Evolutionary Biology of Plants

Marquetta Brownlee

First Edition, 2012

ISBN 978-81-323-3747-8

Published by:
University Publications
4735/22 Prakashdeep Bldg,
Ansari Road, Darya Ganj,
Delhi - 110002
Email: info@wtbooks.com

Table of Contents

Chapter 1 - Evolutionary History of Plants

Chapter 2 - Plant Evolutionary Developmental Biology

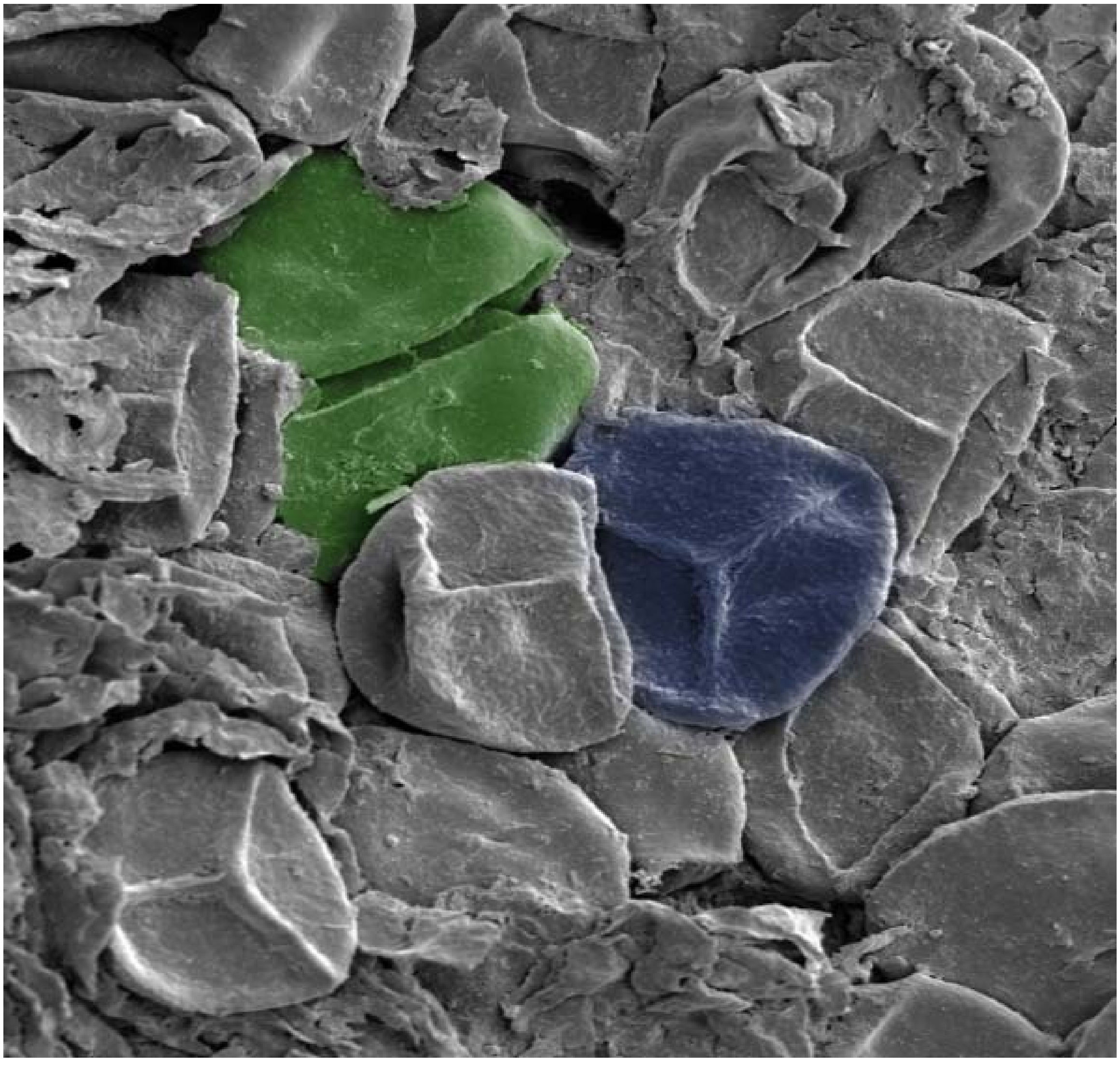
Chapter 3 - Alternation of Generations

Chapter 4 - Plant Reproduction

Chapter 5 - Timeline of Plant Evolution

Chapter- 1

Evolutionary History of Plants



A late Silurian sporangium. **Green**: A spore tetrad. **Blue**: A spore bearing a trilete mark – the *Y*-shaped scar. The spores are about 30-35 µm across

The **evolution of plants** has resulted in increasing levels of complexity, from the earliest algal mats, through bryophytes, lycopods, ferns to the complex gymnosperms and angiosperms of today. While the groups which appeared earlier continue to thrive, especially in the environments in which they evolved, each new grade of organisation has eventually become more "successful" than its predecessors by most measures.

Evidence suggests that an algal scum formed on the land 1,200 million years ago, but it was not until the Ordovician Period, around 450 million years ago, that land plants appeared. These began to diversify in the late Silurian Period, around 420 million years ago, and the fruits of their diversification are displayed in remarkable detail in an early Devonian fossil assemblage from the Rhynie chert. This chert preserved early plants in cellular detail, petrified in volcanic springs. By the middle of the Devonian Period most of the features recognised in plants today are present, including roots, leaves and secondary wood, and by late Devonian times seeds had evolved. Late Devonian plants had thereby reached a degree of sophistication that allowed them to form forests of tall trees. Evolutionary innovation continued after the Devonian period. Most plant groups were relatively unscathed by the Permo-Triassic extinction event, although the structures of communities changed. This may have set the scene for the evolution of flowering plants in the Triassic (~200 million years ago), which exploded in the Cretaceous and Tertiary. The latest major group of plants to evolve were the grasses, which became important in the mid Tertiary, from around 40 million years ago. The grasses, as well as many other groups, evolved new mechanisms of metabolism to survive the low CO_2 and warm, dry conditions of the tropics over the last 10 million years.

Colonisation of land

The Devonian period marks the beginning of extensive land colonization by plants, which through their effects on erosion and sedimentation brought about significant climatic change.

Land plants evolved from chlorophyte algae, perhaps as early as 510 million years ago; their closest living relatives are the charophytes, specifically Charales. Assuming that the Charales' habit has changed little since the divergence of lineages, this means that the land plants evolved from a branched, filamentous, haplontic alga, dwelling in shallow fresh water, perhaps at the edge of seasonally desiccating pools. Co-operative interactions with fungi may have helped early plants adapt to the stresses of the terrestrial realm.

Plants were not the first photosynthesisers on land, though: consideration of weathering rates suggests that organisms were already living on the land 1,200 million years ago, and microbial fossils have been found in freshwater lake deposits from 1,000 million years ago, but the carbon isotope record suggests that they were too scarce to impact the atmospheric composition until around 850 million years ago. These organisms were probably small and simple, forming little more than an "algal scum".

The first evidence of plants on land comes from spores of Mid-Ordovician age (early Llanvirn, ~470 million years ago). These spores, known as cryptospores, were produced either singly (monads), in pairs (diade) or groups of four (tetrads), and their microstructure resembles that of modern liverwort spores, suggesting they share an equivalent grade of organisation. It could be that atmospheric 'poisoning' prevented eukaryotes from colonising the land prior to this, or it could simply have taken a great time for the necessary complexity to evolve.

Trilete spores similar to those of vascular plants appear soon afterwards, in Upper Ordovician rocks. Depending exactly when the tetrad splits, each of the four spores may bear a "trilete mark", a *Y*-shape, reflecting the points at which each cell was squashed up against its neighbours. However, in order for this to happen, the spore walls must be sturdy and resistant at an early stage. This resistance is closely associated with having a desiccation-resistant outer wall – a trait only of use when spores have to survive out of water. Indeed, even those embryophytes that have returned to the water lack a resistant wall, thus don't bear trilete marks. A close examination of algal spores shows that none have trilete spores, either because their walls are not resistant enough, or in those rare cases where it is, the spores disperse before they are squashed enough to develop the mark, or don't fit into a tetrahedral tetrad.

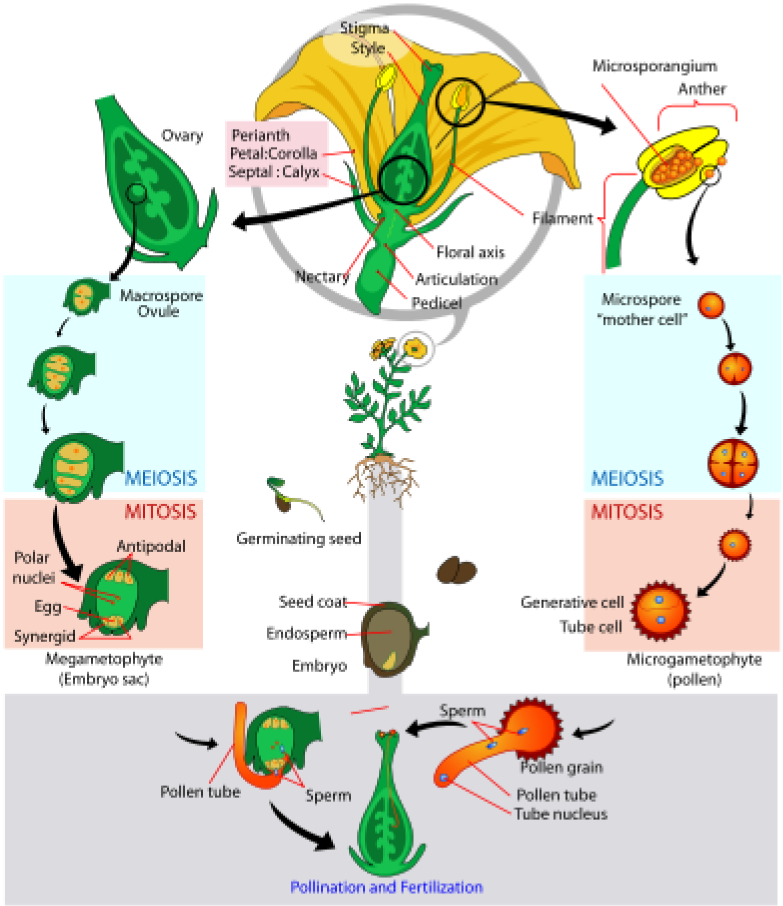
The earliest megafossils of land plants were thalloid organisms, which dwelt in fluvial wetlands and are found to have covered most of an early Silurian flood plain. They could only survive when the land was waterlogged.

Once plants had reached the land, there were two approaches to dealing with desiccation. The bryophytes avoid it or give in to it, restricting their ranges to moist settings, or drying out and putting their metabolism "on hold" until more water arrives. Tracheophytes resist desiccation. They all bear a waterproof outer cuticle layer wherever they are exposed to air (as do some bryophytes), to reduce water loss – but since a total covering would cut them off from CO_2 in the atmosphere, they rapidly evolved stomata – small openings to allow gas exchange. Tracheophytes also developed vascular tissue to aid in the movement of water within the organisms (see below), and moved away from a gametophyte dominated life cycle (see below). Vascular tissue also facilitated upright growth without the support of water and paved the way for the evolution of larger plants on land.

The establishment of a land-based flora permitted the accumulation of oxygen in the atmosphere as never before, as the new hordes of land plants pumped it out as a waste product. When this concentration rose above 13%, it permitted the possibility of wildfire. This is first recorded in the early Silurian fossil record by charcoalified plant fossils. Apart from a controversial gap in the Late Devonian, charcoal is present ever since.

Charcoalification is an important taphonomic mode. Wildfire drives off the volatile compounds, leaving only a shell of pure carbon. This is not a viable food source for herbivores or detritovores, so is prone to preservation; it is also robust, so can withstand pressure and display exquisite, sometimes sub-cellular, detail.

Changing life cycles



Angiosperm life cycle

All multicellular plants have a life cycle comprising two generations or phases. One is termed the **gametophyte**, has a single set of chromosomes (denoted **1N**), and produces gametes (sperm and eggs). The other is termed the **sporophyte**, has paired chromosomes (denoted **2N**), and produces spores. The gametophyte and sporophyte may appear identical – homomorphy – or may be very different – heteromorphy.

The pattern in plant evolution has been a shift from homomorphy to heteromorphy. The algal ancestors to land plants were almost certainly haplobiontic, being haploid for all their life cycles, with a unicellular zygote providing the 2N stage. All land plants (i.e. embryophytes) are diplobiontic – that is, both the haploid and diploid stages are multicellular. Two trends are apparent: bryophytes (liverworts, mosses and hornworts) have developed the gametophyte, with the sporophyte becoming almost entirely dependent on it; vascular plants have developed the sporophyte, with the gametophyte being particularly reduced in the seed plants.

There are two competing theories to explain the appearance of a diplobiontic lifecycle.

The **interpolation theory** (also known as the antithetic or intercalary theory) holds that the sporophyte phase was a fundamentally new invention, caused by the mitotic division of a freshly germinated zygote, continuing until meiosis produces spores. This theory implies that the first sporophytes would bear a very different morphology to the gametophyte, on which they would have been dependent. This seems to fit well with what we know of the bryophytes, in which a vegetative thalloid gametophyte is parasitised by simple sporophytes, which often comprise no more than a sporangium on a stalk. Increasing complexity of the ancestrally simple sporophyte, including the eventual acquisition of photosynthetic cells, would free it from its dependence on a gametophyte, as we see in some hornworts (*Anthoceros*), and eventually result in the sporophyte developing organs and vascular tissue, and becoming the dominant phase, as in the tracheophytes (vascular plants). This theory may be supported by observations that smaller *Cooksonia* individuals must have been supported by a gametophyte generation. The observed appearance of larger axial sizes, with room for photosynthetic tissue and thus self-sustainability, provides a possible route for the development of a self-sufficient sporophyte phase.

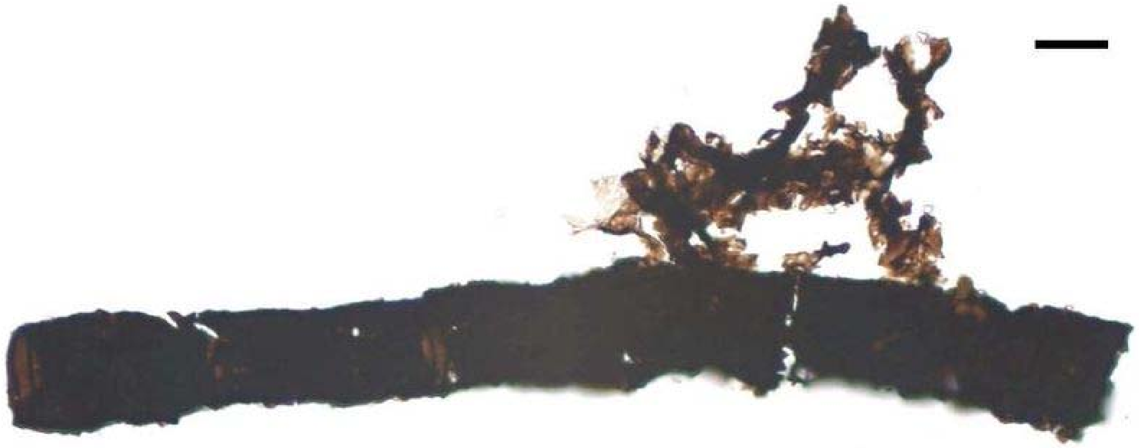
The alternative hypothesis is termed the **transformation theory** (or homologous theory). This posits that the sporophyte appeared suddenly by a delay in the occurrence of meiosis after the zygote germinated. Since the same genetic material would be employed, the haploid and diploid phases would look the same. This explains the behaviour of some algae, which produce alternating phases of identical sporophytes and gametophytes. Subsequent adaption to the desiccating land environment, which makes sexual reproduction difficult, would result in the simplification of the sexually active gametophyte, and elaboration of the sporophyte phase to better disperse the waterproof spores. The tissue of sporophytes and gametophytes preserved in the Rhynie chert is of similar complexity, which is taken to support this hypothesis.

Water transport

In order to photosynthesise, plants must uptake CO_2 from the atmosphere. However, this comes at a price: while stomata are open to allow CO_2 to enter, water can evaporate. Water is lost much faster than CO_2 is absorbed, so plants need to replace it, and have developed systems to transport water from the moist soil to the site of photosynthesis. Early plants sucked water between the walls of their cells, then evolved the ability to control water loss (and CO_2 acquisition) through the use of stomata. Specialised water transport tissues soon evolved in the form of hydroids, tracheids, then secondary xylem, followed by an endodermis and ultimately vessels.

The high CO_2 levels of Silurian-Devonian times, when plants were first colonising land, meant that the need for water was relatively low . As CO_2 was withdrawn from the atmosphere by plants, more water was lost in its capture, and more elegant transport mechanisms evolved. As water transport mechanisms, and waterproof cuticles, evolved, plants could survive without being continually covered by a film of water. This transition from poikilohydry to homoiohydry opened up new potential for colonisation. Plants were then faced with a balance, between transporting water as efficiently as possible and preventing transporting vessels to implode and cavitate.

During the Silurian, CO_2 was readily available, so little water needed expending to acquire it. By the end of the Carboniferous, when CO_2 levels had lowered to something approaching today's, around 17 times more water was lost per unit of CO_2 uptake. However, even in these "easy" early days, water was at a premium, and had to be transported to parts of the plant from the wet soil to avoid desiccation. This early water transport took advantage of the **cohesion-tension** mechanism inherent in water. Water has a tendency to diffuse to areas that are drier, and this process is accelerated when water can be wicked along a fabric with small spaces. In small passages, such as that between the plant cell walls (or in tracheids), a column of water behaves like rubber – when molecules evaporate from one end, they literally pull the molecules behind them along the channels. Therefore transpiration alone provided the driving force for water transport in early plants. However, without dedicated transport vessels, the cohesion-tension mechanism cannot transport water more than about 2 cm, severely limiting the size of the earliest plants. This process demands a steady supply of water from one end, to maintain the chains; to avoid exhausing it, plants developed a waterproof cuticle. Early cuticle may not have had pores but did not cover the entire plant surface, so that gas exchange could continue. However, dehydration at times was inevitable; early plants cope with this by having a lot of water stored between their cell walls, and when it comes to it sticking out the tough times by putting life "on hold" until more water is supplied.



A banded tube from the late Silurian/early Devonian. The bands are difficult to see on this specimen, as an opaque carbonaceous coating conceals much of the tube.

In order to be free from the constraints of small size and constant moisture that the parenchymatic transport system inflicted, plants needed a more efficient water transport system. During the early Silurian, they developed specialized cells, which were lignified (or bore similar chemical compounds) to avoid implosion; this process coincided with cell death, allowing their innards to be emptied and water to be passed through them. These wider, dead, empty cells were a million times more conductive than the inter-cell method, giving the potential for transport over longer distances, and higher CO_2 diffusion rates.

The first macrofossils to bear water-transport tubes *in situ* are the early Devonian pretracheophytes *Aglaophyton* and *Horneophyton*, which have structures very similar to the **hydroids** of modern mosses. Plants continued to innovate new ways of reducing the resistance to flow within their cells, thereby increasing the efficiency of their water transport. Bands on the walls of tubes, in fact apparent from the early Silurian onwards, are an early improvisation to aid the easy flow of water. Banded tubes, as well as tubes with pitted ornamentation on their walls, were lignified and, when they form single celled conduits, are considered to be **tracheids**. These, the "next generation" of transport cell design, have a more rigid structure than hydroids, allowing them to cope with higher levels of water pressure. Tracheids may have a single evolutionary origin, possibly within the hornworts, uniting all tracheophytes (but they may have evolved more than once).

Water transport requires regulation, and dynamic control is provided by stomata. By adjusting the amount of gas exchange, they can restrict the amount of water lost through transpiration. This is an important role where water supply is not constant, and indeed stomata appear to have evolved before tracheids, being present in the non-vascular hornworts.

An endodermis probably evolved during the Silu-Devonian, but the first fossil evidence for such a structure is Carboniferous. This structure in the roots covers the water transport tissue and regulates ion exchange (and prevents unwanted pathogens etc. from entering the water transport system). The endodermis can also provide an upwards pressure, forcing water out of the roots when transpiration is not enough of a driver.

Once plants had evolved this level of controlled water transport, they were truly homoiohydric, able to extract water from their environment through root-like organs rather than relying on a film of surface moisture, enabling them to grow to much greater size. As a result of their independence from their surroundings, they lost their ability to survive desiccation – a costly trait to retain.

During the Devonian, maximum xylem diameter increased with time, with the minimum diameter remaining pretty constant. By the middle Devonian, the tracheid diameter of some plant lineages had plateaued. Wider tracheids allow water to be transported faster, but the overall transport rate depends also on the overall cross-sectional area of the xylem bundle itself. The increase in vascular bundle thickness further seems to correlate with the width of plant axes, and plant height; it is also closely related to the appearance of leaves and increased stomatal density, both of which would increase the demand for water.

While wider tracheids with robust walls make it possible to achieve higher water transport pressures, this increases the problem of cavitation. Cavitation occurs when a bubble of air forms within a vessel, breaking the bonds between chains of water molecules and preventing them from pulling more water up with their cohesive tension.

A tracheid, once cavitated, cannot have its embolism removed and return to service (except in a few advanced angiosperms which have developed a mechanism of doing so). Therefore it is well worth plants' while to avoid cavitation occurring. For this reason, pits in tracheid walls have very small diameters, to prevent air entering and allowing bubbles to nucleate. Freeze-thaw cycles are a major cause of cavitation. Damage to a tracheid's wall almost inevitably leads to air leaking in and cavitation, hence the importance of many tracheids working in parallel.

Cavitation is hard to avoid, but once it has occurred plants have a range of mechanisms to contain the damage. Small pits link adjacent conduits to allow fluid to flow between them, but not air – although ironically these pits, which prevent the spread of embolisms, are also a major cause of them. These pitted surfaces further reduce the flow of water through the xylem by as much as 30%. Conifers, by the Jurassic, developed an ingenious improvement, using valve-like structures to isolate cavitated elements. These torus-margo structures have a blob floating in the middle of a donut; when one side depressurises the blob is sucked into the torus and blocks further flow. Other plants simply accept cavitation; for instance, oaks grow a ring of wide vessels at the start of each spring, none of which survive the winter frosts. Maples use root pressure each spring to force sap upwards from the roots, squeezing out any air bubbles.

Growing to height also employed another trait of tracheids – the support offered by their lignified walls. Defunct tracheids were retained to form a strong, woody stem, produced in most instances by a secondary xylem. However, in early plants, tracheids were too mechanically vulnerable, and retained a central position, with a layer of tough sclerenchyma on the outer rim of the stems. Even when tracheids do take a structural role, they are supported by sclerenchymatic tissue.

Tracheids end with walls, which impose a great deal of resistance on flow; vessel members have perforated end walls, and are arranged in series to operate as if they were one continuous vessel. The function of end walls, which were the default state in the Devonian, was probably to avoid embolisms. An embolism is where an air bubble is created in a tracheid. This may happen as a result of freezing, or by gases dissolving out of solution. Once an embolism is formed, it usually cannot be removed; the affected cell cannot pull water up, and is rendered useless.

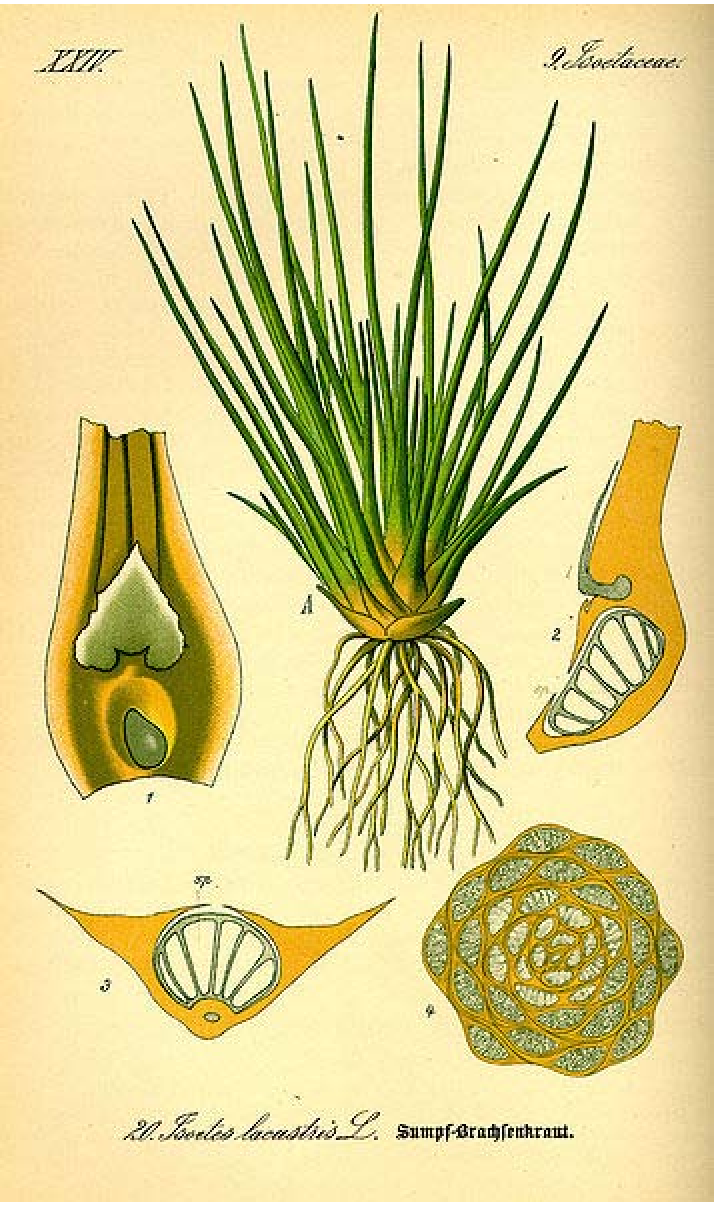
End walls excluded, the tracheids of prevascular plants were able to operate under the same hydraulic conductivity as those of the first vascular plant, *Cooksonia*.

