Phylum Pteridophyta

The Great Majority of Pteridophyta Are Ferns

The Pteridophyta have traditionally been regarded as comprising only the ferns, with the whisk ferns being recognized more recently as reduced ferns not deserving of their status as a separate phylum. Recently, molecular comparisons have indicated that the horsetails, generally regarded as a separate phylum, represent a second major evolutionary line of pteridophytes (see page 399), so that they are now grouped together with ferns in a single phylum, Pteridophyta. Within this phylum, however, their relationships are still under active investigation.

Ferns have been relatively abundant in the fossil record from the Carboniferous period to the present (see pages 374 to 375, and Figure 18–1). There are about 11,000 living species of ferns, the largest and most diverse group of plants other than the angiosperms (Figure 17–22). It appears likely that the differentiation of modern ferns took place in the Upper Cretaceous period, after the formation of diverse forests of angiosperms increased the range of habitats into which ferns could radiate.

The diversity of ferns is greatest in the tropics, where about three-fourths of the species are found. Here, not only are there many species of ferns, but ferns are abundant in many plant communities. Only about 380 species of ferns occur in the United States and Canada, whereas about 1000 occur in the small tropical country of Costa Rica. Approximately a third of all species of tropical ferns grow upon the trunks or branches of trees as epiphytes (Figure 17–22).

Some ferns are very small and have undivided leaves. *Lygodium,* a climbing fern, has leaves with a long, twining rachis (an extension of the leaf stalk, or petiole) that may be up to 30 meters or more in length. Some tree ferns, such as those of the genus *Cyathea* (Figure 17–22b), have been recorded to reach heights of more than 24 meters and to have leaves 5 meters or more in length. Although the trunks of such tree ferns may be 30 centimeters or more thick, their tissues are entirely primary in origin. Most of this thickness is the fibrous root mantle; the true stem is only four to six centimeters in diameter. The herbaceous genus *Botrychium* (see Figure 17–24a) is the only living fern known to form a vascular cambium.

There Are Two Kinds of Sporangia within the Ferns

In terms of the structure and method of development of their sporangia, ferns may be classified as either eusporangiate or leptosporangiate (Figure 17–23). The distinction between these two types of sporangia is important for understanding relationships among vascular plants. In a **eusporangium,** the parent cells, or initials, are located at the surface of the tissue from which the sporangium is produced (Figure 17–23a). These initials divide by the formation of walls parallel to the surface, resulting in the formation of an inner and an outer series of cells. The outer cell layer, by further divisions in both planes, builds up the several-layered wall of the sporangium. The inner layer gives rise to a mass of irregularly oriented cells from which the spore mother cells ultimately arise. In many eusporangia, the inner wall layers are stretched and compressed during the course of development, so that the walls may apparently consist of a single layer of cells at maturity. Eusporangia, which are larger than leptosporangia and contain many more spores, are characteristic of all vascular plants—including the lycophytes—except for the leptosporangiate ferns.

In contrast to the multicellular origin of eusporangia, **leptosporangia** arise from a single superficial initial cell, which divides transversely or obliquely (Figure 17–23b). The inner of the two cells produced by this division may either contribute cells that produce a large part of the sporangial stalk or remain inactive and play no role in the further development of the sporangium, which is the more common condition. By a precise pattern of divisions, the outer cell ultimately gives rise to an elaborate, stalked sporangium, with a globose capsule having a wall that is one cell thick. Within this wall is a nutritive structure two cell layers thick called the **tapetum.** The inner mass of the leptosporangium eventually differentiates into spore mother cells, which undergo meiosis to produce four spores each.

After it nourishes the young dividing cells within the sporangium, the tapetum is deposited around the spores, creating ridges, spines, and other types of surface features that are often characteristic for individual families and genera. The spores are exposed following the development of a crack in the so-called *lip cells* of the sporangium. The sporangia are stalked, and each contains a special layer of unevenly thick-walled cells called an **annulus.** As the sporangium dries out, contraction of the annulus causes tearing in the middle of the capsule. The sudden explosion and snapping back of the annulus to its original position then result in a catapultlike discharge of the spores. In eusporangia, the stalks are more massive and, while there may be preformed lines of dehiscence, there is no annulus and no catapultlike discharge of spores.

