

Q1 EARLY EVOLUTION OF VASCULAR PLANTS

Key Notes

The earliest vascular plants	Earliest fossils of vascular plants, <i>Cooksonia</i> , occur in late Silurian rocks. It had photosynthetic stems but no leaves or roots; only rhizoids anchored to soil. <i>Cooksonia</i> had no stomata. By the early Devonian period, several genera are known. They were low growing plants less than 50 cm high bearing sporangia at the tips (Rhyniopsida), laterally (Zosterophyllopsida) or in bunches (Trimerophytopsida).
Life cycle	Most were probably homosporous. Gametophytes are little known, but some probable gametophyte fossils resemble the sporophytes with cup-like structures at the tips bearing archegonia and antheridia.
Later developments	There was rapid diversification through the Devonian era with developments of monopodial branching and trees belonging to the ferns and other living groups.
Origins and evolution	Compared with an aquatic environment, land plants need to withstand changes in temperature and humidity, wind, rain and desiccation. They need a conducting system for water and nutrients, and mechanical strength. Reproduction must be possible in the air or on a damp soil surface. Most of them probably formed swards a few centimeters high.
Related topics	The bryophytes (P3) Clubmosses and horsetails (Q2) The ferns (Q3)

The earliest vascular plants

Vascular plants probably first appeared in the Silurian era (Table 1). The oldest fossils are those of *Cooksonia* (Fig. 1) in the Rhyniopsida from late Silurian rocks, a little over 400 million years old. Fossils of *Cooksonia* have been found in several places in Europe and North America. These plants had photosynthetic stems up to about 10 cm high that branched **dichotomously**, i.e. into two even branches at each point, but no leaves or roots. Some had **rhizomes**, horizontal underground stems, and subterranean rhizoids, short outgrowths from the rhizomes or stems one cell thick, that may have absorbed water and anchored the plant. The earliest *Cooksonia* fossil species had no stomata and had a simple vascular system with tracheids. The carbon dioxide concentration in the atmosphere was higher than at present and these plants may have obtained sufficient carbon dioxide through diffusion into its stems, or may have absorbed it from the ground through its rhizoids, like living quillworts (Topic Q2). They had sporangia at the branch tips.

At the beginning of the Devonian period, about 395 million years ago, a slightly more complex fossil plant, *Zosterophyllum* (Fig. 2) is found. In slightly younger rocks several genera are known, the most famous being the beautifully

Table 1. Approximate time scale of first appearance of major vascular plant groups in the fossil record

Period	Millions of years ago (start)	Spore-bearing plants other than ferns	Ferns	Seed plants
Present day	1			
Tertiary	65			
Cretaceous	145		Leptosporangiate ferns	Gnetopsida; dicotyledons, monocotyledons
Jurassic	205			Earliest flowering plants?
Triassic	250			Caytoniales ^a , Bennettitales ^a
Permian	290			Ginkgoales
Carboniferous	360	Tree and heterosporous Lycopsidea; tree Equisetopsida	Heterosporous ferns	Cycads Conifers Cordaitales ^a (perhaps earlier)
Devonian	410	Homosporous Lycopsidea and Equisetopsida; progymnosperms ^a other Rhyniopsida ^a , etc.	Eusporangiate ferns (including tree ferns)	Pteridosperms ^a
Silurian	440	<i>Cooksonia</i> ^a (end Silurian); earliest vascular plants?		
Ordovician	500			
Cambrian	570			

^a Extinct groups.

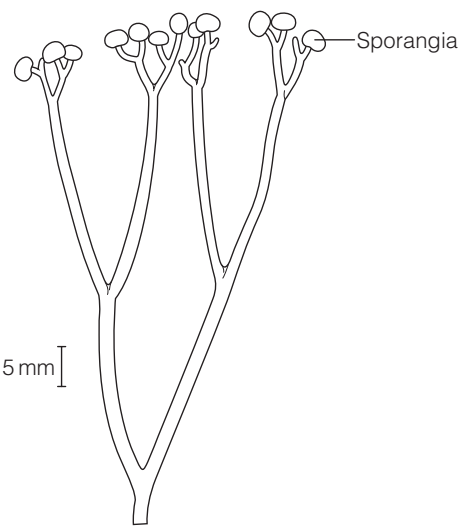


Fig. 1. The earliest known fossil vascular plant, *Cooksonia*.

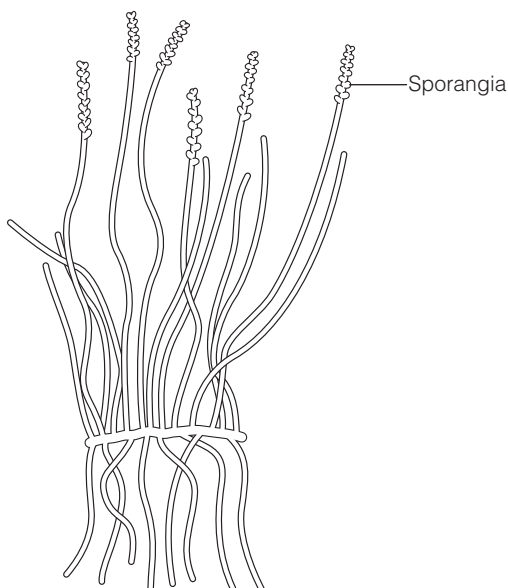


Fig. 2. *Zosterophyllum* (*Zosterophyllopsida*), showing terminal spikes of sporangia.

preserved fossils in siliceous cherts from Rhynie in Scotland, from which the group name, Rhyniopsida, derives (Table 1). Rocks of a similar age from several places, mainly in Europe, have fossils of these and related plants. These plants were more varied and complex, though *Rhynia* itself resembled *Cooksonia* in many ways. All the later plants did have stomata and the potential for gas exchange in the stems. The attachment of these plants to the ground was by means of horizontal or arching rhizomes or a swollen corm-like section of the stem; thin, thread-like rhizoids grew out from these to penetrate the substrate and absorb water and nutrients.

Zosterophyllum had lateral sporangia and some members of the *Zosterophyllopsida* had spine-like outgrowths of the stem resembling tiny leaves, but without any vascular connection with the stem. A third group, the *Trimerophytopsida* (Fig. 3), had a single main branch with side branches, i.e. were **monopodial**, with sporangia in terminal bunches.