The size of tracheids is limited as they comprise a single cell; this limits their length, which in turn limits their maximum useful diameter to 80 µm. Conductivity grows with the fourth power of diameter, so increased diameter has huge rewards; **vessel elements**, consisting of a number of cells, joined at their ends, overcame this limit and allowed larger tubes to form, reaching diameters of up to 500 µm, and lengths of up to 10 m.

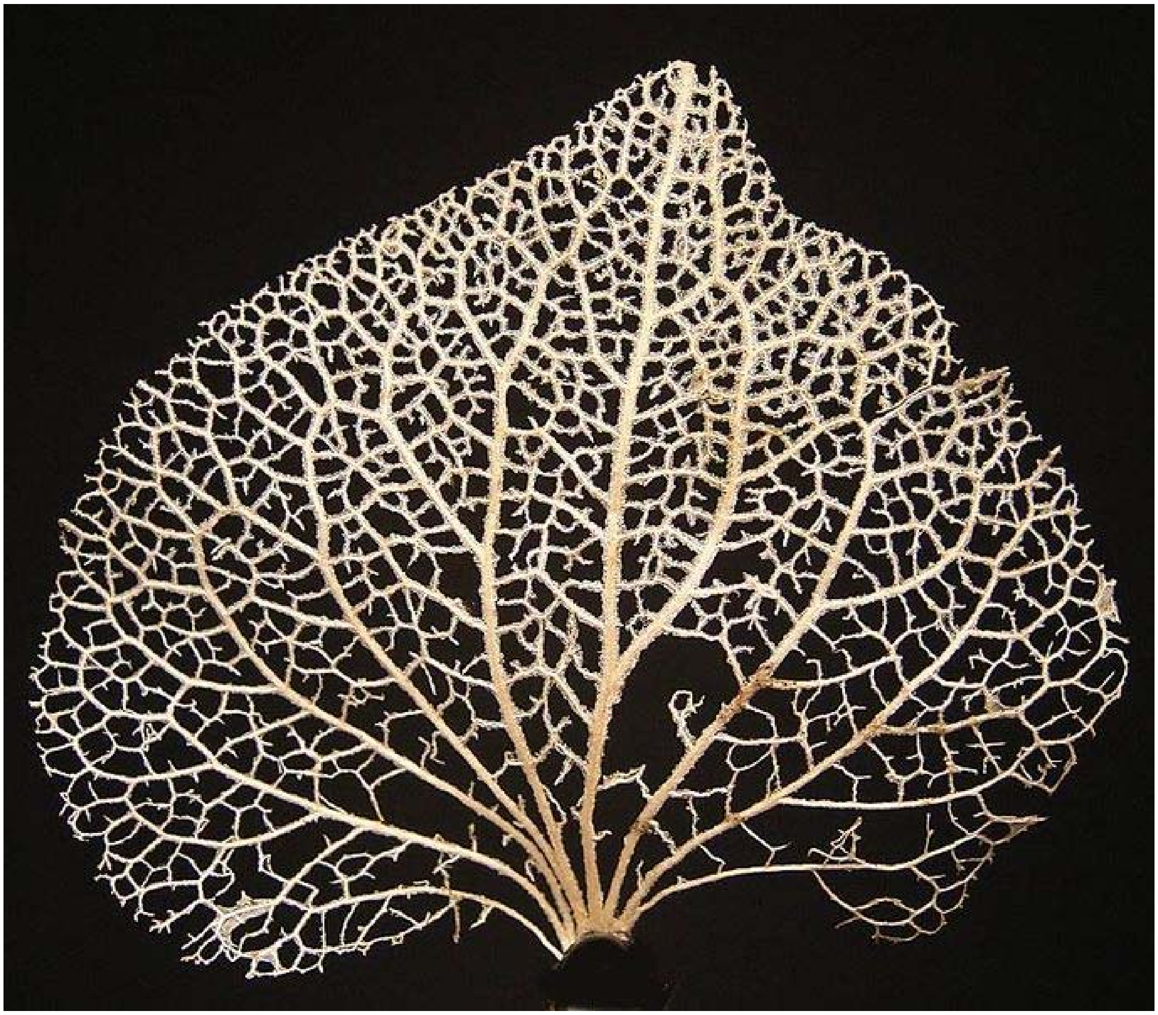
Vessels first evolved during the dry, low CO_2 periods of the late Permian, in the horsetails, ferns and Selaginellales independently, and later appeared in the mid

Cretaceous in angiosperms and gnetophytes. Vessels allow the same cross-sectional area of wood to transport around a hundred times more water than tracheids! This allowed plants to fill more of their stems with structural fibres, and also opened a new niche to vines, which could transport water without being as thick as the tree they grew on. Despite these advantages, tracheid-based wood is a lot lighter, thus cheaper to make, as vessels need to be much more reinforced to avoid cavitation.

Evolution of leaves



The lycopod *Isoetes* bears microphylls with a single vascular trace.



The branching pattern of megaphyll veins may belie their origin as webbed, dichotomising branches.

Leaves today are, in almost all instances, an adaptation to increase the amount of sunlight that can be captured for photosynthesis. Leaves certainly evolved more than once, and probably originated as spiny outgrowths to protect early plants from herbivory.

The rhyniophytes of the Rhynie chert comprised nothing more than slender, unornamented axes. The early to middle Devonian trimerophytes, therefore, are the first evidence we have of anything that could be considered leafy. This group of vascular plants are recognisable by their masses of terminal sporangia, which adorn the ends of axes which may bifurcate or trifurcate. Some organisms, such as *Psilophyton*, bore enations. These are small, spiny outgrowths of the stem, lacking their own vascular supply.

Around the same time, the zosterophyllophytes were becoming important. This group is recognisable by their kidney-shaped sporangia, which grew on short lateral branches close to the main axes. They sometimes branched in a distinctive H-shape. The majority of this group bore pronounced spines on their axes. However, none of these had a vascular trace, and the first evidence of vascularised enations occurs in the Rhynie genus *Asteroxylon*. The spines of *Asteroxylon* had a primitive vasuclar supply – at the very least, leaf traces could be seen departing from the central protostele towards each individual "leaf". A fossil known as *Baragwanathia* appears in the fossil record slightly earlier, in the late Silurian. In this organism, these leaf traces continue into the leaf to form their mid-vein. One theory, the "enation theory", holds that the leaves developed by outgrowths of the protostele connecting with existing enations, but it is also possible that microphylls evolved by a branching axis forming "webbing".

Asteroxylon and *Baragwanathia* are widely regarded as primitive lycopods. The lycopods are still extant today, familiar as the quillwort *Isoetes* and the club mosses. Lycopods bear distinctive microphylls – leaves with a single vascular trace. Microphylls could grow to some size – the Lepidodendrales boasted microphylls over a meter in length – but almost all just bear the one vascular bundle. (An exception is the branching *Selaginella*).

The more familiar leaves, megaphylls, are thought to have separate origins – indeed, they appeared four times independently, in the ferns, horsetails, progymnosperms, and seed plants. They appear to have originated from dichotomising branches, which first overlapped (or "overtopped") one another, and eventually developed "webbing" and evolved into gradually more leaf-like structures. So megaphylls, by this "teleome theory", are composed of a group of webbed branches – hence the "leaf gap" left where the leaf's vascular bundle leaves that of the main branch resembles two axes splitting. In each of the four groups to evolve megaphylls, their leaves first evolved during the late Devonian to early Carboniferous, diversifying rapidly until the designs settled down in the mid Carboniferous.

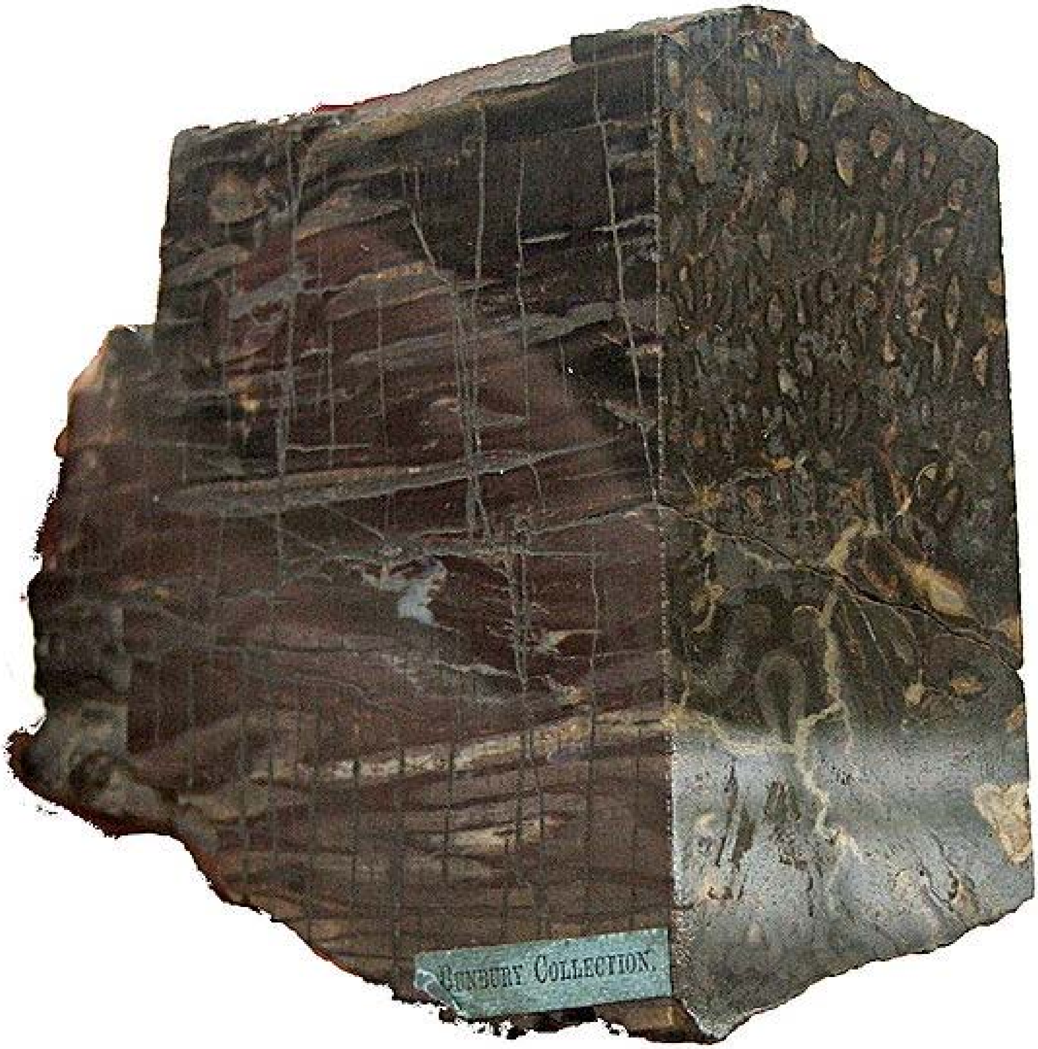
The cessation of further diversification can be attributed to developmental constraints, but why did it take so long for leaves to evolve in the first place? Plants had been on the land for at least 50 million years before megaphylls became significant. However, small, rare mesophylls are known from the early Devonian genus *Eophyllophyton* – so development could not have been a barrier to their appearance. The best explanation so far incorporates observations that atmospheric CO_2 was declining rapidly during this time – falling by around 90% during the Devonian. This corresponded with an increase in stomatal density by 100 times. Stomata allow water to evaporate from leaves, which causes them to curve. It appears that the low stomatal density in the early Devonian meant that evaporation was limited, and leaves would overheat if they grew to any size. The stomatal density could not increase, as the primitive steles and limited root systems would not be able to supply water quickly enough to match the rate of transpiration.

Clearly, leaves are not always beneficial, as illustrated by the frequent occurrence of secondary loss of leaves, famously exemplified by cacti and the "whisk fern" *Psilotum*.

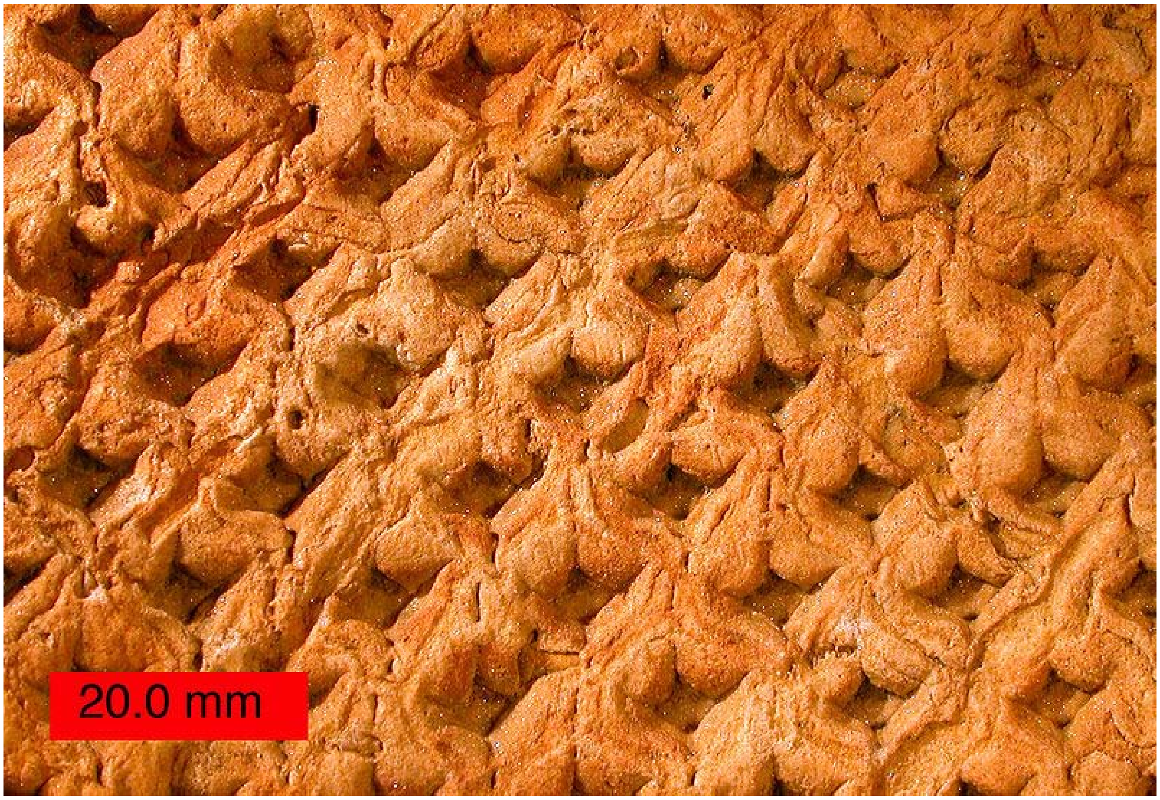
Secondary evolution can also disguise the true evolutionary origin of some leaves. Some genera of ferns display complex leaves which are attached to the pseudostele by an outgrowth of the vascular bundle, leaving no leaf gap. Further, horsetail (*Equisetum*) leaves bear only a single vein, and appear for all the world to be microphyllous; however, in the light of the fossil record and molecular evidence, we conclude that their forbears bore leaves with complex venation, and the current state is a result of secondary simplification.

Deciduous trees deal with another disadvantage to having leaves. The popular belief that plants shed their leaves when the days get too short is misguided; evergreens prospered in the Arctic circle during the most recent greenhouse earth. The generally accepted reason for shedding leaves during winter is to cope with the weather – the force of wind and weight of snow are much more comfortably weathered without leaves to increase surface area. Seasonal leaf loss has evolved independently several times and is exhibited in the ginkgoales, pinophyta and angiosperms. Leaf loss may also have arisen as a response to pressure from insects; it may have been less costly to lose leaves entirely during the winter or dry season than to continue investing resources in their repair.

Evolution of trees



The trunk of early tree fern *Psaronius*, showing internal structure. The top of the plant would have been to the left of the image



External mold of *Lepidodendron* trunk showing leaf scars from the Upper Carboniferous of Ohio

The early Devonian landscape was devoid of vegetation taller than waist height. Without the evolution of a robust vascular system, taller heights could not be attained. There was, however, a constant evolutionary pressure to attain greater height. The most obvious advantage is the harvesting of more sunlight for photosynthesis – by overshadowing competitors – but a further advantage is present in spore distribution, as spores (and, later, seeds) can be blown greater distances if they start higher. This may be demonstrated by *Prototaxites*, thought to be a late Silurian fungus reaching eight metres in height.

In order to attain arborescence, early plants needed to develop woody tissue that would act as both support and water transport. To understand wood, we must know a little of vascular behaviour. The stele of plants undergoing "secondary growth" is surrounded by the vascular cambium, a ring of cells which produces more xylem (on the inside) and phloem (on the outside). Since xylem cells comprise dead, lignified tissue, subsequent rings of xylem are added to those already present, forming wood.

The first plants to develop this secondary growth, and a woody habit, were apparently the ferns, and as early as the middle Devonian one species, *Wattieza*, had already reached heights of 8 m and a tree-like habit.

Other clades did not take long to develop a tree-like stature; the late Devonian *Archaeopteris*, a precursor to gymnosperms which evolved from the trimerophytes, reached 30 m in height. These progymnosperms were the first plants to develop true wood, grown from a bifacial cambium, of which the first appearance is in the mid Devonian *Rellimia*. True wood is only thought to have evolved once, giving rise to the concept of a "lignophyte" clade.

These *Archaeopteris* forests were soon supplemented by lycopods, in the form of lepidodendrales, which topped 50m in height and 2m across at the base. These lycopods rose to dominate late Devonian and Carboniferous coal deposits. Lepidodendrales differ from modern trees in exhibiting determinate growth: after building up a reserve of nutrients at a low height, the plants would "bolt" to a genetically determined height, branch at that level, spread their spores and die. They consisted of "cheap" wood to allow their rapid growth, with at least half of their stems comprising a pith-filled cavity. Their wood was also generated by a unifacial vascular cambium – it did not produce new phloem, meaning that the trunks could not grow wider over time.

The horsetail *Calamites* was next on the scene, appearing in the Carboniferous. Unlike the modern horsetail *Equisetum*, *Calamites* had a unifacial vascular cambium, allowing them to develop wood and grow to heights in excess of 10 m. They also branched multiple times.

While the form of early trees was similar to that of today's, the groups containing all modern trees had yet to evolve.

The dominant groups today are the gymnosperms, which include the coniferous trees, and the angiosperms, which contain all fruiting and flowering trees. It was long thought that the angiosperms arose from within the gymnosperms, but recent molecular evidence suggests that their living representatives form two distinct groups. It must be noted that the molecular data has yet to be fully reconciled with morphological data, but it is becoming accepted that the morphological support for paraphyly is not especially strong. This would lead to the conclusion that both groups arose from within the pteridosperms, probably as early as the Permian.

The angiosperms and their ancestors played a very small role until they diversified during the Cretaceous. They started out as small, damp-loving organisms in the understory, and have been diversifying ever since the mid-Cretaceous, to become the dominant member of non-boreal forests today.

Evolution of roots

The roots (bottom image) of lepidodendrales are thought to be functionally equivalent to the stems (top), as the similar appearance of "leaf scars" and "root scars" on these specimens from different species demonstrates.

Roots are important to plants for two main reasons: Firstly, they provide anchorage to the substrate; more importantly, they provide a source of water and nutrients from the soil. Roots allowed plants to grow taller and faster.

The onset of roots also had effects on a global scale. By disturbing the soil, and promoting its acidification (by taking up nutrients such as nitrate and phosphate), they enabled it to weather more deeply, promoting the draw-down of CO_2 with huge implications for climate. These effects may have been so profound they led to a mass extinction.

But how and when did roots evolve in the first place? While there are traces of root-like impressions in fossil soils in the late Silurian, body fossils show the earliest plants to be devoid of roots. Many had tendrils which sprawled along or beneath the ground, with upright axes or thalli dotted here and there, and some even had non-photosynthetic subterranean branches which lacked stomata. The distinction between root and specialised branch is developmental; true roots follow a different developmental trajectory to stems. Further, roots differ in their branching pattern, and in possession of a root cap. So while Silu-Devonian plants such as *Rhynia* and *Horneophyton* possessed the physiological equivalent of roots, roots – defined as organs differentiated from stems – did not arrive until later. Unfortunately, roots are rarely preserved in the fossil record, and our understanding of their evolutionary origin is sparse.

Rhizoids – small structures performing the same role as roots, usually a cell in diameter – probably evolved very early, perhaps even before plants colonised the land; they are recognised in the Characeae, an algal sister group to land plants. That said, rhizoids probably evolved more than once; the rhizines of lichens, for example, perform a similar role. Even some animals (*Lamellibrachia*) have root-like structures!

More advanced structures are common in the Rhynie chert, and many other fossils of comparable early Devonian age bear structures that look like, and acted like, roots. The rhyniophytes bore fine rhizoids, and the trimerophytes and herbaceous lycopods of the chert bore root-like structure penetrating a few centimetres into the soil. However, none of these fossils display all the features borne by modern roots. Roots and root-like structures became increasingly more common and deeper penetrating during the Devonian period, with lycopod trees forming roots around 20 cm long during the Eifelian and Givetian. These were joined by progymnosperms, which rooted up to about a metre deep, during the ensuing Frasnian stage. True gymnosperms and zygopterid ferns also formed shallow rooting systems during the Famennian period.

The rhizomorphs of the lycopods provide a slightly approach to rooting. They were equivalent to stems, with organs equivalent to leaves performing the role of rootlets. A similar construction is observed in the extant lycopod *Isoetes*, and this appears to be evidence that roots evolved independently at least twice, in the lycophytes and other plants.

A vascular system is indispensable to a rooted plants, as non-photosynthesising roots need a supply of sugars, and a vascular system is required to transport water and nutrients from the roots to the rest of the plant. These plants are little more advanced than their Silurian forbears, without a dedicated root system; however, the flat-lying axes can be clearly seen to have growths similar to the rhizoids of bryophytes today.

By the mid-to-late Devonian, most groups of plants had independently developed a rooting system of some nature. As roots became larger, they could support larger trees, and the soil was weathered to a greater depth. This deeper weathering had effects not only on the aforementioned drawdown of CO_2, but also opened up new habitats for colonisation by fungi and animals.

Roots today have developed to the physical limits. They penetrate many metres of soil to tap the water table. The narrowest roots are a mere 40 µm in diameter, and could not physically transport water if they were any narrower. The earliest fossil roots recovered, by contrast, narrowed from 3 mm to under 700 µm in diameter; of course, taphonomy is the ultimate control of what thickness we can see.

Arbuscular mycorrhizae

The efficiency of many plants' roots is increased via a symbiotic relationship with a fungal partner. The most common are arbuscular mycorrhizae (AM), literally "tree-like fungal roots". These comprise fungi which invade some root cells, filling the cell membrane with their hyphae. They feed on the plant's sugars, but return nutrients generated or extracted from the soil (especially phosphate), which the plant would otherwise have no access to.

This symbiosis appears to have evolved early in plant history. AM are found in all plant groups, and 80% of extant vascular plants, suggesting an early ancestry; a "plant"-fungus symbiosis may even have been the step that enabled them to colonise the land, and indeed AM are abundant in the Rhynie chert; the association occurred even before there were true roots to colonise, and is has even been suggested that roots evolved in order to provide a more comfortable habitat for mycorrhizal fungi.

Evolution of seeds

The fossil seed *Trigonocarpus*

Early land plants reproduced in the fashion of ferns: spores germinated into small gametophytes, which produced sperm. These would swim across moist soils to find the female organs (archegonia) on the same or another gametophyte, where they would fuse with an ovule to produce an embryo, which would germinate into a sporophyte.

