

The Early Tracheophytes



THE LYCOPHYTES

Lycopodium Has a Homosporous Life Cycle
Selaginella Has a Heterosporous Life Cycle
Heterospory Allows for Greater Parental Investment
Isoetes May Be the Only Living Member of the Lepidodendrid Group

THE MONILOPHYTES

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Ophioglossalean Ferns
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True Ferns
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Ferns Have Ecological and Economic Importance

SUMMARY

PLANTS, PEOPLE, AND THE ENVIRONMENT: *Sporophyte Prominence and Survival on Land*

PLANTS, PEOPLE, AND THE ENVIRONMENT: *Coal, Smog, and Forest Decline*

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THE OCCUPATION OF THE LAND

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KEY CONCEPTS

1. Tracheophytes, also called vascular plants, possess lignified water-conducting tissue (xylem). Approximately 14,000 species of tracheophytes reproduce by releasing spores and do not make seeds. These are sometimes called seedless vascular plants. Tracheophytes differ from bryophytes in possessing branched sporophytes that are dominant in the life cycle. These sporophytes are more tolerant of life on dry land than those of bryophytes because water movement is controlled by strongly lignified vascular tissue, stomata, and an extensive cuticle. The gametophytes, however still require a seasonally wet habitat, and water outside the plant is essential for the movement of sperm from antheridia to archegonia.

2. The rhyniophytes were the first tracheophytes. They consisted of dichotomously branching axes, lacking roots and leaves. They are all extinct. They gave rise to two lineages that are still present: the lycophytes and the rest of the tracheophytes. This latter group is again divided into two lineages: seed plants and monilophytes.

3. The lycophytes are a group of plants that diverged very early and currently are represented by three lineages, all of which occur in North America. These plants all have leaves, roots, and laterally attached sporangia. One lineage consists of the genus *Lycopodium* (in addition to a number of new genera segregated from it), which is strictly homosporous and has subterranean gametophytes. Each of the other two lineages consists of a single genus. *Selaginella* is heterosporous. *Isoetes*, also heterosporous and having secondary growth, is likely in the lineage that included the extinct lepidodendrids, a major component of the Coal Age swamp forests.

4. The monilophytes consist of five lineages, four of which are commonly called ferns. The whisk ferns or psilophytes are represented by two living genera: *Psilotum* and *Tmesipteris*. Sporophytes of *Psilotum* are reduced, consisting of a green, branching stem, lacking roots and possessing only highly reduced leaves (enations). *Tmesipteris* is an epiphyte with large leaves. The psilophytes are most closely related to the ophioglossalean ferns. The marattialean ferns are large tropical ferns with upright stems and eusporangia. The horsetails or sphenophytes consist of a single living genus, *Equisetum*. Sporophytes are jointed and ribbed, and their stems have a complex anatomy.

5. The lineage known as monilophytes contains most of the species in the true ferns group. They are diverse in form, and they range from warm tropical regions to the arctic. True ferns are characterized by a distinctive type of sporangium, the leptosporangium, which has a long stalk, a single cell layer making up the wall, and an annulus, which aids in dehiscence. Their leaves are complex and varied. A few aquatic ferns are the only heterosporous species. True ferns have food value and other applications for human use.

23.1 THE OCCUPATION OF THE LAND

When plants first moved onto the land, they responded to the problem of living and reproducing in a dry environment with key innovations, such as surrounding their gametes with sterile jackets (gametangia), producing multicellular sporophytes, and synthesizing cuticle and other substances. However, these early bryophytes could only survive in sites with abundant water. Soon after achieving a foothold in the terrestrial environment, the bryophytes gave rise to another lineage that became spectacularly specialized for life on land and soon predominated: **tracheophytes** (Fig. 23.1).

The story of how bryophytes gave rise to tracheophytes and how these plants became increasingly better adapted to harsh terrestrial environments reveals profound changes in morphology, life cycle, physiology, and biochemistry. These adaptations reduced the dependence of plants on free water in their environment and allowed plants to occupy a wider range of sites.

If humans had been of Earth about 450 million years ago, they would have witnessed the early stages of this tremendous evolutionary explosion that turned our planet's barren rocks green, stabilized our atmosphere, and became the basis for all the intricate webs of terrestrial life. These new ecosystems became cradles of evolution, giving rise not only to a vast array of plant species, but also to countless other kinds of life, from dinosaurs to butterflies. However, the initial terrestrial pioneers of 450 million years ago were only a tangled mat of unimpressive, vertical green stems, patchily distributed across the landscape and no taller than this textbook. Within a mere 40 million years, their descendants had produced a rich diversity of form, including such novel plant structures as roots, wood, leaves, and seeds.

The chapter considers the evolution and diversification of early tracheophytes from their first appearance and initial diversification to the origin of two of the early lineages: lycophytes and monilophytes. Somewhat later, a third lineage of tracheophytes arose with an additional reproductive innovation, the seed.

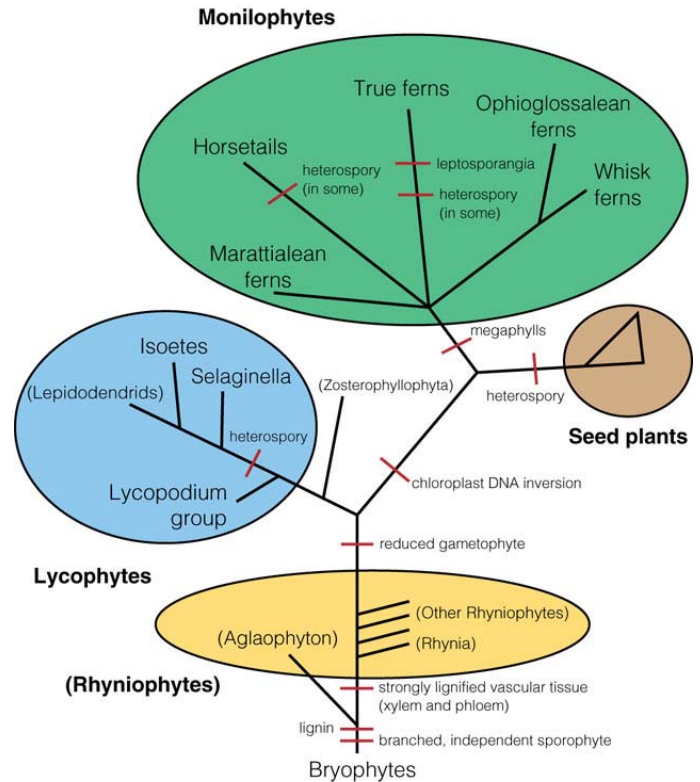


Figure 23.1. A cladogram showing relationships among the early tracheophytes. Relationships among the five lineages of Monilophytes are largely uncertain. Megaphylls and even roots have been lost in some lineages. Names in parentheses represent extinct groups.

These plants are discussed in Chapter 24 and 25. The tracheophytes discussed in this chapter all disperse by spores. Thus, the plants in this group also are called **seedless vascular plants**.

The First Tracheophytes Were Rhyniophytes

Unmistakable evidence of true xylem appears in the fossil record around the middle of the Silurian period, approximately 430 million years ago, but microfossils suggest that tracheophytes were already established more than 40 million years earlier, in the mid-Ordovician period. We have a clear picture of what these early tracheophytes were like because of extremely well-preserved and abundant fossils found in chert near the village of Rhynie, Scotland. One of the most spectacular fossil beds ever found it has yielded a vast amount of information on internal and external features, as well as the ecology of the early tracheophyte flora. A variety of plants have been found in these fossil beds. All were small (no taller than 20 cm) and lacked leaves and roots. They consisted of **dichotomously branching** rhizomes with rhizoids attached to them and vertical aerial stems with sporangia at their tips. The existence of sporangia reveals that these plants were the sporophyte phase of the life cycle (Fig. 23.2a). Unfortunately, few fossil gametophytes have been found.

Rhyniophytes had a simple stem anatomy (Fig. 23.2b). There is evidence, as with many early plants, of endosymbiotic fungi living in the stems. These symbiotic relationships may have been crucial to the success of plants on land. The rhyniophyte group gave rise to all other land plants; thus, it is not monophyletic.

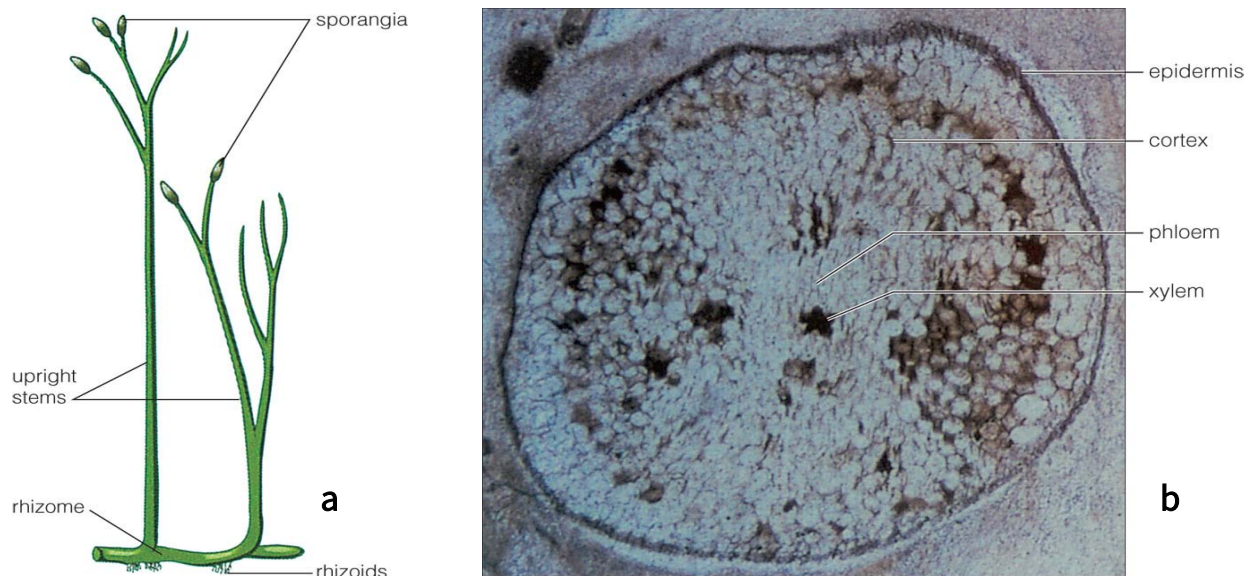


Figure 23.2. *Rhynia*, a vascular plant that lived 400 million years ago. (a) A reconstruction of two plants, about 30 cm tall. (b) A cross-section of the stem approximately 3 mm in diameter. A small cylindrical core of xylem is surrounded by a large cylinder of phloem. An even larger cylinder of cortex, composed of thin-walled parenchyma cells, is packed around the vascular tissue, and the entire stem is covered with an epidermal layer bearing cuticle and stomata.

Tracheophytes Became Increasingly Better Adapted to the Terrestrial Environment

Examination of fossils and cladistic studies of the earliest land plants have yielded some surprises and have enabled us to reconstruct the most likely path of evolution from bryophyte to tracheophyte. Tracheophyte innovations include: (1) a dichotomously branching sporophyte with multiple terminal sporangia; (2) a free-living, nutritionally independent sporophyte that is prominent in the life cycle; (3) a reduced gametophyte; and (4) lignified vascular tissue (xylem) in the sporophyte.

All of these adaptations were likely important in the colonization of the land. Several fossils recently have been discovered that help shed light on how and why these changes might have occurred. Although bryophytes succeeded in moving onto the land, they were severely limited by an inability to control their water balance. Therefore, they must have occupied only discrete islands of habitat where conditions were favorable for growth.

One of the strongest selective pressures at this stage must have been exerted by the high mortality of spores; the overwhelming majority of spores released would have fallen on inhospitable ground and failed to germinate. Early plants could have increased spore production by two possible mechanisms: increasing the number of sporophytes produced on each gametophyte, or increasing the number of sporangia per sporophyte. Plants evolved both solutions. Bryophytes, particularly the mosses, produce many sporophytes on each gametophyte. Tracheophytes, in contrast, branched their sporophyte, thereby increasing the number of sporangia the plant could make. These elaborated sporophytes would have soon required stiffening tissue to hold them up and would eventually have required effective means of transporting water. To continue this trend of enlarging the sporophyte, a new plant architecture, in which a main stem sports smaller lateral branches, would have had to evolve.

If the elaboration of the sporophyte were driven by selection for more spores, it would be expected that plants evolved a branched sporophyte first and only later evolved specialized vascular tissues and lateral branching to solve the secondary problems created by branching the sporophyte. Studies of extremely well-preserved rhyniophyte fossils have shown exactly that. Some of the earliest taxa lacked strongly lignified water-conducting cells (tracheids), although they branched profusely (Fig. 23.3). These so-called protracheophytes are intermediate between the bryophytes, with unligified (or no) vascular systems, and tracheophytes, with highly

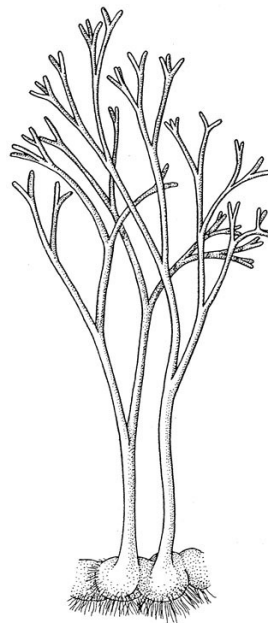


Figure 23.3. Reconstruction of an extinct Devonian plant *Horneophyto lignieri*.

specialized, lignin-stiffened vascular systems. The earliest plants with lignin, such as *Rhynia* (Fig. 23.2b) branched only dichotomously but were eventually superseded by taller plants with a main stem and smaller laterally emerging branches.