Life cycle

Most of the fossil remains of these early vascular plants are of sporophyte plants. There appear to have been no dehiscence mechanisms in the sporangia of *Cooksonia* and some others, though some plants had epidermal cells aligned in spirals, possibly associated with dehiscence. As far as is known most of these plants were **homosporous**, i.e. producing just one type of spore. In living homosporous plants the spores germinate and grow into a gametophyte bearing male and female gametes. A few Devonian *Zosterophyllopsida* bore two sizes of spores and these plants could have been **heterosporous**. Living heterosporous plants bear spores that develop into gametophytes with either male gametes or female gametes but not both. Male gametophytes normally derive from smaller spores than female gametophytes. There is no evidence apart from this for heterospory in these plant groups.

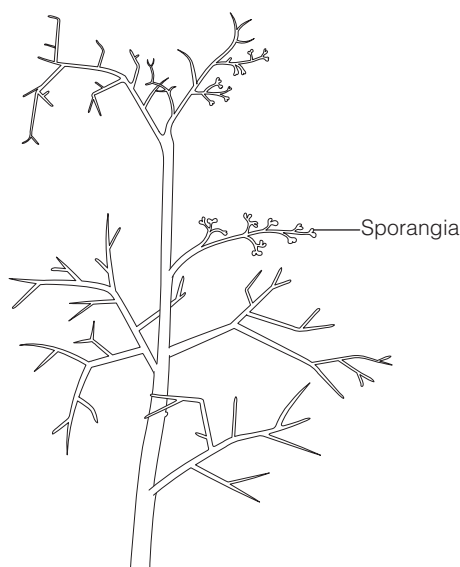


Fig. 3. *Psilophyton* (*Trimerophytopsida*), showing lateral clumps of sporangia.

Gametophytes from these plants are not well known, but some plants that were probably gametophytes were upright, branched structures resembling a sporophyte. Structures resembling archegonia and antheridia were borne in cup-like structures on the tops of the stems, some of which were lobed (Fig. 4). It is likely that rain splashes dispersed the sperm, perhaps often to neighboring archegonia effecting self-fertilization. In many ways the fertile cup-shaped structures must have resembled the 'inflorescences' of some mosses (Topic P4) in habit and function. It also suggests that in some, at least, of these early plants, the alternation of generations may have been **isomorphic**, i.e. between a sporophyte and a gametophyte that resembled each other, as in some algae. If other gametophytes were small and growing on the soil surface, as in living relatives of these plants, it is likely that preservation will be poor. The early evolution of gametophytes remains unknown.

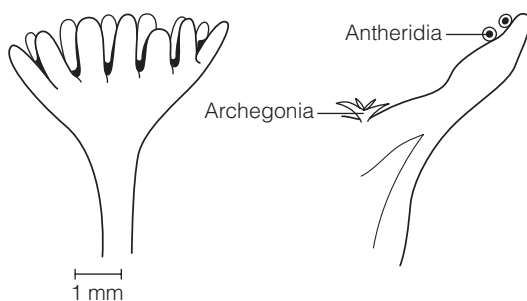


Fig. 4. Tip of stem of a gametophyte, *Lyonophyton*, showing probable antheridia and archegonia. (Redrawn from Stewart and Rothwell (1993). *Paleobotany and the Evolution of Plants*, 2nd Edn. Cambridge University Press.)

Later developments

Increasing numbers of fossil plants appear in rocks of the Devonian era, 410–360 million years ago, suggesting that land plants diversified rapidly during this period (*Table 1*). These fossils include many short herbaceous species like those already described, and some shrubby ones with elaborate rhizome systems. Plants became taller, with monopodial branching and, by the end of the Devonian there were many trees. These mainly belonged to groups with living members, the Lycopsidea, Equisetopsida and Polypodiopsida (ferns).

Origins and evolution

Vascular plants have many similarities with green algae (Chlorophyta; Topic P2), and probably evolved from them. The land provides a different and harsher environment compared with the aquatic or semi-aquatic environment that the algae occupied. Plants on land must be able to withstand large changes in temperature and humidity, wind and rain, and have some means of withstanding desiccation. They need a conducting system throughout the plant for water and nutrients, some structure in the ground to anchor and absorb water and a mechanically strong body. They also need reproductive structures that do not require water. Add to this the fact that the organic component in soils, vital for its nutrient cycling, must have been limited in development with so few land-living organisms.

Land plants are adapted to a low sodium environment and osmoregulate using potassium (K^+), sodium being toxic (Topic I4). Their evolution from marine organisms would require major changes in ion transporters at the cellular level. It is possible that they colonized the land via brackish or fresh water.

Many of the problems mentioned above are eased by small size, and the earliest land plants were no more than about 50 cm high. On the soil surface the environment will be fairly wet, at least after rain, and some aspects of the lives of these plants, particularly sexual reproduction, probably took place there. Sexual reproduction involves motile sperms which need a damp substrate for the sperms to swim in; modern ferns and other spore-bearing plants still have this requirement for sexual reproduction. There is some evidence that these plants mainly occurred in wet environments, perhaps forming swards about 10–20 cm high.

Q2 CLUBMOSES AND HORSETAILS

Key Notes

Vegetative structure of Lycopsidea

There are three groups of living clubmosses and quillworts, comprising about 1000 herbaceous species distributed world-wide. Clubmosses are terrestrial or epiphytic, and the quillworts aquatic. The clubmosses have branched stems with microphyll leaves, roots and, in *Selaginella*, rhizophores; the quillworts have a basal corm and long microphylls.

Reproduction in Lycopsidea

Sporangia are produced in leaf axils, often in separate strobili with small leaves. *Lycopodium* and its relatives are homosporous but *Selaginella* and *Isoetes* heterosporous. Microspores may be very numerous in the sporangia but only four or a small number of megaspores are present in *Selaginella*, and up to one hundred in *Isoetes*.

Gametophyte of Lycopsidea

Homosporous species have green or subterranean gametophytes, sometimes long-lived. Heterosporous species have reduced gametophytes contained within the sporangial wall. Female gametophytes may be dispersed after fertilization.

Fossil Lycopsidea

Fossils go back to Devonian times, similar to current living members, particularly *Selaginella*. Heterosporous trees occur in Carboniferous rocks and they were important constituents of coal.

Vegetative structure of Equisetopsida

There are about 20 species of horsetails, world-wide in distribution. All are herbaceous but can reach 10 m. They have a jointed, ribbed stem with microphylls and whorls of branches and extensive rhizome and root systems. Silica is deposited giving them their roughness.