This mode of reproduction restricted early plants to damp environments, moist enough that the sperm could swim to their destination. Therefore, early land plants were constrained to the lowlands, near shores and streams. The development of heterospory freed them from this constraint.

Heterosporic organisms, as their name suggests, bear spores of two sizes – microspores and megaspores. These would germinate to form microgametophytes and megagametophytes, respectively. This system paved the way for seeds: taken to the extreme, the megasporangia could bear only a single megaspore tetrad, and to complete the transition to true seeds, three of the megaspores in the original tetrad could be aborted, leaving one megaspore per megasporangium.

The transition to seeds continued with this megaspore being "boxed in" to its sporangium while it germinates. Then, the megagametophyte is contained within a waterproof integument, which forms the bulk of the seed. The microgametophyte – a pollen grain which has germinated from a microspore – is employed for dispersal, only releasing its desiccation-prone sperm when it reaches a receptive megagametophyte.

Lycopods go a fair way down the path to seeds without ever crossing the threshold. Fossil lycopod megaspores reaching 1 cm in diameter, and surrounded by vegetative tissue, are known – these even germinate into a megagametophyte *in situ*. However, they fall short of being seeds, since the nucellus, an inner spore-covering layer, does not completely enclose the spore. A very small slit remains, meaning that the seed is still exposed to the atmosphere. This has two consequences – firstly, it means it is not fully resistant to desiccation, and secondly, sperm do not have to "burrow" to access the archegonia of the megaspore.

The first "spermatophytes" (literally:seed plants) – that is, the first plants to bear true seeds – are called **pteridosperms**: literally, "seed ferns", so called because their foliage consisted of fern-like fronds, although they were not closely related to ferns. The oldest fossil evidence of seed plants is of Late Devonian age and they appear to have evolved out of an earlier group known as the progymnosperms. These early seed plants ranged from trees to small, rambling shrubs; like most early progymnosperms, they were woody plants with fern-like foliage. They all bore ovules, but no cones, fruit or similar. While it is difficult to track the early evolution of seeds, we can trace the lineage of the seed ferns from the simple trimerophytes through homosporous Aneurophytes.

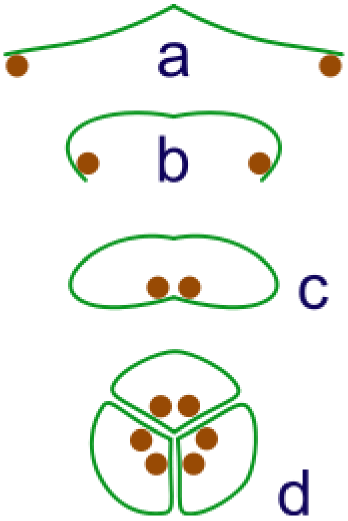
This seed model is shared by basically all gymnosperms (literally: "naked seeds"), most of which encase their seeds in a woody or fleshy (the yew, for example) cone, but none of which fully enclose their seeds. The angiosperms ("vessel seeds") are the only group to fully enclose the seed, in a carpel.

Fully enclosed seeds opened up a new pathway for plants to follow: that of seed dormancy. The embryo, completely isolated from the external atmosphere and hence protected from desiccation, could survive some years of drought before germinating. Gymnosperm seeds from the late Carboniferous have been found to contain embryos, suggesting a lengthy gap between fertilisation and germination. This period is associated with the entry into a greenhouse earth period, with an associated increase in aridity. This suggests that dormancy arose as a response to drier climatic conditions, where it became advantageous to wait for a moist period before germinating. This evolutionary breakthrough appears to have opened a floodgate: previously inhospitable areas, such as dry mountain slopes, could now be tolerated, as were soon covered by trees.

Seeds offered further advantages to their bearers: they increased the success rate of fertilised gametophytes, and because a nutrient store could be "packaged" in with the embryo, the seeds could germinate rapidly in inhospitable environments, reaching a size where it could fend for itself more quickly. For example, without an endosperm, seedlings growing in arid environments would not have the reserves to grow roots deep enough to reach the water table before they expired. Likewise, seeds germinating in a gloomy understory require an additional reserve of energy to quickly grow high enough to capture sufficient light for self-sustenance. A combination of these advantages gave seed plants the ecological edge over the previously dominant genus *Archaeopteris*, this increasing the biodiversity of early forests.

Evolution of flowers

The pollen bearing organs of the early "flower" *Crossotheca*



The evolution of syncarps.
a: sporangia borne at tips of leaf
b: Leaf curls up to protect sporangia
c: leaf curls to form enclosed roll
d: grouping of three rolls into a syncarp

Flowers are modified leaves possessed only by the group known as the angiosperms, which are relatively late to appear in the fossil record. Colourful and/or pungent structures surround the cones of plants such as cycads and gnetales, making a strict definition of the term "flower" elusive.

The flowering plants have long been assumed to have evolved from within the *gymnosperms*; according to the traditional morphological view, they are closely allied to the gnetales. However, as noted above, recent molecular evidence is at odds to this hypothesis, and further suggests that gnetales are more closely related to some gymnosperm groups than angiosperms, and that extant gymnosperms form a distinct clade to the angiosperms, the two clades diverging some 300 million years ago.

The relationship of stem groups to the angiosperms is of utmost importance in determining the evolution of flowers; stem groups provide an insight into the state of earlier "forks" on the path to the current state. If we identify an unrelated group as a stem group, then we will gain an incorrect image of the lineages' history. The traditional view that flowers arose by modification of a structure similar to that of the gnetales, for example, no longer bears weight in the light of the molecular data.

Convergence increases our chances of misidentifying stem groups. Since the protection of the megagametophyte is evolutionarily desirable, it would be unsurprising if many separate groups stumbled upon protective encasements independently. Distinguishing ancestry in such a situation, especially where we usually only have fossils to go on, is tricky – to say the least.

In flowers, this protection is offered by the carpel, an organ believed to represent an adapted leaf, recruited into a protective role, shielding the ovules. These ovules are further protected by a double-walled integument.

Penetration of these protective layers needs something more that a free-floating microgametophyte. Angiosperms have pollen grains comprising just three cells. One cell is responsible for drilling down through the integuments, and creating a conduit for the two sperm cells to flow down. The megagametophyte has just seven cells; of these, one fuses with a sperm cell, forming the nucleus of the egg itself, and another other joins with the other sperm, and dedicates itself to forming a nutrient-rich endosperm. The other cells take auxiliary roles. This process of "double fertilisation" is unique and common to all angiosperms.

The inflorescences of the Bennettitales are strikingly similar to flowers

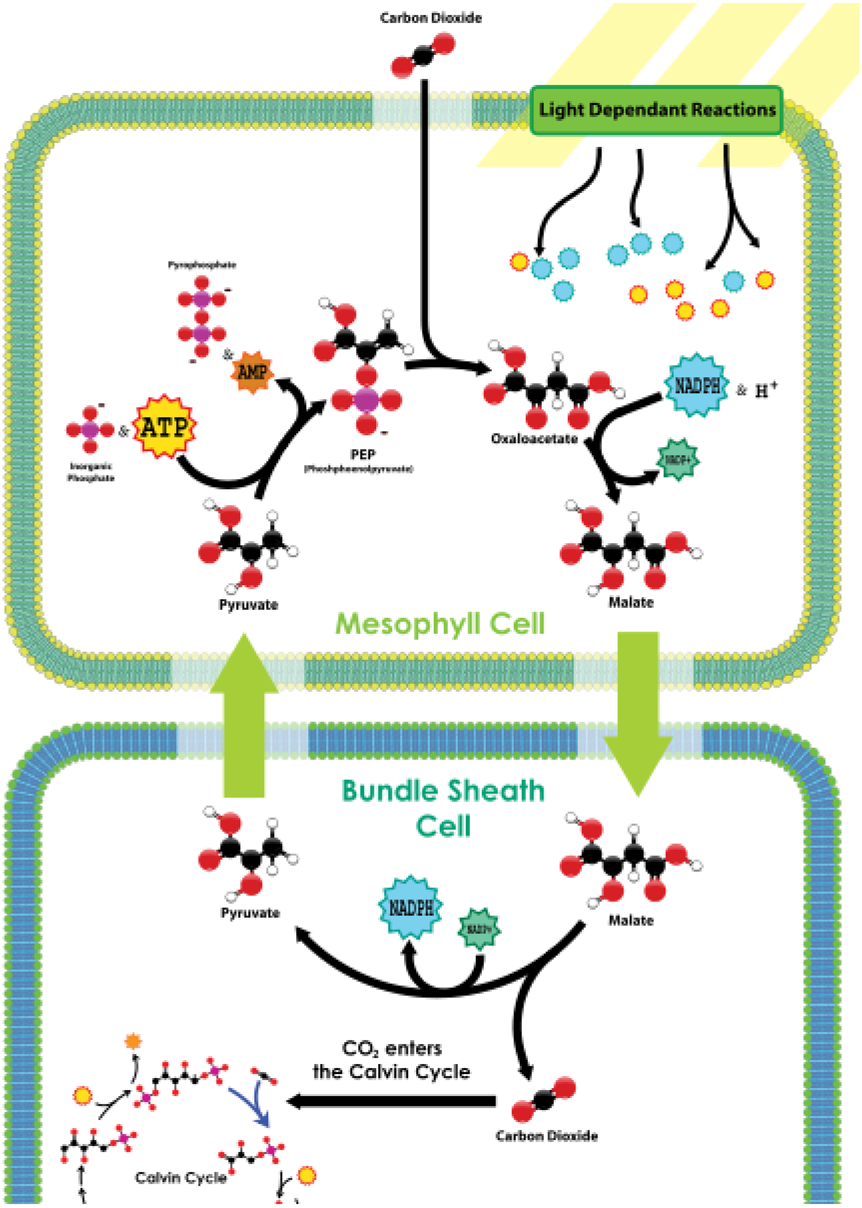
In the fossil record, there are three intriguing groups which bore flower-like structures. The first is the Permian pteridosperm *Glossopteris*, which already bore recurved leaves resembling carpels. The Triassic *Caytonia* is more flower-like still, with enclosed ovules – but only a single integument. Further, details of their pollen and stamens set them apart from true flowering plants.

The Bennettitales bore remarkably flower-like organs, protected by whorls of bracts which may have played a similar role to the petals and sepals of true flowers; however, these flower-like structures evolved independently, as the Bennettitales are more closely related to cycads and ginkgos than to the angiosperms.

However, no true flowers are found in any groups save those extant today. Most morphological and molecular analyses place *Amborella*, the nymphaeales and Austrobaileyaceae in a basal clade dubbed "ANA". This clade appear to have diverged in the early Cretaceous, around 130 million years ago – around the same time as the earliest fossil angiosperm, and just after the first angiosperm-like pollen, 136 million years ago. The magnoliids diverged soon after, and a rapid radiation had produced eudicots and monocots by 125 million years ago. By the end of the Cretaceous 65.5 million years ago, over 50% of today's angiosperm orders had evolved, and the clade accounted for 70% of global species. It was around this time that flowering trees became dominant over conifers

The features of the basal "ANA" groups suggest that angiosperms originated in dark, damp, frequently disturbed areas. It appears that the angiosperms remained constrained to such habitats throughout the Cretaceous – occupying the niche of small herbs early in the successional series. This may have restricted their initial significance, but given them the flexibility that accounted for the rapidity of their later diversifications in other habitats.

Advances in metabolism



The C_4 carbon concentrating mechanism

The most recent major innovation by the plants is the development of the C_4 metabolic pathway.

Photosynthesis is not quite as simple as adding water to CO_2 to produce sugars and oxygen. A complex chemical pathway is involved, facilitated along the way by a range of enzymes and co-enzymes. The enzyme RuBisCO is responsible for "fixing" CO_2 – that is, it attaches it to a carbon-based molecule to form a sugar, which can be used by the plant, releasing an oxygen molecule along the way. However, the enzyme is notoriously inefficient, and just as effectively will also fix oxygen instead of CO_2 in a process called photorespiration. This is energetically costly as the plant has to use energy to turn the products of photorepsiration back into a form that can react with CO_2.

Concentrating carbon

To work around this inefficiency, C_4 plants evolved carbon concentrating mechanisms. These work by increasing the concentration of CO_2 around RuBisCO, thereby increasing the amount of photosynthesis and decreasing photorespiration. The process of concentrating CO_2 around RuBisCO requires more energy than allowing gases to diffuse, but under certain conditions – i.e. warm temperatures (>25°C), low CO_2 concentrations, or high oxygen concentrations – pays off in terms of the decreased loss of sugars through photorespiration.

One, C_4 metabolism, employs a so-called Kranz anatomy. This transports CO_2 through an outer mesophyll layer, via a range of organic molecules, to the central bundle sheath cells, where the CO_2 is released. In this way, CO_2 is concentrated near the site of RuBisCO operation. Because RuBisCO is operating in an environment with much more CO_2 than it otherwise would be, it performs more efficiently.

A second method, CAM photosynthesis, temporally separates photosynthesis from the action of RuBisCO. RuBisCO only operates during the day, when stomata are sealed and CO_2 is provided by the breakdown of the chemical malate. More CO_2 is then harvested from the atmosphere when stomata open, during the cool, moist nights, reducing water loss.

Evolutionary record

These two pathways, with the same effect on RuBisCO, evolved a number of times independently – indeed, C_4 alone arose in 18 different plant families. The C_4 construction is most famously used by a subset of grasses, while CAM is employed by many succulents and cacti. The trait appears to have emerged during the Oligocene, around 25 to 32 million years ago; however, they did not become ecologically significant until the Miocene, -1 million years ago. Remarkably, some charcoalified fossils preserve tissue organised into the Kranz anatomy, with intact bundle sheath cells, allowing the presence C_4 metabolism to be identified without doubt at this time. In deducing their distribution and significance, we resort to the use of isotopic markers. C_3 plants preferentially use the lighter of two isotopes of carbon in the atmosphere, ^{12}C, which is more readily involved in the chemical pathways involved in its fixation. Because C_4 metabolism involves a further chemical step, this effect is accentuated. Plant material can be analysed to deduce the ratio of the heavier ^{13}C to ^{12}C. This ratio is denoted $\delta^{13}C$. C_3 plants are on average around 14‰ (parts per thousand) lighter than the atmospheric ratio, while C_4 plants are about 28‰ lighter. The $\delta^{13}C$ of CAM plants depends on the percentage of carbon fixed at night relative to what is fixed in the day, being closer to C_3 plants if they fix most carbon in the day and closer to C_4 plants if they fix all their carbon at night.

It's troublesome procuring original fossil material in sufficient quantity to analyse the grass itself, but fortunately we have a good proxy: horses. Horses were globally widespread in the period of interest, and browsed almost exclusively on grasses. There's an old phrase in isotope palæontology, "you are what you eat (plus a little bit)" – this refers to the fact that organisms reflect the isotopic composition of whatever they eat, plus a small adjustment factor. There is a good record of horse teeth throughout the globe, and their $\delta^{13}C$ has been measured. The record shows a sharp negative inflection around -1 million years ago, during the Messinian, and this is interpreted as the rise of C_4 plants on a global scale.

When is C_4 an advantage?

While C_4 enhances the efficiency of RuBisCO, the concentration of carbon is highly energy intensive. This means that C_4 plants only have an advantage over C_3 organisms in certain conditions: namely, high temperatures and low rainfall. C_4 plants also need high levels of sunlight in order to thrive. Models suggest that without wildfires removing shade-casting trees and shrubs, there would be no space for C_4 plants. But wildfires have occurred for 400 million years – why did C_4 take so long to arise, and then appear independently so many times? The Carboniferous period (~300 million years ago) had notoriously high oxygen levels – almost enough to allow spontaneous combustion – and very low CO_2, but there is no C_4 isotopic signature to be found. And there doesn't seem to be a sudden trigger for the Miocene rise.

During the Micoene, the atmosphere and climate was relatively stable. If anything, CO_2 increased gradually from 14 to 9 million years ago before settling down to concentrations similar to the Holocene. This suggests that it did not have a key role in invoking C_4 evolution. Grasses themselves (the group which would give rise to the most occurrences of C_4) had probably been around for 60 million years or more, so had had plenty of time to evolve C_4, which in any case is present in a diverse range of groups and thus evolved independently. There is a strong signal of climate change in South Asia; increasing aridity – hence increasing fire frequency and intensity – may have led to an increase in the importance of grasslands. However, this is difficult to reconcile with the North American record. It is possible that the signal is entirely biological, forced by the fire- (and elephant?)- driven acceleration of grass evolution – which, both by increasing weathering and incorporating more carbon into sediments, reduced atmospheric CO_2 levels. Finally, there is evidence that the onset of C_4 from 9 to 7 million years ago is a biased signal, which only holds true for North America, from where most samples originate; emerging evidence suggests that grasslands evolved to a dominant state at least 15Ma earlier in South America.

Evolutionary trends

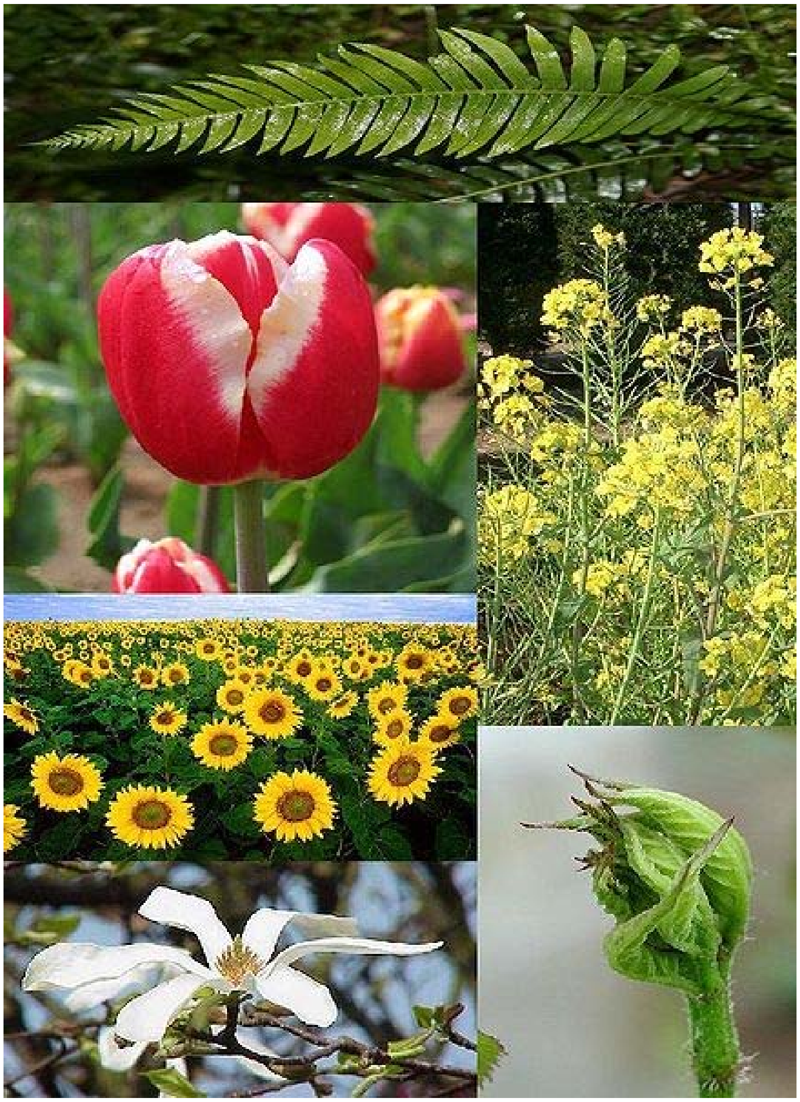
The process of evolution works slightly differently in plants than animals. Differences in plant physiology and reproduction mean that while the same evolutionary principles of natural selection apply, the finer nuances of their effect are radically different.

One major difference is the ability of plants to reproduce clonally, and the totipotent nature of their cells, allowing them to reproduce asexually much more easily than most animals. They are also capable of polyploidy – where more than two chromosome sets are inherited from parents. This allows relatively fast bursts of evolution to occur. The long periods of dormancy that seed plants can employ also makes them less vulnerable to extinction, as they can "sit out" the tough periods and wait until more clement times to leap back to life.

The effect of these differences is most profoundly seen during extinction events. These events, which wiped out between 6 and 62% of terrestrial animal families, had "negligible" effect on plant families. However, the ecosystem structure is significantly rearranged, with the abundances and distributions of different groups of plants changing profoundly. These effects are perhaps due to the higher diversity within families, as extinction – which *was* common at the species level – was very selective. For example, wind-pollinated species survived better than insect-pollinated taxa, and specialised species generally lost out. In general, the surviving taxa were rare before the extinction, suggesting that they were generalists who were poor competitors when times were easy, but prospered when specialised groups went extinct and left ecological niches vacant.

Chapter- 2

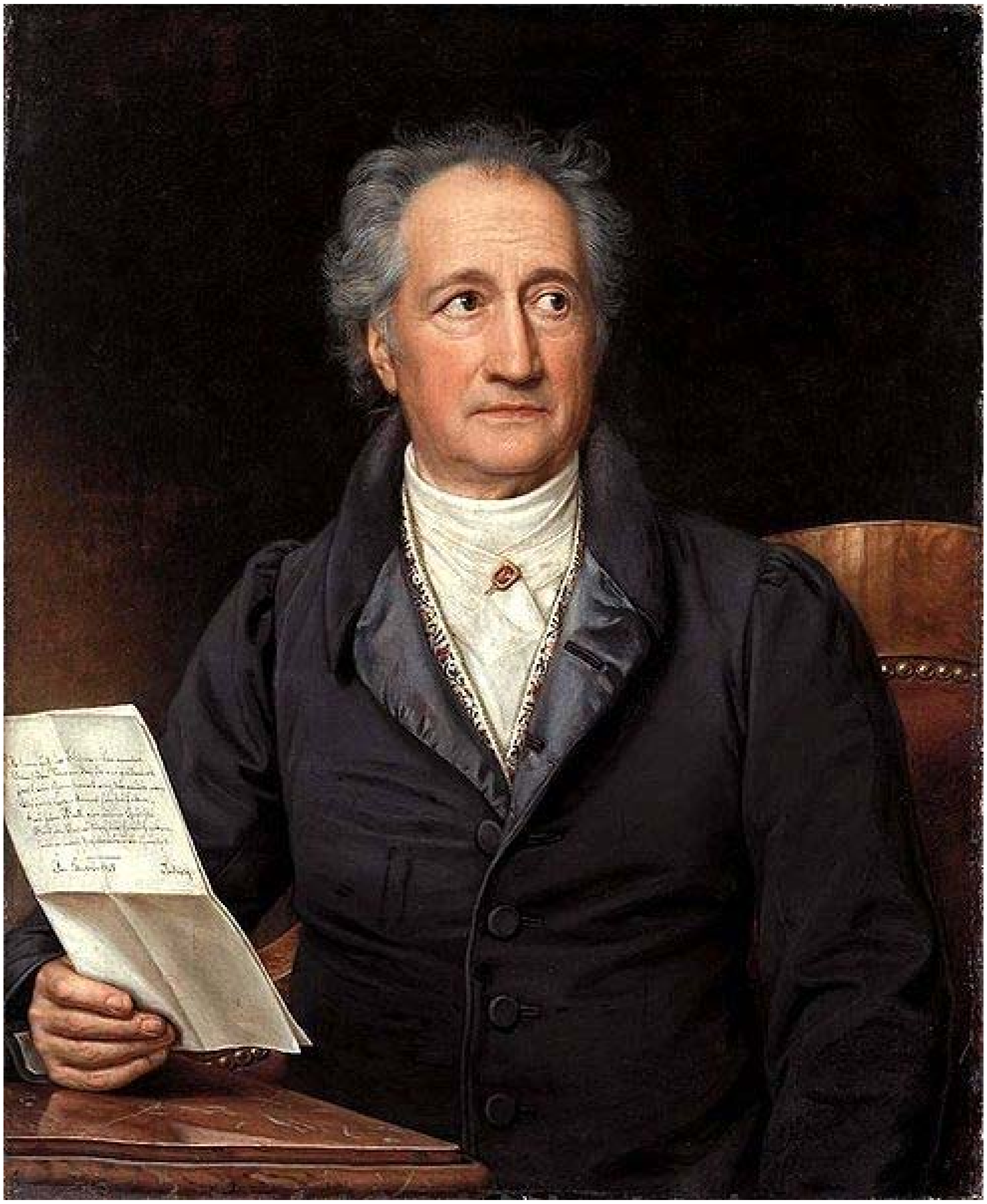
Plant Evolutionary Developmental Biology



Evolutionary developmental biology (evo-devo) refers to the study of developmental programs and patterns from an evolutionary perspective. It seeks to understand the various influences shaping the form and nature of life on the planet. Evo-devo arose as a separate branch of science only in the last decade. Most of the synthesis in evo-devo has been in the field of animal evolution, one reason being the presence of elegant model systems like *Drosophila melanogaster*, *C. elegans*, zebrafish and *Xenopus laevis*. However, in the past couple of decades, a wealth of information on plant morphology, coupled with modern molecular techniques has helped shed light on the conserved and unique developmental patterns in the plant kingdom also.