Most living ferns are homosporous; heterospory is restricted to two orders of living water ferns (see Figure 17–31), which will be discussed further below. A few extinct ferns also were heterosporous.

We shall now consider as examples four very different kinds of ferns: (1) the orders Ophioglossales and Marattiales, as examples of eusporangiate ferns; (2) the Filicales, or homosporous leptosporangiate ferns; (3) the water ferns, orders Marsileales and Salviniales, the heterosporous leptosporangiate ferns; and (4) the whisk ferns, order Psilotales, earlier regarded as a distinct phylum but now seen in context (Figure 17–13) as reduced ferns.

(a)

(b)

(c)

(d)

(e)

(f)

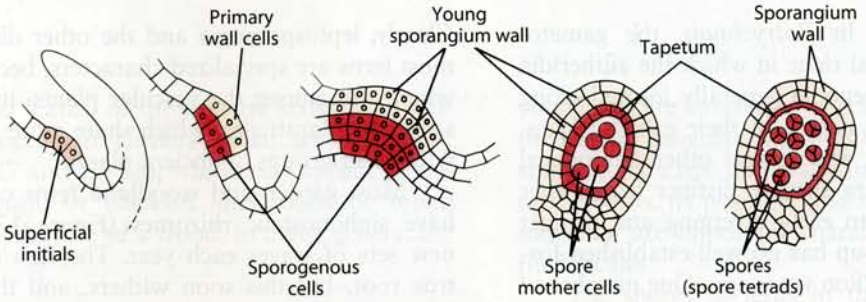
(g)

17–22 Representative ferns *The diversity of ferns, as illustrated by a few genera of the largest order of ferns, Filicales.* ***(a)*** Lindsaea, *Volcán Barba, Costa Rica.* ***(b)*** *A tree fern,* Cyathea, *at Monteverde, Costa Rica.* ***(c)*** Plagiogyria, *with distinct fertile and vegetative leaves, Volcán Poás, Costa Rica.* ***(d)*** Elaphoglossum, *with thick, undivided leaves, near Cuzco, Peru.* ***(e)*** Asplenium septentrionale, *a small fern that occurs all around the Northern Hemisphere, growing on metal-rich soil near a lead-silver mine in Wales.* ***(f)*** Pleopeltis polypodioides, *growing as an epiphyte on a juniper trunk in Arkansas.* ***(g)*** *A species of* Hymenophyllum, *one of the filmy ferns, so-called because of their delicate leaves. Filmy ferns occur as epiphytes primarily in tropical rainforests or wet temperate regions.*

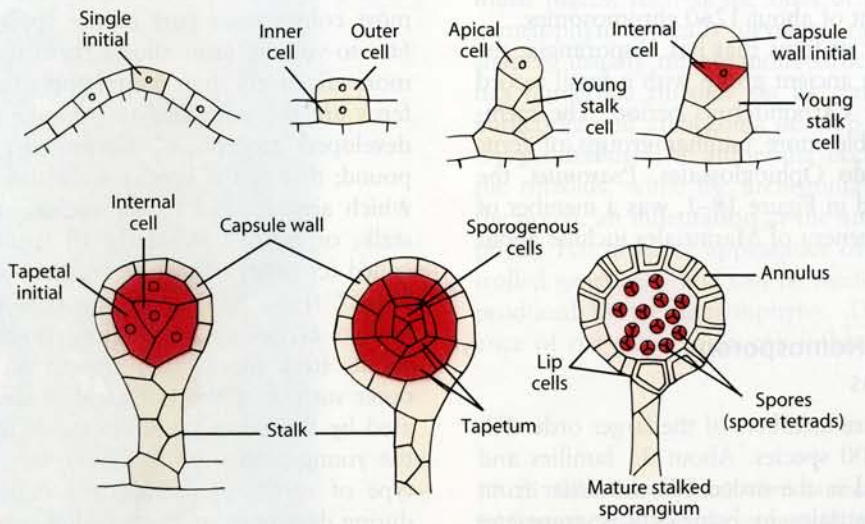
The Orders Ophioglossales and Marattiales Are Eusporangiate Ferns