Relationships among Early Tracheophytes

Traditionally, tracheophytes that reproduce by releasing spores rather than seeds have been divided into four divisions. However, botanists have come to realize that this taxonomic scheme does not accurately reflect the evolutionary history of these plants. Studies using cladistic methods have unequivocally demonstrated that living tracheophytes fall into two major clades, which separated more than 400 million years ago (Fig. 23.1). One lineage currently is represented by lycophytes, whereas the second lineage includes all other tracheophytes. The evidence for this ancient split includes a series of morphological features, but also one distinctive molecular feature. There is a region of about 30,000 base pairs in the chloroplast DNA of all plants. This sequence on the chloroplast chromosome "reads" in one direction in the bryophytes and lycophytes, but in the opposite direction for all other plants. This inversion must have taken place after the lycophytes line split from the main vascular plant lineage.

Recent studies of the nonlycophyte vascular plants involving morphology and DNA sequences from the chloroplast and the nucleus have yielded an unexpected new result. This group of tracheophytes is itself divided into only two major lineages: the seed plants and a diverse group called the monilophytes. This clade is primarily composed of a variety of plants commonly called ferns and includes two small, unusual groups that are traditionally treated as divisions, horsetails and whisk ferns.

Currently, we are unsure of the exact pattern of relationships among monilophytes. There appear to be five lineages, and these are divided into four major clades: whisk ferns plus ophioglossalean ferns, horsetails, marattialean ferns, and true ferns. The exact relationships among these four clades have not yet been worked out.

23.2 THE LYCOPHYTES

The lineage that gave rise to lycophytes separated from other vascular plants early in the history of tracheophytes (Fig. 23.4). Living **lycophytes** thus preserve a set of different solutions to the problems of a terrestrial life than other vascular plants. The lycophyte line originated in the Devonian or Silurian period. The earliest known members of the line are a group called **Zosterophyllophyta**, which is now extinct. Plants in this group lacked leaves and roots, and they branched dichotomously like the rhyniophytes. However, one unique morphological feature distinguished this line from rhyniophytes: the sporangia were attached to stems in a lateral rather than terminal position. The Zosterophyllophyta are important because they either gave rise to or are closely related to the lycophytes. In either case, the lateral sporangial position was present in the common ancestor of both Zosterophyllophyta and lycophytes and is universal among lycophytes.

The lycophyte line reached its peak of diversity and ecological importance in the Coal Age (Fig. 23.5). During this period, Earth's climate was warm, topographical relief was low, and lush swamps covered vast coastal lowlands. These swamps supported forests composed largely of trees in a now extinct lycophyte group called the **lepidodendrids**. One example is *Lepidodendron*, which grew to more than 35 m in height and had secondary growth, although with a different pattern than that of most modern plants (Fig. 23.6).

These trees branched dichotomously in both their aerial and underground portions. The fossilized trunks are covered with distinctive diamond-shaped pads where leaves were attached. The underground stems were similarly covered with roots. Lepidodendrids continue to exert a strong ecological and economic influence today because their abundant bodies, compressed under millions of years of accumulated sediment, have been transformed into the extensive coal deposits currently being mined (see endnote: "PLANTS, PEOPLE, AND THE ENVIRONMENT: Coal, Smog, and Forest Decline.")

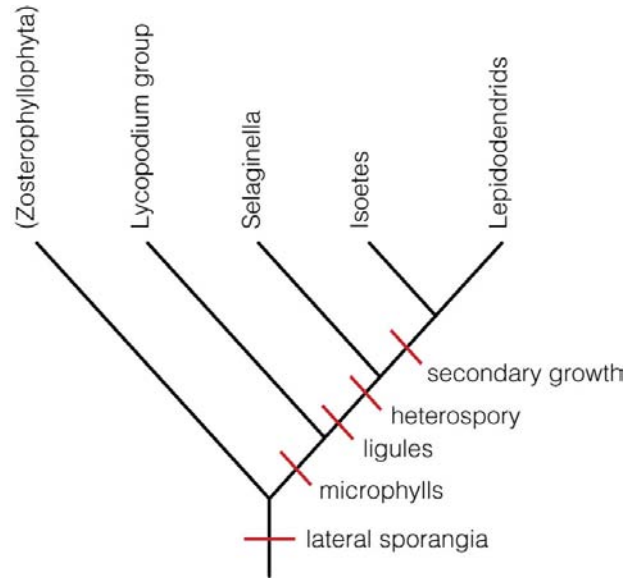


Figure 23.4. A cladogram showing phylogenetic relationships between lycophytes and the Zosterophyllophyta group. The latter, in parentheses, are extinct.



Figure 23.5. A diorama reconstruction of a Coal Age forest.

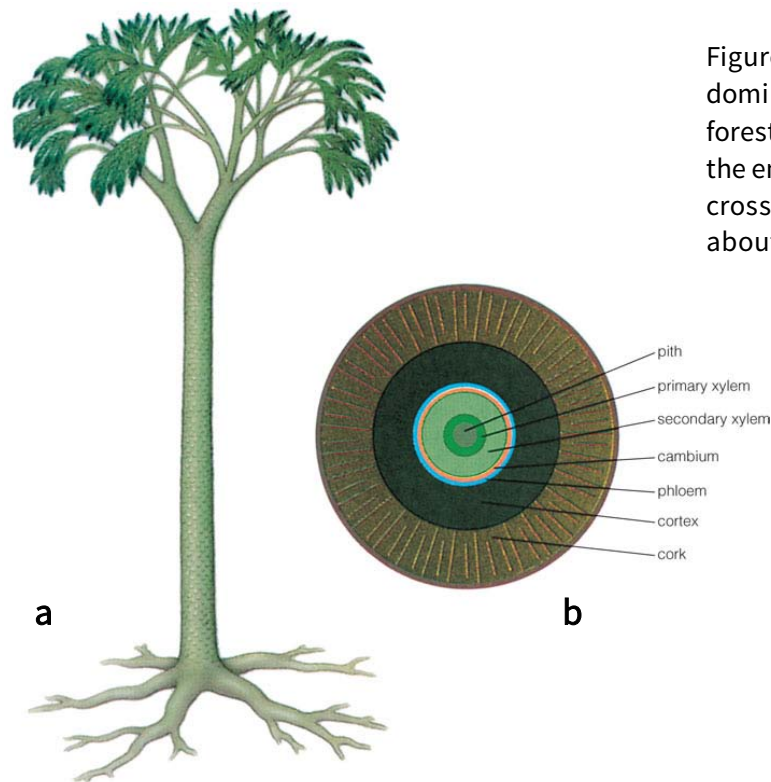


Figure 23.6. *Lepidodendron*, a dominant tree of the Coal Age forest. (a) A reconstruction of the entire tree. (b) A fossilized cross-section of the trunk, about 1 m in diameter.

Lycophytes produce a particular kind of leaf called a microphyll. Although the term suggests small size, some of these leaves were quite large. Microphylls are defined by the presence of a single vascular bundle. This bundle (or trace) does not branch inside the leaf and causes no interruption in the vascular strand of the stem when it peels off to enter the leaf. The most likely candidate for the original structure is a lateral sporangium that was converted to a light-gathering structure to enhance photosynthesis. As the sporangium evolved to gather light more efficiently, it flattened, increased in size, became sterile (lost its spore-producing function), and ultimately became vascularized, forming the microphylls found in all lycophytes, living and extinct.

Today, lycophytes represent a mere remnant of their Coal Age diversity. The group consists of three very different lineages: *Lycopodium* (and related genera), *Selaginella*, and *Isoetes*. Each of these lineages has a worldwide distribution, predominantly in tropical and subtropical forests, but a number occur in temperate and arctic regions. Some have adapted to aquatic environments, completing their entire life cycle fully submerged, whereas others grow in deserts and survive drought much like mosses, by shriveling and becoming dormant.

Lycopodium Has a Homosporous Life Cycle

The lineage that includes the genus *Lycopodium* is familiar to many as the evergreen trailing plants used in making wreaths (Fig. 23.7a). The abundant spores are highly flammable and were once used by magicians and photographers to cause dramatic flashes of light. The spores also were used to coat such latex items as

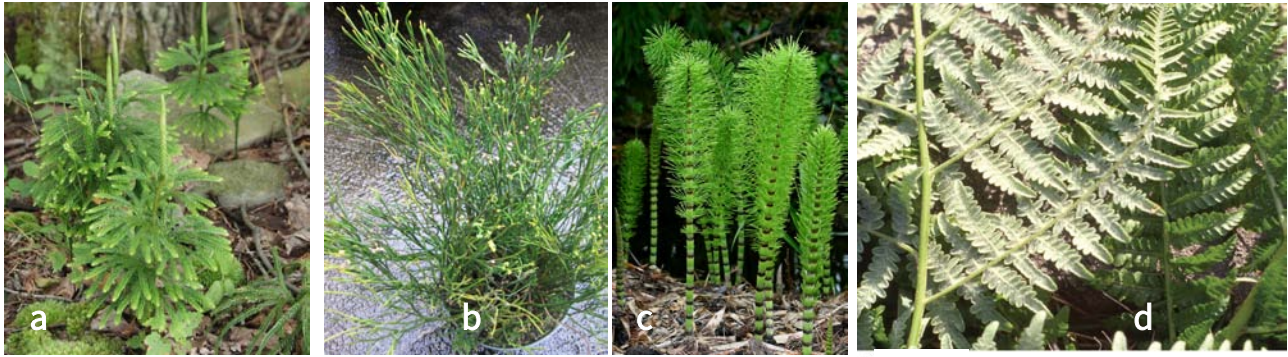


Figure 23.7. Representatives of the groups discussed in this chapter. (a) A club moss, *Lycopodium obscurum*. (b) A whisk fern, *Psilotum nudum*. (c) A horsetail, *Equisetum telmateia*. (d) Chain fern, *Woodwardia fimbriata*.

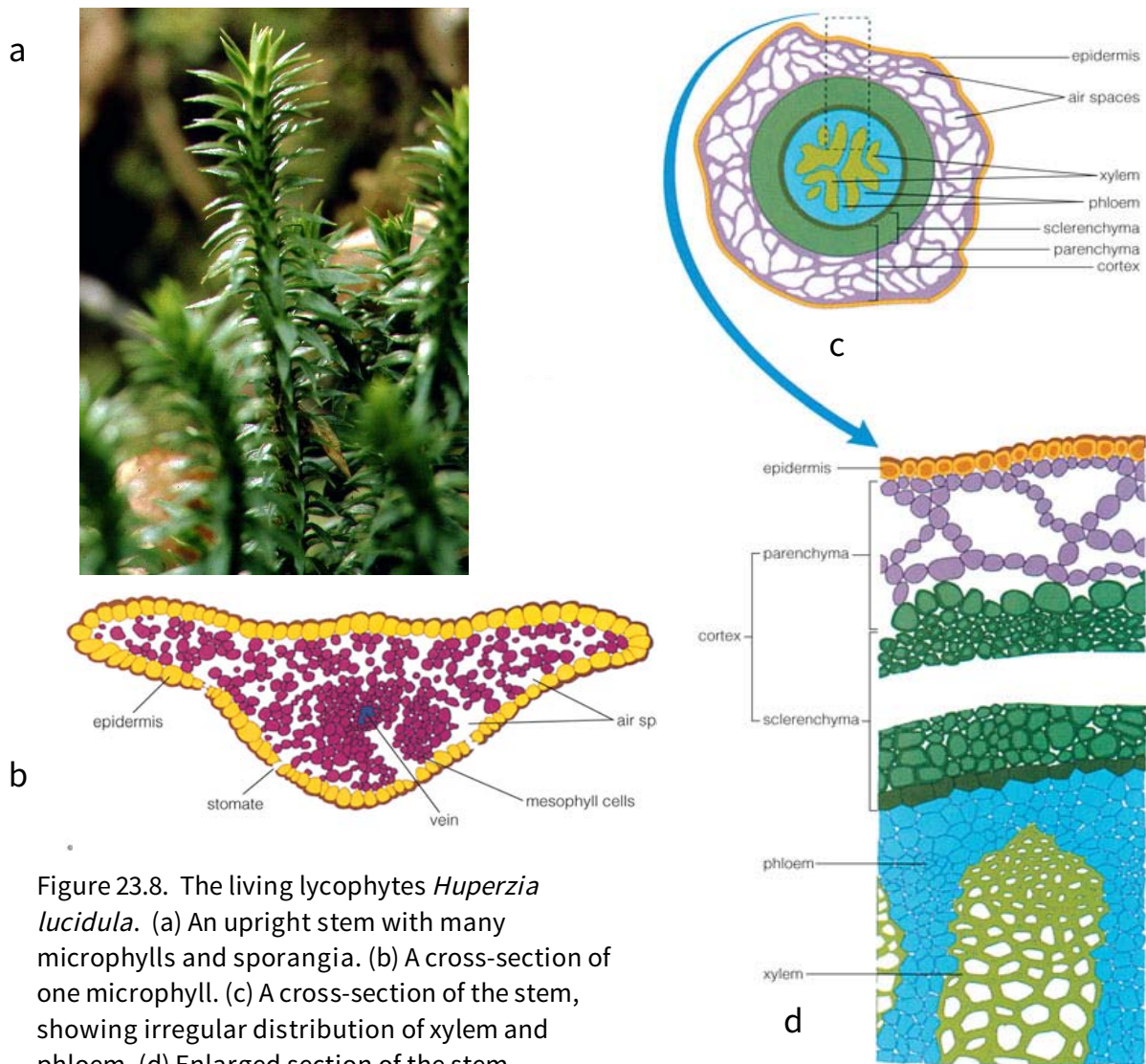


Figure 23.8. The living lycophytes *Huperzia lucidula*. (a) An upright stem with many microphylls and sporangia. (b) A cross-section of one microphyll. (c) A cross-section of the stem, showing irregular distribution of xylem and phloem. (d) Enlarged section of the stem.

gloves and condoms, but it was eventually discovered that they are irritating to the skin, and their use was discontinued. *Lycopodium clavatum* has been shown experimentally to have hypoglycemic effects.