Reproduction in Equisetopsida

Strobili are produced at the ends of shoots, with sporangia at the branch tips. All are homosporous, the spores with elaters.

Gametophyte of Equisetopsida

These are green structures on the soil surface that may bear only antheridia or only archegonia, but archegonial ones produce antheridia as they age.

Fossil Equisetopsida

The earliest fossils come from the Devonian period, and some Carboniferous fossils resemble *Equisetum*. Others are trees up to 20 m tall, some heterosporous.

Related topics

Early evolution of vascular plants (Q1)

Vegetative structure of Lycopsidea

The Lycopsidea or lycopods today consist of about 1000 species of small non-woody plants known as **clubmosses** and **quillworts**, occurring throughout the world. They are mainly terrestrial, and one of the two groups of clubmosses, *Selaginella*

species, can be abundant on the floor of tropical forests. Some are epiphytic while others occur in temperate mountains extending into the Arctic. The Isoetales (quillworts) are mainly aquatic plants. They have no particular human uses.

The living clubmosses (Fig. 1) have a shoot system that branches, often dichotomously, but sometimes with a main stem and side branches. These stems have a central vascular system with no pith and are covered with **microphyll** leaves. Microphylls (literally ‘small leaves’) are generally small, a few millimeters in length, and characterized by a single vascular strand through the middle. There is no gap in the conducting system of the stem where the leaf branches off. By contrast, the leaves of most other vascular plants, known as **megaphylls**, have a network of vascular strands (Topic C5) and there is a gap in the stem vascular system where the leaf branches off.

Rhizomes may be present and roots (Topic D2) branch from them. The roots branch dichotomously and regularly. In *Selaginella*, the roots branch from a curious structure intermediate between stems and roots, called a **rhizophore**. These arise at angles in a stem and are unbranched, often aerial, but form roots when they touch the ground. They may represent a stage at which stems and roots were not fully differentiated.

The quillworts have only a basal **corm**, a short (about 1 cm) swollen stem or rootstock, which can show limited secondary growth (Topic C4) and from which arises a rosette of remarkably long microphylls, often 10 cm or longer, and rhizoids, which, between them, completely conceal the corm. They closely resemble rosettes of aquatic flowering plants with which they often grow and do not resemble the clubmosses.

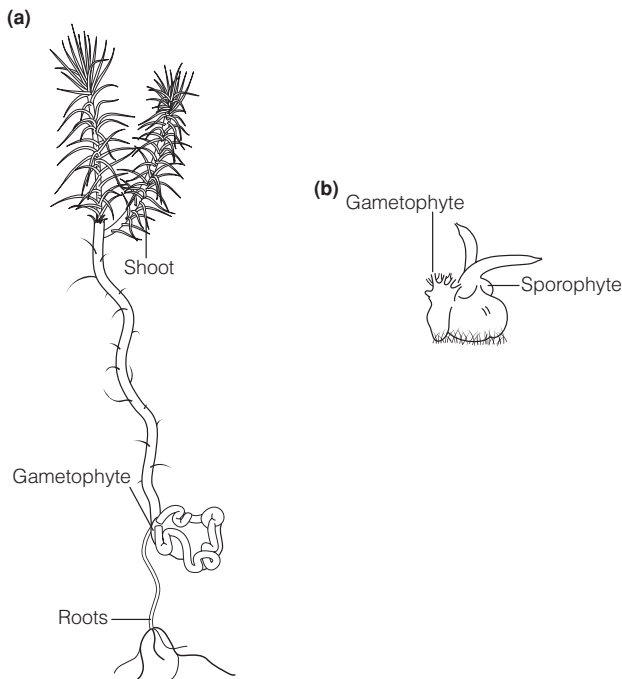


Fig. 1. A clubmoss, *Lycopodium*, showing subterranean gametophyte and sporophyte growing from it. (Redrawn from Foster AS and Gifford EM (1974) Comparative Morphology of Vascular Plants, 2nd edn. WH Freeman.)

Reproduction in Lycopsidea

One group of Lycopsidea, including about 200 species of *Lycopodium* and its relatives, is **homosporous**; the other two groups, *Selaginella* (about 700 species) and *Isoetes* (about 70 species) are **heterosporous** (Topic Q1). In all groups the sporangia are produced singly in the axils of leaves. In a few homosporous species there are fertile sections of the stem but in most there are separate **strobili** (singular strobilus). These consist of specialized scale-like microphylls with a different morphology from the vegetative leaves, often raised above the main stem. Nearly all *Selaginella* species have strobili and in *Isoetes* all leaves may bear sporangia.

The sporangium is normally 1–2 mm across, though larger in *Isoetes*. The sporangium consists of a wall, initially of several cell layers, though the inner layers break down as the spores mature. It dehisces along a line of thin-walled cells. In the heterosporous groups, strobili may contain a mixture of male sporangia and female sporangia, often with female at the base, or bear them in separate strobili. In the male sporangia, or **microsporangia**, there are numerous **microspores**, in *Isoetes* possibly as many as one million. In **megasporeangia** of *Selaginella* there is usually one spore mother cell undergoing meiosis to produce four **megaspores**, though a few species may produce eight or more. In *Isoetes* more than 100 megaspores are produced in each sporangium.

Gametophyte of Lycopsidea

In homosporous forms two types of gametophyte are known, both independent multicellular structures (Fig. 1). One type is cylindrical to 3 mm long and grows near the soil surface, becoming green and branched in the light, with sex organs, usually mixed, at the base of the branches. It lives for up to 1 year. The second type is subterranean or epiphytic and may live for 10 years before reaching 2 cm in length. It is oblong, disc-like or branched and antheridia are produced first in the center, while archegonia are produced later towards the edge. All are infected with fungi that occupy a defined place and are essential for nutrition of the gametophyte and act as mycorrhizae do in angiosperms (Topic M1).

In heterosporous groups the gametophyte is much reduced and develops entirely within the spore wall, beginning development before leaving the sporangium. In microspores the first cell division leads to one vegetative cell known as the **prothallus** cell, and a second cell which divides to form the antheridium. The antheridium consists of a sterile jacket, but this and the prothallus cell disintegrate at maturity. In *Selaginella* biflagellate sperms, usually 128 or 256, all contained within the spore, are produced; in *Isoetes* just four multiflagellate sperms are produced. By this time the microspore has dispersed. The spore wall ruptures to release the sperms. In the megaspore, a gametophyte of many cells grows and the spore wall ruptures. Archegonia similar to those of bryophytes (Topic P4) grow by the break. Dispersal of the female gametophyte occurs at different times in different species but in a few species it is retained until after fertilization and the embryo is growing.