Historical perspective

Before 1900



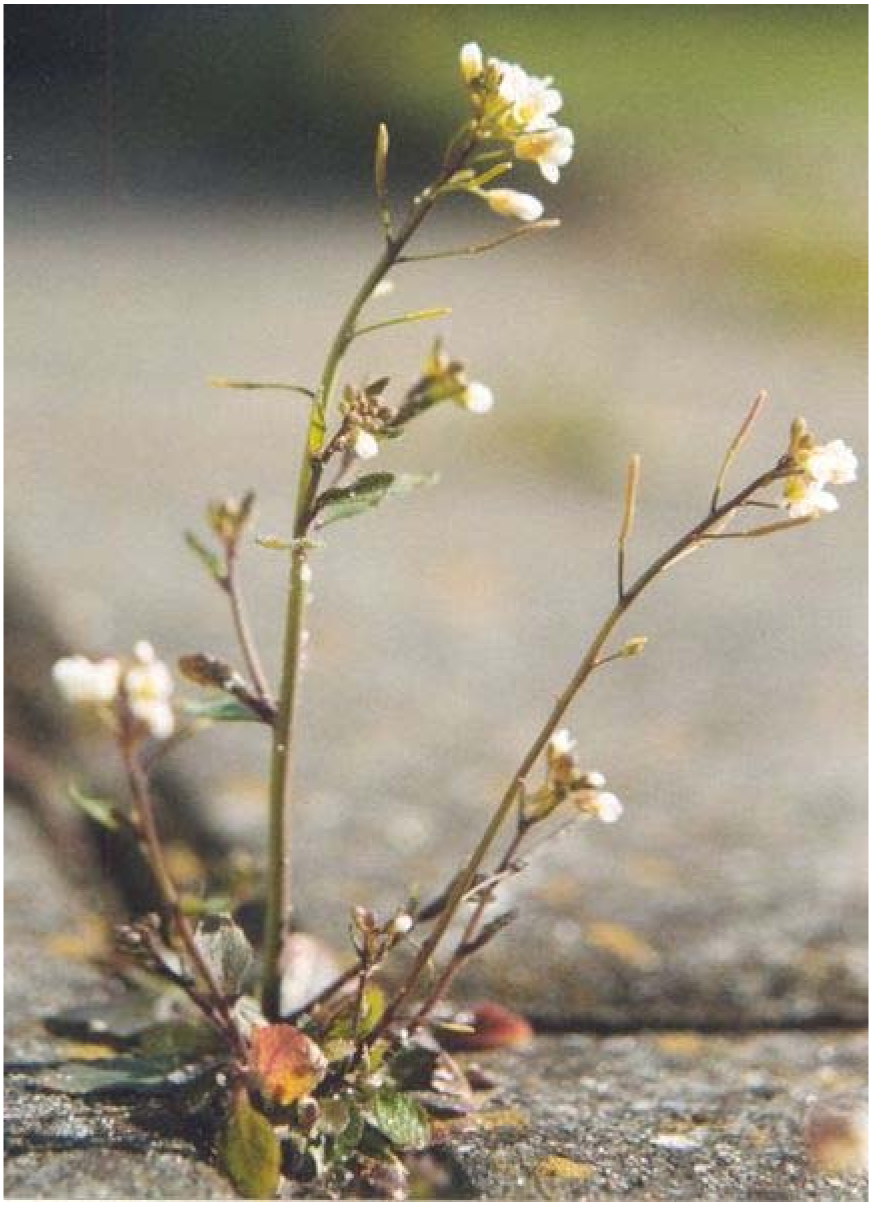
Johann Wolfgang von Goethe

The origin of the term "morphology" is generally attributed to Johann Wolfgang von Goethe (1749–1832). He was of the opinion that there is an underlying fundamental organisation *(Bauplan)* in the diversity of flowering plants. In his book titled The Metamorphosis of Plants, he proposed that the *Bauplan* enabled us to predict the forms of plants that had not yet been discovered. Goethe also was the first to make the perceptive suggestion that flowers consist of modified leaves.

In the middle centuries, several basic foundations of our current understanding of plant morphology were laid down. Nehemiah Grew, Marcello Malpighi, Robert Hooke, Antonie van Leeuwenhoek, Wilhelm von Nageli were just some of the people who helped build knowledge on plant morphology at various levels of organisation. It was the taxonomical classification of Carolus Linnaeus in the eighteenth century though, that generated a firm base for the knowledge to stand on and expand. The introduction of the concept of Darwinism in contemporary scientific discourse also had had an effect on the thinking on plant forms and their evolution.

Wilhelm Hofmeister, one of the most brilliant botanists of his times, was the one to diverge away from the idealist way of pursuing botany. Over the course of his life, he brought an interdisciplinary outlook into botanical thinking. He came up with biophysical explanations on phenomena like phototaxis and geotaxis, and also discovered the alternation of generations in the plant life cycle.

1900 to the present



Arabidopsis thaliana. This flowering plant has been a model system for most of plant molecular studies

The past century witnessed a rapid progress in the study of plant anatomy. The focus shifted from the population level to more reductionist levels. While the first half of the century saw expansion in developmental knowledge at the tissue and the organ level, in the latter half, especially since the 1990s, there has also been a strong impetus on gaining molecular information.

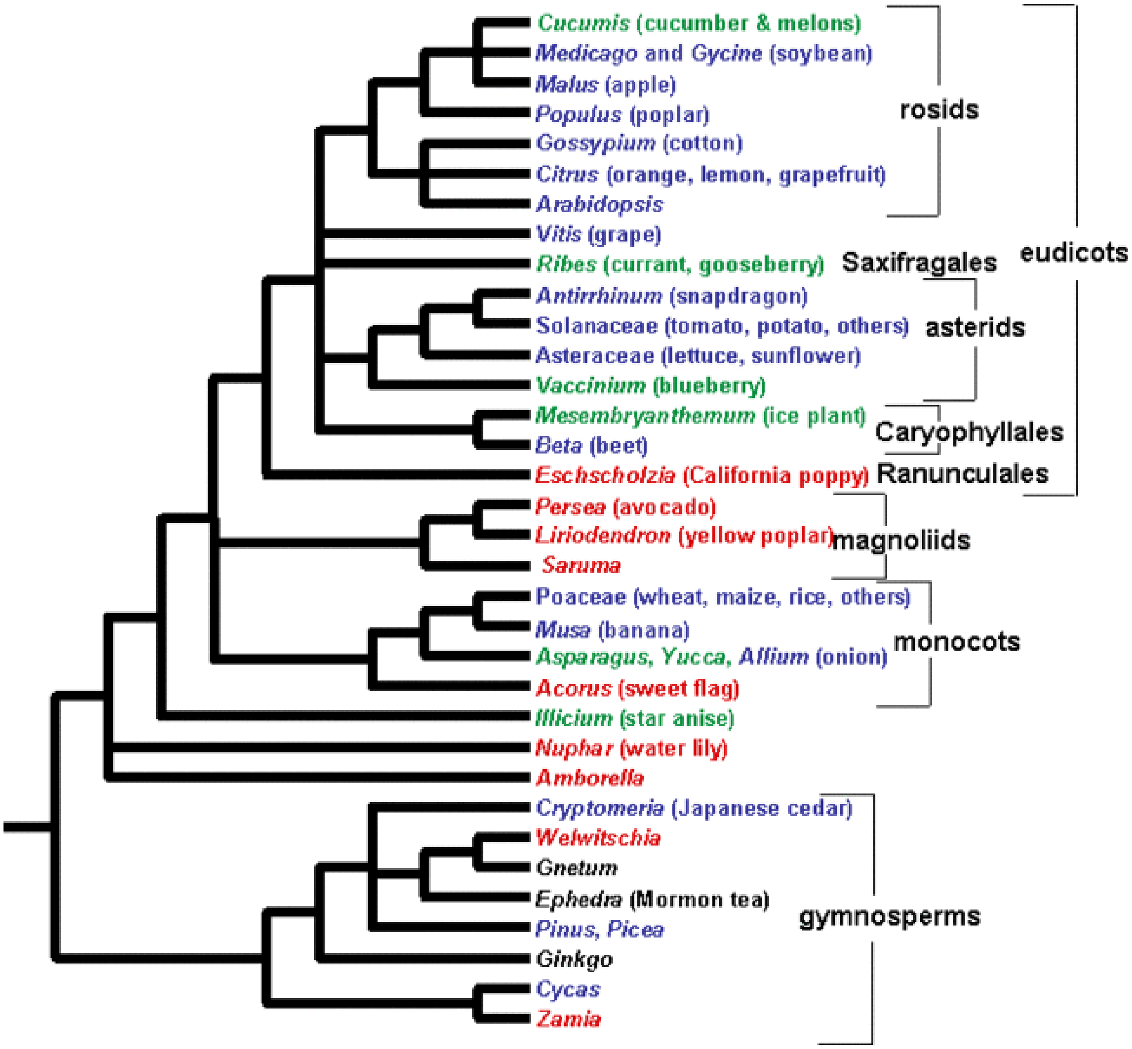
Edward Charles Jeffrey was one of the early evo devo researchers of the 20th century. He performed a comparative analyses of the vasculatures of living and fossil Gymnosperms and came to the conclusion that the storage parenchyma has been derived from tracheids. His research focussed primarily on plant anatomy in the context of phylogeny. This tradition of evolutionary analyses of plant architectures was further advanced by Katherine Esau, best known for her book *The Plant Anatomy*. Her work focussed on the origin and development of various tissues in different plants. Working with Vernon Cheadle, she also explained the evolutionary specialization of the phloem tissue with respect to its function.

In the meantime, by the beginning of the latter half of 1900s, *Arabidopsis thaliana* had begun to be used in some developmental studies. The first collection of *Arabidopsis thaliana* mutants were made around 1945. However it formally became established as a model organism only in 1998.

The recent spurt in information on various plant-related processes has largely been a result of the revolution in molecular biology. Powerful techniques like mutagenesis and complementation were made possible in *Arabidopsis thaliana* via generation of T-DNA containing mutant lines, recombinant plasmids, techniques like Transposon Tagging etc. Availability of complete physical and genetic maps, RNAi vectors, and rapid transformation protocols are some of the technologies that have significantly altered the scope of the field. Recently, there has also been a massive increase in the genome and EST sequences of various non-model species, which, coupled with the Bioinformatics tools existing today, generate interesting opportunities in the field of plant evo devo research.

Cusset provided a detailed in-depth analysis of the history of plant morphology, including plant development and evolution, from its beginnings to the end of the 20th century.

Organisms, databases and tools



The sampling of the Floral Genome Project

The most important model systems in plant development have been arabidopsis and maize. Maize has traditionally been the favorite of plant geneticists, while extensive resources in almost every area of plant physiology and development are available for *Arabidopsis thaliana*. Apart from these, rice, *Antirrhinum majus*, *Brassica*, tomato are also being used in a variety of studies. The genomes of *Arabidopsis thaliana* and rice have been completely sequenced, while the others are in process. It must be emphasized here that the information from these "model" organisms form the basis of our developmental knowledge. While *Brassica* has been used primarily because of its convenient location in the phylogenetic tree in the mustard family, *Antirrhinum majus* is a convenient system for studying leaf architecture. Rice has been traditionally used for studying responses to hormones like abscissic acid and gibberelin as well as responses to stress. However, recently, not just the domesticated rice strain, but also the wild strains have been studied for their underlying genetic architectures.

Some people have objected against extending the results of model organisms to the plant world. One argument is that the effect of gene knockouts in lab conditions wouldn't truly reflect even the same plant's response in the natural world. Also, these supposedly *crucial* genes might not be responsible for the evolutionary origin of that character. For these reasons, a comparative study of plant traits has been proposed as the way to go now.

Since the past few years, researchers have indeed begun looking at non-model, "non-conventional" organisms using modern genetic tools. One example of this is the Floral Genome Project, which envisages to study the evolution of the current patterns in the genetic architecture of the flower through comparative genetic analyses, with a focus on EST sequences. Like the FGP, there are several such ongoing projects that aim to find out conserved and diverse patterns in evolution of the plant shape. Expressed sequence tag (EST) sequences of quite a few non-model plants like Sugarcane, Apple, Lotus, Barley, Cycas, Coffee, to name a few, are available freely online. The Cycad Genomics Project, for example, aims to understand the differences in structure and function of genes between gymnosperms and angiosperms through sampling in the order Cycadales. In the process, it intends to make available information for the study of evolution of structures like seeds, cones and evolution of life cycle patterns. Presently the most important sequenced genomes from an evo-devo point of view include those of *A.thaliana (a flowering plant)*, Poplar *(a woody plant)*, *Physcomitrella patens (a bryophyte)*, Maize *(extensive genetic information)*, and *Chlamydomonas reinhardtii (a green alga)*. The impact of such a vast amount of information on understanding common underlying developmental mechanisms can easily be realised.

Apart from EST and genome sequences, several other tools like PCR, Yeast two hybrid system, microarrays, RNA Interference, SAGE, QTL mapping etc. permit the rapid study of plant developmental patterns. Recently, cross-species hybridization has begun to be employed on microarray chips, to study the conservation and divergence in mRNA expression patterns between closely related species. Techniques for analyzing this kind of data have also progressed over the past decade. We now have better models for molecular evolution, more refined analysis algorithms and better computing power as a result of advances in computer sciences.

Evolution of plant morphology

Overview of plant evolution

Evidence suggests that an algal scum formed on the land 1,200 million years ago, but it was not until the Ordovician period, around 500 million years ago, that land plants appeared. These begun to diversify in the late Silurian period, around 420 million years ago, and the fruits of their diversification are displayed in remarkable detail in an early Devonian fossil assemblage known as the Rhynie chert. This chert preserved early plants in cellular detail, petrified in volcanic springs. By the middle of the Devonian period most of the features recognised in plants today are present, including roots, leaves and seeds. By the late Devonian, plants had reached a degree of sophistication that allowed them to form forests of tall trees. Evolutionary innovation continued after the Devonian period. Most plant groups were relatively unscathed by the Permo-Triassic extinction event, although the structures of communities changed. This may have set the scene for the evolution of flowering plants in the Triassic (~200 million years ago), which exploded the Cretaceous and Tertiary. The latest major group of plants to evolve were the grasses, which became important in the mid Tertiary, from around 40 million years ago. The grasses, as well as many other groups, evolved new mechanisms of metabolism to survive the low CO_2 and warm, dry conditions of the tropics over the last 10 million years.

Evolution of meristems

The meristematic cells give rise to various organs of the plant, and keep the plant growing. The Shoot Apical Meristem (SAM) gives rise to organs like the leaves and flowers. The cells of the apical meristems - SAM and RAM (Root Apical Meristem)- divide rapidly and are considered to be indeterminate, in that they do not possess any defined end fate. In that sense, the meristematic cells are frequently compared to the stem cells in animals, that have an analogous behavior and function.

Diversity in meristem architectures

Is the mechanism of being *indeterminate* conserved in the SAM's of the plant world? The SAM contains a population of stem cells that also produce the lateral meristems while the stem elongates. It turns out that the mechanism of regulation of the stem cell number might indeed be evolutionarily conserved. The *CLAVATA* gene *CLV2* responsible for maintaining the stem cell population in *Arabidopsis thaliana* is very closely related to the Maize gene *FASCIATED EAR 2*(*FEA2*) also involved in the same function. Similarly, in Rice, the *FON1-FON2* system seems to bear a close relationship with the CLV signaling system in *Arabidopsis thaliana*. These studies suggest that the regulation of stem cell number, identity and differentiation might be an evolutionarily conserved mechanism in monocots, if not in angiosperms. Rice also contains another genetic system distinct from *FON1-FON2*, that is involved in regulating stem cell number. This example underlines the innovation that goes about in the living world all the time.

Role of the KNOX-family genes

Note the long spur of the above flower. Spurs attract pollinators and confer pollinator specificity. *(Flower:Linaria dalmatica)*

Complex leaves of *C. hirsuta* are a result of KNOX gene expression

Genetic screens have identified genes belonging to the KNOX family in this function. These genes essentially maintain the stem cells in an undifferentiated state. The KNOX family has undergone quite a bit of evolutionary diversification, while keeping the overall mechanism more or less similar. Members of the KNOX family have been found in plants as diverse as Arabidopsis thaliana, rice, barley and tomato. KNOX-like genes are also present in some algae, mosses, ferns and gymnosperms. Misexpression of these genes leads to formation of interesting morphological features. For example, among members of *Antirrhinae*, only the species of genus *Antirrhinum* lack a structure called spur in the floral region. A spur is considered an evolutionary innovation because it defines pollinator specificity and attraction. Researchers carried out transposon mutagenesis in *Antirrhinum majus*, and saw that some insertions led to formation of spurs that were very similar to the other members of *Antirrhinae*, indicating that the loss of spur in wild *Antirrhinum majus* populations could probably be an evolutionary innovation.

The KNOX family has also been implicated in leaf shape evolution. One study looked at the pattern of KNOX gene expression in *A. thaliana*, that has simple leaves and *Cardamine hirsuta*, a plant having complex leaves. In *A. thaliana*, the KNOX genes are completely turned off in leaves, but in *C.hirsuta*, the expression continued, generating complex leaves. Also, it has been proposed that the mechanism of KNOX gene action is conserved across all vascular plants, because there is a tight correlation between KNOX expression and a complex leaf morphology.

Evolution of the meristem architecture

The meristem architectures do differ between angiosperms, gymnosperms and pteridophytes. The gymnosperm vegetative meristem lacks organization into distinct tunica and corpus layers. They possess large cells called Central Mother Cells in the meristem. In angiosperms, the outermost layer of cells divides anticlinally to generate the new cells, while in gymnosperms, the plane of division in the meristem differs for different cells. However, the apical cells do contain organelles like large vacuoles and starch grains, like the angiosperm meristematic cells.

Pteridophytes, like fern, on the other hand, do not possess a multicellular apical meristem. They possess a tetrahedral apical cell, which goes on to form the plant body. Any somatic mutation in this cell can lead to hereditary transmission of that mutation. The earliest meristem-like organization is seen in an algal organism from group *Charales* that has a single dividing cell at the tip, much like the pteridophytes, yet simpler. One can thus see a clear pattern in evolution of the meristematic tissue, from pteridophytes to angiosperms. Pteridophytes, with a single meristematic cell; gymnosperms with a multicellular, but less defined organization and finally, angiosperms, with the highest degree of organization. The genetic innovations that contributed to this evolution are yet not clearly known.

Evolution of leaves

Origins of the leaf

Leaf lamina. The leaf architecture probably arose multiple times in the plant lineage

Leaves are the primary photosynthetic organs of a plant. Based on their structure, they are classified into two types - microphylls, that lack complex venation patterns and megaphylls, that are large and with a complex venation. It has been proposed that these structures arose independently. Megaphylls, according to the Telome hypothesis, have evolved from plants that showed a three dimensional branching architecture, through three transformations—**plantation**, which involved formation of a planar architecture, **webbing**, or formation of the outgrowths between the planar branches and **fusion**, where these webbed outgrowths fused to form a proper leaf lamina. Studies have revealed that these three steps happened multiple times in the evolution of today's leaves.

It has been proposed that the before the evolution of leaves, plants had the photosynthetic apparatus on the stems. Today's megaphyll leaves probably became commonplace some 360mya, about 40my after the simple leafless plants had colonized the land in the early Devonian period. This spread has been linked to the fall in the atmospheric carbon dioxide concentrations in the Late Paleozoic era associated with a rise in density of stomata on leaf surface. This must have allowed for better transpiration rates and gas exchange. Large leaves with less stomata would have gotten heated up in the sun's heat, but an increased stomatal density allowed for a better-cooled leaf, thus making its spread feasible.

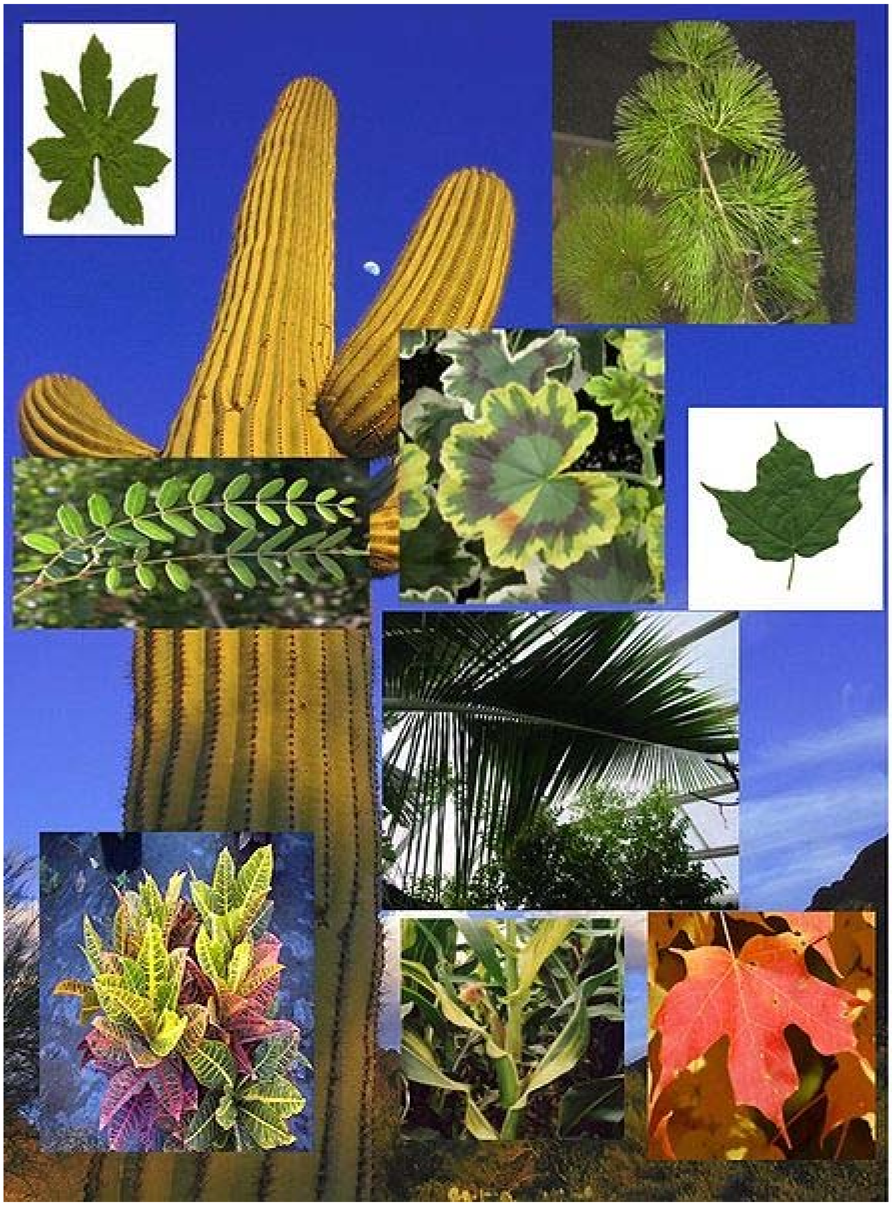
Factors influencing leaf architectures

Spiny leaves of *Aciphylla squarrosa*. It is thought that these leaves evolved as an adaptation against the now extinct Moas

Various physical and physiological forces like light intensity, humidity, temperature, wind speeds etc. are thought to have influenced evolution of leaf shape and size. It is observed that high trees rarely have large leaves, owing to the obstruction they generate for winds. This obstruction can eventually lead to the tearing of leaves, if they are large. Similarly, trees that grow in temperate or taiga regions have pointed leaves, presumably to prevent nucleation of ice onto the leaf surface and reduce water loss due to transpiration. Herbivory, not only by large mammals, but also small insects has been implicated as a driving force in leaf evolution, an example being plants of the genus *Aciphylla*, that are commonly found in New Zealand. The now extinct Moas fed upon these plants, and its seen that the leaves have spines on their bodies, which probably functioned to discourage the moas from feeding on them. Other members of *Aciphylla* that did not co-exist with the moas, do not have these spines.

Genetic evidences for leaf evolution

At the genetic level, developmental studies have shown that repression of the KNOX genes is required for initiation of the leaf primordium. This is brought about by *ARP* genes, which encode transcription factors. Genes of this type have been found in many plants studied till now, and the mechanism i.e. repression of KNOX genes in leaf primordia, seems to be quite conserved. Interestingly, expression of KNOX genes in leaves produces complex leaves. It is speculated that the *ARP* function arose quite early in vascular plant evolution, because members of the primitive group Lycophytes also have a functionally similar gene Other players that have a conserved role in defining leaf primordia are the phytohormone auxin, gibberelin and cytokinin.



The diversity of leaves

One interesting feature of a plant is its phyllotaxy. The arrangement of leaves on the plant body is such that the plant can maximally harvest light under the given constraints, and hence, one might expect the trait to be genetically robust. However, it may not be so. In maize, a mutation in only one gene called *abphyl (ABNORMAL PHYLLOTAXY)* was enough to change the phyllotaxy of the leaves. It implies that sometimes, mutational tweaking of a single locus on the genome is enough to generate diversity. The *abphyl* gene was later on shown to encode a cytokinin response regulator protein.