The genus *Lycopodium* once contained about 400 species, but it has been broken into 10 to 15 smaller genera. There are seven genera in North America (see Table 23.1). Most are trailing plants, with short upright branches that resemble thick mosses or pine seedlings (hence, the common names club moss and ground pine). The stems branch dichotomously and often are prostrate. They are sheathed with numerous spirally arranged microphylls (Fig. 23.8a). The stem has a netlike system of interconnected strands of xylem with phloem between them (Fig. 23.8c,d). The xylem contains tracheids, and the phloem contains sieve cells and parenchyma cells. There is no true endodermis, but typically a layer of sclerenchyma encircles the vascular cylinder. Roots arise at the shoot apical meristems and may grow through the cortex for some distance and emerge on the underside of the horizontal stems.

Lycopodium has a homosporous life cycle, meaning that only one type of spore is made and that the gametophytes are bisexual, producing both archegonia and antheridia (Fig. 23.9). Sporangia are produced on the top surface of **sporophylls** (leaves bearing sporangia). In many members of this group, the sporophylls are aggregated into **strobili** (singular, *strobilus*), soft, conelike structures (Fig. 23.9a).

Meiosis occurs inside sporangia, producing numerous haploid spores (Fig. 23.9c). The spores are shed, germinate on the ground, and develop into gametophytes. These typically are long-living and subterranean, and require an endosymbiotic fungus to survive. Gametophytes of some species grow above ground and are photosynthetic, but they apparently still require the fungus to develop normally (Fig. 23.9d).

Archegonia and antheridia are borne on the surface of the gametophyte (Fig. 23.9e). When biflagellate sperm are liberated from antheridia, they swim through water to fertilize eggs inside archegonia (Fig. 23.9f-h). The resulting zygote develops into an embryo that possesses a well-developed foot, a short primary root, leaf primordia, and a shoot apex (Fig. 23.9i). The young sporophyte (Fig. 23.9j) is initially dependent on the gametophyte, but soon becomes self-sustaining.

***Selaginella* Has a Heterosporous Life Cycle**

Another lineage of lycophytes has a single living genus, *Selaginella* (spike moss), with approximate 700 species. Most are tropical, but a few tolerate relatively dry or cold habitats. Several species are commercially grown as ornamental plants, including *Selaginella lepidophylla* (resurrection plant, rose of Jericho), *Selaginella willdenovii* (peacock fern), and *Selaginella braunii* (treelet spike moss). In Chinese medicine, *Selaginella doederleinii* is added to a stew of lean pork to treat "immobile masses."

The sporophyte consists of a dichotomously branched stem, which is prostrate in some species (Fig. 23.10a) and upright and slender in others. The microphylls frequently are arranged in four rows, or ranks, one row of large leaves on either side of the stem and two rows of smaller leaves on the topside of the stem.

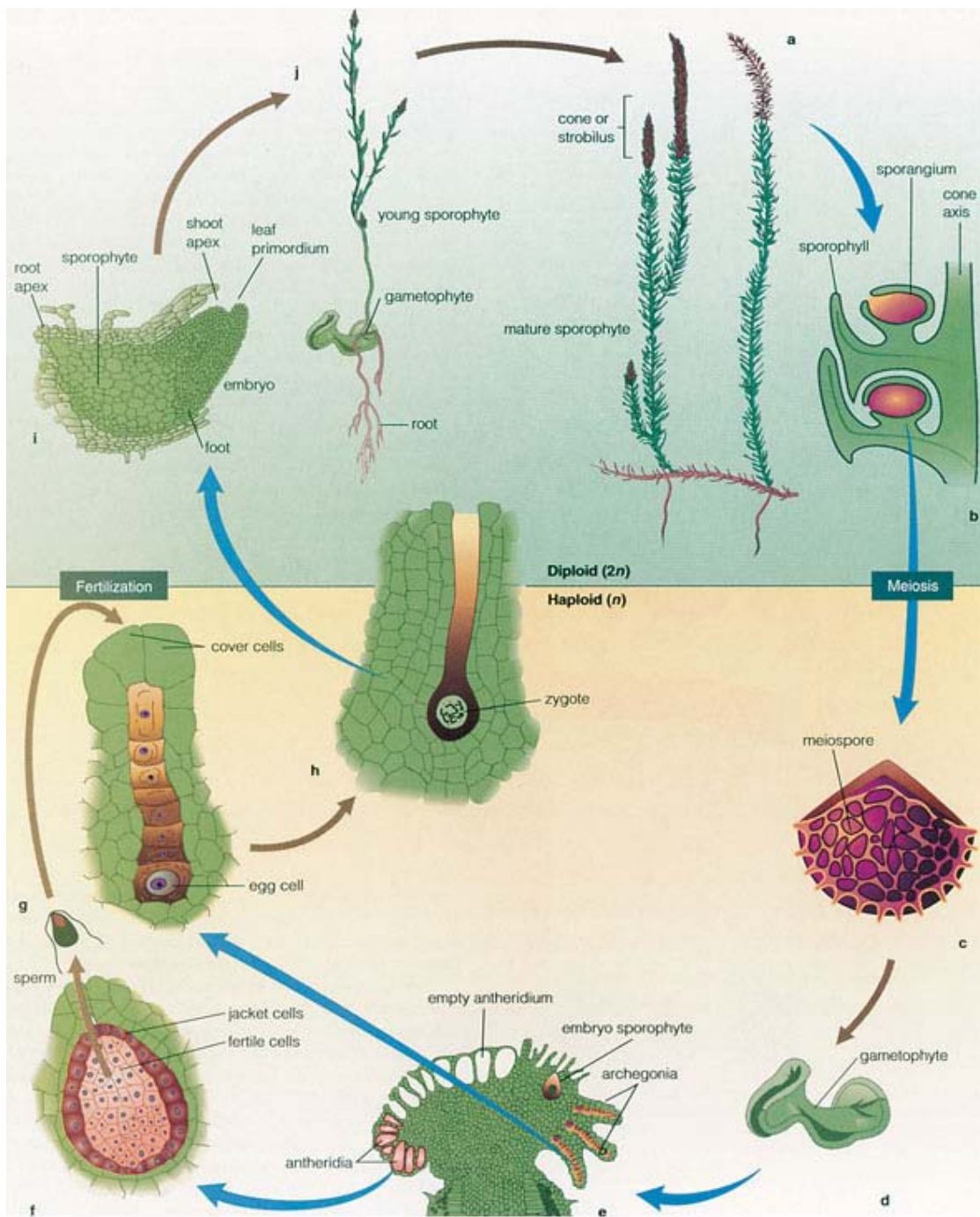


Figure 23.9. The life cycle of a species of *Lycopodium*. (a) A mature sporophyte. (b) A longitudinal section of a strobilus, showing sporangia attached to microphylls (sporophylls). Meiosis within the sporangium produces (c) haploid meiospores, each of which can germinate, multiply by mitosis, and grow into (d) a gametophyte. (e) A longitudinal section of a portion of a gametophyte, showing the location of archegonia and antheridia. (f,g) Biflagellate sperm are released from antheridia and swim in a film of water to archegonia, where one sperm fuses with one egg to create (h) a diploid zygote. The zygote remains embedded in, and dependent on, gametophyte tissue. (i,j) The zygote divides by mitosis and grows into an embryo and then into a mature sporophyte.

The stem and leaves resemble miniature cypress branches. In addition, all leaves of *Selaginella* possess a small structure on their top side called a **ligule**, which secretes protective fluids during leaf development. Ligules can be important in distinguishing *Selaginella* from plants in the *Lycopodium* lineage, which always lack ligules. Special meristems at the branch points produce an organ that is unique to *Selaginella*, called a **rhizophore**. It has characteristics of both a stem and a root and typically grows downward to the soil where it gives rise to true roots. However, under certain conditions (for example, if the shoot tip is lost), the rhizophore can give rise to a stem.

Selaginella has a heterosporous life cycle. Sporophytes produce two types of spores; large **megaspores** are produced by **megasporangia**, and small **microspores** are produced by **microsporangia**. These sporangia are located in the axil of sporophylls, as in *Lycopodium*, but are always aggregated into strobili. A single strobilus usually has both types of sporangia (Fig. 23.10b,c)

Megasporangia are filled with diploid megasporocytes. One of them divides by meiosis to yield four large megaspores; the rest of the sporocytes typically degenerate. Megaspores divide mitotically to form a **megagametophyte**, but all cells remain inside the thick spore wall (Fig. 23.10d). Immature megagametophytes can be passively released from the sporangium or actively ejected by a snapping motion of the peeled-back sporangium wall. When megagametophytes of *Selaginella* reach maturity, the spore wall cracks open and a cushion of gametophyte tissue protrudes. Archegonia develop in this cushion of tissue, and often rhizoids protrude (Fig. 23.10e).

Microsporangia undergo a similar process. They initially are filled with up to several hundred diploid microsporocytes, which divide by meiosis to make four small microspores each (Fig. 23.10f,g). Microspores divide mitotically to form a microgametophyte. This consists of a layer of cells inside the spore wall forming an antheridium with a mass of sperm cells in the center (Fig. 23.10h,i). The mature microgametophyte thus is a minute plant consisting of a single antheridium within a microspore wall.

The sperm cells are liberated when the microspore wall becomes wet, and they swim toward mature archegonia in which a single egg cell resides (Fig. 23.10j). The haploid egg and haploid sperm cell combine to produce a diploid zygote cell, which immediately begins to divide and differentiate into an embryo (Fig. 23.10k,l). The embryo does not become dormant, as it does in a seed, but instead continues to grow into a fully mature sporophyte (returning to Fig. 23.10a).

Heterospory Allows for Greater Parental Investment

Heterospory undoubtedly evolved in *Selaginella* to enhance reproduction. It is a system based on a division of labor. In homosporous species, dispersal of spores is effective, but the spores have no stored food. Consequently, many are viable for only a short time, thereby providing inadequate nutrition to the embryo. Heterosporous plants such as *Selaginella* produce a megaspore, provisioned with a rich store of food. These large, heavy megaspores are not widely dispersed, but the resulting megagametophyte provides nutrition and protection for the zygote, embryo, and young sporophyte. The smaller, lighter microspore has little food resources, but it can disperse over long distances, to bring the sperm to the

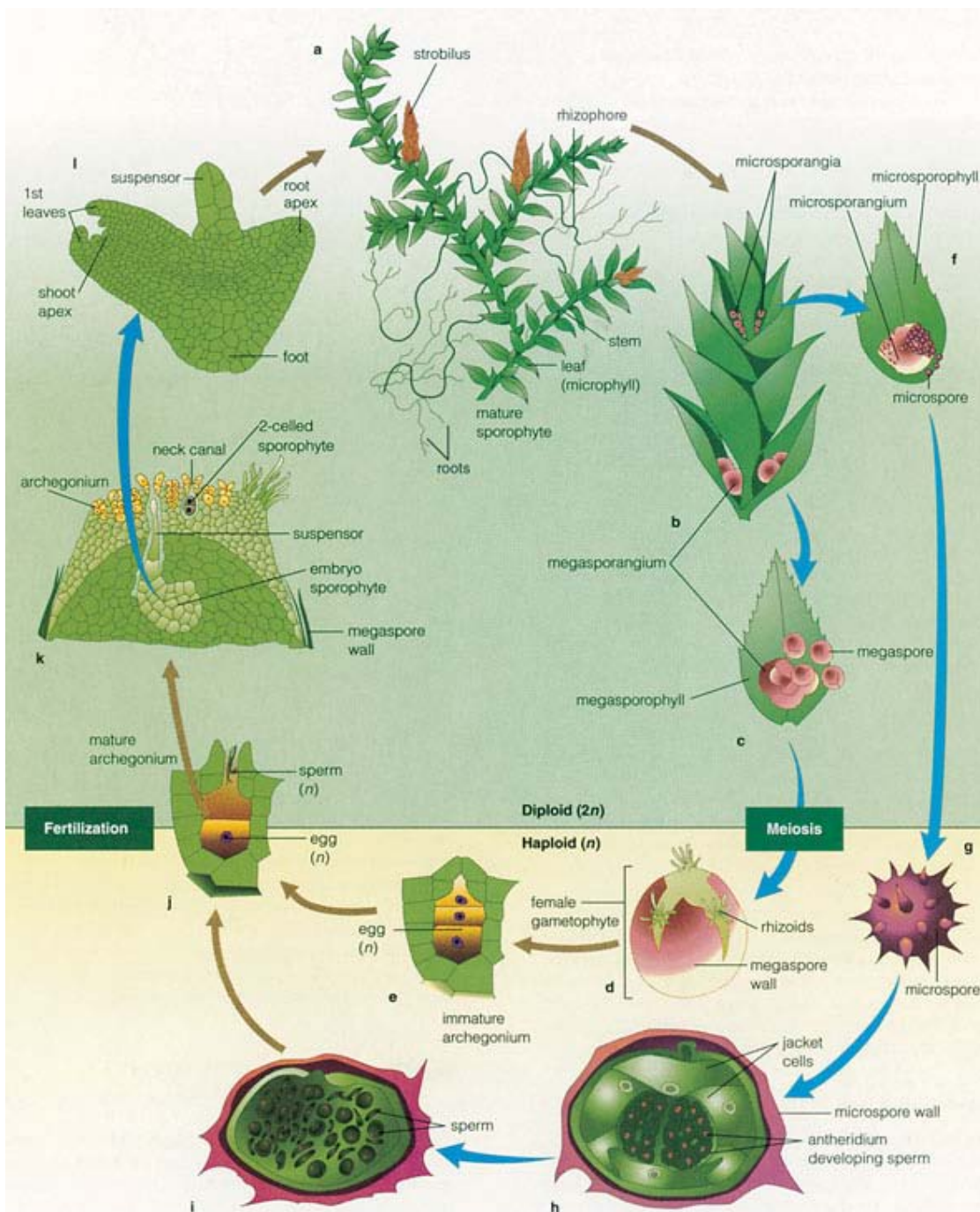


Figure 23.10. The life cycle of *Selaginella*. (a) A mature sporophyte with stems, microphylls, rhizophores, roots, and strobili. (b,c,f) Inside each strobilus are two kinds of sporangia: megasporangia and microsporangia. Meiosis within the larger megasporangium yields four megaspores, each of which divides by mitosis to produce (d) megagametophytes. Meiosis within the smaller microsporangium produces many microspores (g), each of which develops by mitosis into (h,i) microgametophytes, which produce sperm. The motile sperm swim from the antheridium to a nearby archegonium (d,e,j) and each can fertilize one egg. A fertilized egg becomes a zygote, which divides mitotically to form an embryo (k,l) and then a mature sporophyte (a). The zygote and embryo are retained within, and dependent on, gametophyte.

megagametophyte. Heterospory has evolved independently in many plant groups and represents an important, necessary step toward seeds.