Fossil Lycopsidea

The clubmosses and quillworts are living remnants of a once much larger group with a rich fossil record including trees in late Devonian and Carboniferous times. Fossil lycopods are known from the early Devonian period onwards. Devonian lycopods mostly resembled living homosporous clubmosses like *Lycopodium*, being herbaceous and most with dichotomous branching. Sporangia were sometimes stalked and borne on the leaves. By the Carboniferous period, herbaceous plants clearly seen to be heterosporous appear, and so closely resemble *Selaginella* that they are placed in the same genus.

The best known fossil lycopods were trees, measuring ≥ 30 m. They are common fossils, beautifully preserved from the Carboniferous period in Britain and North America, and are important constituents of coal. They can be ascribed to the genus *Lepidodendron* which had a long unbranched trunk with dichotomous branching at its tip (Fig. 2). Strobili were produced at the branch ends and these were heterosporous. Microsporangia and megasporangia were similar to those of living heterosporous lycopods and the gametophytes were enclosed within the spore wall. In at least one species only one megaspore was produced within the sporangium and the whole structure was enclosed by a leaf-like outgrowth, to be dispersed together.

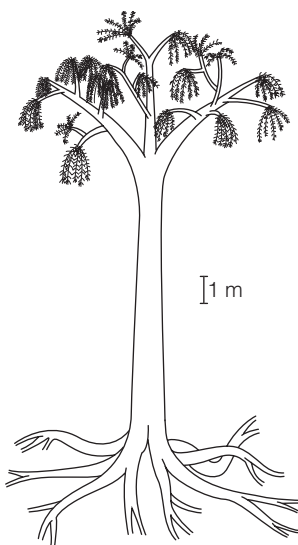


Fig. 2. Reconstruction of fossil lycopoid *Lepidodendron*, from Carboniferous rocks.

Vegetative structure of Equisetopsida

There is only one living genus and about 20 species in the Equisetopsida, known as **horsetails**, *Equisetum*. They are herbaceous perennial plants, mostly up to 1 m in height, world-wide in distribution, but mostly in the northern temperate region where they are quite common. South and Central American species are taller, reaching 10 m, and in these the shoots are perennial. In the smaller northern plants, only the below-ground parts survive the winter.

The living horsetails have a characteristic rough jointed stem (Fig. 3). This is ribbed, with scale-like microphyll leaves at the joints where they readily come apart. Most species have whorls of side branches from the main stem. They have an extensive rhizome system, the rhizomes being similar to the above-ground stem with nodes from which roots arise. This allows horsetails to colonize large patches, and their ability to regrow from a fragment of rhizome means they can be pernicious weeds. The stems have extensive deposits of silica along their length which gives them their rough texture, and their alternative name, 'scouring rushes', refers to the use of some as scourers. Growth abnormalities, such as no internodes or no side branches or dichotomous branching, are frequent in horsetails and this suggests that their growth regulation is poor.

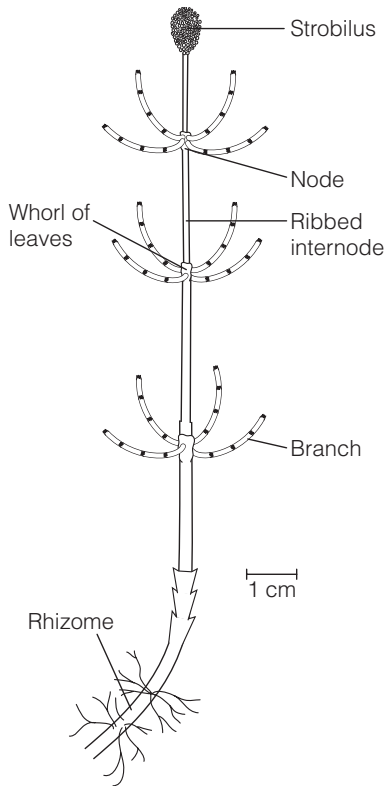


Fig. 3. A horsetail, *Equisetum*, showing vegetative shoot with terminal strobilus.

Reproduction in *Equisetopsida*

Sporangia are produced in strobili at the tip of either a vegetative shoot or a distinct, brownish fertile shoot (Fig. 3). The strobilus has short side branches each with an umbrella-shaped tip bearing 5–10 sporangia on the underside (Fig. 4), similar in structure to those of *Lycopsida*. The **spores** are unusual in that they contain chloroplasts and, at maturity, have four **elaters** (Fig. 4). These are short band-like structures with a spoon-shaped tip that coil around the spore at high humidity and uncoil as they dry, aiding dispersal. All horsetails are homosporous.

Gametophyte of *Equisetopsida*

Although the spores are apparently all identical in horsetails, gametophytes show a partial division of the sexes. They are green structures on a damp soil surface, with a colorless base and a much branched upper part, though they remain <1 cm long. Gametophytes may produce antheridia or archegonia or both, any archegonial plants usually producing antheridia as they get older. The determination of sex seems to be at least partly environmental, and is flexible. The antheridia have a two-layered jacket and produce multi-flagellate sperm; the archegonia are similar to those of bryophytes (Topic P4).

Fossil *Equisetopsida*

The fossil history of the group is rich, with the earliest fossils dating from the Devonian period where rhizomatous herbaceous plants with forked leaves and divided sporangial branches are known. In the Carboniferous other fossils appear, varied in the structure of their strobili, including climbing plants and a

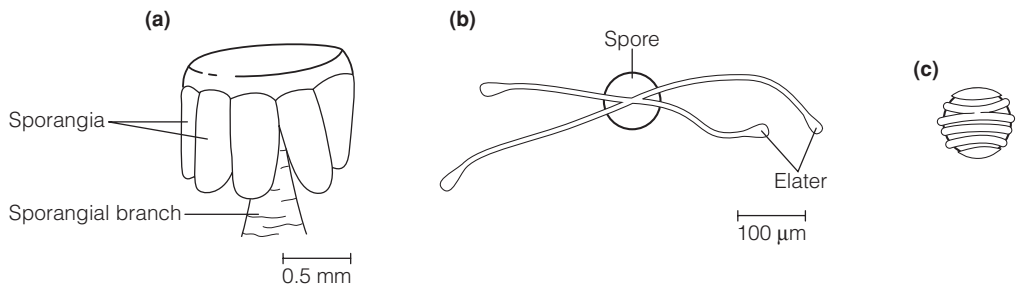


Fig. 4 (a) A branch of the strobilus of a horsetail showing sporangia; (b, c) a spore with attached elaters in dry (b) and moist (c) conditions.

fossil closely resembling *Equisetum* itself, so this may be an ancient genus. The best known fossil Equisetopsids, also from the Carboniferous period, were large trees forming an important constituent of coal, *Calamites* and its relatives.

