produce wood also have seeds, and vice versa; yet here was a fossil with wood, but not seeds. We now have a number of different *Archaeopteris*/*Callixylon* fossil plants, which are classified in an extinct group called the progymnosperms. These finds tell us that woody growth and the development of trees preceded the evolution of seed plant biology – important knowledge that we could not have discovered from living plants alone.

Archaeopteris Tree 3D Illustration - Archaeopteris is one of Earths earliest trees, if not the earliest. Like all Devonian vegetation, it used to grow close to waters. Caption here.

sliced very thinly and observed with a microscope, all of the cell details are visible, providing a wealth of information about their structure and biology. We have learnt two new and particularly important things from the Rhynie fossils. The first is that sporophytes were branched before the evolution of vascular tissue; in living plants, these features always occur together. The second is that in early land plant evolution, the gametophytes were branched and complex like the sporophytes, and had stomata and possibly conducting tissues; these features are absent in gametophytes of living vascular plants.

Glossopteris and Gondwana

Between 250 and 300 million years ago, during the geological age known as the Permian period, the world was a very different place from today. In the southern hemisphere continents, sedimentary rocks deposited during this time now contain massive coal deposits – the fossilized remains of swamp vegetation. These deposits are dominated by a now extinct group of plants in the order Glossopteridales, which includes the genera *Glossopteris* and *Vertebraria*. These were large trees with many distinctive features that make their fossils easily recognizable. Foremost, their leaves were broad



⊳ Gondwana here please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly to the approximate length shown here please Caption here please write acco rdingly to the approximate length shown.

and tongue-shaped (hence the genus name *Glossopteris* – *glosso* is Greek for 'tongue' and *pteris* means 'fern'), with a very characteristic reticulate or net-like vein pattern. Their roots contained numerous air spaces to prevent waterlogging in their swampy home, and they appear jointed when fossilized (hence the genus name *Vertebraria*, because of the superficial resemblance of the roots to a backbone). It was this distribution of glossopterid fossils in South America, Africa, India and Australia that led geologists in the late nineteenth century to first propose that these now separate continents were once connected long ago as the super-continent Gondwana.

⊽ Scott and co please write caption here please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accor dingly. Caption here please write accordingly to the approximate.

GREAT SCOTT!

During British explorer Robert Falcon Scott's ill-fated trek to the South Pole in 1912, *Glossopteris* fossils were discovered in the Transantarctic Mountains. Edward Wilson, the expedition doctor and a keen naturalist, realized their importance to the debate on continental connections, and so the fossils were retained by the group to the very end; the rescue party recovered the specimens the following summer, and they now reside in the Natural History Museum in London. The presence in Antarctica of Permian *Glossopteris* and coal seams, and indeed other plant fossils from as recent as several million years ago, reveals that the continent has only recently become the frozen landscape that we recognize today.

Ⓛ Glossopteris fossil seed fern leavesaccordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly to the approximate length shown here please Caption here please write accordingl.

Ⓥ Cross section of chambered root of glossopterids Vertebraria australis from permineralized peat of the Late Permian Blackwater Coal Measures to the approximate length shown here please

Fossil pollen and flowers

Flowering plants, with more than 250,000 species, dominate the Earth's modern-day vegetation in terms of sheer diversity and variety. The English naturalist Charles Darwin, whose seminal work *On the Origin of Species*, published in 1859, gave us the first formulation of evolutionary theory, was at a loss for an explanation of flowering plants, describing them as an 'abominable mystery' in a letter to his colleague Joseph Hooker in 1879. The ensuing 150 years has seen a vast amount of research piecing together the history and relationships of these important plants, and palaeontology has played a critical role in this.

The earliest definitive evidence of flowering plants in the fossil record are pollen grains from the early Cretaceous period, approximately 145 million years ago, although rare pollen finds from Triassic sediments dating back almost 200 million years are very intriguing. Angiosperm pollen can be recognized by its distinctive cell wall structure, but nothing is known about the plants that produced this early pollen. By the mid-Cretaceous, about 100 million years ago, angiosperms were common enough that their leaves and pollen are well represented in fossil floras. But plant relationships are based largely on the features of their flowers, not their leaves, and since it is the flowers that also produce pollen, fossil flowers provide the most definitive information. Unfortunately, fossil flowers are not often discovered.

Mid-Cretaceous sediments from the eastern seaboard of North America have just the right combination of factors for the preservation of early fossil flowers – they were very fine, silty clays deposited in still water, and have remained unaltered by geological processes such as compression and extreme temperatures. These beds have yielded fragments of flowers at different developmental stages, such as small intact flower buds, stamens that still contain pollen, young fruits with pollen grains on the stigmas, and twigs showing the arrangement of flowers and their parts. This has allowed not only the reconstruction of the flowers and determination of their relationships, but also their link to pollen that is widely distributed in the fossil record but whose affinities were previously unknown.

Plant structures and their functions

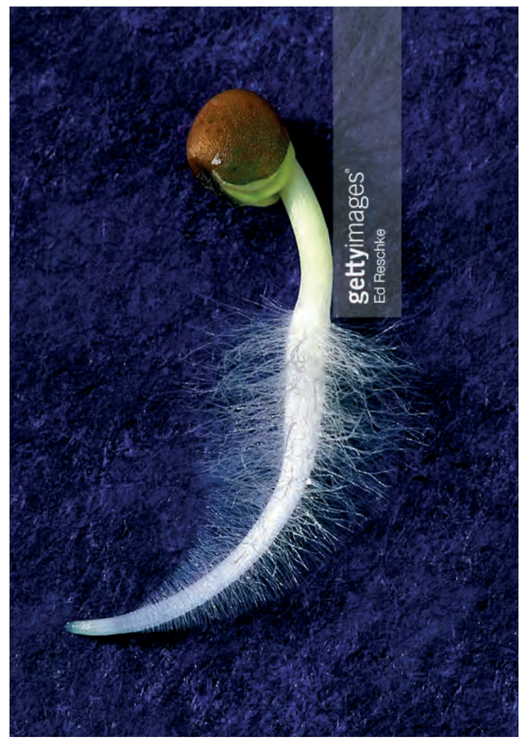
The plant kingdom includes such a wide diversity of form, from the most primitive liverworts to the most complex of flowering plants, that it is impossible to generalize a common structure for all. However, in our ordinary everyday interaction with plants, which for the most part involves the flowering plants and conifers, the enormous diversity of form can be encapsulated into a generalized ground plan, with each component or organ assigned a specific function.

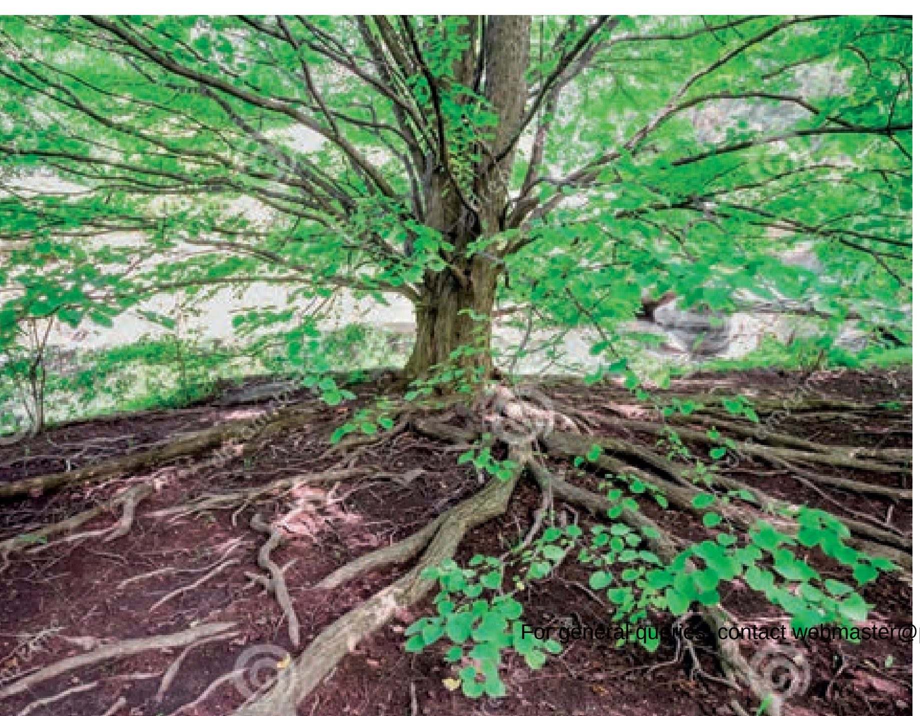
> Root apex here please write accordingly to the approximate length shown here please supply this caption, write accordingly to the approximate length shown here please

v View of Katsura tree and partially exposed root system. to the approximate length shown here please supply this caption, thanks. Caption here please write accor dingly to the approximate length shown here please

Below- and above-ground distinctions

Most plants grow in the ground, and the first obvious distinction is between the root system, which anchors the plant and absorbs water and nutrients from the soil, and the shoot system, the above-ground part of the plant that interacts with the atmosphere. The shoot system is primarily composed of stems and leaves, and intermittently produces the reproductive structures such as flowers in angiosperms and cones in conifers. Despite the enormous diversity of plants, roots and shoots play consistent fundamental roles, and their essential features such as growth, structure and shape are relatively uniform. Indeed, most of the variations we find in plants reflect adaptations of the different organs to allow them to function better in a particular environment.