Once the leaf primordial cells are established from the SAM cells, the new axes for leaf growth are defined, one important (and more studied) among them being the abaxial-adaxial (lower-upper surface) axes. The genes involved in defining this, and the other axes seem to be more or less conserved among higher plants. Proteins of the *HD-ZIPIII* family have been implicated in defining the adaxial identity. These proteins deviate some cells in the leaf primordium from the default abaxial state, and make them adaxial. It is believed that in early plants with leaves, the leaves just had one type of surface - the abaxial one. This is the underside of today's leaves. The definition of the adaxial identity occurred some 200 million years after the abaxial identity was established. One can thus imagine the early leaves as an intermediate stage in evolution of today's leaves, having just arisen from spiny stem-like outgrowths of their leafless ancestors, covered with stomata all over, and not optimized as much for light harvesting.

How the infinite variety of plant leaves is generated is a subject of intense research. Some common themes have emerged. One of the most significant is the involvement of KNOX genes in generating compound leaves, as in tomato. But this again is not universal. For example, pea uses a different mechanism for doing the same thing. Mutations in genes affecting leaf curvature can also change leaf form, by changing the leaf from flat, to a crinky shape, like the shape of cabbage leaves. There also exist different morphogen gradients in a developing leaf which define the leaf's axis. Changes in these morphogen gradients may also affect the leaf form. Another very important class of regulators of leaf development are the microRNAs, whose role in this process has just begun to be documented. The coming years should see a rapid development in comparative studies on leaf development, with many EST sequences involved in the process coming online.

Evolution of flowers

The pollen bearing organs of the early flower *Crossotheca*

A flower is, arguably, one of the most beautiful products of evolution. Flower-like structures first appear in the fossil records some ~130 mya, in the Cretaceous era.

The flowering plants have long been assumed to have evolved from within the gymnosperms; according to the traditional morphological view, they are closely allied to the gnetales. However, recent molecular evidence is at odds to this hypothesis, and further suggests that gnetales are more closely related to some gymnosperm groups than angiosperms, and that gymnosperms form a distinct clade to the angiosperms,. Molecular clock analysis predicts the divergence of flowering plants (anthophytes) and gymnosperms to ~300 mya

The main function of a flower is reproduction, which, before the evolution of the flower and angiosperms, was the job of microsporophylls and megasporophylls. A flower can be considered a powerful evolutionary innovation, because its presence allowed the plant world to access new means and mechanisms for reproduction.

Origins of the flower

Amborella trichopoda : Amborellaceae is considered the sister family of all flowering plants *(magnified image)*

The family Amborellaceae is regarded as the sister family of all living flowering plants. That means members of this family were most likely the first flowering plants.

It seems that on the level of the organ, the leaf may be the ancestor of the flower, or at least some floral organs. When we mutate some crucial genes involved in flower development, we end up with a cluster of leaf-like structures. Thus, sometime in history, the developmental program leading to formation of a leaf must have been altered to generate a flower. There probably also exists an overall robust framework within which the floral diversity has been generated. A example of that is a gene called *LEAFY (LFY)*, which is involved in flower development in *Arabidopsis thaliana*. The homologs of this gene are found in angiosperms as diverse as tomato, snapdragon, pea, maize and even gymnosperms. Interestingly, expression of *Arabidopsis thaliana* LFY in distant plants like poplar and citrus also results in flower-production in these plants. The *LFY* gene regulates the expression of some gene belonging to the MADS-box family. These genes, in turn, act as direct controllers of flower development.

Evolution of the MADS-box family

The members of the MADS-box family of transcription factors play a very important and evolutionarily conserved role in flower development. According to the ABC Model of flower development, three zones - A,B and C - are generated within the developing flower primordium, by the action of some transcription factors, that are members of the MADS-box family. Among these, the functions of the B and C domain genes have been evolutionarily more conserved than the A domain gene. Many of these genes have arisen through gene duplications of ancestral members of this family. Quite a few of them show redundant functions.

The evolution of the MADS-box family has been extensively studied. These genes are present even in pteridophytes, but the spread and diversity is many times higher in angiosperms. There appears to be quite a bit of pattern into how this family has evolved.

Consider the evolution of the C-region gene *AGAMOUS (AG)*. It is expressed in today's flowers in the stamens, and the carpel, which are reproductive organs. It's ancestor in gymnosperms also has the same expression pattern. Here, it is expressed in the strobili, an organ that produces pollens or ovules. Similarly, the B-genes' *(AP3 and PI)* ancestors are expressed only in the male organs in gymnosperms. Their descendants in the modern angiosperms also are expressed only in the stamens, the male reproductive organ. Thus, the same, then-existing components were used by the plants in a novel manner to generate the first flower. This is a recurring pattern in evolution.

Factors influencing floral diversity

The various shapes and colors of flowers

How is the enormous diversity in the shape, color and sizes of flowers established? There is enormous variation in the developmental program in different plants. For example, monocots possess structures like lodicules and palea, that were believed to be analogous to the dicot petals and carpels respectively.It turns out that this is true, and the variation is due to slight changes in the MADS-box genes and their expression pattern in the monocots. Another example is that of a plant called *Linaria vulgaris*, which has two kinds of flower symmetries-radial and bilateral. These symmetries are due to epigenetic changes in just one gene called *CYCLOIDEA*.

Large number of petals in roses has probably been a result of human selection

Arabidopsis thaliana has a gene called *AGAMOUS* that plays an important role in defining how many petals and sepals and other organs are generated. Mutations in this gene give rise to the floral meristem obtaining an indeterminate fate, and many floral organs keep on getting produced. We have flowers like roses, carnations and morning glory, for example, that have very dense floral organs. These flowers have been selected by horticulturists since long for increased number of petals. Researchers have found that the morphology of these flowers is because of strong mutations in the *AGAMOUS* homolog in these plants, which leads to them making a large number of petals and sepals. Several studies on diverse plants like petunia, tomato, Impatiens, maize etc. have suggested that the enormous diversity of flowers is a result of small changes in genes controlling their development.

Some of these changes also cause changes in expression patterns of the developmental genes, resulting in different phenotypes. The Floral Genome Project looked at the EST data from various tissues of many flowering plants. The researchers confirmed that the ABC Model of flower development is not conserved across all angiosperms. Sometimes expression domains change, as in the case of many monocots, and also in some basal angiosperms like *Amborella*. Different models of flower development like the *The fading boundaries model*, or the *Overlapping-boundaries model* which propose non-rigid domains of expression, may explain these architectures. There is a possibility that from the basal to the modern angiosperms, the domains of floral architecture have gotten more and more fixed through evolution.

Flowering time

Another floral feature that has been a subject of natural selection is flowering time. Some plants flower early in their life cycle, others require a period of vernalization before flowering. This decision is based on factors like temperature, light intensity, presence of pollinators and other environmental signals. We know that genes like *CONSTANS (CO)*, *Flowering Locus C* (*FLC*) and *FRIGIDA* regulate integration of environmental signals into the pathway for flower development. Variations in these loci have been associated with flowering time variations between plants. For example, *Arabidopsis thaliana* ecotypes that grow in the cold, temperate regions require prolonged vernalization before they flower, while the tropical varieties, and the most common lab strains, don't. We now know that this variation is due to mutations in the *FLC* and *FRIGIDA* genes, rendering them non-functional.

Quite a few players in this process are conserved across all the plants studied. Sometimes though, despite genetic conservation, the mechanism of action turns out to be different. For example, rice is a short-day plant, while *Arabidopsis thaliana* is a long-day plant. Now, in both plants, the proteins *CO* and *FLOWERING LOCUS T (FT)* are present. But in *Arabidopsis thaliana*, *CO* enhances *FT* production, while in rice, the *CO* homolog represses *FT* production, resulting in completely opposite downstream effects.

Theories of flower evolution

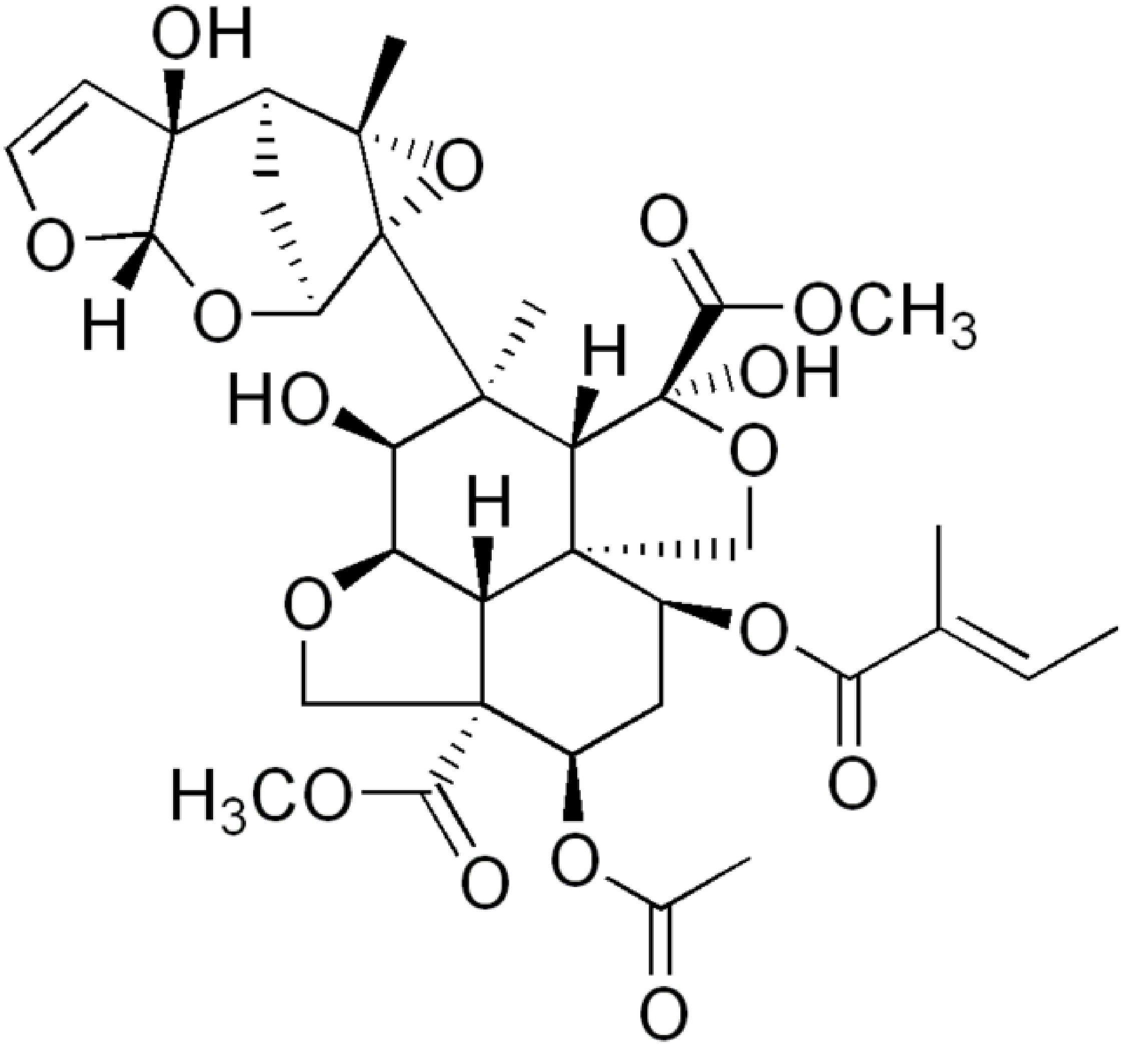
There are many theories that propose how flowers evolved. Some of them are described below.

The *Anthophyte Theory* was based upon the observation that a gymnospermic group Gnetales has a flower-like ovule. It has partially developed vessels as found in the angiosperms, and the megasporangium is covered by three envelopes, like the ovary structure of angiosperm flowers. However, many other lines of evidence show that Gnetales is not related to angiosperms.

The *Mostly Male Theory* has a more genetic basis. Proponents of this theory point out that the gymnosperms have two very similar copies of the gene *LFY* while angiosperms just one. Molecular clock analysis has shown that the other *LFY* paralog was lost in angiosperms around the same time as flower fossils become abundant, suggesting that this event might have led to floral evolution. According to this theory, loss of one of the *LFY* paralog led to flowers that were more male, with the ovules being expressed ectopically. These ovules initially performed the function of attracting pollinators, but sometime later, may have been integrated into the core flower.

One theory also suggests that humans have been one of the reasons for the diversity of flowers. This theory suggests that since the early settlers found flowers beautiful, they may have started selecting for them artificially. The flowers may have evolved to exploit the ecological niche being opened because of humans finding them attractive. The validity of this theory, however, is debatable, not least because flowers started diversifying long before they came into contact with humans.

Evolution of secondary metabolism



Structure of Azadirachtin, a terpenoid produced by the Neem plant, which helps ward off microbes and insects. Many secondary metabolites have complex structures

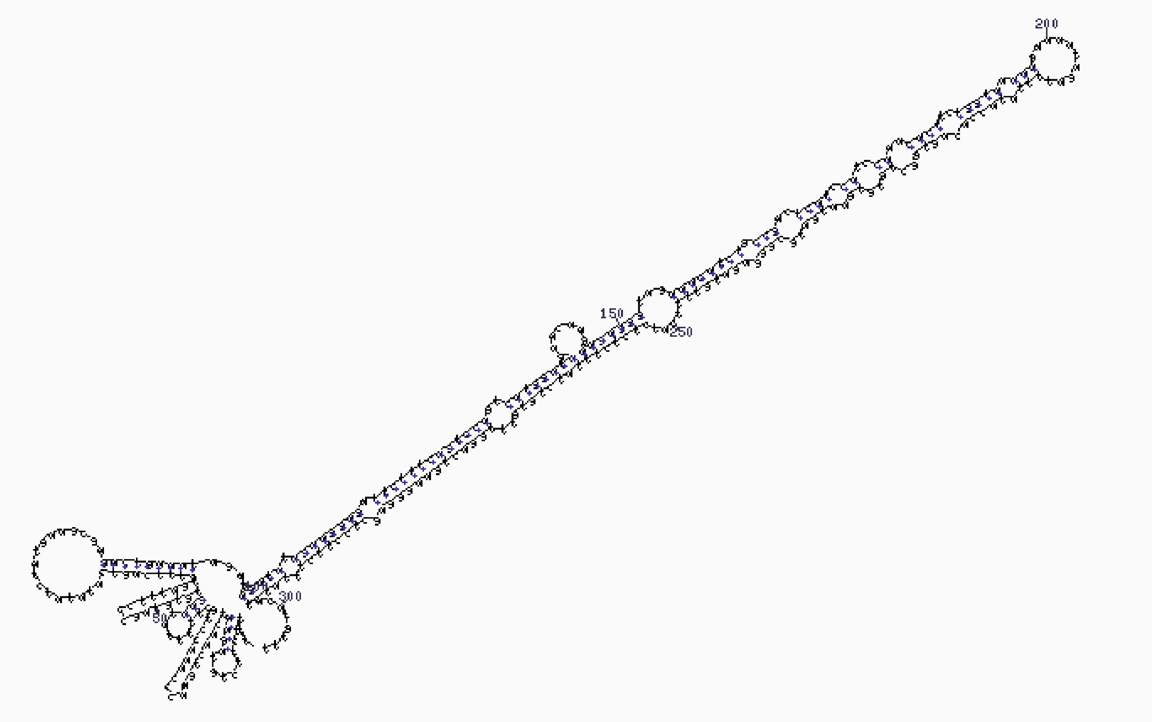
Although we know many secondary metabolites produced by plants, the extent of the same is still unfathomable. Secondary metabolites are essentially low molecular weight compounds, sometimes having complex structures. They function in processes as diverse as immunity, anti-herbivory, pollinator attraction, communication between plants, maintaining symbiotic associations with soil flora, enhancing the rate of fertilization etc., and hence are significant from the evo-devo perspective. The structural and functional diversity of these secondary metabolites across the plant kingdom is so huge that it is estimated that hundreds of thousands of enzymes might be involved in this process in the entire of the plant kingdom, with about 15–25% of the coding genome coding for these enzymes. Despite this, every species has its unique arsenal of secondary metabolites. Many of these metabolites are of enormous medical significance to humans.

What is the purpose of having so many secondary metabolites being produced, with a significant chunk of the metabolome devoted to this activity? It is hypothesized that most of these chemicals help in generating immunity, and in consequence, the diversity of these metabolites is a result of a constant war between plants and their parasites. There is evidence that this may be true in many cases. The big question here is the reproductive cost involved in maintaining such an impressive inventory. Various models have been suggested that probe into this aspect of the question, but a consensus on the extent of the cost is lacking. We still cannot predict whether a plant with more secondary metabolites would be better off than other plants in its vicinity.

Secondary metabolite production seems to have arisen quite early during evolution. Even bacteria possess the ability to make these compounds. But they assume more significant roles in life from fungi onwards to plants. In plants they seem to have spread out using different mechanisms like gene duplications, evolution of novel genes etc. Furthermore, studies have shown that diversity in some of these compounds may be positively selected for.

Although the role of novel gene evolution in the evolution of secondary metabolism cannot be denied, there are several examples where new metabolites have been formed by small changes in the reaction. For example, cyanogen glycosides have been proposed to have evolved multiple times in different plant lineages. There are several such instances of convergent evolution. For example, we now know that enzymes for synthesis of limonene – a terpene – are more similar between angiosperms and gymnosperms than to their own terpene synthesis enzymes. This suggests independent evolution of the limonene biosynthetic pathway in these two lineages.

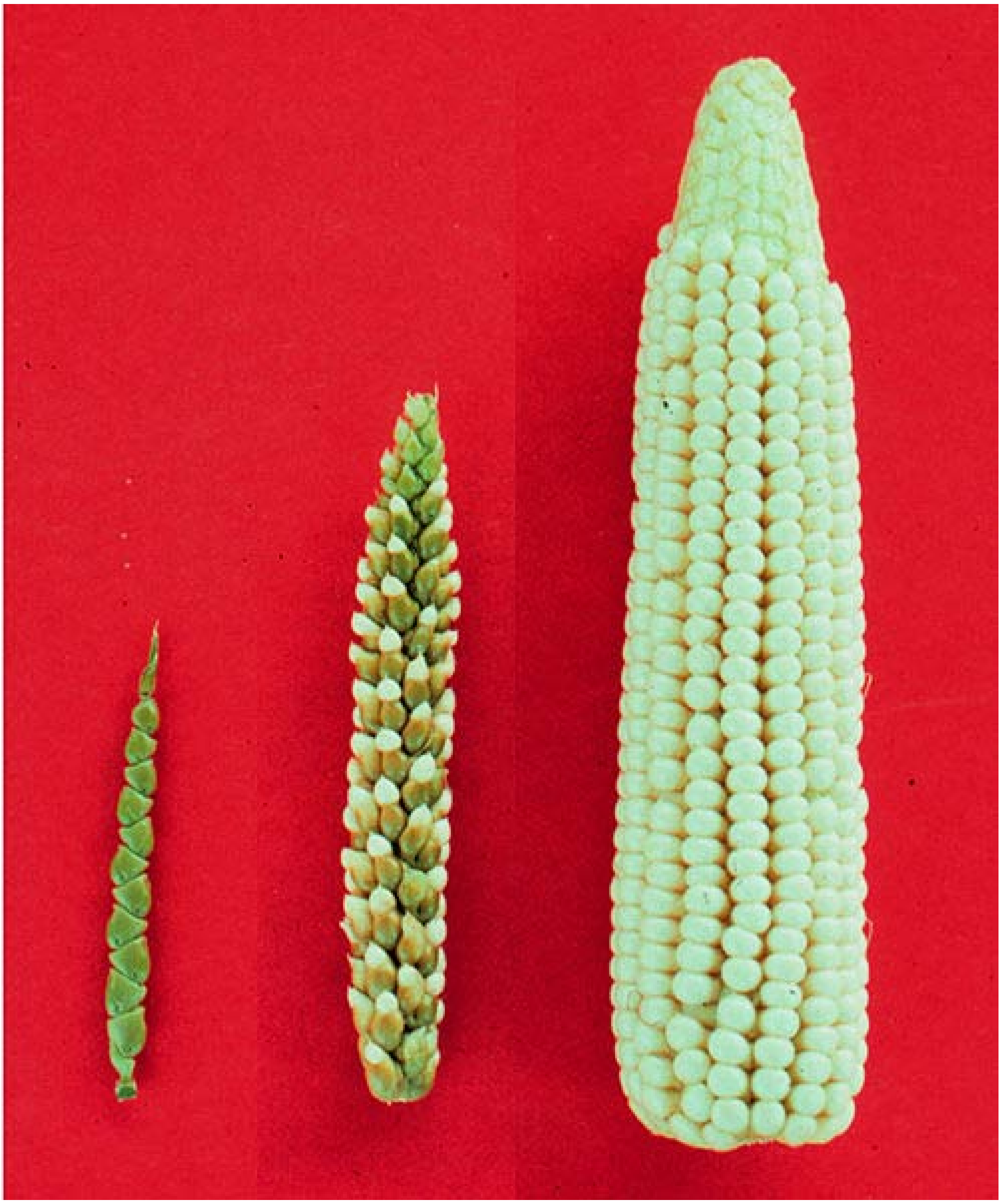
Mechanisms and players in evolution



The stem-loop secondary structure of a pre-microRNA from Brassica oleracea

While environmental factors are significantly responsible for evolutionary change, they act merely as agents for natural selection. Change is inherently brought about via phenomena at the genetic level - mutations, chromosomal rearrangements and epigenetic changes. While the general types of mutations hold true across the living world, in plants, some other mechanisms have been implicated as highly significant.

Polyploidy is a very common feature in plants. It is believed that at least half *(and probably all)* plants are or have been polyploids. Polyploidy leads to genome doubling, thus generating functional redundancy in most genes. The duplicated genes may attain new function, either by changes in expression pattern or changes in activity. Polyploidy and gene duplication are believed to be among the most powerful forces in evolution of plant form. It is not know though, why genome doubling is such a frequent process in plants. One probable reason is the production of large amounts of secondary metabolites in plant cells. Some of them might interfere in the normal process of chromosomal segregation, leading to polypoidy.



Extreme left: teosinte, Extreme right: maize, middle: maize-teosinte hybrid

In recent times, plants have been shown to possess significant microRNA families, which are conserved across many plant lineages. In comparison to animals, while the number of plant miRNA families are lesser than animals, the size of each family is much larger. The miRNA genes are also much more spread out in the genome than those in animals, where we find them clustered. It has been proposed that these miRNA families have expanded by duplications of chromosomal regions. Many miRNA genes involved in regulation of plant development have been found to be quite conserved between plants studied.

Domestication of plants like maize, rice, barley, wheat etc. has also been a significant driving force in their evolution. Some studies have tried to look at the origins of the maize plant and it turns out that maize is a domesticated derivative of a wild plant from

Mexico called teosinte. Teosinte belongs to the genus *Zea*, just as maize, but bears very small inflorescence, 5-10 hard cobs and a highly branched and spread out stem.

Cauliflower : *Brassica oleracea var botrytis*

Interestingly, crosses between a particular teosinte variety and maize yields fertile offsprings that are intermediate in phenotype between maize and teosinte. QTL analysis has also revealed some loci that when mutated in maize yield a teosinte-like stem or teosinte-like cobs. Molecular clock analysis of these genes estimates their origins to some 9000 years ago, well in accordance with other records of maize domestication. It is believed that a small group of farmers must have selected some maize-like natural mutant of teosinte some 9000 years ago in Mexico, and subjected it to continuous selection to yield the maize plant as we know today.

Another interesting case is that of cauliflower. The edible cauliflower is a domesticated version of the wild plant *Brassica oleracea*, which does not possess the dense undifferentiated inflorescence called the curd, that cauliflower possesses.

Cauliflower possesses a single mutation in a gene called *CAL*, controlling meristem differentiation into inflorescence. This causes the cells at the floral meristem to gain an undifferentiated identity, and instead of growing into a flower, they grow into a lump of undifferentiated cells. This mutation has been selected through domestication at least since the Greek empire.

Chapter- 3

Alternation of Generations

Alternation of generations (also known as **alternation of phases** or **metagenesis**) is a term primarily used in describing the life cycle of plants (taken here to mean the Archaeplastida). A multicellular diploid sporophyte, with N paired chromosomes (i.e. 2N in total), alternates with a multicellular haploid gametophyte, with N unpaired chromosomes. A mature sporophyte produces spores by meiosis, a process which results in a reduction of the number of chromosomes by a half. Spores germinate and grow into a gametophyte. At maturity, the gametophyte produces gametes by mitosis. Two gametes (originating from different organisms of the same species or from the same organism) fuse to produce a zygote, which develops into a diploid sporophyte. This cycle, from sporophyte to sporophyte (or equally from gametophyte to gametophyte), is the way in which all land plants and many algae undergo sexual reproduction.