Calamites (Fig. 5) grew to approximately 20 m in height but had many features similar to those of living horsetails. They had jointed ribbed stems, extensive branching and scale-like leaves, though these were often bigger than those of living horsetails. There was an underground rhizome system from which trunks grew and it is likely that these trees formed large patches. The stems had a large central pith but secondary thickening was extensive outside this. Strobili were borne on the side branches rather than at the tips but varied in structure, some having leaf-like bracts by each sporangium, and some clearly showing true heterospory with two different sizes of sporangium. Some species retained the megaspores in their sporangia on the parent plant to be dispersed as a unit.

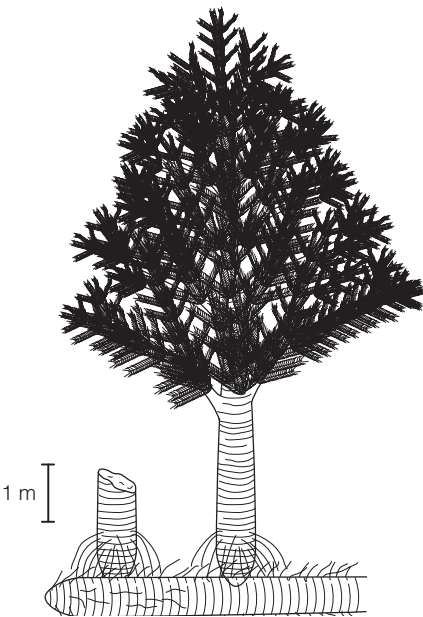


Fig. 5. Reconstruction of Carboniferous member of the Equisetopsida, *Calamites*.

Q3 THE FERNS

Key Notes

General characteristics

Ferns are a large group of plants occurring throughout the world. Most have rhizomes with roots and some have a trunk. Leaves are typically large and pinnate derived from a branch system. A few ferns have a eusporangium similar to those of other spore-bearing plants, but most have a leptosporangium with explosive dehiscence, dispersing the spores. They are homosporous except for one small group.

Eusporangiate ferns

Three small groups, the adderstongues, Marattiaceae and whisk-ferns, are eusporangiate. Adderstongues are small, do not resemble typical ferns and usually have two branches, one bearing the large sporangia. Marattiaceae resemble typical ferns except in the sporangia. Whisk-ferns have no roots or leaves and resemble the earliest vascular plants.

Typical leptosporangiate ferns

These have a stem, usually a rhizome, and roots with no secondary thickening. Leaves are often large and pinnate but may be simple or one cell thick. Sporangia are borne in sori on the underside of leaves or on reproductive leaves separate from the vegetative leaves.

Water ferns

Two small groups of ferns are aquatic, the Marsileaceae on mud and Salviniaceae that float. They are small heterosporous plants and do not resemble typical ferns. Sporangia are on separate branches and do not dehisce. Megaspores usually contain one spore.

The gametophyte

Typical ferns have a green prothallus 1 cm across on damp soil, bearing antheridia and archegonia on its underside. It has rhizoids. Eusporangiate ferns have larger longer-lived prothalli, some being subterranean. The heterosporous ferns have much reduced gametophytes retained within the spore wall.

Ecology of ferns

Though often common they do not dominate, except for bracken. They are mainly found in dense shade in woods or rocky crevices and as pioneers of gaps in rainforest and as epiphytes. Bracken can cover moorland through vegetative growth.

Fossil ferns

Many fossils are known from the mid-Devonian period onwards. They resemble modern ferns, and tree ferns are common in coal. Only eusporangiate ferns are known until the Cretaceous period. Heterospory is known from the Carboniferous period onwards.

Ferns and man

Bracken was formerly used as bedding and kindling, and young shoots of ferns are eaten, although some are carcinogenic. The main use now is ornamental.

Related topics

Early evolution of vascular plants (Q1) Evolution of the seed (Q4)
Clubmosses and horsetails (Q2)

General characteristics

The ferns are a numerous and important group of vascular plants, with about 12 000 species growing throughout the world. They range from small epiphytes to tree ferns 20 m high to floating aquatics. Many ferns have a perennial rhizome, either underground or growing along a branch if epiphytic, with roots attached. Characteristically, ferns have large **pinnate** leaves, i.e. with numerous leaflets, but some have simple leaves and there is a great range in size. The leaves are regarded as flattened and fused branch systems that have become determinate in their growth, i.e. without stem buds, so they cannot continue growing (a few climbing ferns have stem buds in their leaves and these are indeterminate in their growth). This type of leaf has a fundamentally different origin from the microphylls of clubmosses and horsetails and they are known as **megaphylls** (Topic Q2). The conducting system is typical of vascular plants (Topic C3), with the xylem cells being only tracheids except in bracken and some of the water ferns in which there are vessels, perhaps independently evolved from those of flowering plants but almost identical in structure.

The ferns are divided into two main groups based on their sporangia. One group has sporangia similar to those of the clubmosses and horsetails (Topic Q2), known as **eusporangia**. In these, several initial cells form the sporangium and this develops a wall several cells thick. One or more of the cell layers disintegrates to form nutritive tissue for the developing spores. There is a line of weaker cells in the wall which splits to allow spores to be dispersed in the wind. The second type, the **leptosporangium**, is peculiar to the ferns (Fig. 1). It arises from a single initial cell and the mature sporangium always has a wall one cell thick, all other cells disintegrating as the spores mature. The number of spores is always less than in a typical eusporangium, normally 64 or fewer. There is an incomplete ring of cells in the sporangial wall which has a thin cell wall on the outside and thickened inner walls. On drying out at maturity, the thin sections of the cell wall are sucked in and the thickened walls drawn towards each other. This leads to a split in the part of the sporangial wall not covered by the ring of cells and the ring becoming inverted. Considerable tension builds up which eventually leads to a loss of cohesion in the water molecules in the cell; the water then becomes gaseous leading to a sudden release of tension and an explosive return of the sporangium to its original position. Spores are ejected in