Rooted to the spot

Roots live in a tough physical environment. They have soft, delicate tips, yet have to penetrate and grow through firm, abrasive soil. Their growing tips are protected by a cap of cells embedded in mucilage that are continually replaced as they are damaged. Just a few millimetres behind the tip, a zone of root hairs marks the region where water and nutrients are absorbed. Roots absorb water only at their tips; the rest of the root stem develops a thick, protective outer layer, and serves to transport the water from the tips back to the shoot system.

Taking a leaf

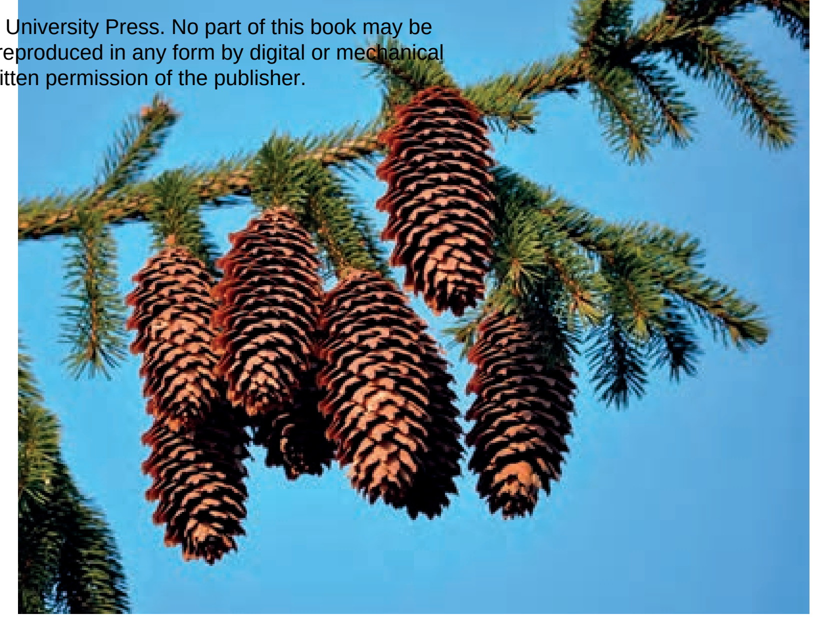
Leaves are predominantly sites of photosynthesis. Their cells are rich in the light-harvesting chlorophyll pigment, and as a consequence they are predominantly some shade of green. They are usually flat and thin, which maximizes their surface-to-volume ratio and provides the largest area for capturing sunlight. Leaves account for most of a plant's surface area and are covered with a waxy cuticle to prevent them from drying out. They have stomata pores on their surface to absorb carbon dioxide from the air, and they have a spongy internal structure to allow air to circulate. Leaves vary enormously in size, shape and texture between species, but these differences usually relate to optimizing the efficiency of photosynthesis while preventing unnecessary water loss.

Stemming the tide

Stems are transport networks that connect the leaves and the roots. They move the energy-containing sugars made by photosynthesis from the leaves, where they are produced, to other parts of the plant, where they are either stored or used for growth. In addition, they transport water from the roots, where it is absorbed, to the leaves to replace moisture that is unavoidably lost through the stomata. Older stems become woody to form trunks and branches, providing structural support in trees and shrubs, but they also continue to play their primary transport role.

Reproductive organs

Reproduction occurs in cones or flowers. In conifers, pollen and seeds are produced in separate cones, and pollen is dispersed by wind. In flowering plants, the pollen organs (stamens) and seed organs (carpels) can be aggregated into a single flower, or born on separate flowers, and are commonly surrounded by an attractive whorl of colourful petals and protective sepals. In general, complex, colourful, perfumed and nectar-producing flowers are pollinated by insects and birds, while simple, drab flowers are wind pollinated.



Cones grow on the branch of spruce tree to the approximate length shown here please supply this caption, thanks. Caption here please write accor dingly to the approximate length shown here please

English Oak (Quercus robur) catkins, to the approximate length shown here please supply this here please write accor dingly to here please supply this here here please supply this here the approximate length shown here please

Sturt's Desert Pea, write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accor dingly to the approximate length shown here please

A short history of plant morphology

We are so familiar with plants and their appearance – firmly rooted in the ground, and with stems that bear leaves and flowers – that we are often unaware that the way we describe their form is just a convention. We are also often unaware that this convention dates back millennia, and that it is not the only perspective.

Plato iin red, Aristotle in blue pictured centre. School of Athens painting to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly to the approximate length.

Early thinkers

We can trace our ideas on plant morphology back to antiquity and the time of the great Greek philosophers Plato and Aristotle in the fourth century BC. These great early thinkers were absorbed with unifying concepts, and they attempted to reconcile plants and animals (including humans) using a common theme. The most basic of these was the concept of psyche (or soul) – plants were said to have a nutritional psyche, animals a sentient psyche, and humans a reasoning psyche. Indeed, the roots of plants were thought to correspond to the mouths of animals.

It was Aristotle's student Theophrastus who first cautioned against an overly rigid plant–animal comparison, and he gave us the first notions of a framework based predominantly on plants. The philosopher divided the plant into permanent parts (root and stem) and temporary parts (leaves, flowers and fruits). He recognized the indeterminate and modular growth of plants, which continually produce new shoots and leaves every year, in contrast to the unitary growth of animals, in which the organs are of fixed and definite number. In keeping with the other ancients, he considered the root to be the primary organ, possibly due to its importance in medicines and the fact that the shoots of many plants die back in winter, only to resprout from the rootstock again the following spring. The leaves attracted little attention; their function was then unknown, and they were considered little more than an accessory to fruit production.

COMMON TERMS

The direct comparison of plants and animals made by the ancient Greek philosophers is the source of some of our current terms and concepts. Examples include the division of both into tissues and organs, and the use of the words 'nerve' for the leaf veins and 'heartwood' for the middle of the trunk. We even refer to the gametes of plants as sperm (motile) and eggs (retained), and convey gender categories of maleness and femaleness on the structures that produce them.

Branch of Norway spruce with male and female flowers supplied. Ideally short caption to say this, offering some connection with the box.

'Everything is leaf'

This notion of plant morphology lasted for 2,000 years. Then in 1790, Johann Wolfgang von Goethe, the famous German statesman, wrote an essay on plant morphology that underpinned a new paradigm. Goethe is best known as a philosopher and poet, and as the author of the great play in which Faust sells his soul to the devil, but he was especially interested in the natural and physical world, and was responsible for a number of important scientific works ranging from natural history to colour theory. During a trip to Italy, he visited the Botanical Garden of Padua, where he observed the European fan palm (*Chamaerops humilis*). Fascinated by the gradation of different-shaped leaves along the stem and their transition into the flowering region, he postulated that they were all variations of the same structure – that they were all types of leaf. Goethe used the phrase '*Alles ist Blatt*', or 'Everything is leaf'. What he really meant was that there was an overarching concept of 'leaf', and that all the variable organs were different manifestations of that archetypal leaf; this reflected a philosophy that had been dominant since Plato, and underscored Goethe's deep metaphysical approach.

Johann Wolfgang von Goethe at age 79 , Artist Joseph Karl Stieler (1781–1858) Caption here please write accordingly to the approximate length shown here please

Goethe's concepts on the "metamorphosis" of plants Caption here please write accordingly to the approximate length shown here please Caption here please write accordingly to the approximate.