All animals develop differently. A mature animal is diploid and so is, in one sense, equivalent to a sporophyte. However, an animal *directly* produces haploid gametes by meiosis. No haploid spores capable of dividing are produced, so neither is a haploid gametophyte. There is no alternation between diploid and haploid forms.

Other organisms, such as fungi, can have life cycles in which different kinds of organism alternate. The term 'alternation of generations' has also been applied to these cases.

Life cycles, such as those of plants, with alternating haploid and diploid phases can be referred to as **diplohaplontic** (the equivalent terms **haplodiplontic**, **diplobiontic** or **dibiontic** are also in use). Life cycles, such as those of animals, in which there is only a diploid phase are referred to as **diplontic**. (Life cycles in which there is only a haploid phase are referred to as **haplontic**.)

Definition

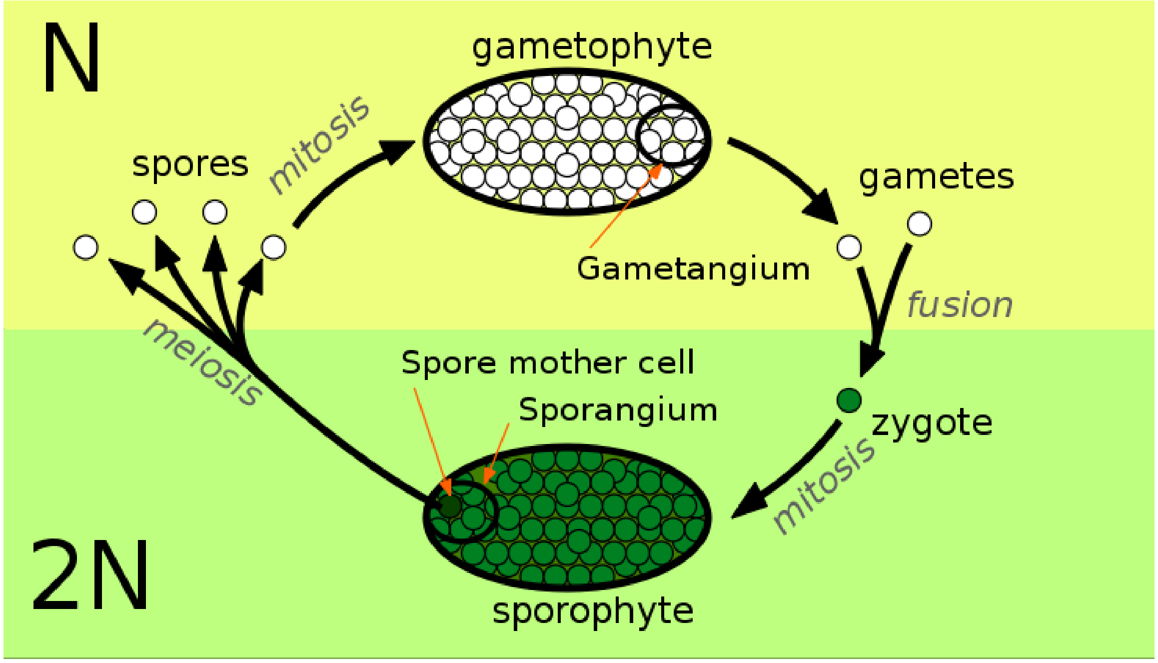
The discussion of 'alternation of generations' above treats the alternation of a multicellular diploid form with a multicellular haploid form as the defining characteristic, regardless of whether these forms are free-living or not. In some species, such as the alga *Ulva lactuca*, the diploid and haploid forms are indeed both free-living independent organisms, essentially identical in appearance. The free-swimming gametes form a zygote which germinates into a diploid sporophyte; the free-swimming spores germinate into a haploid gametophyte. Alternation of *generations* is an appropriate term.

However, in other species, either the sporophyte or the gametophyte is very much reduced and is incapable of free-living. For example, in seed plants, the gametophyte 'generation' develops totally within the sporophyte which protects and nurtures it, with the sole exception of pollen grains, which are the 'male' gametophytes, but which have been reduced to only three cells. Here the notion of two generations is less obvious; as Bateman & Dimichele say "[s]porophyte and gametophyte effectively function as a single organism". The alternative term 'alternation of phases' may then be more appropriate.

Alternation of generations in plants

Fundamental elements

The diagram below shows the fundamental elements of the alternation of generations in plants. It is vital to have a good understanding of these fundamentals before considering the many variations found in different groups of plants. Starting from the right of the diagram, the processes involved are as follows:



- Two single-celled haploid gametes, each containing N unpaired chromosomes, fuse to form a single-celled diploid zygote, which now contains N paired chromosomes, i.e. 2N chromosomes in total.
- The single-celled diploid zygote germinates, dividing by the normal process (mitosis), which maintains the number of chromosomes at 2N. The result is a multi-cellular diploid organism, called the *sporophyte* (because at maturity it produces spores).

- When it reaches maturity, the sporophyte produces one or more **sporangia** (singular sporangium) which are the organs which produce diploid spore mother cells (sporocytes). These divide by a special process (meiosis) which reduces the number of chromosomes by a half. This results in four single-celled haploid spores, each containing N unpaired chromosomes.
- The single-celled haploid spore germinates, dividing by the normal process (mitosis), which maintains the number of chromosomes at N. The result is a multi-cellular haploid organism, called the *gametophyte* (because at maturity it produces gametes).
- When it reaches maturity, the gametophyte produces one or more **gametangia** (singular gametangium) which are the organs which produce haploid gametes. At least one kind of gamete possesses some mechanism for reaching another gamete in order to fuse with it.

The 'alternation of generations' in the life cycle is thus between a diploid (2N) generation of sporophytes and a haploid (N) generation of gametophytes.

Gametophyte of the fern *Onoclea sensibilis* (the flat thallus at the bottom of the picture) with a descendant sporophyte beginning to grow from it (the small frond at the top of the picture).

The situation is quite different in all animals, where the fundamental process is that a diploid (2N) individual *directly* produces haploid (N) gametes by meiosis. Spores (i.e. haploid cells which are able to undergo mitosis) are not produced, so neither is a haploid multi-cellular organism. The single-celled gametes are the only entities which are haploid.

Variations

The diagram shown above is a good representation of the life cycle of some multi-cellular algae (e.g. the genus *Cladophora*) which have sporophytes and gametophytes of very similar, if not identical, appearance, and which do not have different kinds of spores or gametes.

However, there are many possible variations on the fundamental elements of a life cycle which has alternation of generations. Each variation may occur separately or in combination, resulting in a bewildering variety of life cycles. The terms used by botanists in describing these life cycles can be equally bewildering. As Bateman and Dimichele say "[...] the alternation of generations has become a terminological morass; often, one term represents several concepts or one concept is represented by several terms."

Possible variations are:

- *Relative importance of the sporophyte and the gametophyte.*
    - *Equal* (**homomorphy** or **isomorphy**).
      Filamentous algae of the genus *Cladophora*, which are predominantly found in fresh water, have diploid sporophytes and haploid gametophytes which are externally indistinguishable. No living land plant has equally dominant sporophytes and gametophytes, although some theories of the evolution of alternation of generations suggest that ancestral land plants did.
    - *Unequal* (**heteromorphy** or **anisomorphy**).

Gametophyte of *Mnium hornum*, a moss.

- *Dominant gametophyte* (**gametophytic**).
  In liverworts, mosses and hornworts, the dominant form is the haploid gametophyte. The diploid sporophyte is not capable of an independent existence, gaining most of its nutrition from the parent gametophyte, and having no chlorophyll when mature.

Sporophyte of *Blechnum discolor*, a fern.

- *Dominant sporophyte* (**sporophytic**).
  In ferns, both the sporophyte and the gametophyte are capable of living independently, but the dominant form is the diploid sporophyte. The haploid gametophyte is much smaller and simpler in structure. In seed plants, the gametophyte is even more reduced (at the minimum to only three cells), gaining all its nutrition from the sporophyte. The extreme reduction in the size of the gametophyte and its retention within the sporophyte means that when applied to seed plants the term 'alternation of generations' is somewhat misleading: "[s]porophyte and gametophyte effectively function as a single organism". Some authors have preferred the term 'alternation of phases'.

- *Differentiation of the gametes.*
  - *Both gametes the same* (**isogamy**).
    Like other species of *Cladophora*, *C. callicoma* has flagellated gametes which are identical in appearance and ability to move.
  - *Gametes of two distinct sizes* (**anisogamy**).
    - *Both of similiar motility*.
      Species of *Ulva*, the sea lettuce, have gametes which all have two flagella and so are motile. However they are of two sizes: larger 'female' gametes and smaller 'male' gametes.
    - *One large and sessile, one small and motile* (**oogamy**). The larger sessile megagametes are eggs (ova), and smaller motile

microgametes are sperm (spermatazoa, spermatozoids). The degree of motility of the sperm may be very limited (as in the case of flowering plants) but all are able to move towards the sessile eggs. When (as is almost always the case) the sperm and eggs are produced in different kinds of gametangia, these are called **antheridia** (singular antheridium) and **archegonia** (singular archegonium) respectively.

Gametophyte of *Pellia epiphylla* with sporophytes growing from the remains of archegonia.

- *Antheridia and archegonia occur on the same gametophyte,* which is then called **monoicous**. (Many sources, particularly those concerned with bryophyes, use the term 'monoecious' for this situation and 'dioecious' for the opposite. Here 'monoecious' and 'dioecious' are used only for sporophytes.)
  The liverwort *Pellia epiphylla* has the gametophyte as the dominant generation. It is monoicous: the small reddish antheridia are scattered along the midrib while the archegonia grow nearer the tip of divisions of the plant.
- *Antheridia and archegonia occur on different gametophytes,* which are then called **dioicous**.
  The moss *Mnium hornum* has the gametophyte as the dominant generation. It is dioicous: male plants produce

only antheridia in terminal rosettes, female plants produce only archegonia in the form of stalked capsules. Seed plants are also dioicous; however, the extreme reduction of the gametophyte, particularly the microgametophyte, means that the antheridia and archegonia are microscopic.

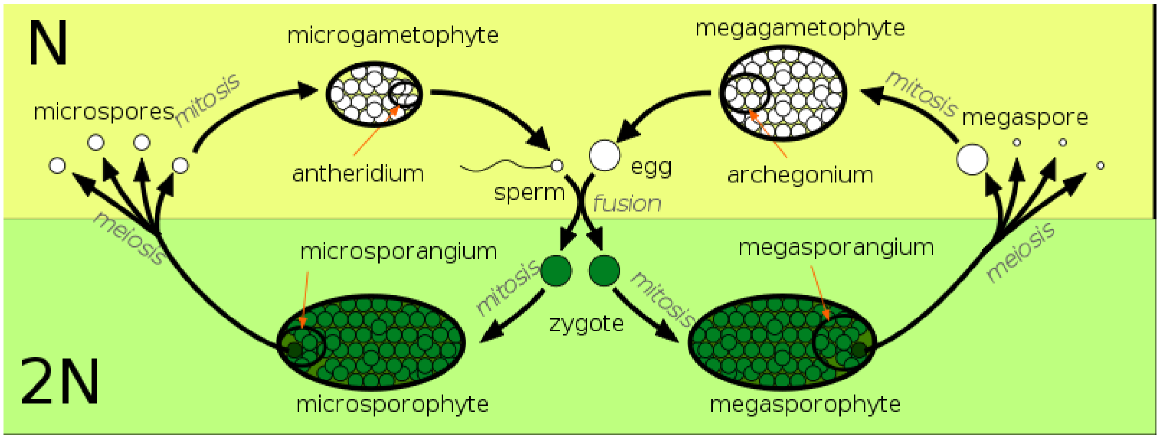
- *Differentiation of the spores.*
    - *All spores the same size* (**homospory** or isospory).
      Horsetails (species of *Equisetum*) have spores which are all of the same size.
    - *Spores of two distinct sizes* (**heterospory** or anisospory): larger **megaspores** and smaller **microspores**. When the two kinds of spore are produced in different kinds of sporangia, these are called **megasporangia** and **microsporangia**. A megaspore often (but not always) develops at the expense of the other three cells resulting from meiosis, which abort.
        - *Megasporangia and microsporangia occur on the same sporophyte,* which is then called **monoecious**.
          Most flowering plants fall into this category. Thus the flower of a lily contains six stamens (the microsporangia) which produce microspores which develop into pollen grains (the microgametophytes), and three fused carpels (the megasporangia) which produce megaspores which develop into ovules (the megagametophytes). In other plants, such as hazel, some flowers have only stamens, others only carpels, but the same plant (i.e. sporophyte) has both kinds of flower and so is monoecious.

Flowers of European Holly, a dioecious species: male above, female below (leaves cut to show flowers more clearly)

- *Megasporangia and microsporangia occur on different sporophytes,* which are then called **dioecious**.
  An individual tree of the European holly (*Ilex aquifolium*) produces either 'male' flowers which have only functional stamens (microsporangia) producing microspores which develop into pollen grains (microgametophytes) or 'female' flowers which have only functional carpels (megasporangia) producing megaspores which develop into ovules (megagametophytes).

There are some correlations between these variations, but they are just that, correlations, and not absolute. For example, in flowering plants, microspores ultimately produce microgametes (sperm) and megaspores ultimately produce megagametes (eggs). However, in pteridophytes there are groups with undifferentiated spores but differentiated gametophytes. For example, the fern *Ceratopteris thalictrioides* has spores of only one kind, which vary continuously in size. Smaller spores tend to produce gametophytes which have only sperm-producing antheridia.

A complex life cycle



The diagram shows the alternation of generations in a species which is heteromorphic, sporophytic, oogametic, dioicous, heterosporic and dioecious. A seed plant example is a willow tree (genus *Salix*). Starting in the centre of the diagram, the processes involved are:

- An immobile egg, typically remaining in the archegonium, fuses with a mobile sperm, released from an antheridium. The resulting zygote is either 'male' or 'female'.
- A 'male' zygote develops by mitosis into a microsporophyte, which at maturity produces one or more microsporangia. Microspores develop within the microsporangium by meiosis.
  In a willow (like all seed plants) the zygote first develops into a seed within the ovule (megasporangium). Later the seed is shed and grows into a mature tree. A 'male' willow tree (a microsporophyte) produces flowers with only stamens, the anthers of which are the microsporangia.

- Microspores germinate producing microgametophytes; at maturity one or more antheridia are produced. Sperm develop within the antheridia.
  In a willow, microspores are not liberated from the anther (the microsporangium), but develop into pollen grains (microgametophytes) within it. The whole pollen grain is moved (typically by an insect) to an ovule (megagametophyte), where a sperm is produced which moves down a pollen tube to reach the egg.
- A 'female' zygote develops by mitosis into a megasporophyte, which at maturity produces one or more megasporangia. Megaspores develop within the megasporangium; typically one of the four spores produced by meiosis gains bulk at the expense of the remaining three, which disappear.
  'Female' willow trees (megasporophytes) produce flowers with only carpels (the megasporangia).
- Megaspores germinate producing megagametophytes; at maturity one or more archegonia are produced. Eggs develop within the archegonia.
  In a willow, megaspores develop into ovules (megagametophytes) within the carpels (megasporangia). An archegonium develops within the ovule and produces an egg. All of this happens within the carpel (the megasporangium). The whole of the gametophytic 'generation' remains within the protection of the sporophyte except for pollen grains (which have been reduced to just three cells).

Life cycles of different plant groups

The term 'plants' is taken here to mean the Archaeplastida, i.e. the glaucophytes, red and green algae and land plants.

Alternation of generations occurs in almost all multicellular red and green algae, both freshwater forms (such as *Cladophora*) and seaweeds (such as *Ulva*). In most, the generations are homomorphic (isomorphic) and free-living. Some species of red algae have a complex triphasic alternation of generations, in which there is a gametophyte phase and two distinct sporophyte phases.

Land plants all have heteromorphic (anisomorphic) alternation of generations, in which the sporophyte and gametophyte are distinctly different. All bryophytes, i.e. liverworts, mosses and hornworts, have the gametophyte generation as the most conspicuous. As an illustration, consider a monoicous moss. Antheridia and archegonia develop on the mature plant (the gametophyte). In the presence of water, the biflagellate sperm from the antheridia swim to the archegonia and fertilisation occurs, leading to the production of a diploid sporophyte. The sporophyte grows up from the archegonium. Its body comprises a long stalk topped by a capsule within which spore-producing cells undergo meiosis to form haploid spores. Most mosses rely on the wind to disperse these spores.

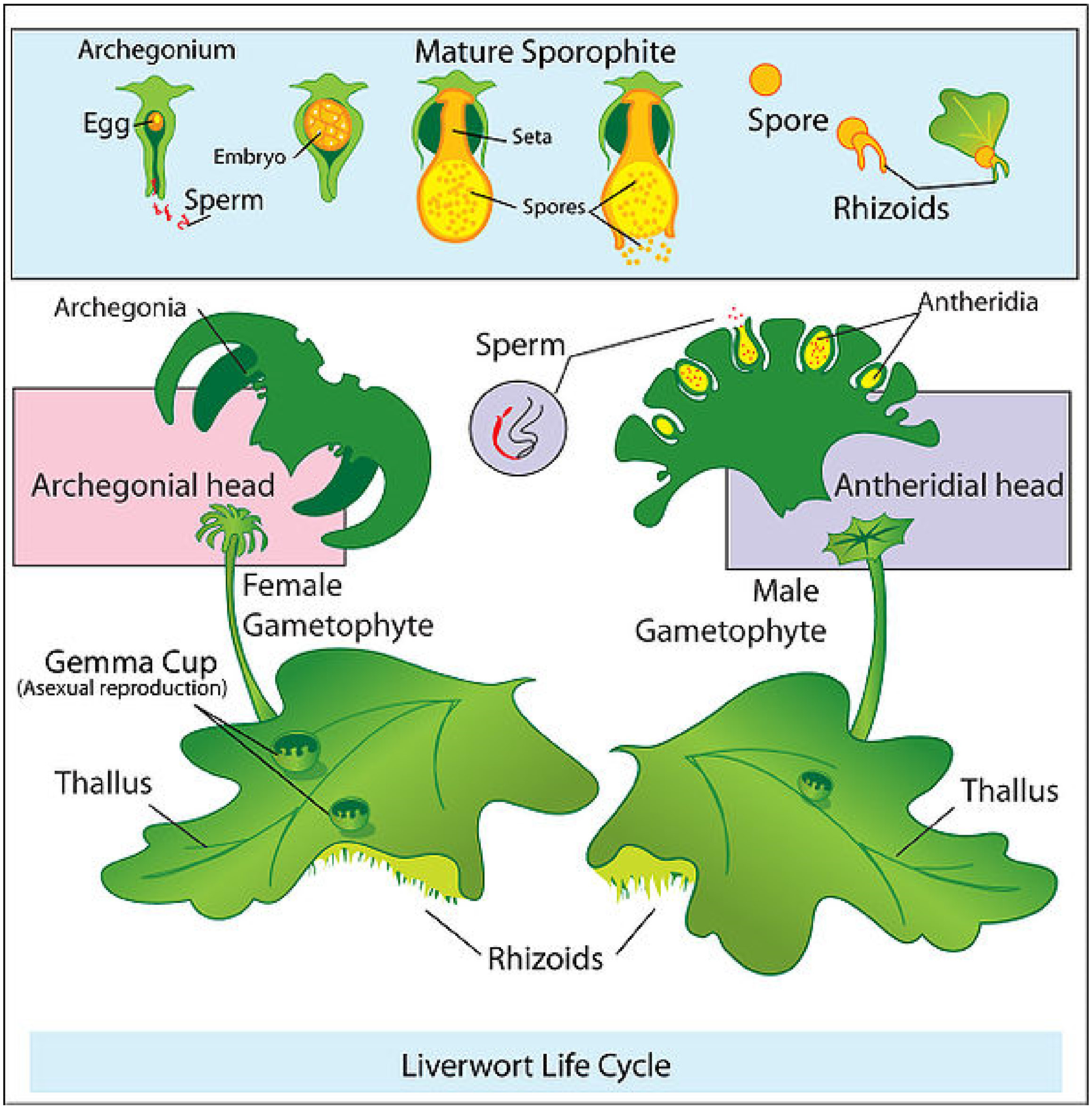
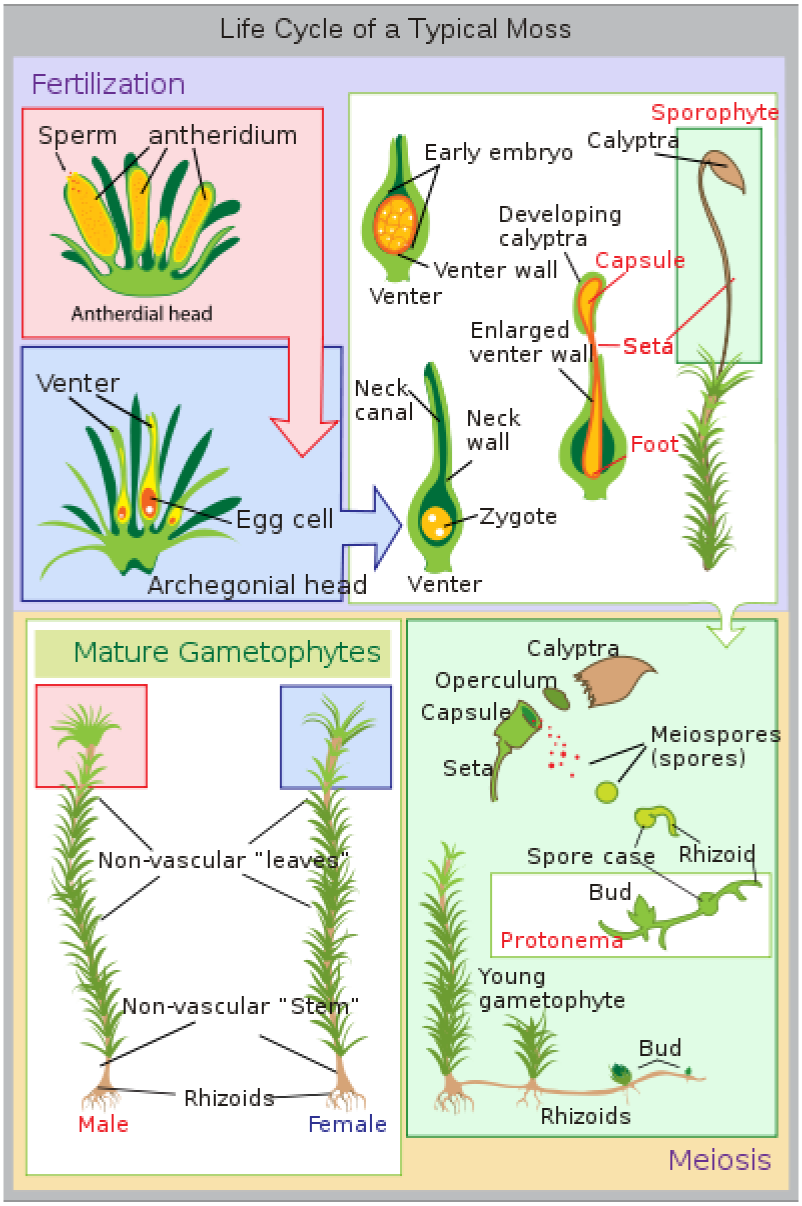
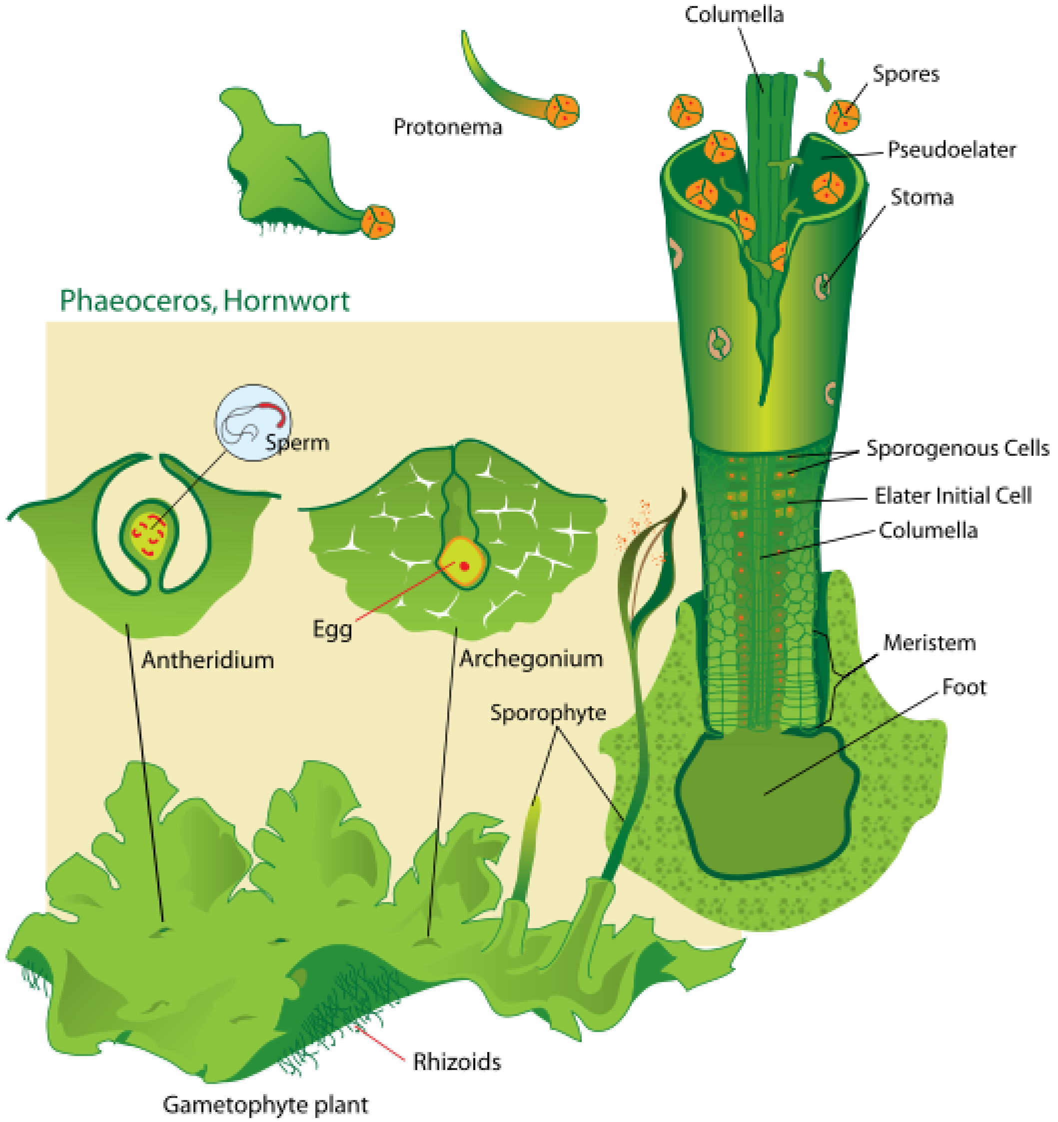


Diagram of alternation of generations in liverworts.