***Isoetes* May Be the Only Living Member of the Lepidodendrid Group**

The third extant lineage of lycophytes contains the single genus *Isoetes*, commonly called quillwort or Merlin's grass. *Isoetes* contains more than 125 species distributed worldwide in aquatic habitats. All are small plants, which typically grow submerged in water for part or all of their life cycle. The plant body consists of a lobed cormlike structure that undergoes secondary growth and produces roots and a tuft of microphylls that resemble grass leaves. The microphylls are filled with large air chambers and have prominent ligules. Most, if not all, microphylls are sporophylls. The entire plant has been likened to a strobilus attached to a bit of stem (Fig. 23.11).

Isoetes is heterosporous. Unlike *Selaginella*, however, each megasporangium produces several hundred megaspores, and each microsporangium produces more than a million microspores. Sperm cells are multiflagellate, whereas those of other living lycophytes are biflagellate. This strange plant shares a number of features with the extinct tree lycophytes of the Carboniferous, including heterospory, ligules, secondary growth, and a distinctive root morphology. Indeed, recent cladistic analyses and the fossil record suggest that *Isoetes* is a living member of the ancient lepidodendrid group.

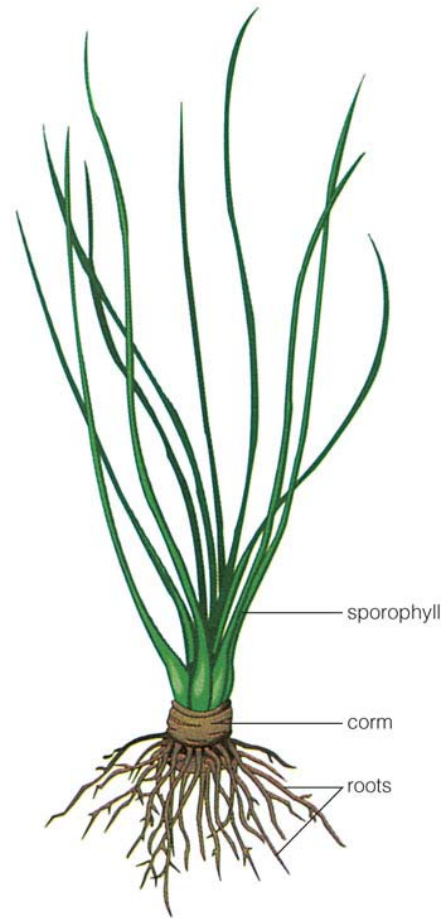


Figure 23.11. *Isoetes*, a living member of the lycophytes lineage. The plants are small (3-6 cm tall) and typically grow submerged in shallow water for part of each year.

23.3 THE MONILOPHYTES

The lineage that includes all seedless tracheophytes besides the lycophytes consists predominantly of plants commonly called ferns. **Monilophytes** are distributed worldwide. They are typically herbaceous today, but previously some reached tree size

and were important members of Coal Age swamp forests. Because the monilophyte line split from the lycophytes before their common ancestor had evolved roots, leaves, secondary growth, the tree habit, heterospory, and multiflagellated sperm, the subsequent appearance of all these features in both lineages represents a remarkable series of evolutionary convergences every bit as spectacular as the independent evolution of wings in birds, bats, and pterosaurs.

Secondary growth in monilophytes occurs in a different way than in lycophytes. The roots of each group also are distinctively different, but the variation in leaf form and development is particularly revealing. The lycophytes all possess microphylls. The monilophytes produce a different kind of leaf called a **megaphyll**. More than one vascular strand enters a megaphyll, and the strands branch extensively in the leaf. In addition, the vascular strands cause an interruption in the xylem of the stem (called a leaf gap) where they branch off to enter the leaf. The difference between microphylls and megaphylls reflects their different evolutionary origins. Microphylls are thought to have originated from lateral appendages, such as sporangia. Megaphylls, in contrast, are thought to have resulted from the modification of a branch system (Fig. 23.12).

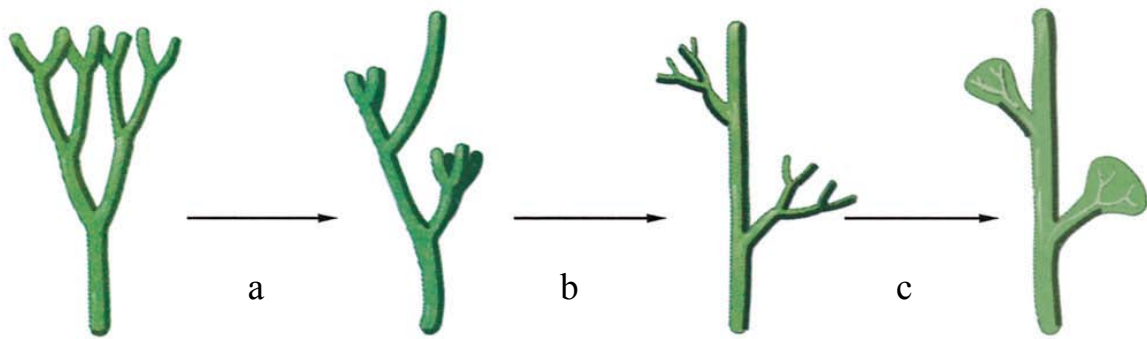


Figure 23.12. Hypothetical stages in the evolution of megaphylls. (a) A dichotomously branched, leafless plant begins to branch unequally, so that at each fork there is a longer main stem axis and shorter side branches. (b) The side branches become splayed into a plane, like a miniature espalier. (c) The splayed branch system becomes webbed. The webbing becomes the leaf blade and the branches become veins.

Whisk Ferns

Whisk ferns, or psilophytes, are unusual plants, and until recently, there has been debate about where they fit in the phylogeny of plants. Some of them look superficially like rhyniophytes, and some botanists have proposed that they are direct descendants of this group. DNA analysis has shown definitively, however, that psilophytes are in the monilophytes clade.

Psilophytes have no known fossil record. There are two living genera: *Psilotum* (Fig. 23.7b) and *Tmesipteris*. These are relatively uncommon herbaceous plants that grow in tropical and subtropical regions, often as epiphytes. *Psilotum* occurs widely through the Pacific Islands, including Hawaii, Africa, and Asia. It also has been reported in a variety of locations across the southern part of the United States, although there is some question as to whether it is truly native in all of its

range. It commonly appears uninvited in greenhouses, and it may have been introduced by humans in many places. *Tmesipteris* is restricted to the South Pacific and Australia.

Psilotum lacks roots and consists of a dichotomously branched rhizome system covered with rhizoids. Cortex cells of the rhizome are infected with mycorrhizal fungi that extend into the soil. The upright, aerial stems also branch dichotomously, and the sporophyte typically is less than 60 cm in height. The aerial stems bear **enations**, small stem outgrowths that are leaflike but lack vascular tissue (Fig. 23.13). *Psilotum* is usually described as lacking leaves, but these enations most likely originated from true leaves.

This simple body, lacking roots and possessing only highly reduced leaflike structures, is unique among living tracheophytes but was once common among extinct rhyniophytes and Zosterophyllophyta. In psilophytes, these simple traits are likely adaptations to an epiphyte lifestyle. They have strong associations to mycorrhizal fungi.

The internal stem anatomy is unlike that of the rhyniophytes (Fig. 23.14). Rhizomes have a central strand of solid xylem, sometimes ridged or lobed; stems have a pith with fibers, surrounded by a cylinder of xylem. To the outside of the xylem is an endodermis with a Casparian strip, then a cortex with several zones of

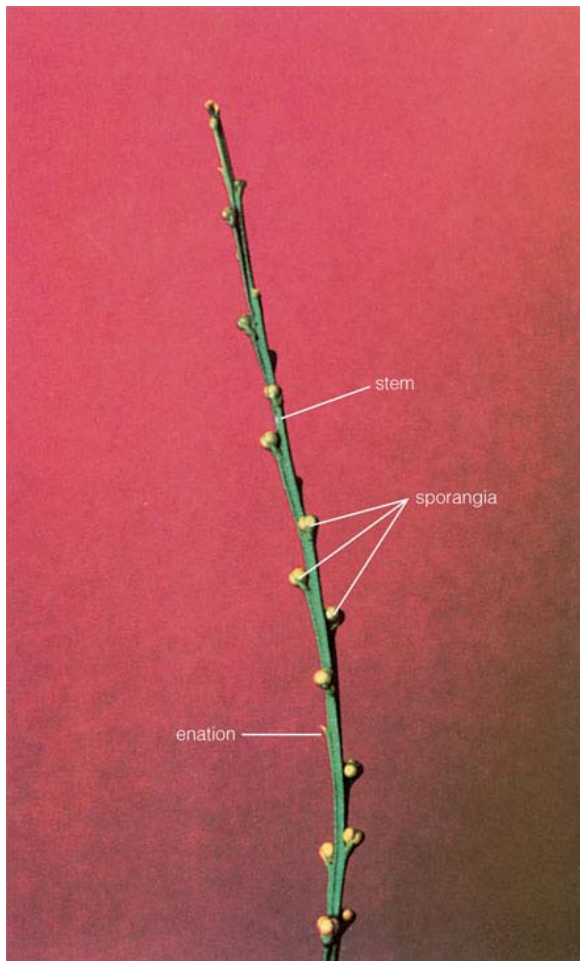


Figure 23.13. A branch of the whisk fern *Psilotum nudum*. Sporangia in all species of this genus occur in aggregations of three (or occasionally more) that are fused together.

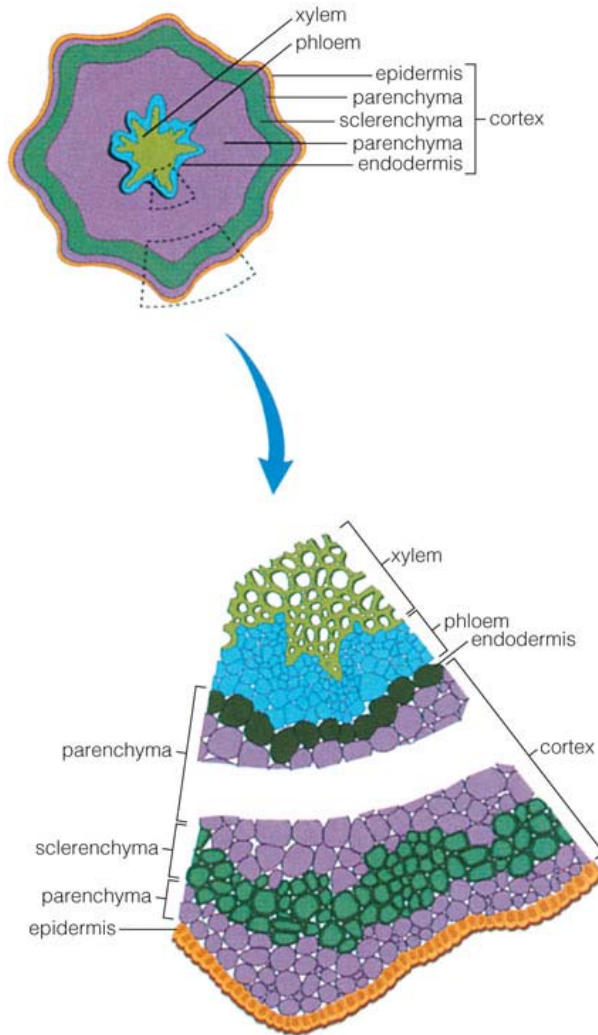


Figure 23.14. A cross section of a *Psilotum* stem

different cell types, and finally an epidermis with a thick cuticle and many stomata. Cortex cells often contain chloroplasts, making the entire stem appear green.

Psilophytes are homosporous. Sporangia are borne on short stalks in the axils of enations and typically are fused into groups of two (*Tmesipteris*) or three (*Psilotum*). Meiosis occurs inside sporangia, forming tetrads of spores. The spores are released and, if they land in a suitable habitat, germinate and form a bisexual gametophyte.

The gametophytes lack chlorophyll and associate with endomycorrhizal fungi. Because they are nonphotosynthetic and are fed by fungi, the gametophytes may grow below the soil surface or in crevices in rocks or bark. When mature, they are quite elaborate. They bear rhizoids, grow from an apical meristem, and branch dichotomously. Some even have vascular tissue. Gametangia are scattered over the surface of the gametophyte; flask-shaped archegonia contain one egg each, and spherical antheridia contain spirally coiled, multiflagellate sperm.

The other genus, *Tmesipteris*, is an epiphyte with dangling branches. Although it lacks roots like *Psilotum*, it has leaves. The leaves have a single,

unbranched vascular strand, but they have evolved independently of the microphylls of lycophytes.

Ophioglossalean Ferns

The closest relative of the psilophytes (as determined by DNA comparisons) is a group of about 75 species of unusual plants called **ophioglossalean ferns**. These consist of several genera, including *Botrychium*, the grape fern (Fig. 23.15a) and *Ophioglossum*, the adder's-tongue fern (Fig. 23.15b). These small plants are members of the spring flora in temperate regions and also are found in disturbed or open tropical sites. A few are epiphytes. *Ophioglossum* has the greatest number of chromosomes of any plant, $2n$ being as high as 1,260 in some species.

Ophioglossalean ferns have unusual leaves divided into two segments: a spikelike fertile segment with an embedded sporangium, and a sterile segment expanded for photosynthesis. Unlike true ferns, the leaves are not coiled when young (see Fig. 23.21), the stems are upright rather than horizontal, and the sporangia are not of the distinctive type found in true ferns.