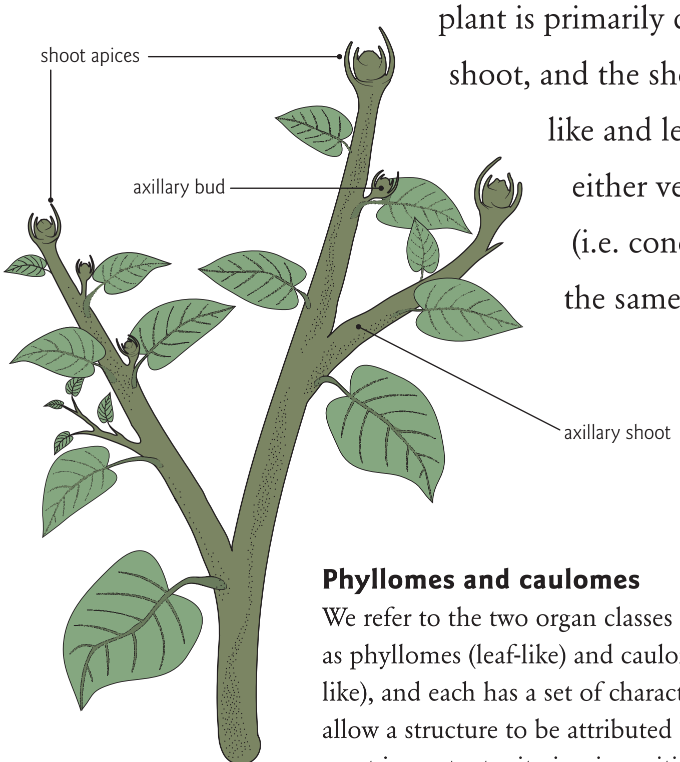
Goethe's idea had a profound impact, and it has influenced plant morphology to the current day. The past 200 years have seen relative disinterest in the root, and a concentration of interest in the shoots and flowers based largely on Goethe's concept of a dichotomy between leaf-like and stem-like organs. This is reflected in the most commonly applied model of plant construction, the classical or leaf–stem model.

Chamaerops humilis Caption here please write caption here please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly.

Applying a model of plant morphology

The classical or leaf–stem model of plant construction is the modern formal articulation of Goethe's idea (see page 00). The plant is primarily divided into roots and shoot, and the shoot is further divided into stem-like and leaf-like structures. Shoots can be either vegetative (i.e. leafy stems) or fertile (i.e. cones or flowers), but their parts bear the same relationship to one another.

Southern magnolia (Magnolia grandiflora). Called Evegreen Magnolia, supply this caption, thanks. Caption here please write accordingly to the approximate length shown here please Caption here please write accordingly.



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Phyllomes and caulomes

We refer to the two organ classes of the shoot as phyllomes (leaf-like) and caulomes (stem-like), and each has a set of characteristics that allow a structure to be attributed to it. The most important criterion is position on the plant, which reflects the organ's mode of formation. Phyllomes are formed near the tip of the growing stem, on the flank of the apical meristem. Caulomes are formed in the axils of phyllomes – the angle between the phyllome and the axis that bears it. Thus, phyllomes are lateral structures, and caulomes are axillary and subtended by a phyllome.

This positional relationship is at the heart of the repetitive architecture inherent in most plants – stems bearing lateral leaves (phyllomes), which in turn have shoots in their axils. These shoots consist of the stem (caulome), which in turn produces its own leaves, and so on. This continuous reiteration of shoots is what gives plants their modular construction and stands them apart from the growth form of animals, which typically develop from embryo directly to adult.

Other associated features

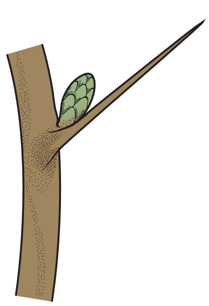
Apart from position, there are several other features associated with phyllomes and caulomes, but these can be variable and their application requires come caution. Phyllomes are typically bilaterally symmetrical structures (i.e. flattened), and have determinate,

or limited, growth. Caulomes are typically radially symmetrical (i.e. round), and have indeterminate, or unlimited, growth. Most leaves clearly fit into the category of phyllomes, and most stems are unarguably caulomes. However, when some of the features conflict, such as round leaves or flattened stems, we invoke their lateral or axillary position as the true indicator of their identity.

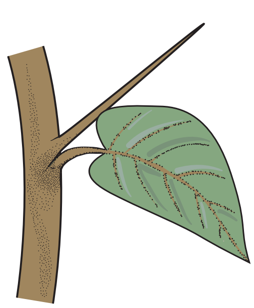
In the classical theory, flowers are considered to be fertile shoots; the axis is a caulome, and the sepals, petals, stamens and carpels are phyllomes. Indeed, flowers themselves are axillary structures, and are usually subtended by a truly lateral structure (a leaf or bract).

A SPINY PROBLEM

Spines can be either phyllomes or caulomes, depending on where they are located. Some species have spines that are in a lateral position and replace leaves; these are phyllomes, and they even have new shoot buds in their axils. Other species have spines that form in the axil of a leaf; these are modified shoots, or caulomes. In common gorse (*Ulex europaeus*) (left), both the leaves and axillary shoots are similarly spiny, but they can be distinguished by their position.



phyllome



caulome

IT'S ALL IN THE DETAIL

Plants in the genus *Ruscus*, closely related to the genus *Asparagus*, attracted the attention of Theophrastus because they appear to bear flowers on the centre of the leaves. However, if we look closely at the foliage, it is clear that each unit – which is green, flattened and of limited growth – actually sits in the axil of a small papery bract. The foliage unit is thus axillary, and from its position is a caulome; the bract is the truly lateral structure, and is interpreted as the phyllome. Note also that the flower sits in the axil of a bract that was produced by the foliage unit. We call these foliage units of *Ruscus* phylloclades, because they combine features of both leaves (flat and determinate) and branches (axillary position), but architecturally they are axillary stems that have been modified as photosynthetic organs.

Ruscus aculeatus. Losar de la Vera caption here please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly.

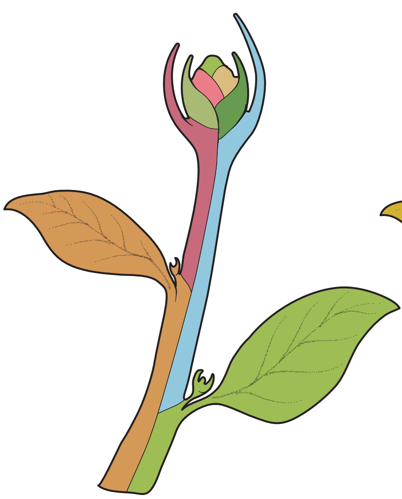
Alternative ways of looking at plants

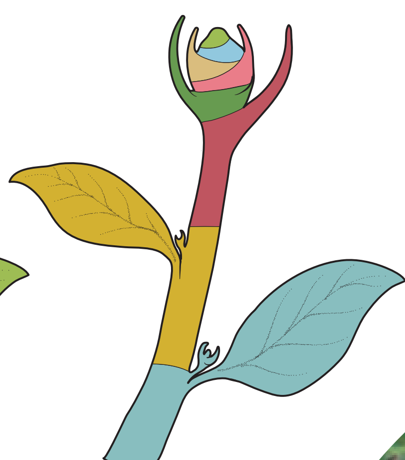
The leaf–stem model works well for interpreting most plants, particularly flowering plants, and even for unusual structures like the phylloclades of *Ruscus* (see box on page 00). However, it does not work for primitive land plants that have not yet evolved a level of complexity that distinguishes stems from leaves, and even within flowering plants there are examples where the leaf–stem model is unsatisfactory. To overcome these limitations, other models of plant construction have been proposed.

The phytonic and metameric models

The differences between the various models of plant morphology largely depend on how they deconstruct the plant. The classical model makes the major distinction between the leaf and the stem, but of course the leaf is continuous with the stem, and our desire to separate them is only arbitrary. Take, for example, the shoot of the Australian winged wattle (*Acacia alata*); it is not clear exactly where to delineate leaf from stem – indeed, the terms 'leaf' and 'stem' are not very useful in this instance.

Two alternative models that deconstruct the plant in different ways are the phytonic and metameric models. The phytonic model divides the shoot longitudinally into sectors; each sector includes a leaf and the adjoining stem as far as the next leaf directly below. This is a good model for describing the shoot of a winged wattle. In contrast, the metameric model divides the plant horizontally into segments; each segment includes an internode and a node, and the lateral organs arising from the node. This is a good model for plants with sympodial growth, where each segment of the axis is produced from a different apical meristem.





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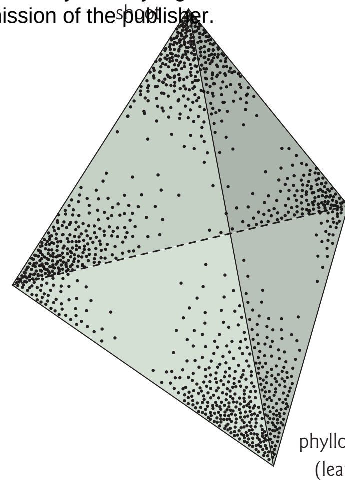
Acacia alata please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly to the approximate length shown here please Caption here please write accordingly to the approximate length.

The continuum model

A third model, called the continuum model, takes a different approach. It dismisses exclusive categories such as leaf and stem in favour of a continuous morphological space. In this space, most organs tend to cluster with character combinations we associate with either phyllomes or caulomes, or other categories such a trichomes (hairs), but intermediate organs can occupy any of the space between them.