Of the three genera of the order Ophioglossales, *Botrychium*, the grape ferns (Figure 17–24a), and *Ophioglossum*, the adder's tongues (Figure 17–24b), are widespread in the north temperate region. In both of these genera, a single leaf typically is produced each year from the stem. Each leaf consists of two parts: (1) a vegetative portion, or blade, which is deeply dissected in *Botrychium* and undivided in most species of *Ophioglossum*, and (2) a fertile segment. In *Botrychium*, the fertile segment is dissected in the same way as the vegetative portion and bears two rows of eusporangia on the outermost segments. In *Ophioglossum*, the fertile portion is undivided and bears two rows of sunken eusporangia.

The gametophytes of *Botrychium* and *Ophioglossum* are subterranean, tuberous, elongate structures with numerous rhizoids; they have endophytic fungi and resemble the



(a) **Eusporangium development**



(b) **Leptosporangium development**

17–23 Eusporangia and leptosporangia *Development and structure of the two principal types of fern sporangia.* ***(a)*** *The eusporangium originates from a series of superficial parent cells, or initials. Each eusporangium develops a wall two or more layers thick (although at maturity the inner wall layers may be crushed) and a high number of spores.* ***(b)*** *The leptosporangium originates from a single initial cell, which first produces a stalk and then a capsule. Each leptosporangium gives rise to a relatively small number of spores.*

(a)

(b)

17–24 Ophioglossales *Representatives of the two genera of Ophioglossales that occur in North America.* ***(a)*** Botrychium parallelum. *In the genus* Botrychium, *the lower, vegetative portion of the leaf is divided. This is the only fern genus to form a vascular cambium.* ***(b)*** *In* Ophioglossum, *the lower portion of the leaf is undivided. In both genera, the erect, fertile, upper part of the leaf is sharply distinct from the vegetative portion.*

gametophytes of Psilotales. In *Botrychium,* the gametophytes usually possess a dorsal ridge in which the antheridia are embedded, with the archegonia generally located along the sides of the ridge. In the nature of their gametophytes, the structure of their leaves, and several other anatomical details, the Ophioglossales are sharply distinct from other living ferns and are clearly an early diverging and distinct group. Unfortunately, the group has no well-established fossil record before about 50 million years ago. One member of the Ophioglossales, *Ophioglossum reticulatum,* has the highest chromosome number known in any living organism, with a diploid complement of about 1260 chromosomes.

The only other order of ferns that has eusporangia, the tropical Marattiales, is an ancient group with a fossil record that extends back to the Carboniferous period. The members of this order resemble more familiar groups of ferns more closely than they do Ophioglossales. *Psaronius,* the extinct tree fern illustrated in Figure 18–1, was a member of this order. The six living genera of Marattiales include about 200 species.

Filicales Is an Order of Homosporous Leptosporangiate Ferns

Nearly all familiar ferns are members of the larger order Filicales, with at least 10,500 species. About 35 families and 320 genera are recognized in the order. Filicales differ from Ophioglossales and Marattiales in being leptosporangiate; they differ from the water ferns, which we shall discuss next, in being homosporous. All ferns other than Ophioglossales and Marattiales, in fact, are leptosporangiate, and very few have the subterranean gametophytes with endophytic fungi that are characteristic of the Ophioglossales and Marattiales. Clearly, leptosporangia and the other distinctive features of most ferns are specialized characters, because they occur nowhere else among the vascular plants, including Ophioglossales and Marattiales, which share more features in common with other groups of ancient plants.