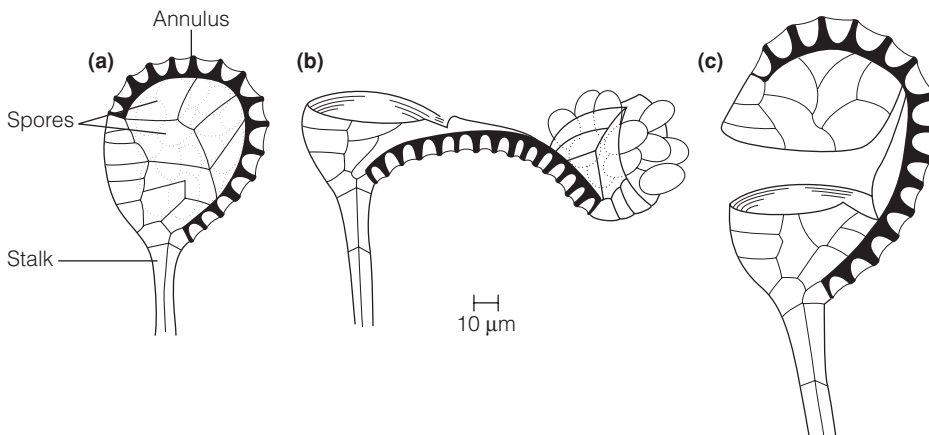


Fig. 1. A leptosporangium. (a) Before dehiscence; (b) drying out; (c) after dehiscence.

the process. The ring of thick-walled cells is at one end of the sporangial wall in some ferns, in others obliquely or transversely positioned. A few ferns, such as the royal ferns, are intermediate between eusporangiate and leptosporangiate types.

All eusporangiate and most leptosporangiate ferns are homosporous but two small groups of leptosporangiate ferns are heterosporous.

Eusporangiate ferns

There are three small groups of eusporangiate ferns: the adderstongues and moonworts, the tropical Marattiaceae and the whisk-fern, *Psilotum*, and its relatives. The **adderstongue** group consists of small, rather insignificant, plants that do not resemble normal ferns but have one vegetative and one fertile leaf (occasionally more), possibly the remains of a dichotomously branching stem (Fig. 2). The large eusporangia are borne in lines on the fertile leaf, each dehiscing with a slit at the tip to produce 2000 or more spores. They are regarded as a remnant of an ancient group of ferns and one of their most peculiar features is the large number of chromosomes, presumably derived from high polyploidy. One species of adderstongue, *Ophioglossum reticulatum*, has approximately 1260 chromosomes, the largest number known for any living organism. The **Marattiaceae** closely resemble typical ferns in their large pinnate leaves with sporangia on the lower surface. The sporangia are typical eusporangia, large with numerous spores and dehiscing by a slit at the tip.

The **whisk-fern** group consists of two genera, *Psilotum* (Fig. 3) and *Tmesipteris*, of such simple vegetative construction that they resemble fossils of some of the first vascular land plants (Topic Q1), and were long thought to be related to them, though with no intermediate fossil record. They are regarded as ferns owing to their resemblance to some southern hemisphere ferns. They have branched stems, dichotomous in *Psilotum* and with flattened side branches in *Tmesipteris*, a branched rhizome but no leaves or roots. The sporangia are large and, in *Psilotum*, three are fused together at each point, associated with a small scale.

Typical leptosporangiate ferns

Typical ferns are leptosporangiate and **homosporous** (Topic Q2) and are by far the largest and most familiar group of ferns (Fig. 4). The stem is usually an underground or epiphytic rhizome and most produce leaves only at their tip. A few have a branching rhizome, like bracken and, in tree ferns, the stem is a trunk. This trunk has no secondary thickening and often is of a similar width throughout its length, although they frequently have dead roots near the base of the trunk forming a 'skirt'. Many fern leaves are large and pinnate but others are simple, as

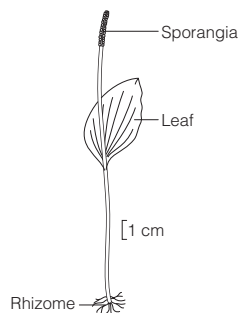


Fig. 2. An adderstongue, *Ophioglossum*.

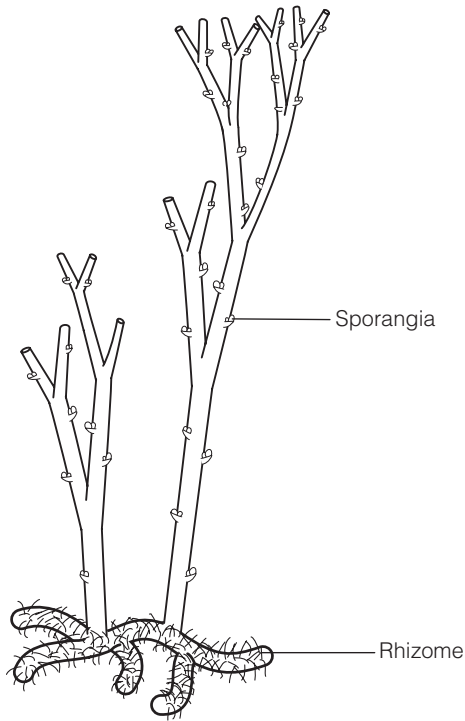


Fig. 3. A whisk-fern, *Psilotum*.

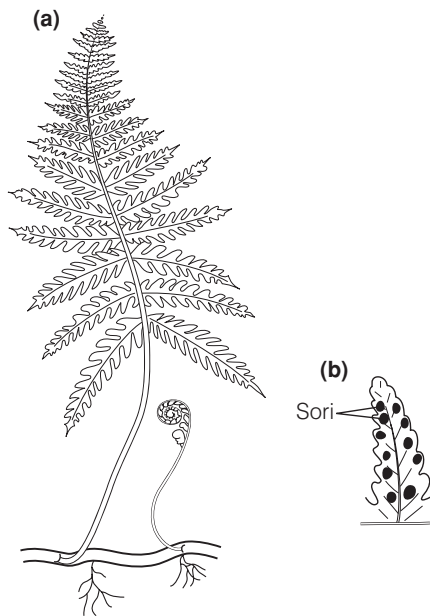


Fig. 4. A typical leptosporangiate fern, *Phegopteris*. (a) Leaf with developing leaf; (b) under-side of leaflet showing sori.

in the British hartstongue and the tropical birdsnest fern (both *Asplenium*) and some tropical climbing ferns have branched leaves of indeterminate growth. In the filmy ferns, *Hymenophyllum*, the leaf is one cell thick, as in mosses. Simple leaves are regarded as derived from pinnate leaves. Fern leaves unfurl from a tight spiral giving the characteristic ‘fiddle’ heads (Fig. 4).