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Complementary views

All three models can be applied to all plants to various degrees – in other words, they are complementary rather than exclusive. None of them is right or wrong, or even more right or more wrong than another; they are just different ways of looking at plants. Certainly, for a given plant or purpose, one model may be more appropriate than another, but being aware of these different views allows one to look at plants from a variety of different perspectives.

A HOLISTIC APPROACH

The small herbaceous plant commonly known as cleavers or goosegrass (*Galium aparine*), in the coffee family (Rubiaceae), is a familiar garden weed that scrambles through shrubs. Apart from its sticky stems and fruits, the most characteristic feature is its foliage: whorls of six identical leaves that are regularly spaced along the stem. But first appearances can be deceiving. Only two leaves in each whorl were formed as primordia at the apical meristem, and hence qualify positionally as 'true leaves' or phyllomes. The other four structures arose later, two on either side of the 'true leaf' primordia, and are considered to be stipules – appendages associated with the bases of leaves. Indeed, close inspection reveals that axillary buds only ever arise in the angle of the true leaves, not in the angles of the 'stipular' leaves.

The continuum model would emphasize the similar form of the leaves and stipules to equate these structures, while a classical approach would distinguish them based on their position. So being able to look at cleavers from both points of view allows a more enlightening and holistic appreciation of the plant.

Galium aparine
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Evolution and development

The past two decades have seen enormous advances in the evolution of development, or evo-devo, and our understanding of the developmental genetics of organisms. Many of the advances have been in human and animal biology, particularly driven by medical research, but a vastly increased knowledge of the genes and genetic processes that control plant development has provided a new way of looking plant structure.

Ⓥ leaves of an eucalyptus tree write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accor dingly to the approximate length shown here please

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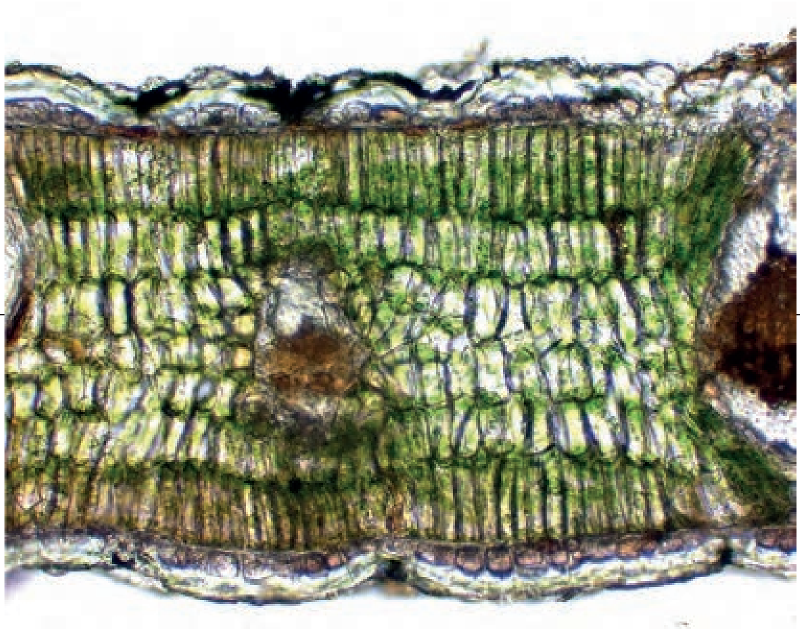
The ABC of flowers

Much of this new knowledge has resulted from experiments with thale cress (*Arabidopsis thaliana*), a small plant in the cabbage family (Brassicaceae) that is widely used in laboratory studies. It is easily manipulated and contains a relatively small number of genes, vast quantities can be cultivated in a limited space, and its speedy maturation from seedling to adult plant allows many generations to be grown in a short time.

One idea that has been turned on its head as a result of this research is the classical notion of the flower as a fertile shoot, with the leaves replaced by successive whorls of sepals, petals, stamens and carpels. Experiments with thale cress have revealed that this seemingly precise order for different floral parts is due to three classes of gene that are expressed across the four whorls of the developing flower; these genes are termed A, B and C, and hence it is referred to as the ABC model.

In a region where only gene A is expressed, sepals are produced. If only gene C is expressed, carpels are produced. Genes A and B expressed together results in petals, and a combination of B and C results in stamens. In the normal situation, the four zones express A alone (sepals), A and B (petals), B and C (stamens), and C alone (carpels). But mutant plants that lack one or other of these genes can produce flowers with missing and substituted parts. For example, plants lacking a C gene can produce only sepals (A expressed alone) and petals (A and B expressed together).

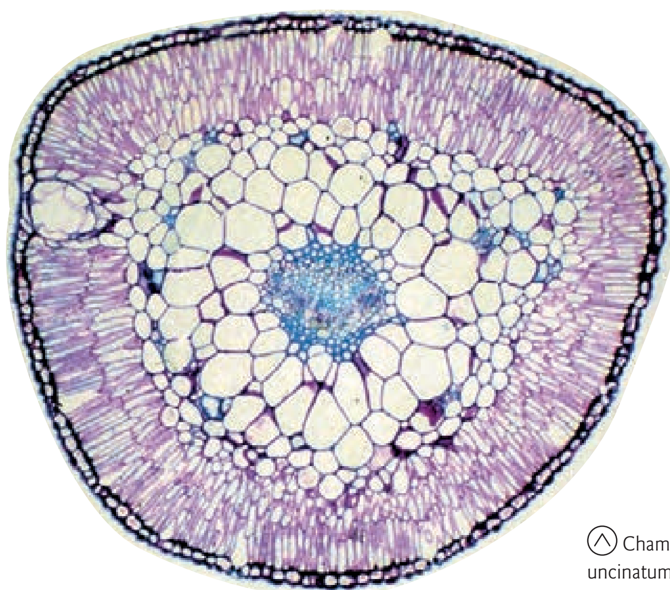
It is easy to see how an imprecise expression of this developmental pattern



could lead to the 'mutant' flowers that are prized in horticulture, such as the multi-petalled roses (*Rosa* spp.) and carnations (*Dianthus* spp.), which are very different from their strictly five-petalled wild ancestors. Indeed, varying expressions of the A, B and C genes could explain much of the enormous variation in flower structure.

The genetics of leaf development

Another set of genes is implicated in leaf development. Typical leaves have a flat blade in which the upper and lower halves have a different cell structure; typically, the upper half has elongated, column-like cells called palisade mesophyll, which is perfect for light capture, and the lower half has stomata (breathing pores) on the surface and internal spongy cells for absorbing carbon dioxide. We now know that different sets of genes determine the identity of the tissue types in these regions. If the genes for spongy tissue are deactivated, both halves of the leaf will have elongate palisade cells, and if the genes for the palisade cells are deactivated, both halves of the leaf will be spongy. It is the interaction of the genes in the two halves of the leaf that determines its bilateral symmetry (flatness); when one gene is missing, the leaves are needle-shaped, with radial symmetry.



Chamelaucium uncinatum write caption here please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly.

Chamelaucium TS leaf write caption here please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly.

GENETIC MODIFICATIONS

The gene experiments on leaves point to possible explanations for atypical leaves found in nature. *Eucalyptus* leaves are isobilateral, and hang vertically to minimize their exposure to the hot sun. Because they do not present 'upper' and 'lower' surfaces, both halves of the leaf are the same and have elongate palisade mesophyll. Many arid plants have terete, or cylindrical leaves, which reduces the surface area-to-volume ratio and hence minimizes water loss to the environment. We do not yet know the developmental genetic basis for these leaves, but it would not be surprising to discover that it was accompanied by a modification of these or similar genes.

Plant cells, tissues and organs

Like all living organisms, plants are made up of cells. There are many different types of plant cells with different functions, and these cells are arranged into tissues that have a precise function. Some cell and tissue types are characteristic of particular organ structures, such as the light-harvesting cells in the leaves, but others are found throughout the plant. The cells themselves can be observed only with a microscope, but the tissues and tissue systems are obvious at a larger scale, such as wood, bark and the veins of the leaf.