Most garden and woodland ferns of temperate regions have siphonostelic rhizomes (Figure 17–25) that produce new sets of leaves each year. The fern embryo produces a true root, but this soon withers, and the rest of the roots arise from the rhizomes near the bases of the leaves. The leaves, or **fronds,** are megaphylls, and they represent the most conspicuous part of the sporophyte. Their high surface-to-volume ratio allows them to capture sunlight much more effectively than the microphylls of the lycophytes. The ferns are the only seedless vascular plants to possess well-developed megaphylls. Commonly, the fronds are compound; that is, the lamina is divided into leaflets, or **pinnae,** which are attached to the **rachis,** an extension of the leaf stalk, or petiole. In nearly all ferns, the young leaves are coiled (circinate); they are commonly referred to as "fiddleheads" (Figure 17–26). This type of leaf development is known as **circinate vernation.** Uncoiling of the fiddlehead results from more rapid growth on the inner than on the outer surface of the leaf early in development and is mediated by the hormone auxin (see Chapter 27), produced by the young pinnae on the inner side of the fiddlehead. This type of vernation protects the delicate embryonic leaf tip during development. Both fiddleheads and rhizomes are usually clothed with either hairs or scales, both of which are epidermal outgrowths; the characteristics of these structures are important in fern classification.

The sporangia of Filicales, all of which are homosporous, occur on the margins or lower surfaces of the leaves,

(a) (b)

17–24 Ophioglossales *Representatives of the two genera of Ophioglossales that occur in North America.* ***(a)*** Botrychium parallelum. *In the genus* Botrychium, *the lower, vegetative portion of the leaf is divided. This is the only fern genus to form a vascular cambium.* ***(b)*** *In* Ophioglossum, *the lower portion of the leaf is undivided. In both genera, the erect, fertile, upper part of the leaf is sharply distinct from the vegetative portion.*

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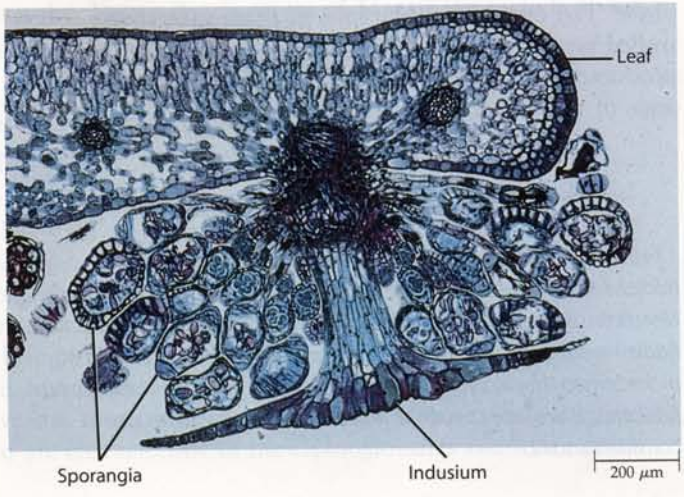
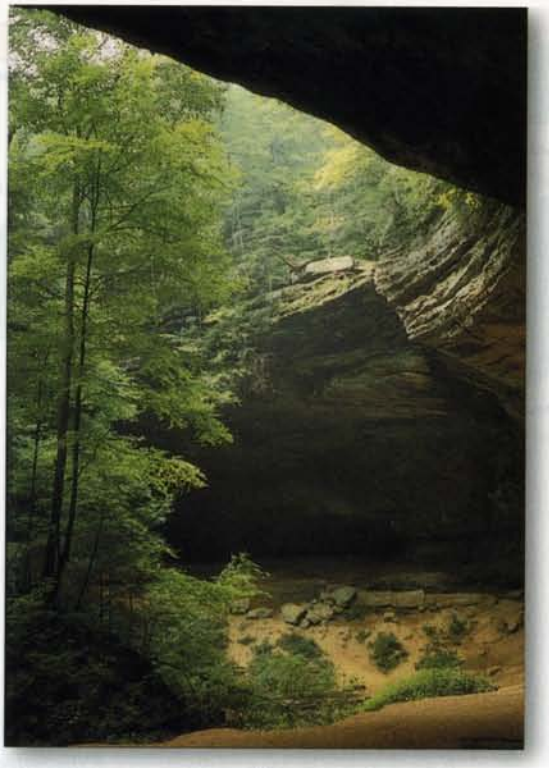
The sporangia of Filicales, all of which are homosporous, occur on the margins or lower surfaces of the leaves,