In many ferns, all leaves are similar and these may bear sporangia, usually on the underside in groups known as **sori** (singular sorus) (Fig. 4) that, in some species, are covered by a protective flap from the leaf, the **indusium**. Some ferns have separate fertile leaves of a different shape, usually with narrower segments and sometimes with the lamina much reduced.

Water ferns

The aquatic ferns do not resemble typical ferns and are the only **heterosporous** ferns. Members of one of the two families, the Marsileaceae, have a rhizome submerged or in mud and aerial leaves a few centimeters high resembling clover with two or four leaves, or grass. The sporangia derive from one cell, so are leptosporangiate but have no specialized dispersal. They are borne on separate short stems in a hard oblong or spherical body a few millimeters long covered with rough hairs, the ‘pills’ of the pillwort (*Pilularia*; Fig. 5). They produce sori inside these, each sorus bearing both megasporangia and microsporangia. Only one spore matures in each megasporangium. Spores are released into water.

The two genera of floating water ferns are not attached to a substrate and both spread vegetatively in a similar way to other floating flowering plants. *Salvinia* (Fig. 6) has whorls of three simple leaves 3–10 mm long on each rhizome and no roots. *Azolla* has a tiny two-lobed leaf, with a cavity in the lower lobe

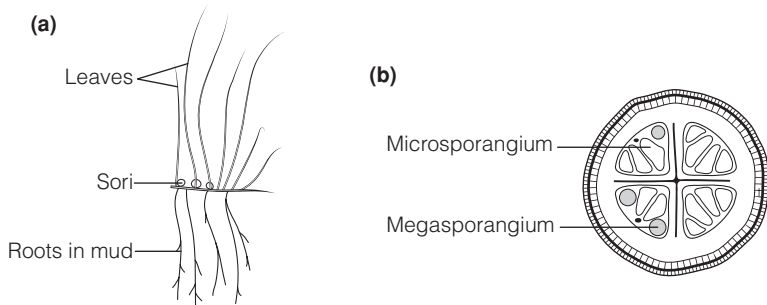


Fig. 5. Pillwort, *Pilularia*. (a) Whole plant; (b) cross-section through sorus.

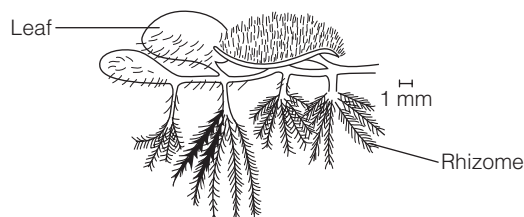


Fig. 6. The floating fern *Salvinia* (side view). (Redrawn from Ingrouille M (1992). Diversity and Evolution of Land Plants. Kluwer Academic Publishers.)

containing a cyanobacterium that fixes nitrogen (Topic M2) and roots trailing into the water from the nodes. Megasporangia and microsporangia are produced separately on the undersides of the leaves and spores released are into the water. In *Azolla* there is one megaspore per sporangium, but *Salvinia* has more than one.

The gametophyte

In typical ferns, the gametophyte is a prothallus that is most commonly a small green heart-shaped structure up to about 1 cm across that lives on the surface of damp soil (Fig. 7), sometimes in dense patches. The body of the prothallus consists of undifferentiated parenchyma cells with a thickened central part bearing rhizoids that absorb water. Antheridia and archegonia are produced on the underside. The antheridium is a rounded jacket containing 16–32 motile sperm. The archegonia are produced mainly near the notch, slightly later than the antheridia. Each archegonium has a neck of several cells surrounding two canal cells that degenerate at maturity, and an egg cell at their base, similar to those of bryophytes (Topic P4).

The eusporangiate ferns and royal ferns have larger and longer-lived prothalli than typical ferns and all have fungi associated with them acting as mycorrhizae (Topic M1); some are colorless and subterranean. The heterosporous water ferns have much reduced gametophytes that develop within the spore wall, as in heterosporous lycopods (Topic Q2). They develop in similar ways to *Selaginella*, although they are unrelated. In the floating group, the microspores aggregate together and hooked hairs develop that may aid attachment to the megasporangia.

Ecology of ferns

Although often common, ferns rarely dominate the vegetation. They mainly frequent damp places since most are limited in their distribution by the need for damp ground for spore germination and gametophyte growth. The enormous numbers and wide distribution of spores makes them good colonizers of suitable sites and many are pioneers, quick to exploit gaps. They are frequently

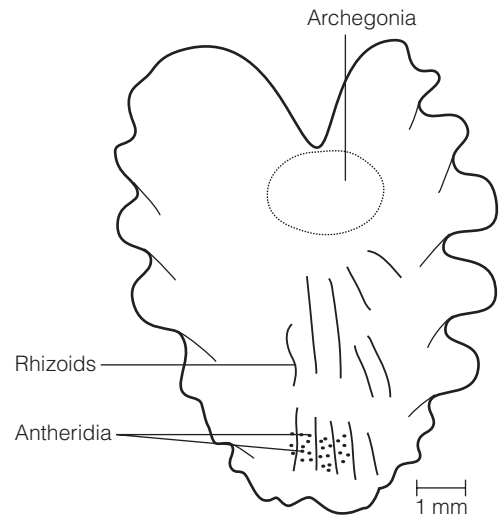


Fig. 7. Typical fern prothallus viewed from below.

found in shady situations under dense tree canopy or in rocky crevices. In the tropics, many ferns are epiphytic and they can be among the commonest epiphytes in drier parts of the rainforest; epiphytic ferns include the birdsnest fern which can grow to 3 m across. Several species, such as **bracken**, *Pteridium aquilinum*, spread vegetatively with branching rhizomes. These can spread to cover large areas, usually where the soil has eroded or degraded as a result of cultivation or forest clearance, and often well away from damp ground. Bracken is one of the world's most common plants, sometimes covering areas of moorland, and in places is considered a serious plant pest.

Very few animals eat ferns although there are a number of specialist insect feeders. Grazing animals may eat developing shoots. Some ferns contain high concentrations of insect molting hormone which may make them toxic.