Moss life cycle diagram



Hornwort life cycle diagram

In ferns and their allies, including clubmosses and horsetails, the conspicuous plant observed in the field is the diploid sporophyte. The haploid spores develop in sori on the underside of the fronds and are dispersed by the wind (or in some cases, by floating on water). If conditions are right, a spore will germinate and grow into a rather inconspicuous plant body called a prothallus. The haploid prothallus does not resemble the sporophyte, and as such ferns and their allies have a heteromorphic alternation of generations. The prothallus is short-lived, but carries out sexual reproduction, producing the diploid zygote that then grows out of the prothallus as the sporophyte.

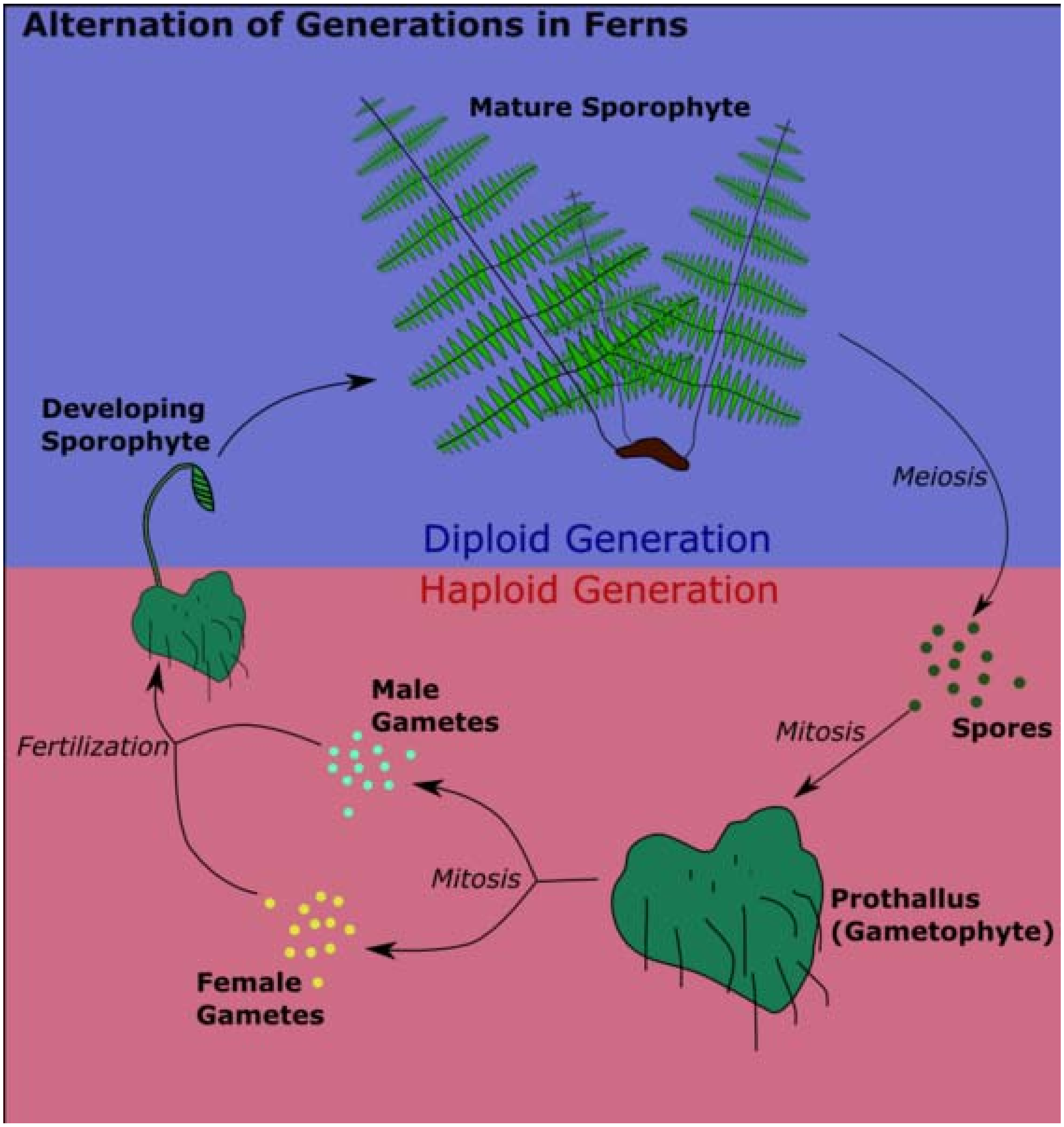


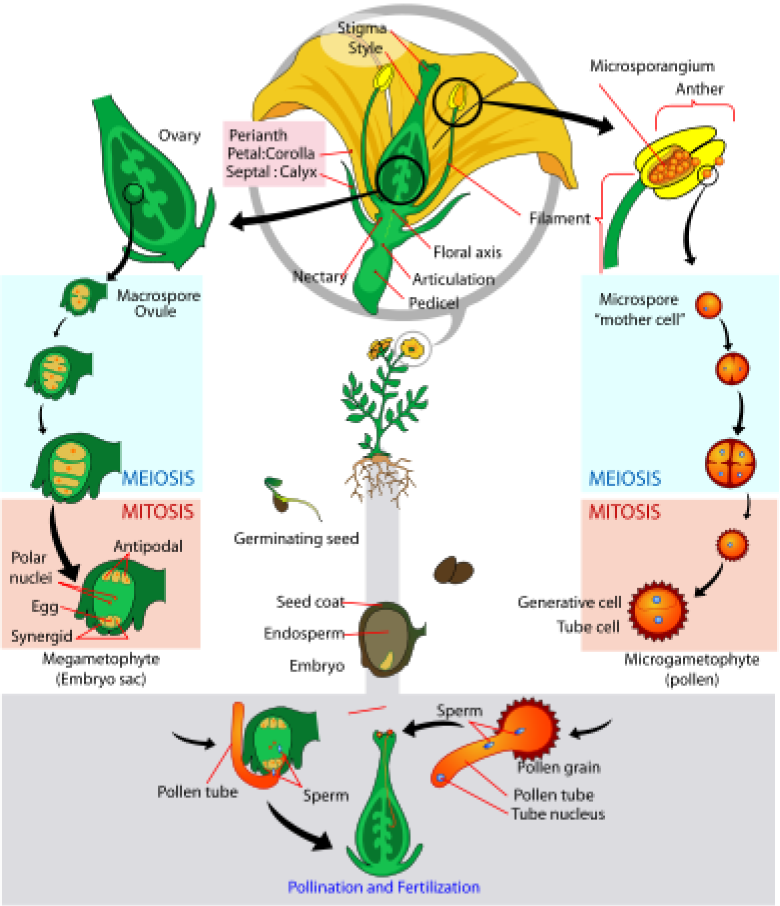
Diagram of alternation of generations in ferns.

A gametophyte (prothallus) of *Dicksonia sp.*


A sporophyte of *Dicksonia antarctica*.

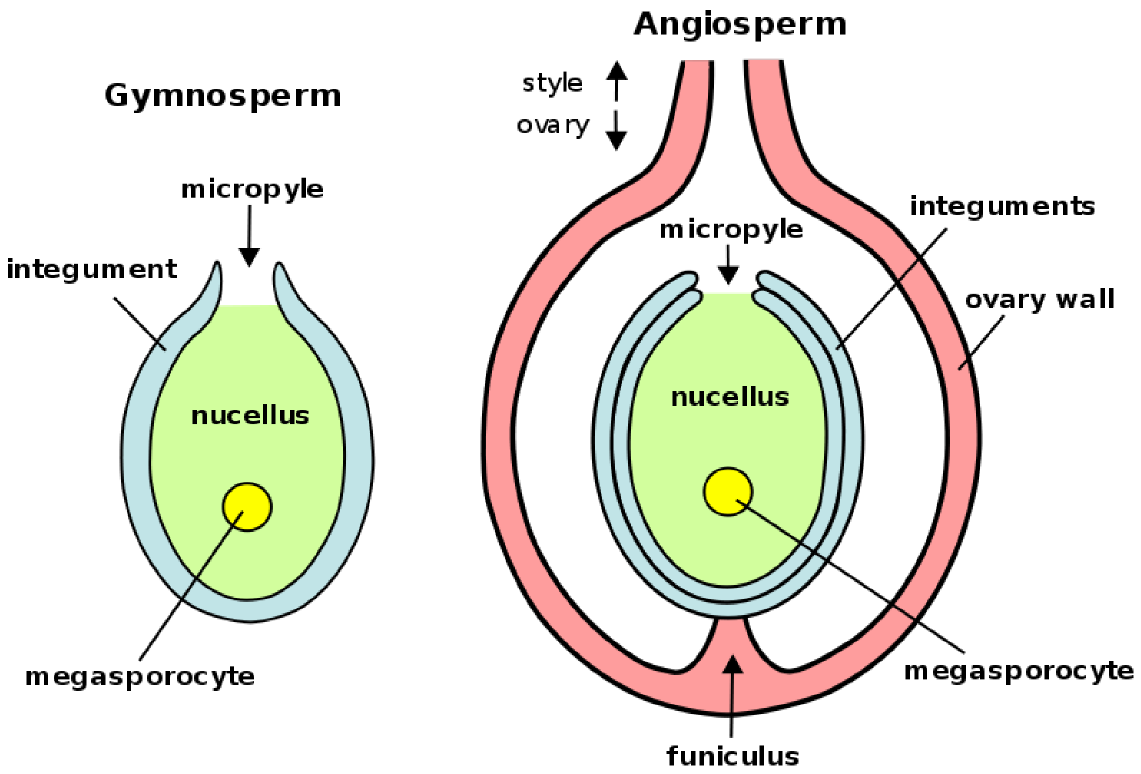
The underside of a *Dicksonia antarctica* frond showing the sori, or spore-producing structures.

In the spermatophytes, the seed plants, the sporophyte is the dominant multicellular phase; the gametophytes are strongly reduced in size and very different in morphology. The entire gametophyte generation, with the sole exception of pollen grains (microgametophytes), is contained within the sporophyte. The life cycle of a dioecious flowering plant (angiosperm), the willow, has been outlined in some detail in an earlier section (A complex life cycle). The life cycle of a gymnosperm is similar. However, flowering plants have in addition a phenomenon called 'double fertilization'. Two sperm nuclei from a pollen grain (the microgametophyte), rather than a single sperm, enter the archegonium of the megagametophyte; one fuses with the egg nucleus to form the zygote, the other fuses with two other nuclei of the gametophyte to form 'endosperm', which nourishes the developing embryo.

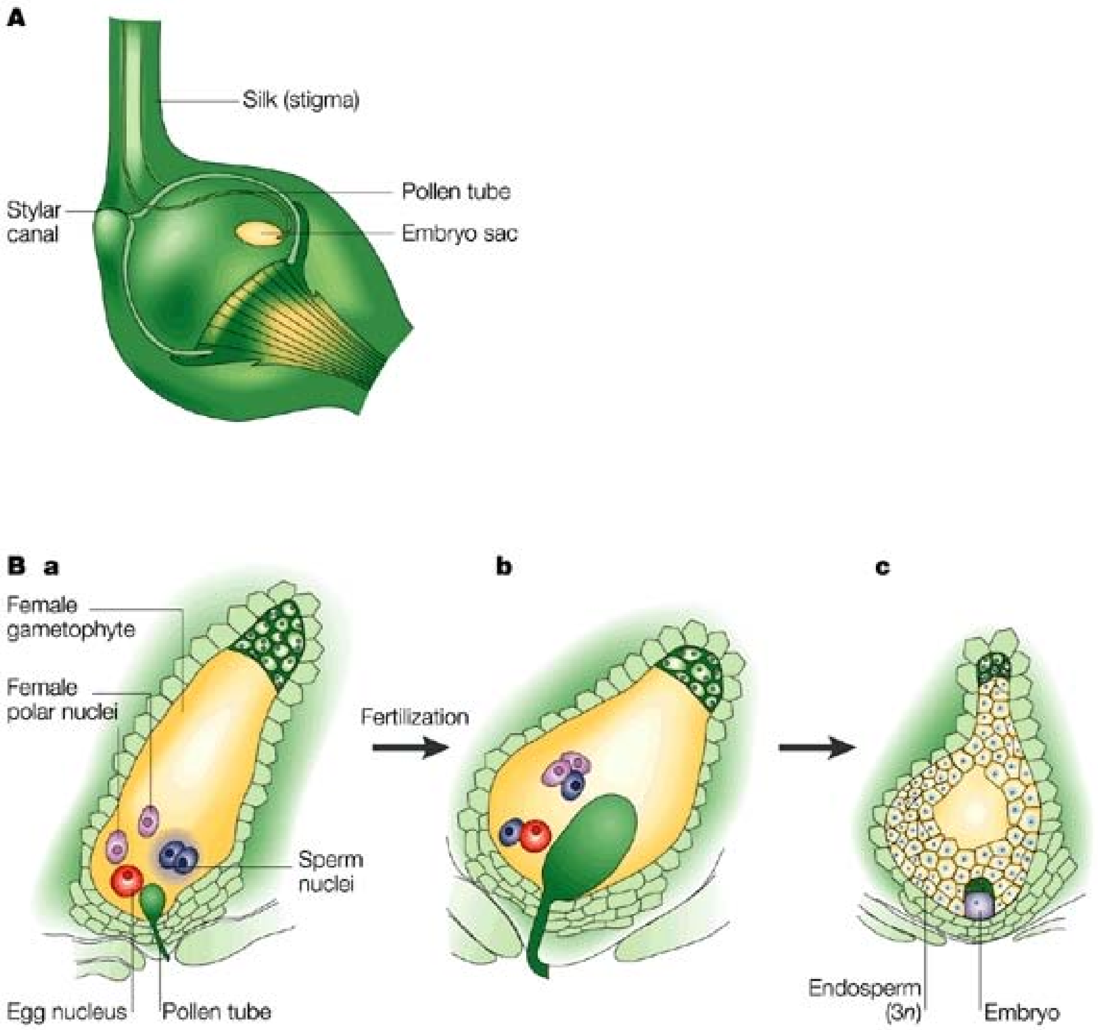


Angiosperm life cycle

Tip of tulip stamen showing pollen (microgametophytes)



Plant ovules (megagametophytes): Gymnosperm ovule on left, angiosperm ovule (inside ovary) on right



Nature Reviews | Genetics

Double fertilization

Other groups of organism

Some organisms currently classified in the Chromalveolata, and thus not plants in the sense used here, exhibit alternation of generations. Kelp are an example of a brown alga with a heteromorphic alternation of generations. Species from the genus *Laminaria* have a large sporophytic thallus that produces haploid spores which germinate to produce free-living microscopic male and female gametophytes. Foraminifera undergo a heteromorphic alternation of generations between haploid ***gamont*** and diploid ***agamont*** forms. The single-celled haploid organism is typically much larger than the diploid organism.

Fungal mycelia are typically haploid. When mycelia of different mating types meet, they produce two multinucleate ball-shaped cells, which join via a "mating bridge". Nuclei move from one mycelium into the other, forming a ***heterokaryon*** (meaning "different nuclei"). This process is called ***plasmogamy***. Actual fusion to form diploid nuclei is called ***karyogamy***, and may not occur until sporangia are formed. Karogamy produces a diploid zygote, which is a short-lived sporophyte that soon undergoes meiosis to form haploid spores. When the spores germinate, they develop into new mycelia.

The life cycle of slime molds is very similar to that of fungi. Haploid spores germinate to form swarm cells or ***myxamoebae***. These fuse in a process referred to as *plasmogamy* and *karyogamy* to form a diploid zygote. The zygote develops into a plasmodium, and the mature plasmodium produces, depending on the species, one to many fruiting bodies containing haploid spores.

In some animals, there is an alternation between parthenogenic and sexually reproductive phases (**heterogamy**). Although in some ways similar to alternation of generations, the genetics of heterogamy is significantly different.

Chapter- 4

Plant Reproduction

Plant reproduction is the production of new individuals or offspring in plants, which can be accomplished by sexual or asexual means. Sexual reproduction produces offspring by the fusion of gametes, resulting in offspring genetically different from the parent or parents. Asexual reproduction produces new individuals without the fusion of gametes, genetically identical to the parent plants and each other, except when mutations occur. In seed plants, the offspring can be packaged in a protective seed, which is used as an agent of dispersal.

Asexual reproduction

Plants have two main types of asexual reproduction in which new plants are produced that are genetically identical clones of the parent individual. "Vegetative" reproduction involves a vegetative piece of the original plant (budding, tillering, etc.) and is distinguished from "apomixis", which is a "replacement" for sexual reproduction, and in some cases involves seeds. Apomixis occurs in many plant species and also in some non-plant organisms.

Natural vegetative reproduction is mostly a process found in herbaceous and woody perennial plants, and typically involves structural modifications of the stem or roots and in a few species leaves. Most plant species that employ vegetative reproduction, do so as a means to perennialize the plants, allowing them to survive from one season to the next and often facilitating their expansion in size. A plant that persists in a location through vegetative reproduction of individuals constitutes a clonal colony, a single ramet, or apparent individual, of a clonal colony is genetically identical to all others in the same colony. The distance that a plant can move during vegetative reproduction is limited, though some plants can produce ramets from branching rhizomes or stolons that cover a wide area, often in only a few growing seasons. In a sense, this process is not one of "reproduction" but one of survival and expansion of biomass of the individual. When an individual organism increases in size via cell multiplication and remains intact, the process is called "vegetative growth". However, in vegetative reproduction, the new plants that result are new individuals in almost every respect except genetic. A major disadvantage to vegetative reproduction, is the transmission of pathogens from parent to daughter plants; it is uncommon for pathogens to be transmitted from the plant to its seeds, though there are occasions when it occurs.

Seeds generated by apomixis are a means of asexual reproduction, involving the formation and dispersal of seeds that do not originate from the fertilization of the embryos. Hawkweed (*Hieracium*), dandelion (*Taraxacum*), some Citrus (*Citrus*) and Kentucky blue grass (*Poa pratensis*) all use this form of asexual reproduction. Pseudogamy occurs in some plants that have apomictic seeds, where pollination is often needed to initiate embryo growth, though the pollen contributes no genetic material to the developing offspring. Other forms of apomixis occur in plants also, including the generation of a plantlet in replacement of a seed or the generation of bulbils instead of flowers, where new cloned individuals are produced.

Natural vegetative structures

The **rhizome** is a modified underground stem serving as an organ of vegetative reproduction, e. g. Polypody, Iris, Couch Grass and Nettles.

Prostrate aerial stems, called **runners** or **stolons** are important vegetative reproduction organs in some species, such as the strawberry, numerous grasses, and some ferns.

Adventitious buds form on roots near the ground surface, on damaged stems (as on the stumps of cut trees), or on old roots. These develop into above-ground stems and leaves.

A form of budding called **suckering** is the reproduction or regeneration of a plant by shoots that arise from an existing root system. Species that characteristically produce suckers include Elm (*Ulmus*), Dandelion (*Taraxacum*), and members of the Rose Family (*Rosa*).

Another type of a vegetative reproduction is the production of bulbs. Plants like onion (*Allium cepa*), hyacinth (*Hyacinth*), narcissus (*Narcissus*) and tulips (*Tulipa*) reproduce by forming bulbs.

Other plants like potatoes (*Solanum tuberosum*) and dahlia (*Dahlia*) reproduce by a method similar to bulbs: they produce tubers.

Gladioli and crocuses (*Crocus*) reproduce by forming a bulb-like structure called a corm.

Human uses of asexual reproduction

The most common form of plant reproduction utilized by people is seeds, but a number of asexual methods are utilized which are usually enhancements of natural processes, including: cutting, grafting, budding, layering, division, sectioning of rhizomes or roots, stolons, tillers (suckers) and artificial propagation by laboratory tissue cloning. Asexual methods are most often used to propagate cultivars with individual desirable characteristics that do not come true from seed. Fruit tree propagation is frequently performed by budding or grafting desirable cultivars (clones), onto rootstocks that are also clones, propagated by layering.

In horticulture, a "cutting" is a branch that has been cut off from a mother plant below an internode and then rooted, often with the help of a rooting liquid or powder containing hormones. When a full root has formed and leaves begin to sprout anew, the clone is a self-sufficient plant, genetically identical to the mother plant. Examples include cuttings from the stems of blackberries (*Rubus occidentalis*), African violets (*Saintpaulia*), verbenas (*Verbena*) to produce new plants. A related use of cuttings is grafting, where a stem or bud is joined onto a different stem. Nurseries offer for sale trees with grafted stems that can produce four or more varieties of related fruits, including apples. The most common usage of grafting is the propagation of cultivars onto already rooted plants, sometimes the rootstock is used to dwarf the plants or protect them from root damaging pathogens.

Since vegetatively propagated plants are clones, they are important tools in plant research. When a clone is grown in various conditions, differences in growth can be ascribes to environmental effects instead of genetic differences.

Sexual reproduction

Sexual reproduction involves two fundamental processes, meiosis which rearranges the genes and reduces the number of chromosomes, and fusion of gametes which restores the chromosome to a complete diploid number. In between these two processes, different types of plants vary. In plants and algae that undergo alternation of generations, a gametophyte is the multicellular structure, or phase, that is haploid, containing a single set of chromosomes:

The gametophyte produces male or female gametes (or both), by a process of cell division called mitosis. The fusion of male and female gametes produces a diploid zygote, which develops by repeated mitotic cell divisions into a multicellular sporophyte. Because the sporophyte is the product of the fusion of two haploid gametes, its cells are diploid, containing two sets of chromosomes. The mature sporophyte produces spores by a process called meiosis, sometimes referred to as "reduction division" because the chromosome pairs are separated once again to form single sets. The spores are therefore once again haploid and develop into a haploid gametophyte. In land plants such as ferns, mosses and liverworts the gametophyte is very small, as in ferns and their relatives. In flowering plants (angiosperms) It is reduced to only a few cells, where the female gametophyte (embryo sac) is known as a megagametophyte and the male gametophyte (pollen) is called a microgametophyte.

History of sexual reproduction

Unlike animals, plants are immobile, and cannot seek out sexual partners for reproduction. In the evolution of early plants, abiotic means, including water and wind, transported sperm for reproduction. The first plants were aquatic and released sperm freely into the water to be carried with the currents. Primitive land plants like liverworts and mosses had motile sperm that swam in a thin film of water or were splashed in water droplets from the male reproduction organs onto the female organs. As taller and more complex plants evolved, modifications in the alternation of generations evolved; in the Paleozoic era progymnosperms reproduced by using spores dispersed on the wind. The seed plants including seed ferns, conifers and cordaites, which were all gymnosperms, evolved 350 million years ago; they had pollen grains that contained the male gametes for protection of the sperm during the process of transfer from the male to female parts. It is believed that insects fed on the pollen, and plants thus evolved to use insects to actively carry pollen from one plant to the next. Seed producing plants, which include the angiosperms and the gymnosperms, have heteromorphic alternation of generations with large sporophytes containing much reduced gametophytes. Angiosperms have distinctive reproductive organs called flowers, with carpels, and the female gametophyte is greatly reduced to a female embryo sac, with as few as eight cells. The male gametophyte consists of the pollen grains. The sperm of seed plants are non-motile, except for two older groups of plants, the Cycadophyta and the Ginkgophyta, which have flagellated sperm.