17–27 Sori *Clusters of sporangia, or sori, are found on the undersides or margins of the leaves of ferns.* ***(a)*** *In* Polypodium virginianum *and other ferns of this genus, the sori are bare.* ***(b)*** *In the bracken fern* (Pteridium aquilinum) *shown here, as well as in the maidenhair ferns* (Adiantum), *the sori are located along the margins of the leaf blades, which are rolled back over them.* ***(c)*** *In the evergreen wood fern* (Dryopteris marginalis), *the sori, which are also located near the margins of the leaf blades, are completely covered by kidney-shaped indusia.* ***(d)*** *In* Onoclea sensibilis, *the sori are enfolded by globular lobes of the pinna (leaflet) and therefore not visible. After overwintering, the lobes separate slightly, and the spores are released early in the spring, often over the snow.*



17–28 Sorus with an indusium *Transverse section of a leaf of* Cyrtomium falcatum, *a homosporous fern, showing a sorus on the lower surface. The sporangia are in different stages of development and are protected by an umbrellalike indusium.*



(a)

(b)

(c)

system is primarily inbreeding or outcrossing. Water is required for the multiflagellated sperm to swim to the eggs.

Early in its development, the embryo, or young sporophyte, receives nutrients from the gametophyte through a foot. Development is rapid, and the sporophyte soon becomes an independent plant, at which time the gametophyte disintegrates.