The roots of many ophioglossalean ferns also are distinctive. They run horizontally through the soil and produce shoot buds at intervals, allowing the plant to spread vegetatively. In addition, the roots have strong mycorrhizal relationships and lack root hairs.

Horsetails

The **horsetails**, or **sphenophytes**, consist of only one living genus, *Equisetum*, with about 25 species (Fig. 23.7c). *Equisetum* has a worldwide distribution, except for Australia and New Zealand. Many of these species live in moist habitats, but a few, such as *Equisetum arvense*, can grow in seasonally dry places. *Equisetum* contains silica in its stem epidermis, making it abrasive. In pioneer days, *Equisetum* was used to scour pots and pans--hence, it was commonly referred to as scouring rush. The bushy, branching structure of some species gives the genus its other common name, horsetail.



Figure 23.15. Two ophioglossalean ferns. (a) Grape fern. (b) Adder's tongue fern.

Horsetails can be weedy, and some are toxic to livestock and humans because they contain enzymes that break down thiamine. If ingested regularly, symptoms of deficiency can occur. Horsetails have been used medicinally throughout the world for urinary and kidney problems, as well as to reduce bleeding. Native Americans ate the young shoots raw or boiled as a spring green, before silica was deposited in the stems. The strobili were especially prized. Consuming horsetail was considered cleansing and good for the blood.

Sphenophytes originated in the Devonian period, and like the lycophytes they were important members of the Coal Age swamp forests. They were quite diverse, ranging from vines to trees. One example, *Calamites*, looked very much like a giant version of *Equisetum*, with creeping rhizomes and secondary growth, and it grew in dense stands (Fig. 23.16). The sporophytes of all sphenophytes, living and extinct, are easily recognized by their jointed and ribbed stems and their whorled appendages.

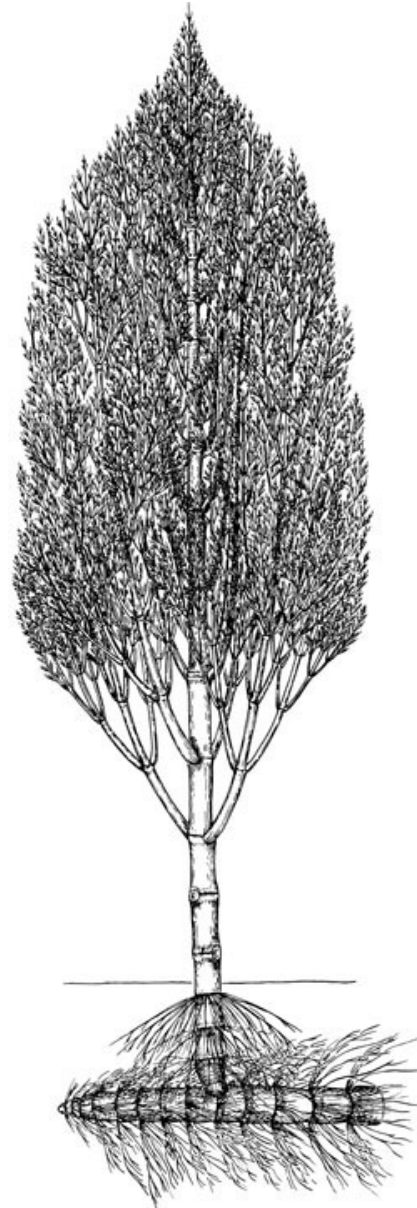


Figure 23.16. a reconstruction of *Calamites*, a Coal Age tree, showing the aboveground system of branching stems, the horizontal rhizome, and roots.

Living horsetails are typically less than 2 m tall, but one tropical species reaches 5 m in height. All horsetails are perennial and have a branched rhizome from which upright stems arise. Depending on the species, the upright stems may branch profusely, sparingly, or not at all. They are marked by vertical riblike ridges and distinctly jointed nodes. A whorl of branches or leaves, or both, occurs at each node. The leaves are relative small and lack chlorophyll. The leaves of living *Equisetum* are microphylls, but they were derived by reduction from megaphylls. (Many extinct sphenophytes had megaphylls.) Roots emerge from rhizome nodes but may also arise from stem nodes if the stem is in contact with moist soil.

The stem anatomy of *Equisetum* is quite distinctive, with a large central cavity surrounded by a ring of vascular bundles and smaller cavities, called **vallecular canals** (Fig. 23.17). The stems are hollow except at the nodes, where a diaphragm of tissue forms a solid joint (not shown in Fig. 23.17). The biophysicist Karl Niklas has shown that these hollow stems are remarkable strong and rigid per unit of weight—stronger, in fact, than solid stems. Smaller canals, called **carinal canals**, are in the center of each vascular bundle. Each bundle consists of two arms of xylem extending from the carinal canal, and phloem lies between the arms. Some species contain vessels with the xylem, but most contain only tracheids. An endodermis may surround each bundle or it may encircle the stem and include all vascular bundles. The cortex consists of parenchyma and chlorenchyma; thus, the stems appear green.

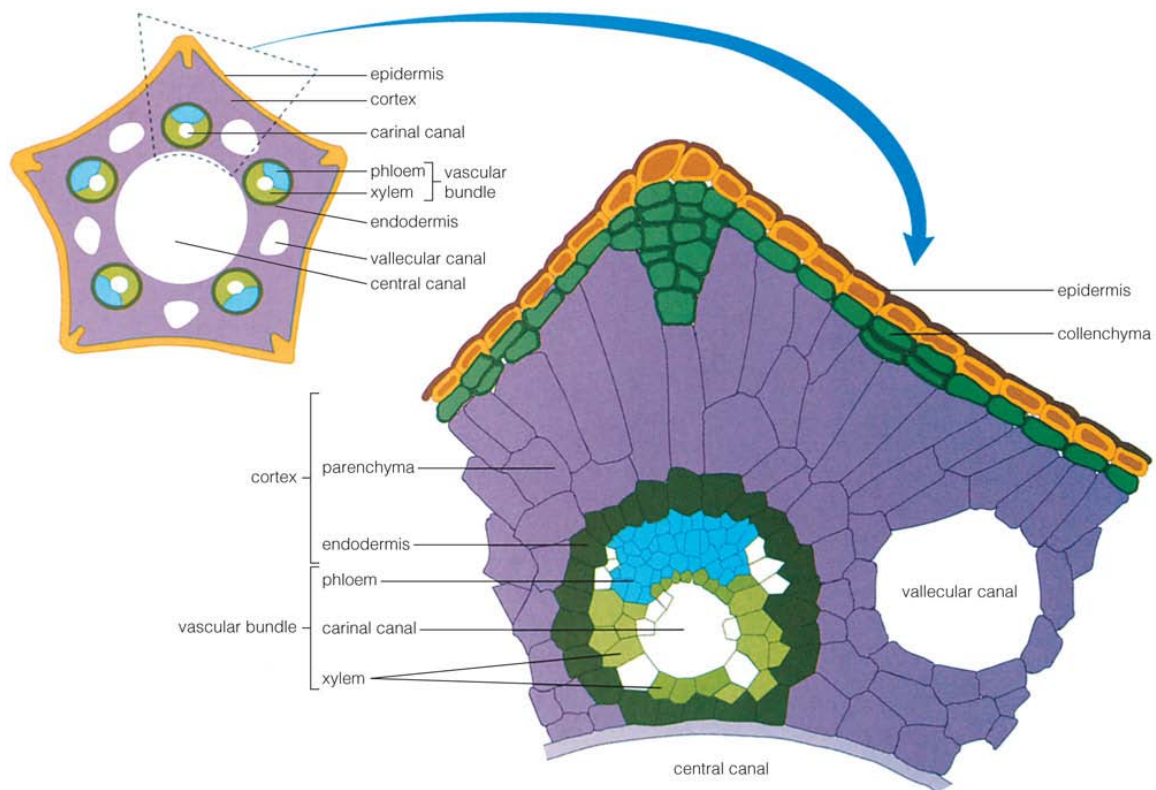
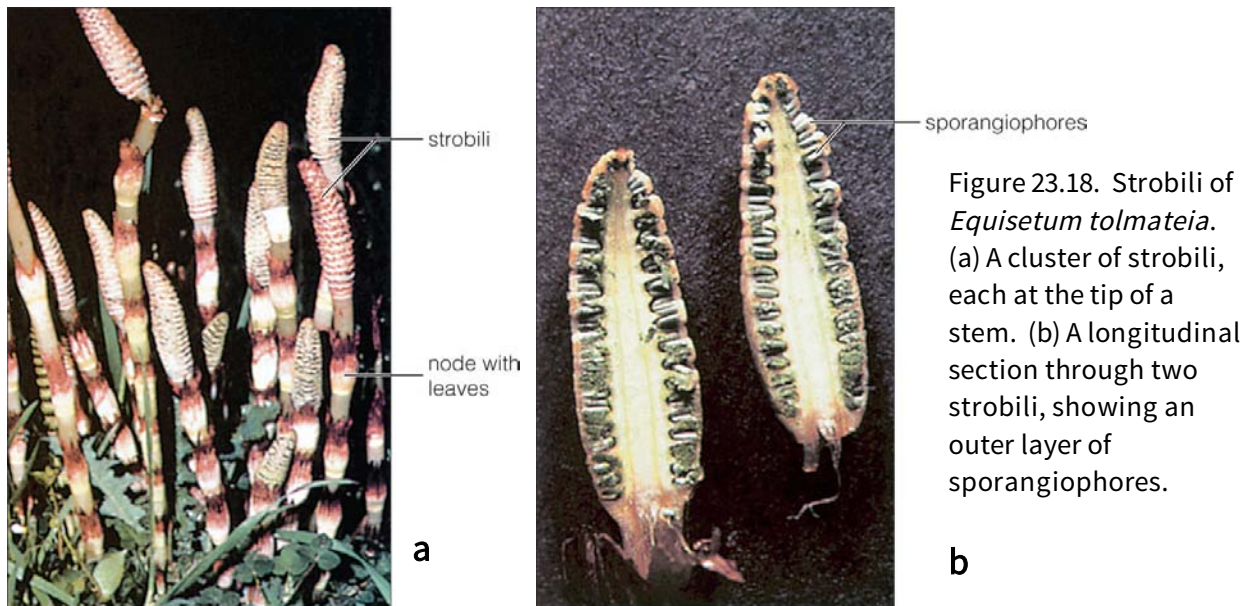


Figure 23.17. A cross-section of a horsetail (*Equisetum*) stem.

Sporangia are borne in strobili on special structures called **sporangiophores** (sporangium-bearing stalks). These are umbrella-shaped structures borne at right angles to the long axis of the strobilus (Fig. 23.18). In most species, strobili occur at the apex of ordinary shoots, but in a few species, they occur only on special shoots that may lack chlorophyll.



Equisetum is considered to be homosporous because it produces one kind of spore. Surprisingly, however, some gametophytes are unisexual. Some extinct sphenophytes were heterosporous. Horsetail spores are green and thin-walled, with long, ribbon-like elaters attached to the spore wall. The elaters coil and uncoil in response to humidity, and they help disperse the spores when the sporangium splits open at maturity.

Marattialean Ferns

In appearance, **marattialean ferns** are similar to true ferns, possessing compound leaves that are coiled when young (Fig 23.19). A synonym for the large, compound leaves that characterize marattalian ferns and true ferns is **frond**. However, like ophioglossalean ferns, they have upright stems, and they possess a distinctive sporangium, which is different from those of true ferns. These plants are largely tropical and possess gigantic leaves that arch above short, squat stems. Having a long and extensive fossil record, they were an important element in the Coal Age swamp forest flora.

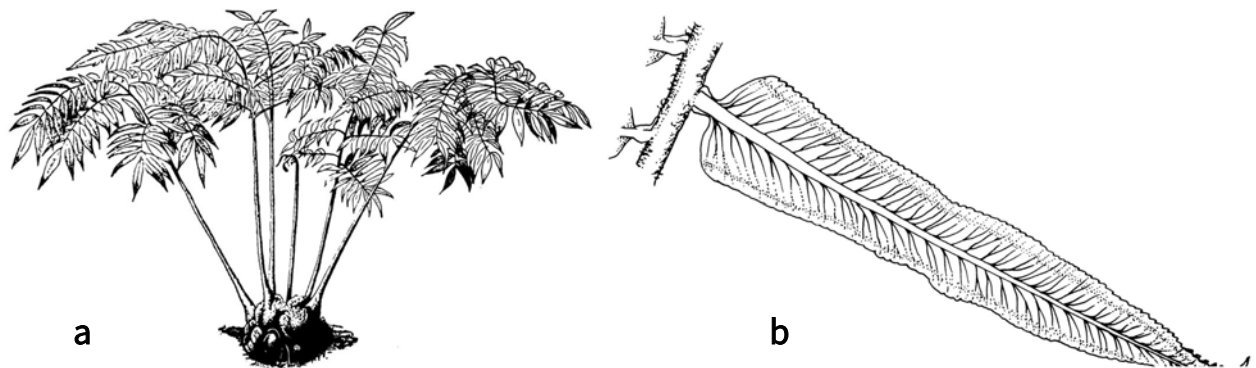


Figure 23.19. A marattialean fern. *Angiopteris evecta*. (a) The above-ground stem and leaves. (b) One pinna.

True Ferns

True ferns make up the majority of living monilophytes, with at least 12,000 species known (Fig. 23.7d). Traditional taxonomic treatments of the ferns divide them into five orders to encompass the vast diversity of forms. Systematic studies have revealed that two of those taxonomic orders, Marattiales and Ophioglossales are not in the true fern lineage, and that two other orders, Salviniiales and Marsileales, are really an unusual subclade of the true fern lineage (see endnote "PLANTS, PEOPLE, AND THE ENVIRONMENT: Diversity among the Ferns")

The true fern lineage contains the ferns familiar to us as ornamentals and wild plants of shady woods and streams (Fig. 23.20). They are readily distinguished from other monilophytes by a single feature: a unique type of sporangium called a **leptosporangium** (Fig. 23.20a). Leptosporangia are distinctive in that they each originate from a single cell in the leaf, have a long thin stalk, have a wall one cell layer in thickness, and have an active form of splitting open--a strip of thick-walled cells called an **annulus** flicks the spores out of the sporangium. The sporangia of all other tracheophytes are called **eusporangia**; these originate from several initial cells, have very short or absent stalks, have thick walls, and never have an annulus. Because this single character reliably identifies true ferns, they sometimes are called leptosporangiate ferns.