Fossil ferns

Fossils of ferns are numerous from the mid-Devonian period onwards. They were important in the coal measures of the Carboniferous period. There were many tree ferns and non-woody species with various branching patterns. The fossils provide evidence, mainly from leaf form, that ferns probably evolved from the Trimerophytopsida (Topic L2). Sporangia of all the early ferns were eusporangiate. True leptosporangia, as seen in most modern ferns, probably did not appear until the Cretaceous period (Topic Q1, *Table 1*). Living leptosporangiate ferns evolved in parallel with the flowering plants in recent epochs.

Several fossil ferns from the mid-Carboniferous period and later were heterosporous. They are not directly related to the living heterosporous water ferns and it is clear that heterospory has evolved several times within the ferns.

Ferns and man

Considering their abundance, our uses of ferns have been limited, although bracken was extensively used for animal bedding and as kindling in Europe. The young developing leaves of bracken and some other ferns have been harvested as food for centuries, sometimes much sought after as a delicacy and still eaten, particularly in the Far East. Unfortunately some are carcinogenic and there is a relationship between regular eating of fern shoots and throat or esophageal cancer.

The main current use for ferns is as ornamentals. Their feathery leaves have long been admired and some rare species have been much sought after, as a result becoming rarer. Leaves are used in flower arrangements as background and orchids and other epiphytes are often grown on pieces of tree fern trunk or in a fibrous soil made from crushed fern leaves.

Q4 EVOLUTION OF THE SEED

Key Notes

Evolution of the seed

Seeds (known as ovules before fertilization) derive from the megasporangia of heterosporous plants that develop only one spore and are retained on the parent plant. The gametophytes are reduced and enclosed within the spore wall. They have a protective integument, perhaps formed from sterile megasporangia. Microspores are known as pollen grains.

Progymnospermopsida

These were trees of Devonian and Carboniferous times and had a combination of wood resembling that of conifers, leaves that may have been microphylls and sporangia resembling those of eusporangiate ferns. They may be ancestral to seed plants and/or ferns.

Seed plants

Seed plants first appeared in the Devonian period and may be descended from ferns or Trimerophytopsida. Some Devonian fossils, known as seed-ferns, had fern-like leaves and were heterosporous, showing intermediate stages in integument development.

Related topics

- The flower (D1)
Pollen and ovules (D2)
The seed (D3)
- The ferns (Q3)
Early seed plants (R1)

Evolution of the seed

The seed habit derives from a **heterosporous** condition similar to what is seen in some living lycopsids and ferns (Topics Q2 and Q3). In these there are two types of spore, **microspores** that give rise to the **microgametophyte** bearing sperms but no eggs, and **megaspores** that give rise to the **megagametophyte** bearing an egg or eggs. The gametophyte of both sexes is much reduced in size in all heterosporous plants, and, in most, it grows entirely within the spore wall. In many, the whole megasporangium is retained on the parent plant until the megagametophyte is fertilized. The seed derives from such a heterosporous condition, the seed itself being the megasporangium. It is a megasporangium that always matures just one spore, the three others produced by meiosis aborting and is known as the ovule before fertilization. It does not dehisce and the main body of the sporangium becomes a mass of parenchyma cells known as the **nucellus** (Topic D3). The microspores are usually (but not always) smaller than the megaspores and the microgametophyte is limited to a few cells inside the spore wall. The microspores of seed plants are the **pollen** grains, the microsporangium the **anther** (Topic D2).

In the seed the nucellus (megasporangium) is surrounded, except for a small opening, by another structure, the **integument** and it is this structure that distinguishes a seed from other heterosporous plants (Topic D1). The origin of the integument is obscure, though the most likely possibility is that it is derived from the fusion of a number of sterile sporangia surrounding the fertile one.

There are some intermediate stages represented among early fossil seed plants. The megagametophyte is reduced in size and retained entirely within the spore wall (itself retained in the sporangium), and it ruptures by the gap in the integument. All seed plants except the flowering plants and some Gnetales (Topic R3) produce recognizable archegonia by the rupture. In the flowering plants the megagametophyte is reduced to the embryo sac (Topic D2), normally eight nuclei, within the spore wall, the synergid cells perhaps representing what remains of the archegonium. In all seed plants the seed is retained on the parent sporophyte until after a new embryo starts to grow and only then is it dispersed as a whole unit. It will be seen that this seed consists of parts of three different genetic constitutions: an outer integument and nucellus (megasporangium) from the parent sporophyte, the haploid female gametophyte inside this and the new developing sporophyte inside this.

In all the **gymnosperms** (literally 'naked seed') the seed is exposed, usually on a modified leaf, but in the flowering plants, or **angiosperms** (literally 'hidden seed') it is enclosed by the **ovary** that becomes the fruit at maturity. It is suggested that this derives from a cup-like outgrowth from the sporophyte which is seen in some gymnosperms (Topic R4).

Progymnospermopsida

The Progymnospermopsida are regarded as the likely ancestral group of all seed plants. It is an entirely fossil group found early on in the evolution of land plants from mid Devonian to early Carboniferous rocks (see Topic Q1, *Table 1*). They were trees with well-developed trunks and lateral branches. The trunks had marked secondary thickening, unlike any ferns, and closely resembled trunks of living conifers (Topics C4 and R2). Their leaves were quite small but densely packed on the lateral branches and resembled microphylls (Topic Q2). Some of the side branches terminated in sporangia, of the eusporangiate type (Topic Q3), like contemporary fossil ferns, but some may have been heterosporous.

The striking feature of this group is its combination of sporangia typical of primitive ferns with wood typical of conifers and leaves that may be of the microphyll type. The progymnosperms are regarded by some as the ancestors of modern ferns as well as seed plants. Whatever the precise origins of the other seed plants, the progymnosperms clearly occupy an intermediate position and provide a fascinating link between early spore-bearing plants and seed plants.

Seed plants

Fossil seed plants first appear in Devonian rocks and they are abundantly represented as fossils from the mid-Devonian period onwards. The relationship between seed plants and ferns is not clear, with some researchers maintaining that all seed plants evolved from a fern-like ancestor, others suggesting an independent origin from the Trimerophytopsida (Topic Q1) or other primitive group for some or all seed plants. Seed plants are highly variable in structure and it is possible that the seed habit has evolved more than once.

Many fossils of vegetative parts that closely resemble ferns from the mid-Carboniferous period onwards were heterosporous, and some retained the megagametophyte on the leaves until after fertilization with the embryo beginning to grow. These show intermediate stages in the evolution of the integument, and are regarded as the earliest seed plants, the 'seed-ferns' or **pteridosperms** (Topic R1).