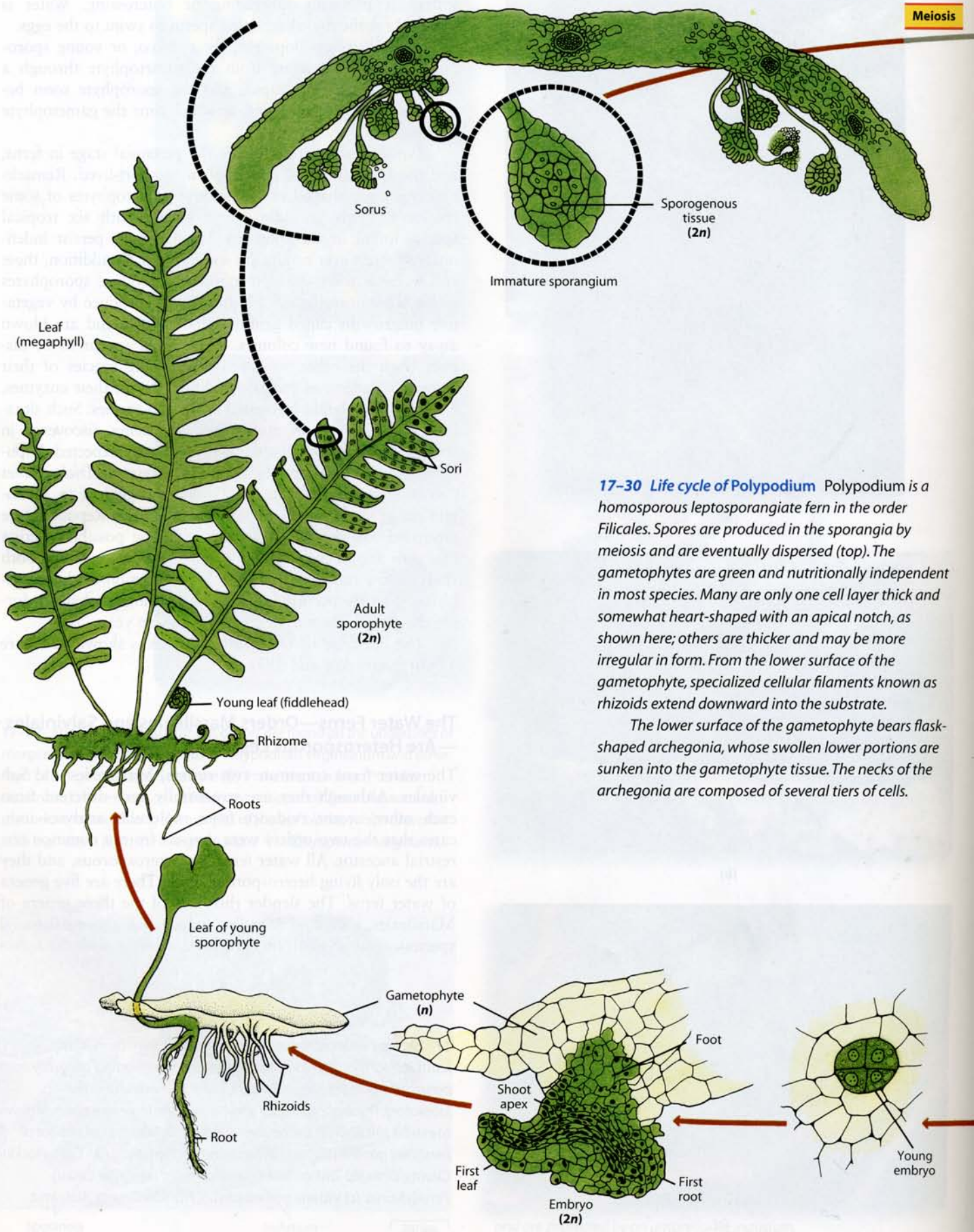
Typically, the sporophyte is the perennial stage in ferns, and the small, thalloid gametophyte is short-lived. Remarkably, the strap-shaped or filamentous gametophytes of some species of ferns, including three genera with six tropical species found in the southern Appalachians, persist indefinitely without ever producing sporophytes. In addition, these species have never yet been induced to produce sporophytes in the laboratory (Figure 17–29). They reproduce by vegetative outgrowths called gemmae that fall off and are blown away to found new colonies. These ferns appear to be distinct from the other, sporophyte-producing species of their respective genera, as judged by differences in their enzymes, and probably should be treated as distinct species. Such situations are common in mosses and are being discovered in ferns much more widely than was previously expected. Populations of perennial, free-living gametophytes of *Trichomanes speciosum*, discovered in the Elbsandsteingebirge (a mountain range shared by Germany and the Czech Republic), are estimated to be over 1000 years old. The possibility exists that they are relics of former populations that included both sporophytes and gametophytes. The extinction of the sporophytes possibly occurred as a result of climatic changes during the glacial intervals of the last 2 million years.

The life cycle of one of the Filicales is shown in Figure 17–30 (pages 396 and 397).

The Water Ferns—Orders Marsileales and Salviniales —Are Heterosporous Leptosporangiate Ferns