The leptosporangia are grouped into distinctive clusters called **sori** (singular, *sorus*). Sometimes each sorus is protected by an overarching umbrella-like structure called an **indusium** (Fig. 23.20b,c), and sometimes the sori are protected by the edge of the leaf curling over them as a false indusium (Fig. 23.20d).

True Fern Sporophytes Typically Have Underground Stems

True fern sporophytes typically extend themselves by an underground perennial rhizome. The rhizome grows from its tip. Roots and leaves arise from nodes (Fig. 23.21). The rhizome can remain alive for centuries in some fern species, spreading over a considerable area. Some bracken fern (*Pteridium aquilinum*) clones are thought to be 500 years old. Most ferns have no stems aboveground; only leaves are visible. Young fern leaves are at first tightly coiled **fiddleheads**. Coiling protects their delicate meristematic tissue as it is pushed up through the soil by the elongating petiole. Above the soil, the leaf uncoils from the base upward, continuing to grow by cell division at the tip.

A typical leaf has a well-developed epidermis with stomata, particularly on the lower surface. The leaf mesophyll may be differentiated into palisade and spongy layers. The petiole is prolonged into a **rachis** on which are attached secondary and tertiary leaflets, called **pinnae** and **pinnules**, respectively.

The vascular tissue of fern stems is occasionally a solid strand, but more typically it has a well-defined pith of parenchyma cells surrounded by vascular bundles. The xylem of a few genera, such as the bracken fern and the aquatic fern *Marsilea*, contains vessels. Sieve cells are present in the phloem (Fig. 23.22).

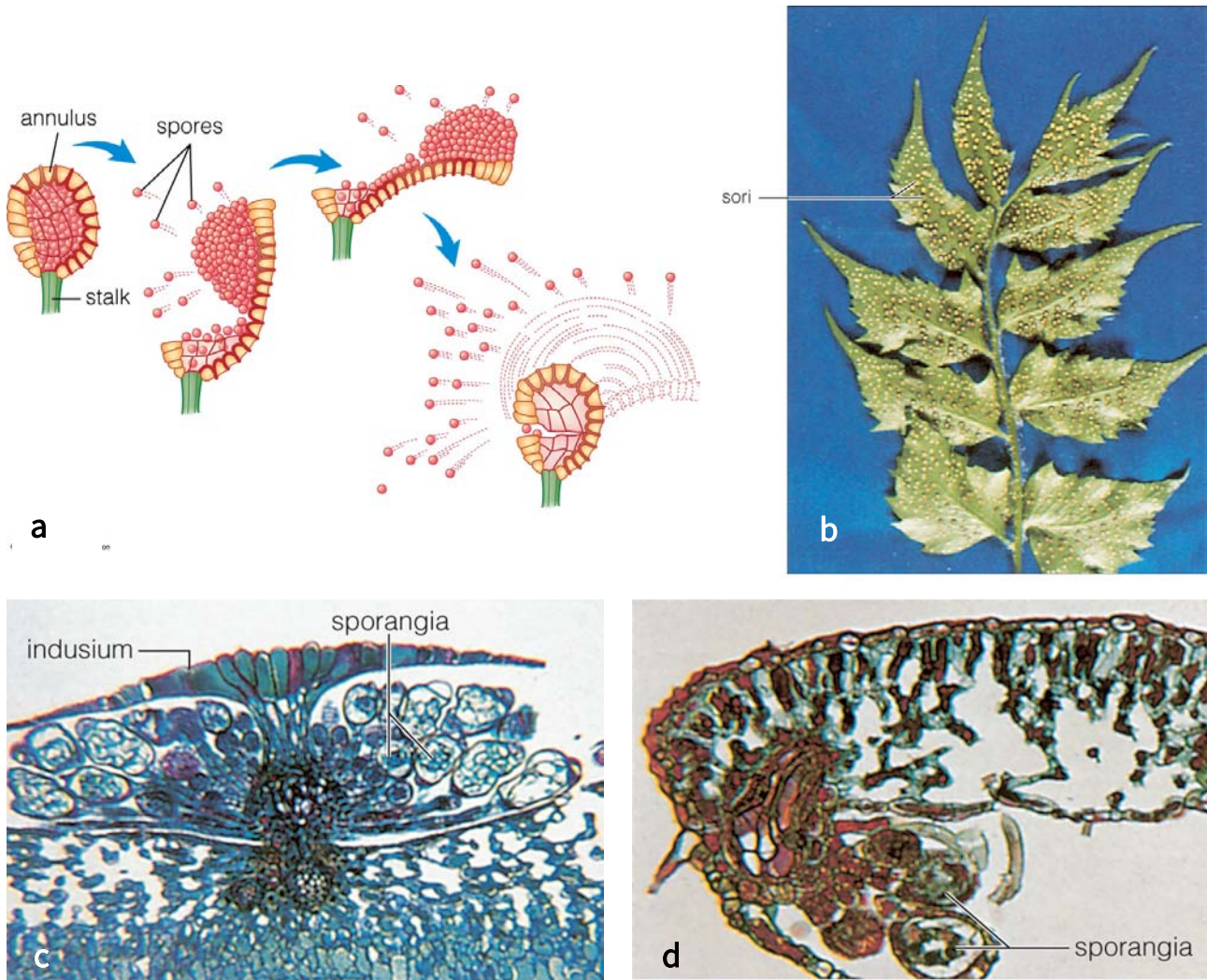


Figure 23.20. Components of true ferns. (a) A leptosporangium and the role of the annulus in spore dispersal. (b) The underside of a holly fern (*Cyrtomium falcatum*) leaf, showing many scattered sori. (c) A section of one sorus (of the fern *Crotonium*), showing the umbrella-like indusium that shelters the sporangia. (d) The false indusium (the rolled leaf edge of cliff brake (*Pellaea rotundifolia*)).

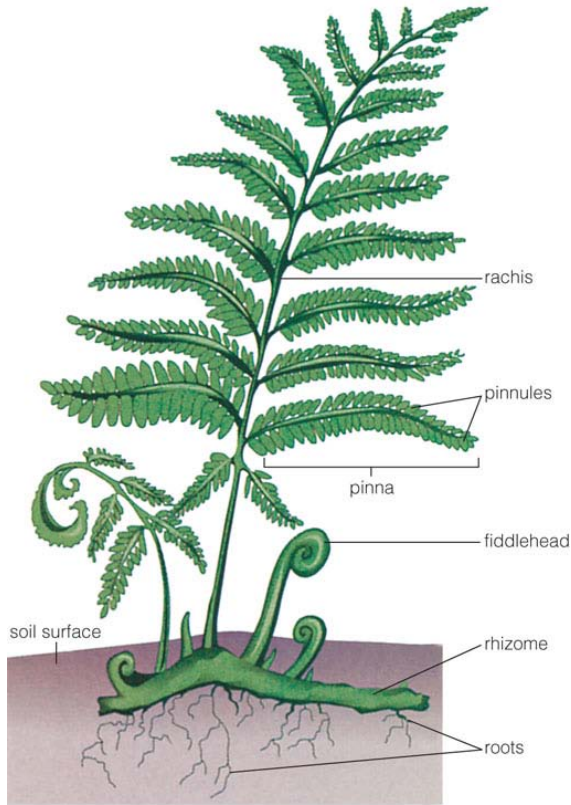


Figure 23.21. The lady fern, *Athyrium filix-femina*. The stem is a horizontal, underground rhizome. Only the leaves (fronds) project above ground. Young leaves emerge through the soil as tightly coiled fiddleheads. Roots anchor the rhizome to the soil and take up nutrients and water.

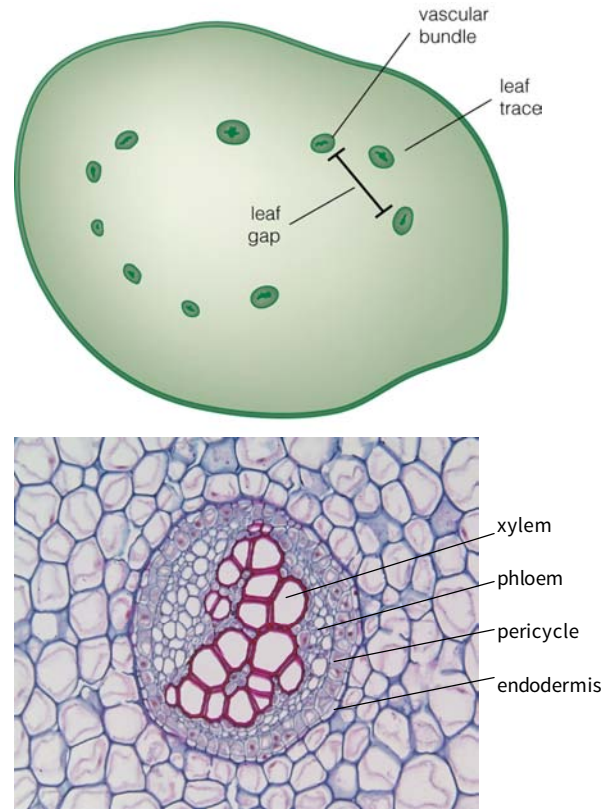


Figure 23.22. A *Polypodium* stem cross section. (top) The entire rhizome, showing the arrangement of the vascular system. In this species, the vascular cylinder surrounding the pith is broken into discrete bundles by gaps where vascular tissue (leaf traces) peel off to enter megaphylls. In three dimensions, the bundles merge and gaps form in other places. (bottom) Details of one vascular bundle.

Sexual Reproduction Usually Is Homosporous

The life cycle of a true fern is shown in Figure 23.23. Fern sporophytes become sexually mature in 1 to 10 years. When the fern is mature, sporangia develop. Not all leaves are fertile (capable of producing spores), and in some species fertile leaves have a different shape than nonfertile leaves. Clusters of leptosporangia occur most commonly on the lower surface or margins of pinnae along veins. The indusium that covers them (Fig. 23.23b) protects immature sporangia and may shrivel and fall away before spores are shed.

Spores develop within the stalked sporangia (Fig. 23.23c). The annulus in the sporangium wall plays a role in spore dispersal. As it dries, it bends backward,

ripping the sporangium open and then snaps forward, flinging the ripe spores as far as 1 to 2 m. Gravity, wind, water, and even electrostatic factors may carry the spores even farther. In temperate zones, spores tend to be released in the fall, at the end of the growing season; in the tropics, they may be released any month of the year. Charles Darwin, sailing hundreds of kilometers from shore on the Beagle, recorded in his journal that some of the air samples he collected contained fern spores (see the endnote: "PLANTS, PEOPLE, AND THE ENVIRONMENT: Fern Spores).

Fern spores contain phytochrome and other unidentified pigments. Some contain chlorophyll, and the spores of many species require light to germinate. Some species can be inhibited from germinating by exposure to far-red light and stimulated to germinate by red light. Their requirement for red light inhibits spores from germinating if there is not enough sunlight present for adequate growth.

When a spore germinates, a short filament of cells is produced, resembling a moss protonema. Soon, the apical cell of the filament begins to divide in many directions, producing a green thallus. It is usually heart-shaped and 1 to 2 cm across (Fig. 23.23d); however, it can be mitten-shaped, ribbon-shaped, or filamentous and highly branched. Rhizoids attached to the lower surface anchor the plant to the soil. Most fern gametophytes require 2 to 3 months to mature, but extremes exist. Some species colonizing disturbed habitats can mature in only 4 to 6 weeks, whereas the chain fern *Woodwardia radicans*, an inhabitant of the understory of cold-temperate conifer forests, requires 2 years.

We would expect the homosporous true ferns to have bisexual gametophytes. Yet some species produce functionally unisexual gametophytes, because the first gametophyte in a particular location to develop archegonia releases a substance that stimulates younger gametophytes to produce only antheridia. This mechanism prevents self-fertilization. Self-fertilization does occur in a few species with bisexual gametophytes; but in many cases, the gametangia mature at different times.

Sperm are helical, with as many as 100 flagella. When free water is present, the antheridium bursts (Fig. 23.23e), releasing the sperm. Archegonia produce an attractant, which guides the sperm toward them. Archegonial necks spread open in the presence of free water, making a path for sperm to reach the egg (Fig. 23.23f). As soon as one sperm has penetrated an egg, the plasma membrane of the egg changes, and no other sperm cells can penetrate.

The diploid zygote cell develops into an embryo, with foot, shoot, and root regions (Fig. 23.23g,h). Although one gametophyte may contain many zygotes, only one or two will mature into embryos. In a short time, an embryo develops into a young sporophyte that is larger than the parent gametophyte (Fig. 23.23i) and becomes nutritionally independent of the gametophyte.

Ferns Have a Variety of Alternative Means of Reproduction

Ferns have a number of ways to propagate vegetatively. In some species, miniature plantlets form on mature leaves and break off, growing into new plants. Other species, called walking ferns, produce propagules at the tip of a frond where it touches the soil. The fern can thus "walk" forward by sequentially forming new plants at the tip of each new frond. Gametophytes also can reproduce vegetatively.