Tissue systems

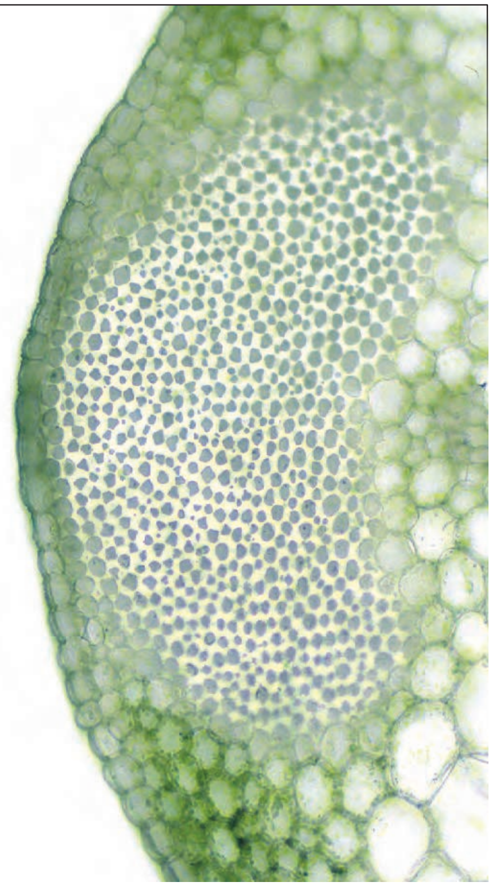
At the most fundamental level, plants consist of three broad tissue systems – the dermal, vascular and ground systems. The dermal system, as its name suggests, is the 'skin' of the plant. In its simplest form, it consists of a single layer of cells that covers the entire surface of the plant, and it is the main interface between the plant and the environment. It is covered with a waxy layer of cuticle to prevent the plant drying out, it contains stomata for taking up carbon dioxide from the atmosphere, and it is often expanded into hairs or prickles as a first layer of defence against herbivory.

The vascular system is the plant's conducting system, and is responsible for transporting substances around the plant. The xylem tissue transports water from the roots, where it is absorbed from the soil, to the leaves. The phloem tissue transports sugars that are made during photosynthesis from the leaves to growing regions or storage organs. The vascular system includes the wood in the stem and the veins in the leaves.

Dicotyledon leafplease write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly to the approximate length shown here please Caption here please write accordingly to the approximate length.

CELLULOSE VS. LIGNIN

The stringy bits on a stalk of celery are bundles of cells called collenchyma. Collenchyma cells are long and narrow, and their corners are thickened with extra layers of the cell wall material cellulose. Cellulose is a flexible material, and collenchyma is produced in places where plants need flexible structural support. When plants require rigid structural support, or a tough, hard texture, they thicken their cells walls with a layer of lignin.



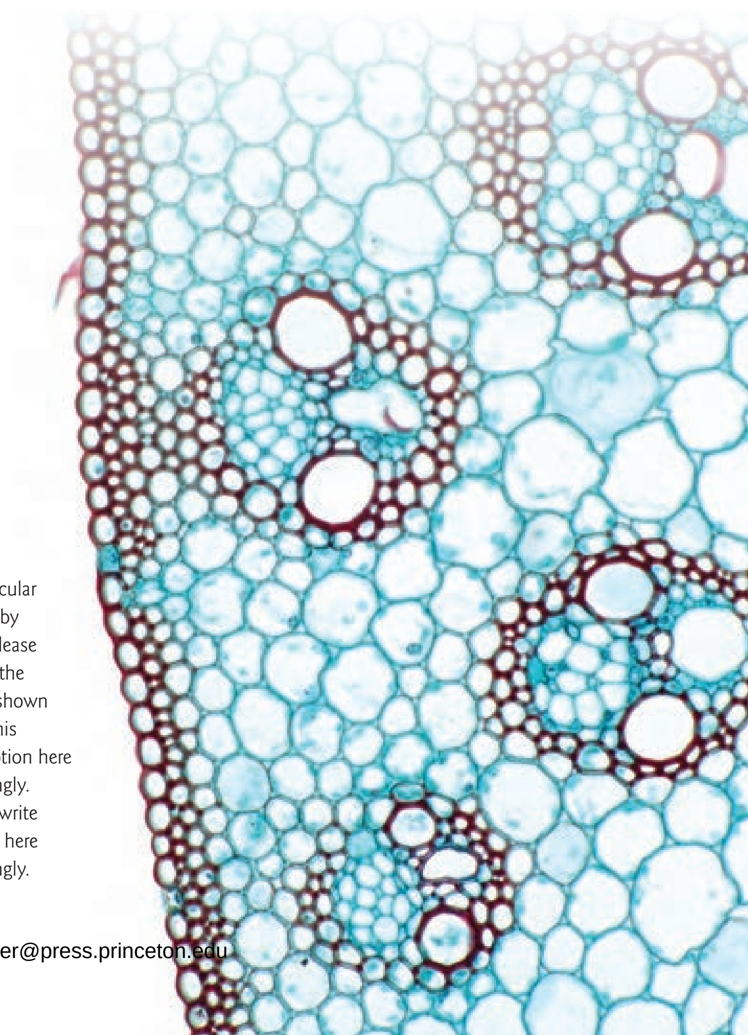
Celery collenchyma write caption here please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly.

Celery slices please write caption here please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly.

The remainder of the plant is referred to as the ground system, and consists of simple tissues that are variously adapted for storage or structural support. For example, a potato is made up almost entirely of thin-walled parenchyma cells filled with starch grains as a food storage, and the strings of a celery stalk are specially thickened collenchyma cells that provide flexible structural support for the leaf (see box).

Cell walls

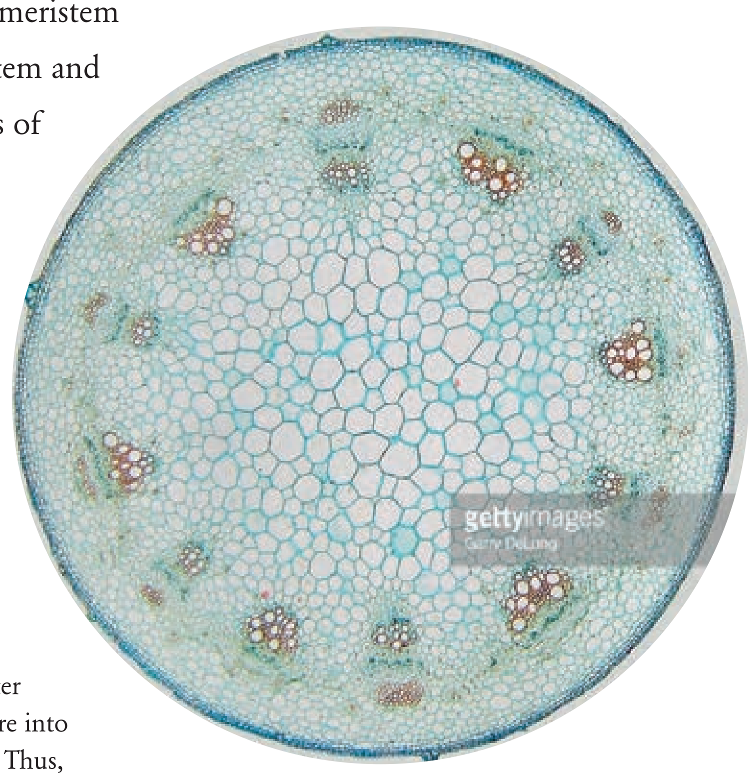
The chemical composition of the plant's cell walls is one of the most important features contributing to its function and texture. All plant cells are primarily made of cellulose, which is a soft, flexible material. Some types of cells are additionally thickened with lignin, a very hard, inflexible material that makes the cell walls hard and rigid. Lignified cells primarily provide structural support, and give plant stems their woody texture.



corn stem – vascular bundles surrounded by sclerenchyma here please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly. Caption here please write accordingly. Caption here please write accordingly.

Plant growth: external form

We have already seen that the shoot apical meristem is crucially important for elongation of the stem and the development of the early cells and tissues of the plant. However, the apical meristem also plays an important role in the external form of plants.

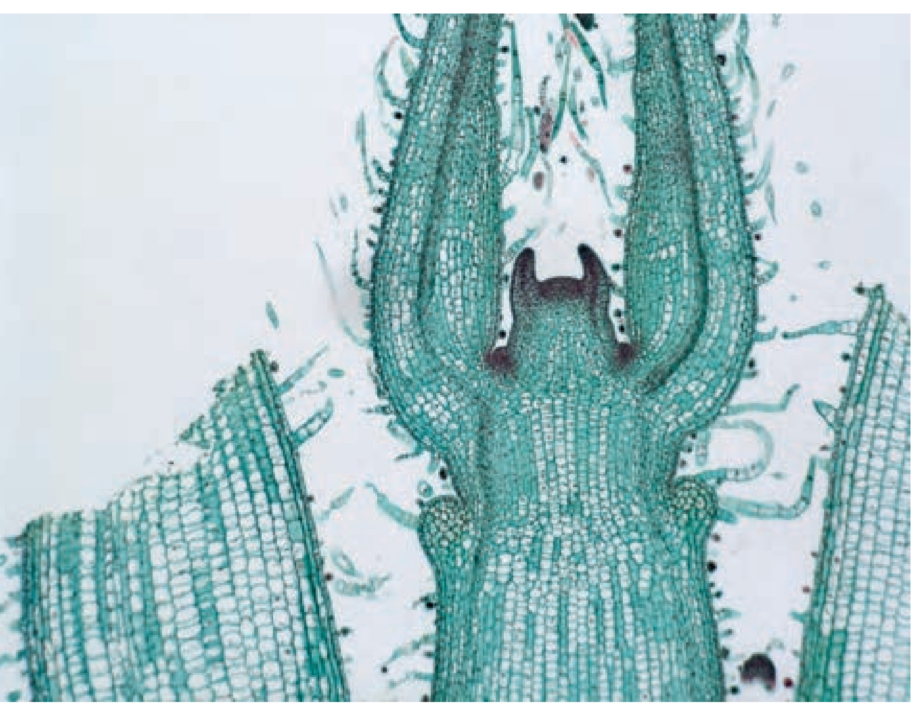


Primary growth

Plants grow from their tips. At the very ends of the seedling shoot and root are regions of cell division and proliferation known as apical meristems. The cells of these meristems are continually dividing, and they leave new daughter cells behind them that in turn mature into the tissues of the stem and the root. Thus, apical meristems add length to the stems and roots. The apical meristems are called the primary meristems, and the cells and tissues derived from them are referred to as primary growth.