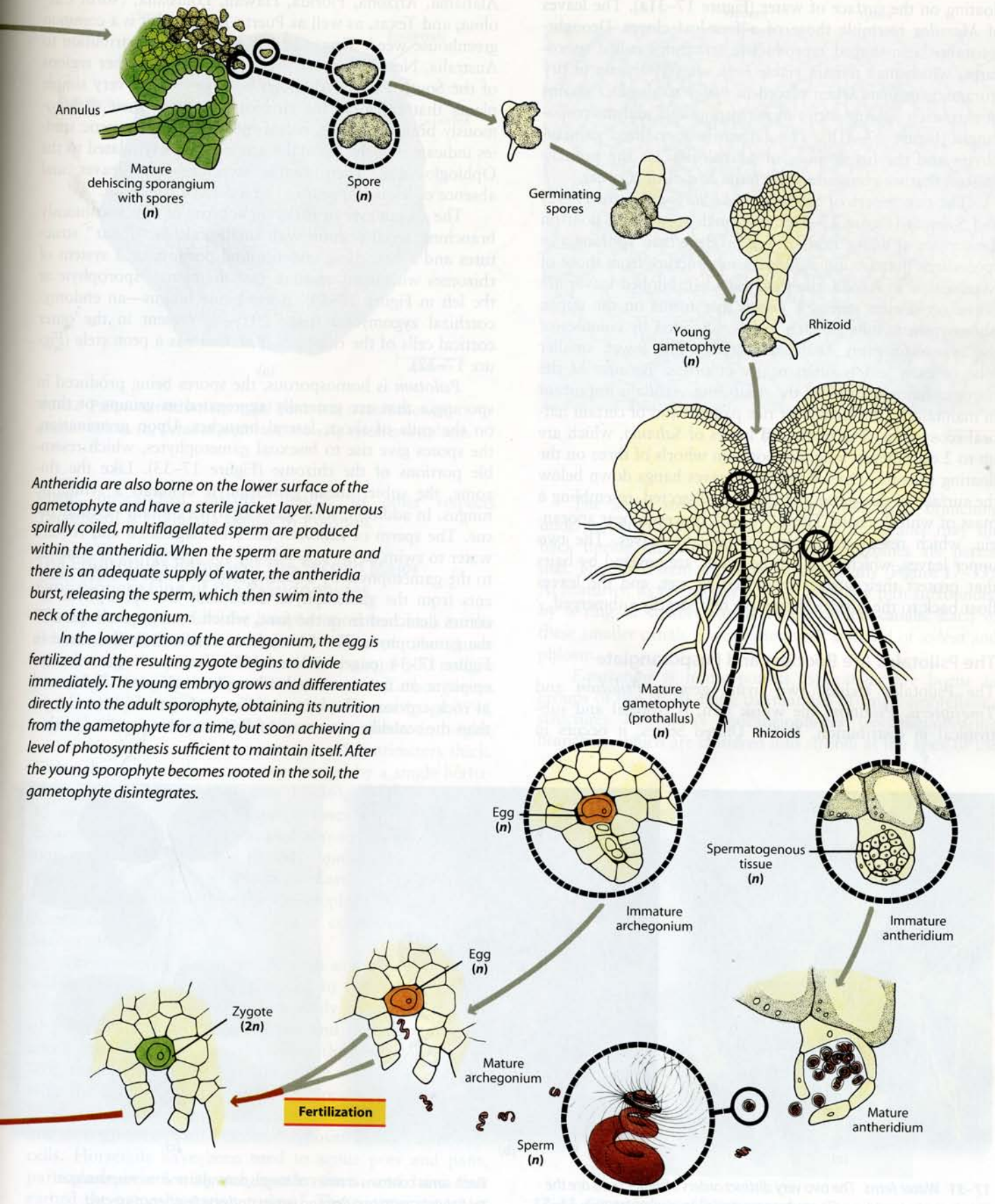
The water ferns constitute two orders, Marsileales and Salviniales. Although they are structurally very different from each other, recent evidence from molecular analyses indicates that the two orders were derived from a common terrestrial ancestor. All water ferns are heterosporous, and they are the only living heterosporous ferns. There are five genera of water ferns. The slender rhizomes of the three genera of Marsileales, including *Marsilea* (which has about 50 to 70 species), grow in mud, on damp soil, or often with the leaves

17–29 Asexually reproducing ferns *In some ferns from widely scattered parts of the world, the gametophytes reproduce asexually and persist; sporophytes are not formed, either in the field or in the laboratory. These photographs show two of the three fern genera known to exhibit this habit in the eastern United States.* ***(a)*** *Typical habitat of persistent gametophytes of* Vittaria *and* Trichomanes, *Ash Cave, Hocking County, Ohio.* ***(b)*** Trichomanes *gametophytes, Lancaster County, Pennsylvania.* ***(c)*** Vittaria *gametophytes, Franklin County, Alabama.*



***17–30 Life cycle of* Polypodium** Polypodium *is a homosporous leptosporangiate fern in the order Filicales. Spores are produced in the sporangia by meiosis and are eventually dispersed (top). The gametophytes are green and nutritionally independent in most species. Many are only one cell layer thick and somewhat heart-shaped with an apical notch, as shown here; others are thicker and may be more irregular in form. From the lower surface of the gametophyte, specialized cellular filaments known as rhizoids extend downward into the substrate.*

The lower surface of the gametophyte bears flask-shaped archegonia, whose swollen lower portions are sunken into the gametophyte tissue. The necks of the archegonia are composed of several tiers of cells.