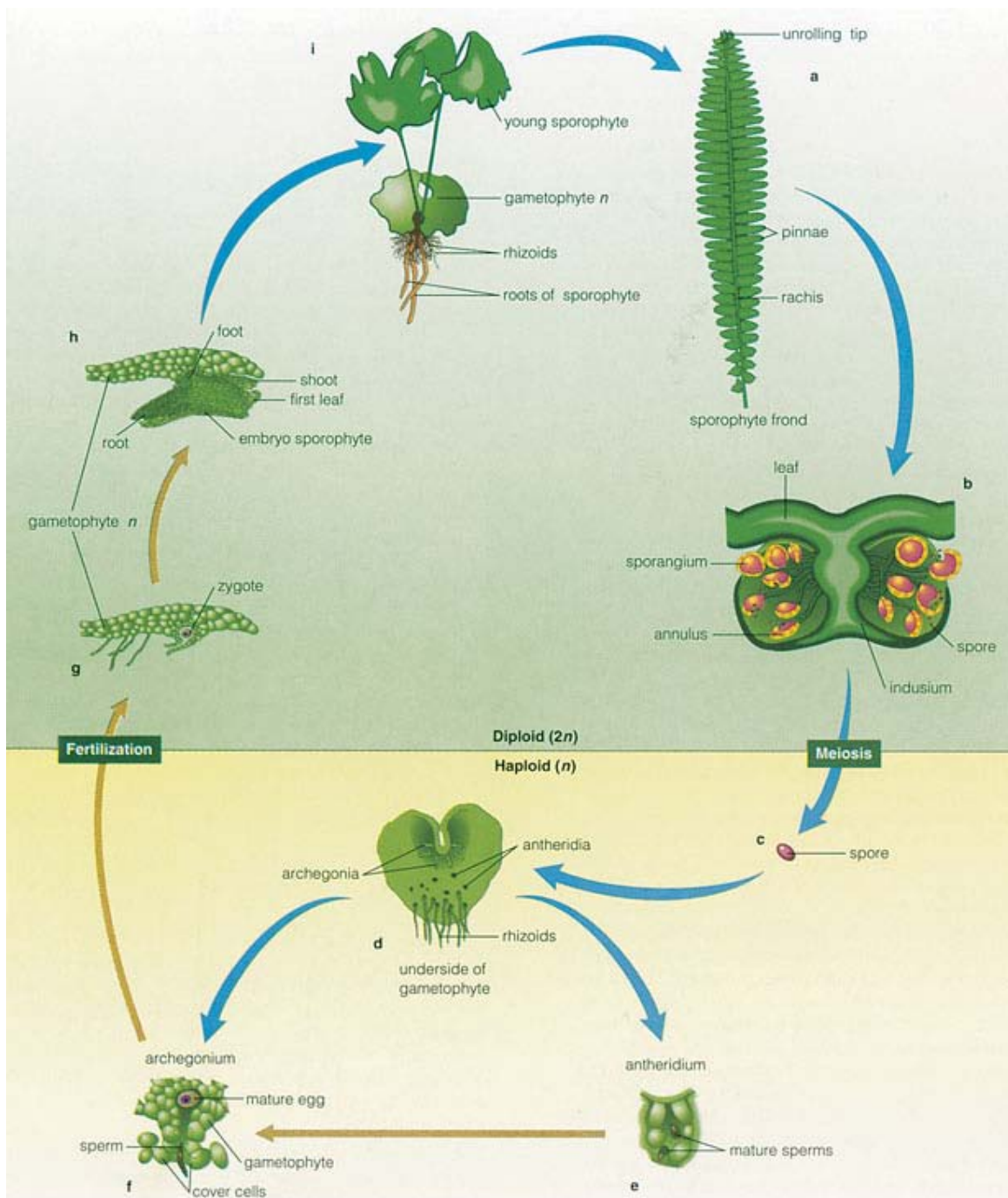


Figure 23.23. The life cycle of a true fern. (a,b) On the underside of a sporophyte leaf are many clusters (sori) of leptosporangia. (c) Meiosis occurs in each leptosporangium, resulting in many haploid spores. (d,e,f) A spore can germinate and grow by mitosis into a heart-shaped gametophyte. The sperm produced by the antheridia are motile and swim through a film of water to reach archegonia and fuse with an egg. (g,h,i) The resulting zygote cell is retained within and nourished by gametophyte tissue. It develops into an embryo and then into a young sporophyte that is rooted in the soil and independent of the gametophyte.

There also are several variants to the normal alternation of generations in a life cycle. A surprising number of fern species can, under certain conditions, produce diploid gametophytes directly out of sporophyte tissue (usually leaf tissue). These gametophytes function normally, but the gametes they produce also are diploid. On fertilization, the resulting sporophyte will have double the chromosome number of the previous generation. This form of reproduction is called **apospory** (without spores). In effect, a new species has been created by a single fertilization event. Many ferns have large numbers of chromosomes, the result of numerous past apospory events.

Some ferns engage in **apogamy** (without gametes), in which gametophytes produce sporophytes without any fusion of gametes. This variation occurs when free water for fertilization is lacking. The resulting sporophytes will be haploid, but eventually can undergo normal meiosis by compensating for the haploid chromosome number. Apospory is a relative rare event, but some ferns reproduce routinely or solely by apogamy.

Ferns Have Ecological and Economic Importance

Ferns are most common in the understory of humid-temperate and tropical forests. They are widely distributed, however, and also grow in arctic and alpine tundra, saline mangrove swamps, semiarid deserts, and on coastal rocks swept by salt spray. Ferns can provide the bulk of biomass in some tropical forests and dominate the understories of some temperate conifer forests. Some ferns--such as *Lygodium* (climbing fern), *Salvinia* (water fern), and *Pteridium aquilinum* (bracken)--are weeds; they smother other vegetation, clog waterways, and poison livestock.

Throughout their life cycle, ferns are remarkably independent of animals. Animals are not essential vectors for spores, sperm, or embryos. Although ferns rarely have mechanical defenses such as thorns, stinging hairs, or hard leaves, animals generally avoid feeding on ferns because of poisonous or unpalatable chemicals present in many species.

Humans have found uses for certain ferns at certain life cycle stages. In the fiddlehead stage, leaves of some species are edible, and these are eaten by people in many cultures. The leaves of other ferns are used as basket-making material. Florists mix fern fronds with flower arrangements, and nurseries propagate ferns as popular indoor houseplants and outdoor landscaping plants. Biologists have found fern gametophytes to be excellent subjects for research on physiology and plant development.

KEY TERMS

annulus	megaspores
apogamy	microsporangia
apospory	microspores
carinal canals	monilophytes
dichotomously branching	ophioglossalean ferns
enation	pinnae
eusporangia	pinnules
frond	rachis
fiddleheads	rhizophore
heterospory	seedless vascular plants
horsetails	sori
indusium	sphenophytes
lepidodendrids	sporangiophores
leptosporangium	sporophyll
ligule	strobili
lycophytes	tracheophytes
marattialean ferns	vallecular canals
megagametophyte	whisk ferns
megaphyll	zosterophyllophyta
megasporangia	

SUMMARY

1. Early tracheophytes, the seedless vascular plants, number about 14,000 species. Their shared traits include a well-developed, lignified vascular system containing tracheids and, rarely, vessels, a branched independent sporophyte, and a free-living but reduced gametophyte. The life cycle is sporophyte-dominant, and the sporophytes have a well-developed epidermis with cuticle and stomata. Sporophyte dominance was key to success on land.
2. Early tracheophytes were leafless and rootless stems, but evolution was rapid during the 40-million-year Devonian period. Microphylls, megaphylls, true roots, secondary growth, wood, and seeds all appeared for the first time in the Devonian.
3. Early tracheophytes predominated in the world's vegetation during much of the Paleozoic era. Diversity of form peaked in the Carboniferous period, 360 to 286 million years ago. *Calamites* and *Lepidodendron*, related to modern horsetails and club mosses, were major forest trees during this period. Their fossil remains are mined today as coal. Other Carboniferous plants included ferns and early seed plants, the seed ferns. Many forms of early tracheophytes were extinct by the end of the Paleozoic.

4. The first tracheophytes were rhyniophytes. These bridged the gap between bryophytes, with relatively small sporophytes and unlignified vascular systems, and vascular plants, with branched sporophytes and lignified xylem tissue. Tracheophytes divided into two major lineages: lycophytes and monilophytes. Monilophytes later gave rise to the seed plants.
5. The lycophytes consist of three living lineages, all of which occur in North America: *Lycopodium* (and a number of related genera), *Selaginella*, and *Isoetes*. The lepidodendrids are an extinct group related to *Isoetes*. All share microphylls and laterally attached sporangia.
6. Sporophytes of *Lycopodium* and related genera (club mosses) have true roots, stems, and microphylls. Sporangia are borne on special microphylls called sporophylls, which may or may not be clustered into cones or strobili near the ends of upright stems. Club mosses are homosporous, and the spores produce small gametophytes that are usually subterranean, surviving by a symbiotic relationship with fungi.
7. *Selaginella* (spike moss) is heterosporous, having megasporangia that produce megaspores and microsporangia that generate microspores. Megaspores develop within the spore wall into megagametophytes; microspores grow within the spore wall into microgametophytes. Gametophytes are reduced relative to those of homosporous plants. The developing embryo is fed by the megagametophyte.
8. Sporophytes of *Isoetes* (quillwort) have a small tuft of grasslike microphylls and a basal corm. They grow in wet areas, often beneath standing water. They are heterosporous and have secondary growth.
9. The monilophytes include four distinct, closely related lineages. Most of the monilophytes have traditionally been thought of as ferns. The monilophytes all have megaphylls or leaves reduced from megaphylls. Most have roots, and they all share a distinct order of genes on the chloroplast chromosome, which differs from the order found in the bryophytes and lycophytes.
10. The psilophytes, or whisk ferns, are represented by only two living genera, *Psilotum* and *Tmesipteris*. Sporophytes of *Psilotum* consist of a branched, underground rhizome with rhizoids and an upright, green, branched stem with highly reduced leaves called enations. Psilophytes are homosporous, and the spores produce small, non-photosynthetic gametophytes, which are nourished by symbiotic fungi. Each gametophyte produces both male and female gametes. The embryo sporophyte is at first dependent on the gametophyte but in time becomes independent. The ophioglossalean ferns are closely related to the psilophytes. These are small temperate and tropical plants with unusual leaves consisting of a sterile, photosynthetic segment and a fertile, sporangium-bearing segment.
11. The sphenophytes, or horsetails, consist of a single genus, *Equisetum*. Sporophytes have uniquely jointed, ribbed, hollow stems. Whorls of reduced leaves

and/or branches are present at the nodes. True roots are present, and vessels are found in the xylem of some species. Sporangia are borne on sporangiophores grouped into complex strobili. Horsetails are homosporous, and spores produce small, photosynthetic gametophytes. Extinct sphenophytes were heterosporous trees or vines and were important members of the Coal Age swamp flora.

12. The marattialean ferns are a distinct lineage that resemble the true ferns, but lack leptosporangia and rhizomatous stems. They are large tropical plants.

13. The true ferns consist of about 12,000 species. This large clade contains a number of subclades, including two traditional orders of aquatic ferns--the Marsileales and the Salviniaceae--and the tree ferns. The group is homosporous, except for the aquatic ferns, and is distinguished by leptosporangia. These form from a single initial cell, have a thin, stalk and wall around the spores, and usually have an annulus that aids in splitting open the sporangium and dispersing the spores.

14. All true ferns are herbs (no secondary growth), and except in the tree ferns, the stem is an underground rhizome; only fern leaves (fronds) appear above ground. Leaves are megaphylls. Vessels are present in some species. Sporangia, located on the underside of leaves, are usually clustered into sori and often protected by an indusium. Spores germinate to produce small, photosynthetic, thalloid gametophytes.

15. Fern gametophytes and sporophytes sometimes develop by alternative pathways in the life cycle. Gametophytes can produce haploid sporophytes by the process of apogamy, and sporophytes can produce diploid gametophytes by the process of apospory.

Questions

1. The early tracheophytes include several lineages that today are relicts of what they once were. Explain in what ways these groups are relicts.
2. Why did the plant invasion of land not occur until the Silurian (or possibly Ordovician) period?
3. During which periods and eras were early (seedless) tracheophytes the dominant form of vegetation on land? Describe the composition of a Carboniferous (Coal Age) forest as an example of vegetation dominated by early tracheophytes.
4. In what ways do seedless tracheophytes exercise more control over their internal water balance than do bryophytes?
5. Why can one say that *Psilotum* is not a relict of the rhyniophytes?

6. Describe the difference between a homosporous and a heterosporous life cycle.

7. In mosses, the sporophyte is attached to and dependent on the gametophyte. In ferns, however, the two generations live independent lives. How might this separation be important for the development of the larger, more complex fern sporophyte?

PLANTS, PEOPLE, AND THE ENVIRONMENT: *Sporophyte Prominence and Survival on Land*

Two conspicuous trends in early land plant evolution are the elaboration of the sporophyte and the reduction of the gametophyte. Natural selection for more spores might explain the elaboration of the sporophyte but not its prominence in the life cycle, nor the corresponding reduction of the gametophyte. Why was the sporophyte phase favored over the gametophyte phase in the early stages of land plant evolution? Several hypotheses have been put forward to explain this trend. Some scientists propose that the sporophyte is protected against many deleterious mutations in its genes, because it is diploid and can thus carry harmful mutations as recessive alleles. The haploid gametophyte, with only one set of genes, is unable to compensate for a mutated gene by balancing it with a normal version. Evolution, therefore, favored a reduced role in the life cycle for the vulnerable gametophyte and increased prominence of the sporophyte. In addition, the greater genetic diversity of the sporophyte, with two sets of genes, over the gametophyte would have given it greater capacity to respond to the environment.