(>) Cross section of young Sunflower (Helianthus sp.) stem. to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly to the appro ximate length shown here please

(V) Shoot apex here please write accordingly to the approximate length shown here please Caption here please write accordingly to the approximate.



Secondary growth

The primary growth of a stem is not very extensive – often less that 5 mm ($\frac{3}{16}$ in) in diameter, and usually much less than the thickness of the average pencil. After all, the main function of the shoot apical meristem is to make the plant taller. But as the plant gets larger, the amount of water that must be transported from the roots to the ever more numerous leaves, and the sugars that need to be transported in the other direction to supply the ever-increasing root system, far exceed the capacity of the narrow primary stem. To overcome this constraint, the plant develops another type of meristem, the vascular cambium, which contributes more vascular tissue to the stem. This vascular cambium is in the shape of a cylinder in the stem, and it generates new xylem to the inside and new phloem to the outside. The xylem from the vascular cambium is the wood of the stem, and as it accumulates, the diameter – and hence the girth – of the branch or trunk increases. Just as the apical

PUT A CORK IN IT

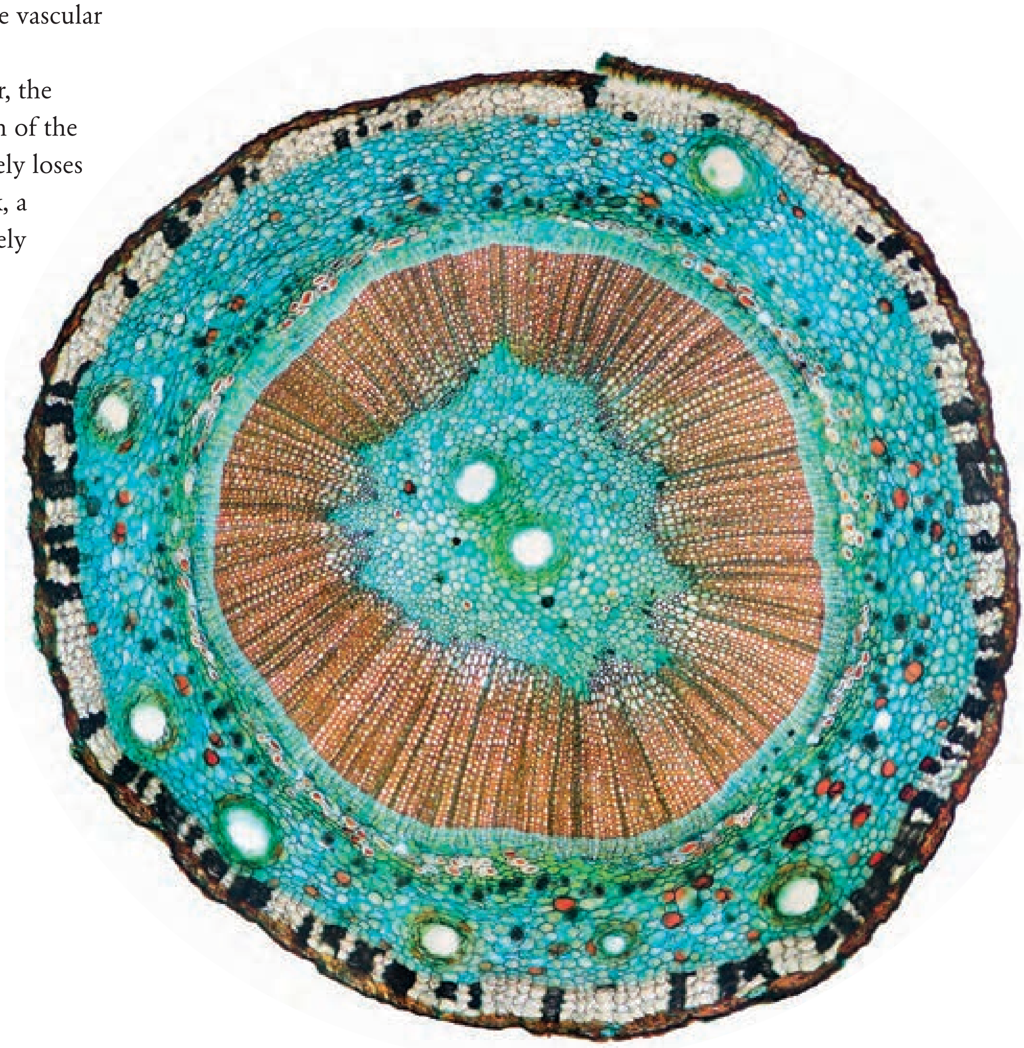
Cork has cell walls that are impregnated with suberin, a waterproof substance that gives the tissue its protective properties on the outside of the stem. This is also the feature that keeps wine in bottles. Wine corks are made from the outer bark of the cork oak (*Quercus suber*). This outer bark can be harvested sustainably; as long as the phloem and the vascular cambium is left intact, new cork meristems regenerate from the phloem.

Cork oak bark here please write caption here please write accordingly to the approximate length shown here please supply this caption, thanks.

meristem adds length to the stem, the vascular cambium adds width.

As the stem itself becomes thicker, the epidermis that forms the original skin of the plant becomes stretched and ultimately loses its integrity. It is replaced by the cork, a waterproof zone of cells that ultimately contributes to the bark. The vascular cambium and the cork meristem are referred to as secondary meristems, and the wood and bark tissue derived from them are secondary growth. A similar scenario occurs in the roots.

By the time a stem is as woody as a pencil, all of its component tissues are secondary growth; the small amount of primary tissue has either been shed with the bark or crushed into the centre.



Cross-section of the stem of a Gínkgo bilóba shoot please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly.

Plant growth: external form

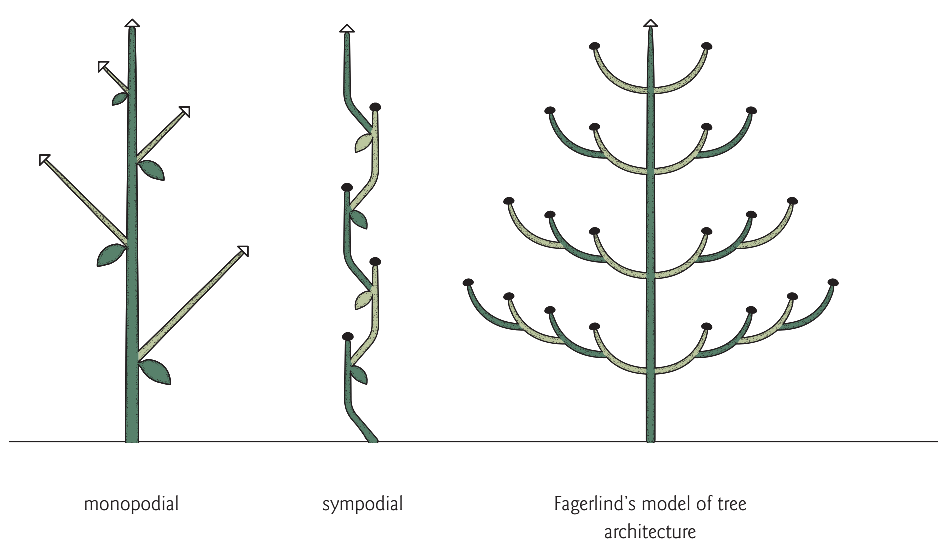
We have already seen that the shoot apical meristem is crucially important for elongation of the stem and the development of the early cells and tissues of the plant. However, the apical meristem also plays an important role in the external form of plants.

Campfire plant (Crassula capitella ssp. thyrsiflora) to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly to the approximate length shown here please

Helianthus sunflower here please write accordingly to the approximate length shown here please Caption here please write accordingly to the approximate. Caption here please write accordingly

Leaf development

Leaves develop as small bumps called primordia on the side of the meristem very close to the apex. In their primordial stage they are closely, but precisely, packed around the apex, and they are spaced out into their final positions – which are not randomly arranged – as the stem elongates. This precise arrangement of leaves is termed phyllotaxy, and although there are a number of different phyllotactic patterns in plants, they are all determined by the position of the primordia at the shoot apex.