Antheridia are also borne on the lower surface of the gametophyte and have a sterile jacket layer. Numerous spirally coiled, multiflagellated sperm are produced within the antheridia. When the sperm are mature and there is an adequate supply of water, the antheridia burst, releasing the sperm, which then swim into the neck of the archegonium.

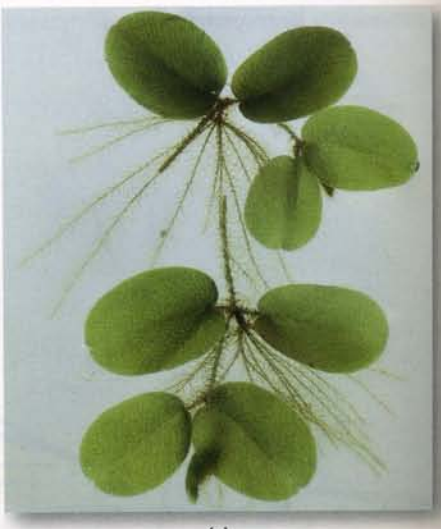
In the lower portion of the archegonium, the egg is fertilized and the resulting zygote begins to divide immediately. The young embryo grows and differentiates directly into the adult sporophyte, obtaining its nutrition from the gametophyte for a time, but soon achieving a level of photosynthesis sufficient to maintain itself. After the young sporophyte becomes rooted in the soil, the gametophyte disintegrates.

floating on the surface of water (Figure 17–31a). The leaves of *Marsilea* resemble those of a four-leaf clover. Drought-resistant, bean-shaped reproductive structures called **sporocarps,** which may remain viable even after 100 years of dry storage, germinate when placed in water to produce chains of sori, each bearing series of megasporangia and microsporangia (Figure 17–31b). The extremely specialized gametophytes and the heterospory of Marsileales are the primary reasons that we recognize these ferns as a distinct order.

The two genera of Salviniales, *Azolla* (see Figure 29–12) and *Salvinia* (Figure 17–31c), are small plants that float on the surface of water. Both genera produce their sporangia in sporocarps that are quite different in structure from those of Marsileales. In *Azolla,* the tiny, crowded, bilobed leaves are borne on slender stems. A pouch that forms on the upper, photosynthetic lobe of each leaf is inhabited by colonies of the cyanobacterium *Anabaena azollae.* The lower, smaller lobe of each leaf is often nearly colorless. Because of the nitrogen-fixing abilities of the *Anabaena, Azolla* is important in maintaining the fertility of rice paddies and of certain natural ecosystems. The undivided leaves of *Salvinia,* which are up to 2 centimeters long, are borne in whorls of three on the floating rhizome. One of the three leaves hangs down below the surface of the water and is highly dissected, resembling a mass of whitish roots. These "roots," however, bear sporangia, which reveals that they are actually leaves. The two upper leaves, which float on the water, are covered by hairs that protect their surface from getting wet, and the leaves float back to the surface if they are temporarily submerged.

(a)

(b)



(c)

17–31 Water ferns *The two very distinct orders of water ferns are the only living heterosporous ferns.* ***(a)*** Marsilea polycarpa, *with its leaves floating on the surface of the water, photographed in Venezuela.* ***(b)*** Marsilea, *showing the germination of a sporocarp, with chains of sori. Each sorus contains a series of megasporangia and microsporangia.* ***(c)*** Salvinia, *with two floating leaves and one feathery dissected, submerged leaf at each node. These two genera are representatives of the orders Marsileales and Salviniales, respectively.*