Another hypothesis suggests that plants elaborated their sporophytes not because of a genetic superiority of the sporophyte but because gametophytes were limited by the sperm's need to swim to the archegonium. In the competition for resources such as light, water, and nutrients, the gametophytes could grow no larger than the effective dispersal range of the sperm and were limited to locations where water for the sperm to swim was present. The sporophyte, on the other hand, was not subject to these constraints and was able to increase in size to compete with nearby plants. In an aquatic environment, gametes and spores are equally good at dispersing, and in many algal groups, both are flagellated. On land, spores lost their flagella, became surrounded by weather-resistant walls, and were aided in dispersal by complex sporangial mechanisms, such as the peristome teeth in moss capsules. They became very effective at getting around. Gametes, however, need to fuse with one another to accomplish sexual reproduction. For this, they need water. Gametes are poorly adapted to a terrestrial environment. Thus evolution may have favored

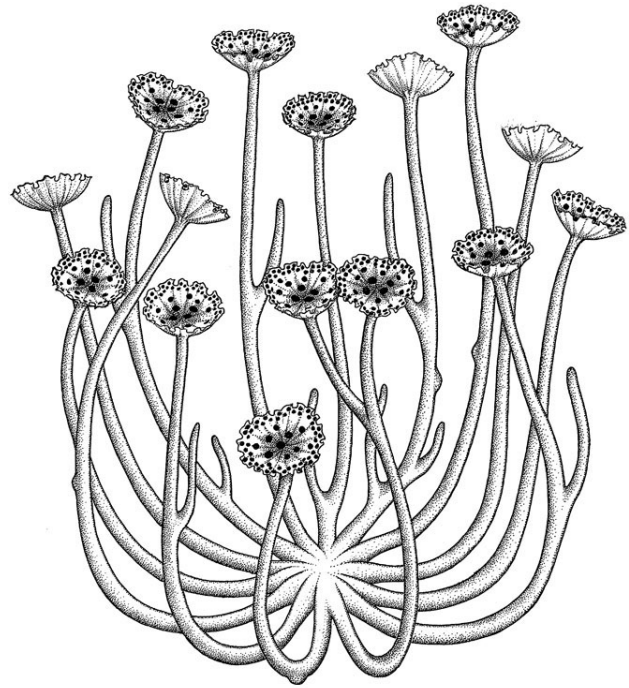


Figure. A reconstruction of the Devonian gametophyte *Sciadophyton*. Gametangia are borne on the terminal disk-shaped gametangiophores. (Kenrick and Crane 1997. P. 304. Fig. 7.29)

an increase in the prominence of the sporophyte, and a decrease in the prominence of the gametophyte, in the life cycle of the plants.

The shift from gametophyte prominence in the bryophytes to sporophyte prominence in the tracheophytes is dramatic, and no living intermediate plant exists. However, it has been recently discovered that some early fossil plants, such as *Sciadophyton*, are actually gametophytes of protracheophytes. These gametophytes were as large as the sporophytes, grew upright, branched profusely, and bore sunken gametangia at the tips of their stems (Figure).

PLANTS, PEOPLE, AND THE ENVIRONMENT: *Coal, Smog, and Forest Decline*

All human societies burn fuel, thereby releasing byproducts into the environment. The particular material that is used as fuel and the conditions under which it is burned produce very different types and volumes of byproducts. Technological societies today use fuel for heating, cooking, industrial processes such as smelting, producing mechanical energy, and creating electricity. Although water, wind, sunlight, and nuclear fission are also used for some of the same objectives, most of our demand for energy is met by the carbon-based fuels of wood, natural gas, and crude oil.

It is ironic that we depend on carbon-based fuels, because carbon is a rather uncommon element. It makes up only 0.04% of the earth's mass. Recall that photosynthesis does not create carbon; it merely rearranges it from part of a gas to part of a sugar. The supply of carbon is finite on Earth; therefore, the rate at which it cycles through the biosphere is very critical to life.

Coal is not just a form of carbon, like graphite or diamonds. It is a mixture of organic substances, moisture, and minerals. The major elements that make up the chemical compounds are carbon, hydrogen, oxygen, nitrogen, and sulfur. Coal begins as plant debris deposited in such a way that oxygen is limited. Consequently, the litter is only partially decomposed. Over time, the deposit of litter thickens. The next process in coalification is burial of the organic material in sediment. Over time, if the sediment is deep enough, pressure and heat compress the material further, turning it into a soft rock we call coal.

The heat released by coal when it burns depends upon the pressure and heat it was subjected to over geologic time. Standard names are given to coal of different heat value: lignite (which is the lowest grade), subbituminous coal, bituminous coal, and anthracite. Heat is typically measured in BTUs (British thermal units). One BTU = 252 calories, and 100,000 BTUs = 1 therm = 25,200 kilocalories. On average 1 metric ton of coal contains 278 therms. Coal satisfies about 30% of the world's annual energy demand.

Coal reserves are not uniformly distributed throughout the world. Of the earth's estimated recoverable coal reserves of 10 trillion metric tons, the United States has nearly 50%.

The availability of coal has been an economic boon but an ecological disaster for those countries with large coal reserves. Byproducts of coal burning include soot, volatile hydrocarbons, and oxides of nitrogen and sulfur. When the English had exhausted their wood reserves for fuel in the seventeenth century and began to burn coal, London became a notoriously dirty and noxious place to live. Fogs became thicker, because fog droplets could condense around soot particles. Fog became smog (smoke + fog). Another health hazard came from the nitrogen and sulfur oxides, which become strong acids in water and can cause respiratory diseases. As its population and its air pollution climbed in the twentieth century, London became infamous for "killer smogs"--smogs so unhealthy that people, particularly young people and the elderly, actually died from their effects. Tall smokestacks alleviated some of the problem locally, but winds then carried the pollutants elsewhere; in the case of England, the smog blew into the Baltic countries and into central Europe. The burning of soft coal, high in sulfur, is no longer allowed in London.

Central and Eastern Europe created their own problems. After World War II, Poland, Czechoslovakia, and Germany became heavily industrialized, burning sulfur-rich coal without smokestack scrubbers to remove sulfur oxides before they reach the atmosphere. As a result, millions of hectares of conifer forest in central and eastern Europe suffered a decline, especially noticeable after 1980. Symptoms include premature shedding of needles and cones, discoloration of needles, abnormal branching patterns, loss of mycorrhizal associations, slowed growth, and death. The combination of symptoms and the wide diversity of affected species do not suggest any known biologically caused disease. Forest ecologists believe that the decline is caused primarily by acid rain from coal burning and automobile exhaust.

In North America, major coal-fields exist in the Northwest Territories of Canada, in the Appalachian and Midwest regions of the United States, in North and South Dakota, and in the Four Corners area of Utah, Colorado, New Mexico, and Arizona (Figure). Much of the eastern coal has been mined in underground shafts, whereas western coalfields are open pits. In both cases, non-coal refuse is left above ground as polluting mine spoil that is very difficult for plants to invade.

Despite the ecological problems that result from the mining and burning of coal, it is likely to remain a prime source of energy for the world for decades to come. Alternative energy sources, such as nuclear fission and hydroelectric dams, have equally damaging or potentially more damaging consequences. We can expect continued technological advances that will clean up coal prior to burning, trap and recycle by-products after combustion, and restore the landscape after mining has ceased.

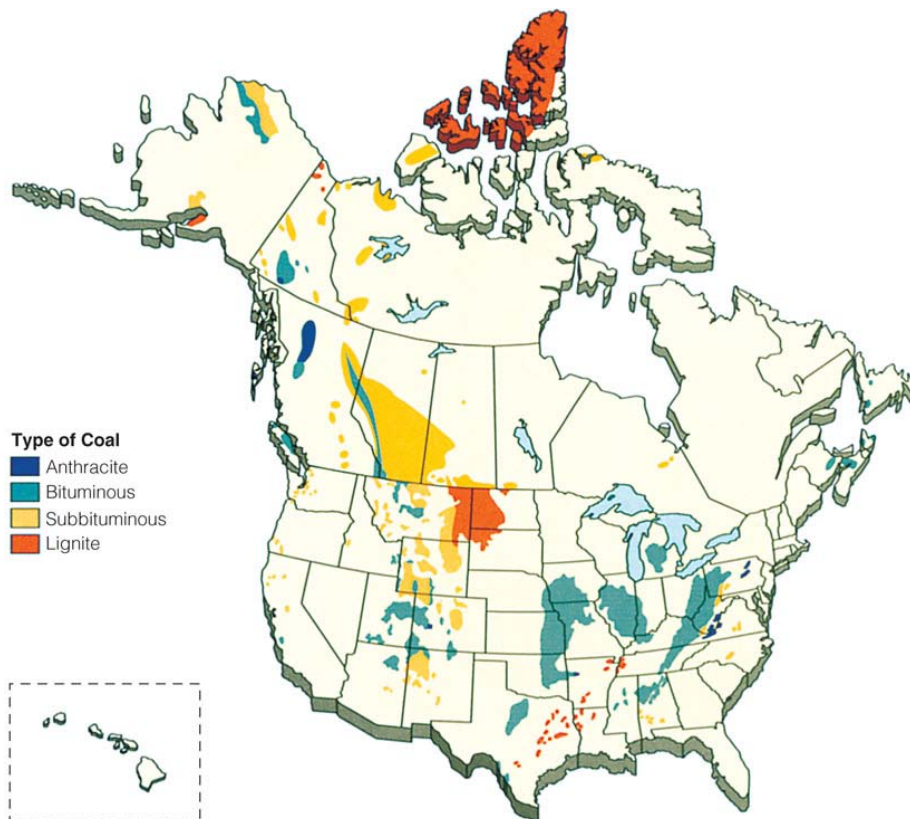


Figure. Locations of major coalfields in North America.

PLANTS, PEOPLE, AND THE ENVIRONMENT: *Diversity among the Ferns*

True ferns have an amazing variety of growth forms, besides the familiar lacy-leaved, moisture- and shade-loving herbs familiar to most of us. Some of them are so different from typical ferns that many people would fail to recognize them as ferns

One unusual group, called the climbing ferns, has leaves that grow continuously, eventually reaching lengths of over 30 m. Several of these, such as the Old World climbing fern, *Lygodium microphyllum*, have become serious pests in the southeastern United States, smothering trees and creating dangerous fire conditions.

One highly unusual group of ferns completes its life cycle floating or submersed in water. They are heterosporous and make hard, bean-shaped reproductive structures, which, like seeds, are extremely decay-resistant and may last years in the environment, enabling the plant to survive prolonged drought.

The lineage of water ferns is divided into two clades. In one clade, consisting of two genera, the plants are free-floating and never become attached to any substrate. One genus, *Azolla* (mosquito fern), lives in symbiosis with nitrogen-fixing bacteria and is used as a green manure to fertilize rice paddies in Asia. Three species are native in North America. Another genus is not native to North America but has been imported from the tropics and now grows wild in the warmer parts of the United States. Several species of *Salvinia* (Fig. 1a) can become pernicious weeds, clogging waterways and pushing out native vegetation. *Salvinia* has round leaves and lacks roots but has a modified leaf that is highly branched and looks superficially root-like.

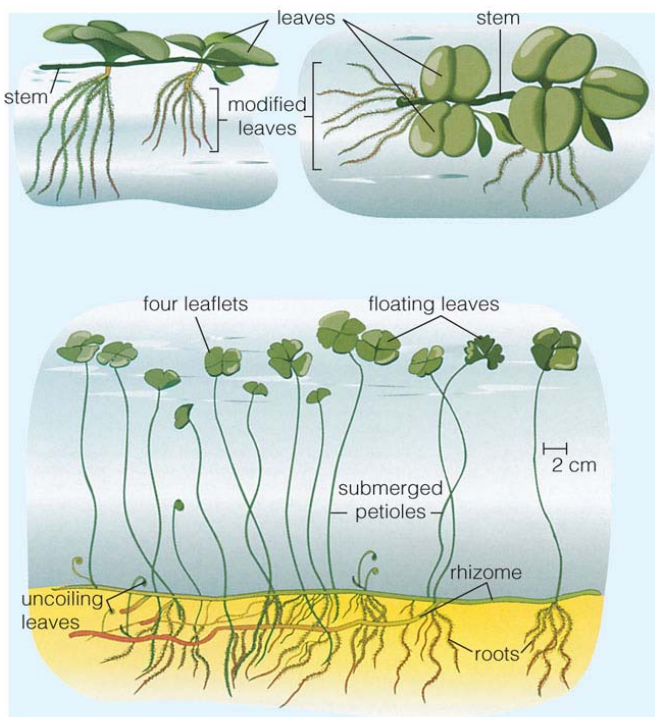


Figure. (a) *Salvinia*, a free-floating, heterosporous, aquatic fern. Each node has two round floating leaves and a third modified leaf, that is highly dissected and appears root-like. (b) *Marsilea*, a heterosporous, aquatic fern, which is rooted in mud. These ferns produce hard bean-shaped reproductive structures. (c) The tree fern *Alsophila* in a Puerto Rican forest.

The other clade of aquatic ferns has three genera: *Marsilea*, *Pilularia*, and *Regnellidium*. These ferns are rooted in mud and may be submersed, floating, or emergent. *Marsilea* (Fig. 1b) resembles a four-leaf clover (and is sometimes sold as such), while *Pilularia* lacks a leaf blade altogether. The petioles, however, coil like typical fern leaves. Both of these genera are native to North America.

Another clade of about 1,000 species of true ferns has achieved tree size, although no secondary growth occurs (Fig. 1c). Tree ferns are largely tropical, but they can be grown indoors as ornamental plants. They may form monocultures on disturbed sites and are abundant in some areas. Some species are endangered by land clearing for agriculture. The fibrous parts of the stems are used in the nursery trade as an epiphyte-growing substrate.

One strange group of ferns, the filmy ferns (family Hymenophyllaceae) has reversed the trend toward sporophyte dominance in vascular plants. Filmy ferns sometimes can persist indefinitely in the gametophyte stage of the life cycle, reproducing asexually. In some species, a sporophyte has never been seen.

PLANTS, PEOPLE, AND THE ENVIRONMENT: *Fern Spores*



Fern spores are incredibly hardy. They are resistant to ultraviolet radiation, low humidity, and very low temperatures. *Dryopteris* (wood fern) spores, for example, have been experimentally held at -254°C for 11 hours without their viability being affected. Fern spores can remain alive from several months to several years in the environment, but most of them land in inhospitable terrain and perish.

Consequently, fern spores are produced in prodigious numbers. Individual leaves typically release up to 750 million spores per year, and most ferns have 10-20 leaves per plant. *Dryopteris pseudo mas* probably holds the spore production record, releasing 1 billion spores per day per plant! The large number of spores produced by ferns, and their resistance to physical stresses, explain why ferns are the first plants to repopulate devastated areas.

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PPE (Sporophyte Prominence...) Kennick and Crane 1997, p. 304, Fig. 7.29.
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