Apical meristem please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write acco rdingly to the approximate length shown here please Caption here please write accordingly.

An architectural model

New branches arise from buds that are formed in the axils of leaves (the angle between the leaf and the stem), and these branches have apical meristems that produce their own leaves. So, a combination of the arrangement of the leaves and the axillary nature of the branching both determines and constrains the architecture of the shoot.

However, not all axillary buds immediately emerge to become branches. Some abort; others remain dormant, only to emerge if the main branch is damaged; and yet others develop into flowering structures. The developmental fate of particular buds is predetermined at the level of the whole plant, and the resulting growth pattern results in a correspondingly predictable whole-plant architecture. Because there are relatively few developmental fates of a bud, the possible variation in whole plant architecture is limited. Indeed, although there are about 300,000 plant species, they conform to just 27 different architectural models.

THE GOLDEN ANGLE

Leaves are precisely arranged on stems in a regular pattern that is formed at the apical meristem. One of the most common patterns is a spiral arrangement with an angle between each successive leaf of 137.5 degrees (called the golden angle), which conforms to the mathematical Fibonacci sequence, named after a twelfth-century Italian mathematician. This sequence approximates the shape of the logarithmic spiral, which is common in nature – the shape of a ram's horn, the spiral of a snail's shell, the curve of a tiger's claw. It is the only spiral that maintains its shape as it increases in size – an important feature for growing organisms.

Houseleek; Sempervivum accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly to the approximate length shown here please accordingly

MONOPODIAL VS. SYMPODIAL GROWTH

Most shoots grow from a permanent apical meristem at the tip, and the entire length of stem is the product of this meristem; this is called monopodial growth. However, other shoots have growing tips with limited growth – they produce a segment of stem, then cease growth (often terminating in a flower), and are superseded by a branch from below that forms the next segment of stem, and so on; this is referred to as sympodial growth. These two types of growth can be combined in the same plant – for example, a monopodial main trunk with sympodial lateral branches is the basis for Fagerlind's model

Plant morphology and classification

A very familiar concept in biology is the fact that related organisms have a similar structure, and that the closer the relationship, the more similar the organisms are to one another. In evolutionary terms, this means that the closer the relationship, the less time the organisms have had to diverge. In fact, we use similarities between organisms to infer relationship.

Erigeron 'Dunkelste Aller' (Fleabane 'Darkest of All') Asteraceae family length shown here please supply this caption, thanks. Caption here please write acco rdingly. Caption here please write acco rdingly.

Defining characters

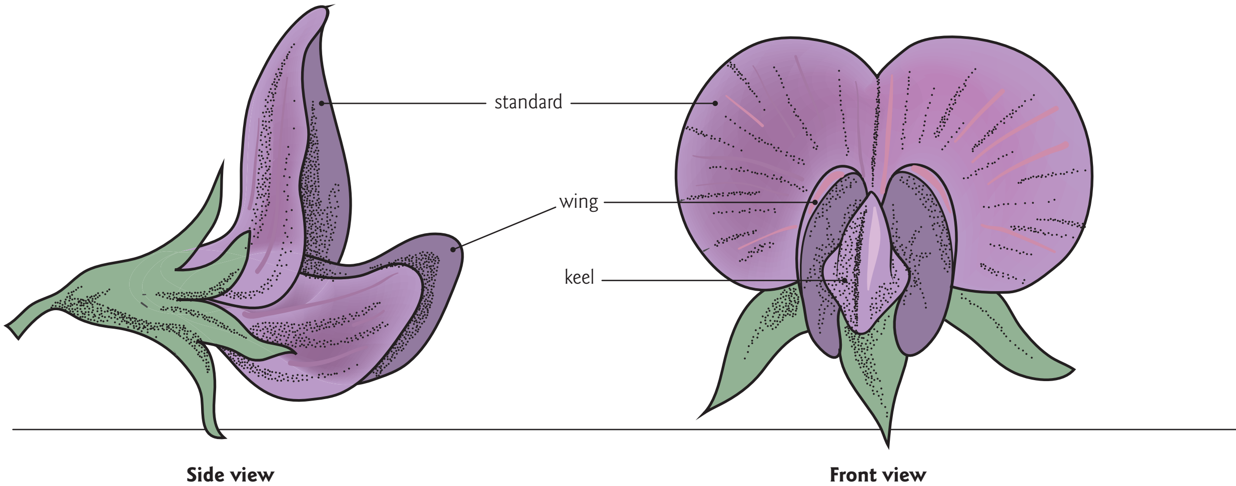
In the classification of plants, the major divisions such as gymnosperms or angiosperms are further divided into orders, families and genera. For example, all species of apples belong to the genus *Malus* and species of pear belong to the genus *Pyrus*. Both *Malus* and *Pyrus* belong to the rose family (Rosaceae), which in turn is classified in the order Rosales. The flowers and fruit of pears and apples are structurally quite similar, which reflects their close relationship. In the classification of plants, it is at the family level that the defining characters are most generally recognizable.

When it comes to determining relationships, reproductive structures such as cones and flowers are more reliable indicators than vegetative features such as leaves or the habit of the plant (its overall shape). This is most likely because vegetative features are permanently present, and are adapted for the particular environment favoured by the species. Flowers, on the other hand, are short-lived and temporary, and so do not become so modified through selection to such a great extent.

Peas and daisies

Two plant families that display a very uniform flower structure but widely variable vegetative morphology are the legume family (Fabaceae) and daisy family (Asteraceae). The scientific name for the legume family used to be Papilionaceae, in reference to the shape of the flower – the Latin word *papilio* means 'butterfly'.

Sweet pea flower here please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly to the approximate length shown here please Caption here please write accordingly to the approximate length shown here please Caption here please write accordingly to the approximate.

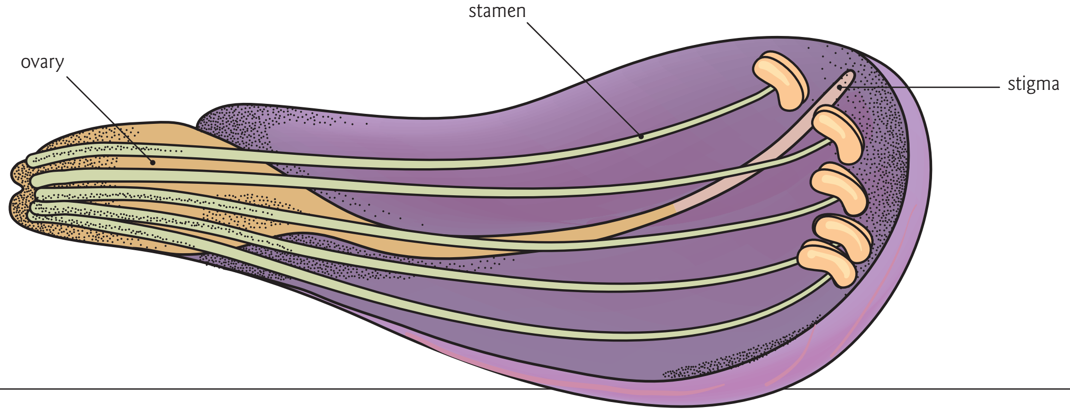


The flowers of species in the family are remarkably consistent, with five petals (one standard, two wings and two that fuse to form the keel) arranged so as to give the overall structure a single plane of symmetry. There are ten stamens, of which commonly nine are united to form a tube and the other is solitary. In the middle of the flower is a single carpel (female part), which develops into a fruit called a legume – pea and bean pods are typical legumes. The plants themselves differ wildly, however, and can range from tiny herbaceous clovers that stay close to the ground, to climbing lianas, arid shrubs with small, spiny leaves, and tall rainforest trees.

Flowers of members of the daisy family are small (they are termed florets) and are arranged in tight clusters surrounded by either papery, fleshy or spiny bracts. This cluster of florets, called an inflorescence, presents itself to pollinators as a coherent unit, so is functioning like the single flower of other plants. There are two different types of floret in typical daisies (although some daisies have only one type): the petal-like ray florets, often arranged around the outside of the cluster; and the more tubular disc florets, located in the centre. The habit of the plants, like the peas, ranges from small herbs to large trees, with shrubby and climbing forms in between. Again, however, the flower is a common character – so much so, in fact, that the typical composite daisy inflorescence gave rise to the earlier family name of Compositae.

Ⓐ Bee on sunflower write caption here please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write acco rdingly.

Ⓑ Craspedia canens here please write caption here please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly.