Flowering plants

Flowering plants are the dominant plant form on land and they reproduce by sexual and asexual means. Often their most distinguishing feature is their reproductive organs, commonly called flowers. Sexual reproduction in flowering plants involves the production of male and female gametes, the transfer of the male gametes to the female ovules in a process called pollination. After pollination occurs, fertilization happens and the ovules grow into seeds with in a fruit. After the seeds are ready for dispersal, the fruit ripens and by various means the seeds are freed from the fruit and after varying amounts of time and under specific conditions the seeds germinate and grow into the next generation.

The anther produces male gametophytes, the sperm is produced in pollen grains, which attach to the stigma on top of a carpel, in which the female gametophytes (inside ovules) are located. After the pollen tube grows through the carpel's style, the sex cell nuclei from the pollen grain migrate into the ovule to fertilize the egg cell and endosperm nuclei within the female gametophyte in a process termed double fertilization. The resulting zygote develops into an embryo, while the triploid endosperm (one sperm cell plus two female cells) and female tissues of the ovule give rise to the surrounding tissues in the developing seed. The ovary, which produced the female gametophyte(s), then grows into a fruit, which surrounds the seed(s). Plants may either self-pollinate or cross-pollinate. Nonflowering plants like ferns, moss and liverworts use other means of sexual reproduction.

Adaptations

An Orchid flower.

Flowers of wind pollinated plants tend to lack petals and or sepals. Typically large amounts of pollen are produced and pollination often occurs early in the growing season before leaves can interfere with the dispersal of the pollen. Many trees and all grasses and sedges are wind pollinated, as such they have no need for large fancy flowers. In plants that use insects or other animals to move pollen from one flower to the next, plants have developed greatly modified flower parts to attract pollinators and to facilitate the movement of pollen from one flower to the insect and from the insect back to the next flower. Plants have a number of different means to attract pollinators including color, scent, heat, nectar glands, eatable pollen and flower shape. Along with modifications involving the above structures two other conditions play a very important role in the sexual reproduction of flowering plants, the first is timing of flowering and the other is the size or number of flowers produced. Often plant species have a few large, very showy flower while others produce many small flowers, often flowers are collected together into large inflorescences to maximize their visual effect, becoming more noticeable to passing pollinators. Flowers are attraction strategies and sexual expressions are functional strategies used to produce the next generation of plants, with pollinators and plants having co-evolved, often to some extraordinary degrees, very often rendering mutual benefit.

Flower heads showing disk and ray florets.

The largest family of flowering plants is the orchids (Orchidaceae), estimated by some specialists to include up to 35,000 species, which often have highly specialized flowers used to attract insects and facilitate pollination. The stamens are modified to produce pollen in clusters called pollinium, which are attached to insects when crawling into the flower. The flower shapes are modified to force insects to pass by the pollen, which is "glued" to the insect. Some orchids are even more highly specialized, with flower shapes that mimic the shape of insects to attract them to 'mate' with the flowers, a few even have scents that mimic insect pheromones.

Another large group of flowering plants is the Asteraceae or sunflower family with close to 22,000 species, which also have highly modified inflorescences that are flowers collected together in heads composed of a composite of individual flowers called florets.

Heads with florets of one sex, when the flowers are pistillate or functionally staminate, or made up of all bisexual florets, are called homogamous and can include discoid and liguliflorous type heads. Some radiate heads may be homogamous too. Plants with heads that have florets of two or more sexual forms are called heterogamous and include radiate and disciform head forms, though some radiate heads may be heterogamous too.

Ferns

Ferns typically produce large diploid sporophytes with rhizomes, roots and leaves; and on fertile leaves called sporangium, spores are produced. The spores are released and germinate to produce short, thin gametophytes that are typically heart shaped, small and green in color. The gametophytes or thallus, produce both motile sperm in the antheridia and egg cells in separate archegonia. After rains or when dew deposits a film of water, the motile sperm are splashed away from the antheridia, which are normally produce on the top side of the thallus, and swim in the film of water to the antheridia where they fertilize the egg. To promote out crossing or cross fertilization the sperm are released before the eggs are receptive of the sperm, making it more likely that the sperm will fertilize the eggs of different thallus. A zygote is formed after fertilization, which grows into a new sporophytic plant. The condition of having separate sporephyte and gametophyte plants is call alternation of generations. Other plants with similar reproductive means include the *Psilotum*, *Lycopodium*, *Selaginella* and *Equisetum*.

Bryophytes

The bryophytes, which include liverworts, hornworts and mosses, reproduce both sexually and vegetatively. The gametophyte is the most commonly known phase of the plant. An early developmental stage in the gametophyte of mosses (immediately following germination of the meiospore) is called the protonema. All are small plants found growing in moist locations and like ferns, have motile sperm with flagella and need water to facilitate sexual reproduction. These plants start as a haploid spore that grows into the dominate form, which is a multicellular haploid body with leaf-like structures that photosynthesize. Haploid gametes are produced in antherida and archegonia by mitosis. The sperm released from the antherida respond to chemicals released by ripe archegonia and swim to them in a film of water and fertilize the egg cells thus producing a zygote. The zygote divides by mitotic division and grows into a sporophyte that is diploid. The multicellular diploid sporophyte produces structures called spore capsules, which are connected by seta to the archegonia. The spore capsules produce spores by meiosis, when ripe the capsules burst open and the spores are released. Bryophytes show considerable variation in their breeding structures and the above is a basic outline. Also in some species each plant is one sex while other species produce both sexes on the same plant.

Sexual expression

Many plants have evolved a complex sexuality, which is expressed in different combinations of their reproductive organs. Some species have separate male and female individuals, some have separate male and female flowers on the same plant, abut the majority of plants have both male and female parts in the same flower. Some plants change their gender expression depending on a number of factors like age, time of day, or because of environmental conditions. Plant sexuality also varies within different populations of some species.

Chapter- 5

Timeline of Plant Evolution

Here we, attempts to place key plant innovations in a geological context. It concerns itself only with novel adaptations and events that had a major ecological significance, not those that are of solely anthropological interest. The timeline displays a graphical representation of the adaptations; the text attempts to explain the nature and robustness of the evidence.

Plant evolution is an aspect of the study of biological evolution, involving predominantly evolution of plants suited to live on land, greening of various land masses by the filling of their niches with land plants, and diversification of groups of land plants.

Earliest classifiable plants

In the strictly modern sense, the name *plant* refers to the biological classification kingdom Plantae. However, other photosynthetic organisms, including protists, green algae, and cyanobacteria have evolutionary significance to modern plants. While here directly about the evolutionary history of the Plant kingdom, these other organisms provide clues to the evolution of all photosynthetic organisms. All of these organisms - plants, green algae, and the protists - are primary photosynthetic eukaryotic organisms.

Scientists start the search for fossil evidence of plants with indirect evidence for their presence, the evidence of photosynthesis in the geological record. The evidence for photosynthesis in the rock record is varied, but primary evidence comes from around 3000 Ma, in rock records and fossil evidence of cyanobacteria, photosynthesizing prokaryotic organisms. Cyanobacteria use water as a reducing agent, thereby producing atmospheric oxygen as a byproduct, and profoundly changing the early reducing atmosphere of the earth to one in which modern aerobic organisms eventually evolved. This oxygen liberated by cyanobacteria then oxidized dissolved iron in the oceans, the iron precipitated out of the sea water, and fell to the ocean floor to form sedimentary layers of oxidized iron called Banded Iron Formations (BIFs). These BIFs are part of the geological record of evidence for the evolutionary history of plants by identifying when photosynthesis originated. This also provides deep time constraints upon when enough oxygen could have been available in the atmosphere to produce the ultraviolet blocking stratospheric ozone layer. The oxygen concentration in the ancient atmosphere subsequently rose, acting as a poison for anaerobic organisms, and resulting in a highly oxidizing atmosphere, and opening up niches on land for occupation by aerobic organisms.

Evidence for the cyanobacteria also comes from the presence of stromatolites in the fossil record deep into the Precambrian. Stromatolites are layered structures thought to have been formed by the trapping, binding, and cementation of sedimentary grains by microorganisms, such as cyanobacteria. The direct evidence for cyanobacteria is less certain than the evidence for their presence as primary producers of atmospheric oxygen. Modern day stromatoloid structures containing cyanobacteria can be found on the west coast of Australia.

Chloroplasts in eukaryotic plants evolved from an endosymbiotic relationship between cyanobacteria and other prokaryotic organisms producing the lineage that eventually led to photosynthesizing eukaryotic organisms in marine and freshwater environments. These earliest photosynthesizing single-celled autotrophs later led to organisms such as Charophyta, a group of freshwater green algae.

Palæozoic flora

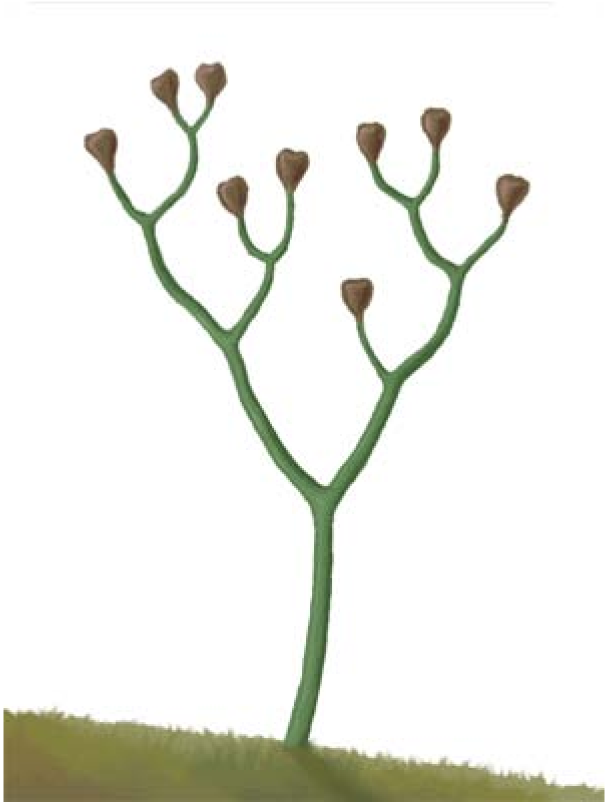
Cambrian flora

Early plants were small, unicellular or filamentous, composed mostly of soft body tissues, with simple branching. The identification of plant tissues in Cambrian strata is an uncertain area in the evolutionary history of plants because of the small and soft-bodied nature of these plants. It is also difficult in a fossil of this age to distinguish among various similar appearing groups with simple branching patterns, and not all of these groups are plants. One exception to the uncertainty of fossils from this age is the calcareous green algae, Dasycladales found in the fossil record since the middle Cambrian. This algae does not belong to the lineage that is ancestral to the land plants. Other major groups of green algae had been established by this time. Generally it is accepted that there were no land plants with vascular tissues at this time although some Biologists believe that the molecular clock points to an earlier Cambrian or perhaps Precambrian origin because the molecular clock states that land plants appeared around 480–440 Ma and fungi appeared on land around 1 Ga but however there is debate over whether the fossil evidence supports this interpretation of the molecular clock.

Ordovician flora

The evidence for plant evolutionary history changes dramatically in the Ordovician with the first extensive appearance of spores in the fossil record (Cambrian spores have been found, also). The first terrestrial plants appeared in the form of tiny plants resembling liverworts when, around the Middle Ordovician, evidence for the beginning of the terrestrialization of the land is found. These early plants did not have conducting tissues, severely limiting their size. They were, in effect, tied to wet terrestrial environments by their inability to conduct water, like extant liverworts, hornworts, and mosses, although they reproduced with spores, important dispersal units that have hard protective outer coatings, allowing for their preservation in the fossil record, in addition to protecting the future offspring against the desiccating environment of life on land. With spores, plants on land could have sent out large numbers of spores that could grow into an adult plant when sufficient environmental moisture was present.

Silurian flora



Artist's impression of *Cooksonia*

The first fossil records of vascular plants, that is, land plants with vascular tissues, appeared in the Silurian period. The earliest known representatives of this group are *Cooksonia* (mostly from the northern hemisphere) and *Baragwanathia* (from Australia). A primitive Silurian land plant with xylem and phloem but no differentiation in root, stem or leaf, was much-branched *Psilophyton*, reproducing by spores and breathing through stomata on every surface, and probably photosynthesizing in every tissue exposed to light. Rhyniophyta and primitive lycopods were other land plants that first appear during this period.

Devonian flora

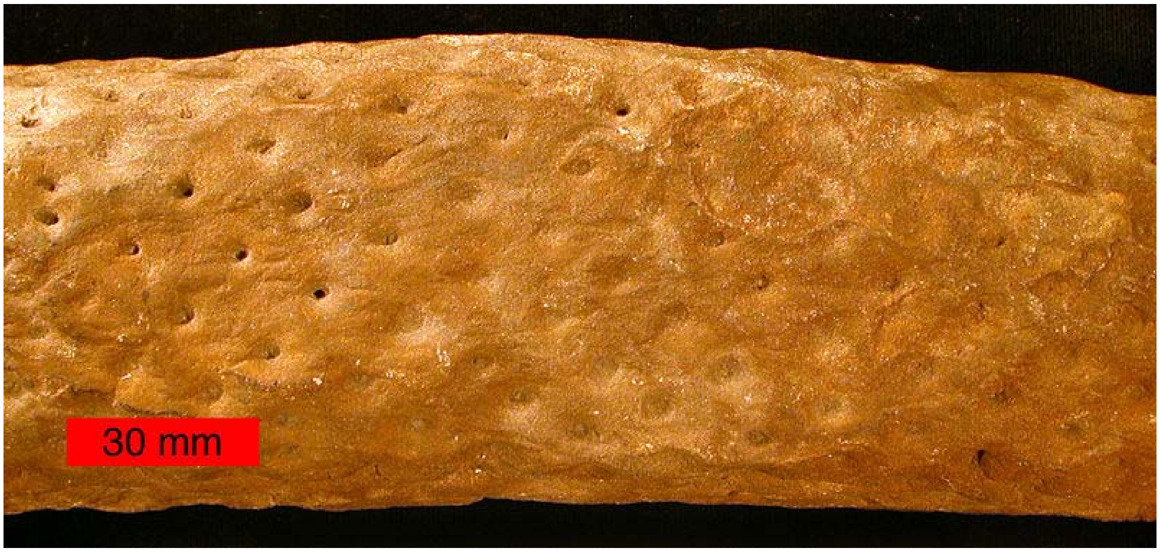
By the Devonian Period, life was well underway in its colonization of the land. The bacterial and algal mats were joined early in the period by primitive plants that created the first recognizable soils and harbored some arthropods like mites, scorpions and myriapods. Early Devonian plants did not have roots or leaves like the plants most common today, and many had no vascular tissue at all. They probably spread largely by vegetative growth, and did not grow much more than a few centimeters tall.

By the Late Devonian, forests of small, primitive plants existed: lycophytes, sphenophytes, ferns, and progymnosperms had evolved. Most of these plants have true roots and leaves, and many were quite tall. The tree-like ancestral fern *Archaeopteris* and the giant cladoxylopsid trees grew as a large tree with true wood. These are the oldest known trees of the world's first forests. Prototaxites was the fruiting body of an enormous fungus that stood more than 8 meter tall. By the end of the Devonian, the first seed-forming plants had appeared. This rapid appearance of so many plant groups and growth forms has been called the "Devonian Explosion". The primitive arthropods co-evolved with this diversified terrestrial vegetation structure. The evolving co-dependence of insects and seed-plants that characterizes a recognizably modern world had its genesis in the late Devonian. The development of soils and plant root systems probably led to changes in the speed and pattern of erosion and sediment deposition.

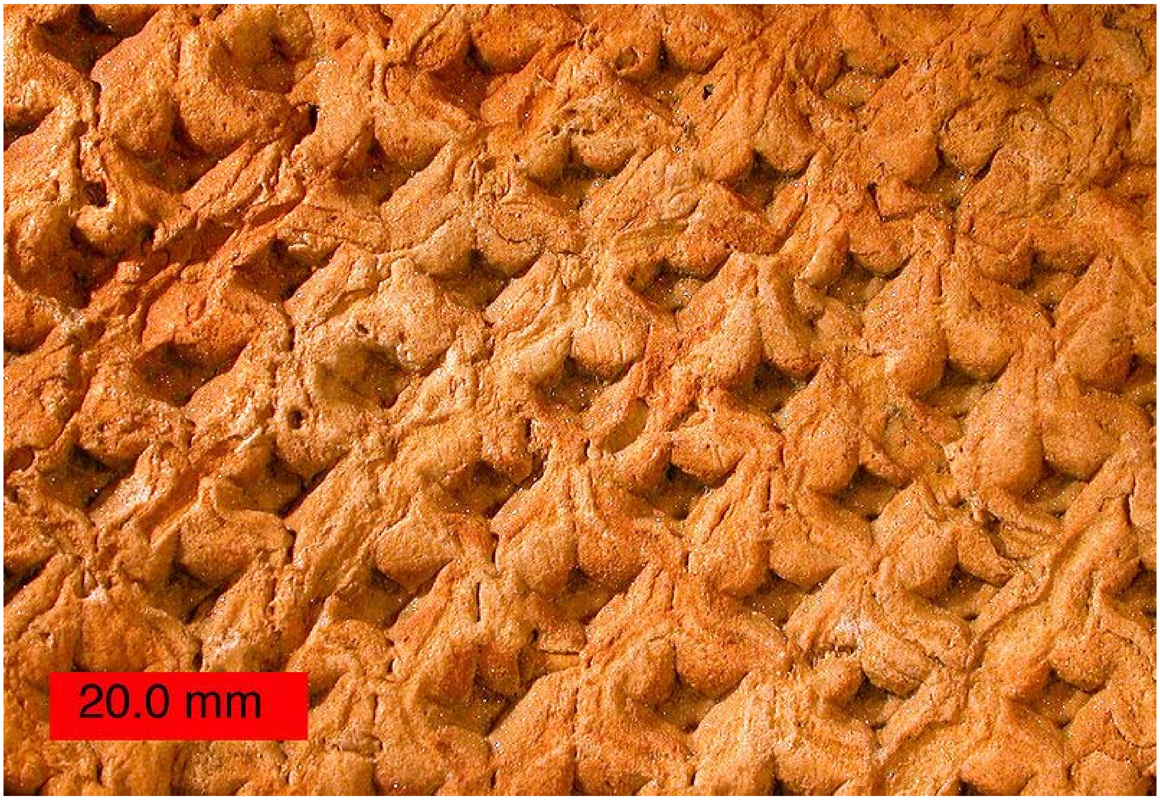
The 'greening' of the continents acted as a carbon dioxide sink, and atmospheric levels of this greenhouse gas may have dropped. This may have cooled the climate and led to a massive extinction event.

Also in the Devonian, both vertebrates and arthropods were solidly established on the land.

Carboniferous Flora



Stigmaria, a fossil tree root. Upper Carboniferous of northeastern Ohio.



External mold of *Lepidodendron* from the Upper Carboniferous of Ohio.

Early Carboniferous land plants were very similar to those of the preceding Latest Devonian, but new groups also appeared at this time.

The main Early Carboniferous plants were the Equisetales (Horse-tails), Sphenophyllales (scrambling plants), Lycopodiales (Club mosses), Lepidodendrales (scale trees), Filicales (Ferns), Medullosales (previously included in the "seed ferns", an artificial assemblage of a number of early gymnosperm groups) and the Cordaitales. These continued to dominate throughout the period, but during late Carboniferous, several other groups, Cycadophyta (cycads), the Callistophytales (another group of "seed ferns"), and the Voltziales (related to and sometimes included under the conifers), appeared.

The Carboniferous lycophytes of the order Lepidodendrales, which are cousins (but not ancestors) of the tiny club-moss of today, were huge trees with trunks 30 meters high and up to 1.5 meters in diameter. These included *Lepidodendron* (with its fruit cone called *Lepidostrobus*), *Halonia*, *Lepidophloios* and *Sigillaria*. The roots of several of these forms are known as *Stigmaria*.

The fronds of some Carboniferous ferns are almost identical with those of living species. Probably many species were epiphytic. Fossil ferns and "seed ferns" include *Pecopteris*, *Cyclopteris*, *Neuropteris*, *Alethopteris*, and *Sphenopteris*; *Megaphyton* and *Caulopteris* were tree ferns.

The Equisetales included the common giant form *Calamites*, with a trunk diameter of 30 to 60 cm and a height of up to 20 meters. *Sphenophyllum* was a slender climbing plant with whorls of leaves, which was probably related both to the calamites and the lycopods.

Cordaites, a tall plant (6 to over 30 meters) with strap-like leaves, was related to the cycads and conifers; the catkin-like inflorescence, which bore yew-like berries, is called *Cardiocarpus*. These plants were thought to live in swamps and mangroves. True coniferous trees (*Walchia*, of the order Voltziales) appear later in the Carboniferous, and preferred higher drier ground.

Permian flora

The Permian began with the Carboniferous flora still flourishing. About the middle of the Permian there was a major transition in vegetation. The swamp-loving lycopod trees of the Carboniferous, such as Lepidodendron and Sigillaria, were replaced by the more advanced conifers, which were better adapted to the changing climatic conditions. Lycopods and swamp forests still dominated the South China continent because it was an isolated continent and it sat near or at the equator. Oxygen levels were probably high there. The Permian saw the radiation of many important conifer groups, including the ancestors of many present-day families. The ginkgos and cycads also appeared during this period. Rich forests were present in many areas, with a diverse mix of plant groups. The gigantopterids thrived during this time; some of these may have been part of the ancestral flowering plant lineage, though flowers evolved only considerably later.

Mesozoic flora

Triassic flora

On land, the holdover plants included the lycophytes, the dominant cycads, ginkgophyta (represented in modern times by *Ginkgo biloba*) and glossopterids. The spermatophytes, or seed plants came to dominate the terrestrial flora: in the northern hemisphere, conifers flourished. *Glossopteris* (a seed fern) was the dominant southern hemisphere tree during the Early Triassic period.

Jurassic flora

The arid, continental conditions characteristic of the Triassic steadily eased during the Jurassic period, especially at higher latitudes; the warm, humid climate allowed lush jungles to cover much of the landscape. Conifers dominated the flora, as during the Triassic; they were the most diverse group and constituted the majority of large trees. Extant conifer families that flourished during the Jurassic included the Araucariaceae, Cephalotaxaceae, Pinaceae, Podocarpaceae, Taxaceae and Taxodiaceae. The extinct

Mesozoic conifer family Cheirolepidiaceae dominated low latitude vegetation, as did the shrubby Bennettitales. Cycads were also common, as were ginkgos and tree ferns in the forest. Smaller ferns were probably the dominant undergrowth. Caytoniaceous seed ferns were another group of important plants during this time and are thought to have been shrub to small-tree sized. Ginkgo-like plants were particularly common in the mid- to high northern latitudes. In the Southern Hemisphere, podocarps were especially successful, while Ginkgos and Czekanowskiales were rare.

Cretaceous flora

Artist's restoration of *Archaeamphora longicervia*, the earliest known carnivorous plant

Flowering plants, also known as angiosperms, spread during this period, although they did not become predominant until near the end of the period (Campanian age). Their evolution was aided by the appearance of bees; in fact angiosperms and insects are a good example of coevolution. The first representatives of many modern trees, including figs, planes and magnolias, appeared in the Cretaceous. At the same time, some earlier Mesozoic gymnosperms, like Conifers continued to thrive, although other taxa like Bennettitales died out before the end of the period.

Cenozoic flora

The Cenozoic is just as much the age of savannas, or the age of co-dependent flowering plants and insects. At 35 Ma, grasses evolved from among the angiosperms. About ten thousand years ago, humans in the Fertile Crescent of the Middle East develop agriculture. Plant domestication begins with cultivation of Neolithic founder crops. This process of food production, coupled later with the domestication of animals caused a massive increase in human population that has continued to the present. In Jericho (modern Israel), there is a settlement with about 19,000 people. At the same time, Sahara is green with rivers, lakes, cattles, crocodiles and monsoons. At 8 ka, Common (Bread) wheat (*Triticum aestivum*) originates in southwest Asia due to hybridisation of emmer wheat with a goat-grass, *Aegilops tauschii*. At 6.5 ka, two rice species are domesticated: Asian rice, *Oryza sativa*, and African rice *Oryza glaberrima*.

Species Differentiation

- Development of rooted plants
- Flowering plants vs. Conifers
- Ferns and other primitive plants
- Borderline species such as coliform protists