Section view

Modifications of form due to extreme function and habitat

The structural features some plants have evolved in order to function in different environments are so extreme that they defy almost every attempt at interpretation. Sometimes, it is only one organ that is affected, but at other times the whole plant is modified. Some bizarre examples are seen in parasitic plants, and plants that have adapted to aquatic habitats.

Caption here please write caption here please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly.

Weird and wonderful

Structural modifications of plant parts as an adaptation to particular environments are common. For example, many plant families contain succulent species that are especially good at storing and conserving water. But even in the most unusual cacti, we can recognize a fleshy barrel-shaped stem with spiny leaves and axillary shoots that develop from apical meristems and associated primordia. In other words, they are weird, but we can interpret them in our normal framework. In contrast, many parasitic plants appear to have dispensed with some of their typical structures and developed, either in part or in the whole plant, an entirely new morphology to cope with the demands of their modified existence.

MINIATURE MARVELS

Duckweeds in the genera *Lemna* and *Wolffia* are among the smallest of all angiosperms. They are free-floating aquatic plants found in still freshwater environments, and their tiny size and simplicity of structure make their interpretation difficult. Each plant consists of a small elliptical module, called a frond, which buds off new modules from special growing zones. A root dangles down into the water. Most reproduction is by vegetative budding, but flowers consisting of a single stamen or carpel are produced if environmental conditions are suitable.

Rootless duckweed (Wolffia arrhiza, Lemna arrhiza), write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly.

SECRET IDENTITY

Riverweeds in the family Podostemaceae attach to rocks in fast-flowing streams and rivers. They are thalloid – in other words, they have an amorphous body that is not differentiated into stems and leaves – and are more reminiscent of liverworts than flowering plants. Even the root system is unusual, and develops to adhere the plant to the rock like the holdfast of a marine alga. Riverweeds flower only when the water level drops and their habitat is exposed, thus revealing their identity as flowering plants.

Under the mistletoe

Mistletoes, parasitic flowering plants in the families Loranthaceae and Santalaceae, have seeds that are spread to the branches of other trees by birds. The seeds germinate, but rather than producing a root system they develop structures called haustoria, or sinkers, that penetrate the host branch and connect with its vascular tissue. In this manner, the mistletoe gets its water directly from the host. Normally, host and mistletoe can coexist, but a heavy infestation of mistletoes can kill a host. Extreme drought conditions in Australia can kill mistletoes while leaving their hosts alive, because the cells of *Eucalyptus* and *Acacia* trees can cope better under extreme water stress.

The shoots of mistletoes are otherwise normal, consisting of stems and leaves, but many species exhibit a strange mimicry, whereby their leaves are similar in appearance to those of the host plant. One explanation for this phenomenon is that it makes it harder for herbivores to distinguish the palatable mistletoe leaves from those of the unpalatable host.

Amyema quandang, approximate length shown here please supply this caption, thanks. Caption here please write accordingly to the approximate length shown here please Caption here please write accordingly to the approximate length shown here please

The branching holdfast of a mistletoe bush beneath a side branch on an old apple tree drawing food nutrients from its host here please supply this caption, thanks. Caption here please write accordingly to the approximate length shown here please Caption here.

Dealing with constraints

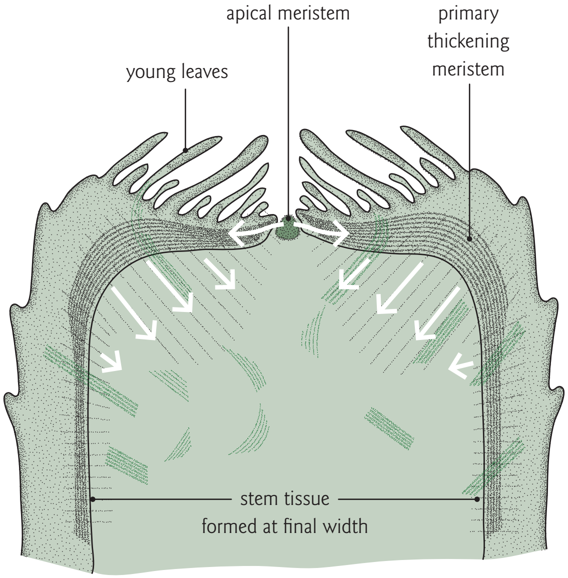
The function of plants is constrained by their structure, which is in turn constrained by their development. Indeed, the history of plant life on land has been one of increasing developmental and structural complexity to exploit the terrestrial environment in new and better ways. On occasion, however, plants find themselves down an evolutionary pathway that compromises some of their abilities; in these situations, they can either adapt to their new constraints, or they can develop ways to overcome them.

Caption here please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly to the approximate length shown here please

Palm trees please write accordingly to the approximate length shown here please Caption here please write accordingly to the approximate.

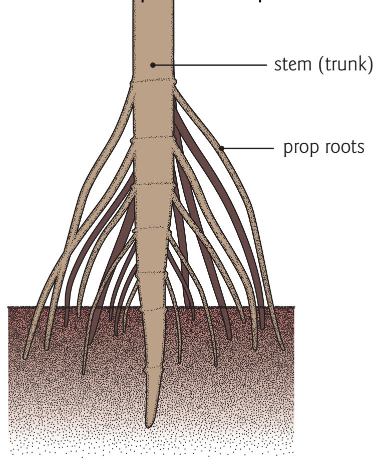
Arborescent monocots

In typical trees such as giant redwood conifers or mountain ash eucalypts, the small shoot apical meristem at the growing tip produces a thin, slender stem. As the plant grows larger in size and produces more leaves, the canopy needs to be supplied with increasing quantities of water from the roots, and the enlarging root system needs to be supplied with more nutrition produced by photosynthesis in the leaves. To increase the transport capacity of the stem, the plant develops the vascular cambium – the meristem that adds new transporting tissue, xylem and phloem, to the stem. This product of the vascular cambium is called

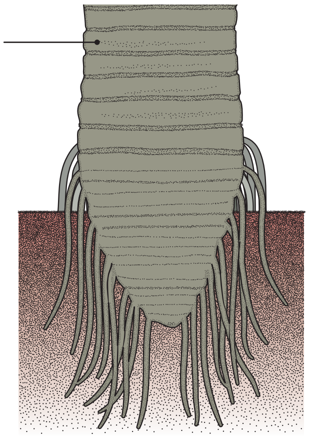


secondary growth, and it leads to woody stems whose function is to maintain the connection between the canopy and the roots.

Within the angiosperms is a large group that has lost the ability to produce a vascular cambium. These plants are the monocotyledons, or monocots, and include grasses, lilies and orchids. Because they do not develop a woody stem, they are, on the whole, relatively small herbaceous plants. However, some monocots do develop into large tree-like, arborescent plants, despite their lack of a vascular cambium and their inability to increase their conducting tissue through secondary growth. Prominent among these arborescent monocots are palms and screw palms (*Pandanus* spp.), which have solved the transport problem with a combination of clever features.



Some palms have prop roots that support the plant and bypass the narrow base of the stem.



Date palms produce their roots from the below-ground portion of the stem.

Transport solution

When palm seedlings emerge from the seed, they have a typical small shoot apical meristem, which produces a narrow stem. But as the seedling grows, the region immediately below the growing tip widens into a new zone of growth, the primary thickening meristem, which in turn produces an increasingly wider stem behind. In some palms, the shoot apex can eventually attain a diameter of 30 cm (12 in), producing the thick stem that is familiar in palm trees.

There is still an inherent constraint, however, because the first portion of the stem, produced when the seedling was small and the apical meristem was narrow, remains slender, with no mechanism for secondary thickening; there is no way for the now robust stem above to maintain an adequate connection with the roots below. Palm trees therefore dispense with the normal tap-root system, and instead produce new roots directly from the stem. As these roots appear higher up in the stem, they bypass the narrow lower region and deliver water directly from the soil to the thicker parts of the stem. In some palms, and in *Pandanus* species, the roots arise well above ground level and form spectacular prop roots that also provide structural support – sometimes even suspending the rest of the plant in mid-air. In other palms, such as date palms (*Phoenix dactylifera*) and coconut trees (*Cocos nucifera*), the seedling apex completes its widening process before it emerges from the ground, and the adventitious roots mostly emerge from the below-ground portion of the trunk.

Ⓟ Prop roots and palm roots please write caption here please write acco rdingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly.

Ⓥ Corn roots please write caption here please write accordingly to the approximate length shown here please supply this caption, thanks. Caption here please write accordingly.

ROOTING FOR MONOCOTS

The inability to maintain a viable root–shoot continuum due to the absence of a vascular cambium is a feature of all monocots, and all solve the problem by forgoing a tap root, instead producing adventitious roots from the stem, usually at the nodes where the leaves appear. Smaller grasses have a matted, fibrous root system, but in larger species such as maize (*Zea mays*), the adventitious roots can clearly be seen arising from the basal nodes of the stem.