Plant Systematics: a Phylogenetic Approach (2nd ed.)
Judd et al. (2002)
Pp. 185-213

8 Lycophytes, Ferns and Their Allies, and Extant Gymnosperms

This chapter and Chapter 9 survey the diversity of tracheophytes. *Tracheo* refers to the presence of tracheids—cells specialized for transport of liquids—and the Greek root *phyte* means plant. Tracheophytes form a well-supported monophyletic group of generally large plants with branched sporophyte axes (Figure 8.1) and well-developed tissues (with tracheids in the xylem and sieve cells in the phloem) for the transport of water and carbohydrates within the plant. As described in Chapter 7, they form a major clade within the embryophytes (or land plants), nested within the paraphyletic "bryophytes" (see Figure 7.6). This implies the derivation of tracheophyte characteristics from those found in the bryophyte lineages, in which the small, unbranched sporophyte is nutritionally dependent on the dominant gametophyte phase of the life cycle.

There are two major lineages within the tracheophytes: the lycophytes and the euphyllophytes (see Figure 7.8). The euphyllophytes in turn comprise two major lineages, the monilophytes (ferns and their allies, including Psilotaceae and Equisitaceae) and the spermatophytes (seed plants). Finally, within the spermatophytes there are five major extant lineages: Cycadales, Ginkgoales, Coniferales, Gnetales, and the angiosperms (flowering plants). The first four of these groups have "naked" seeds, and are thus

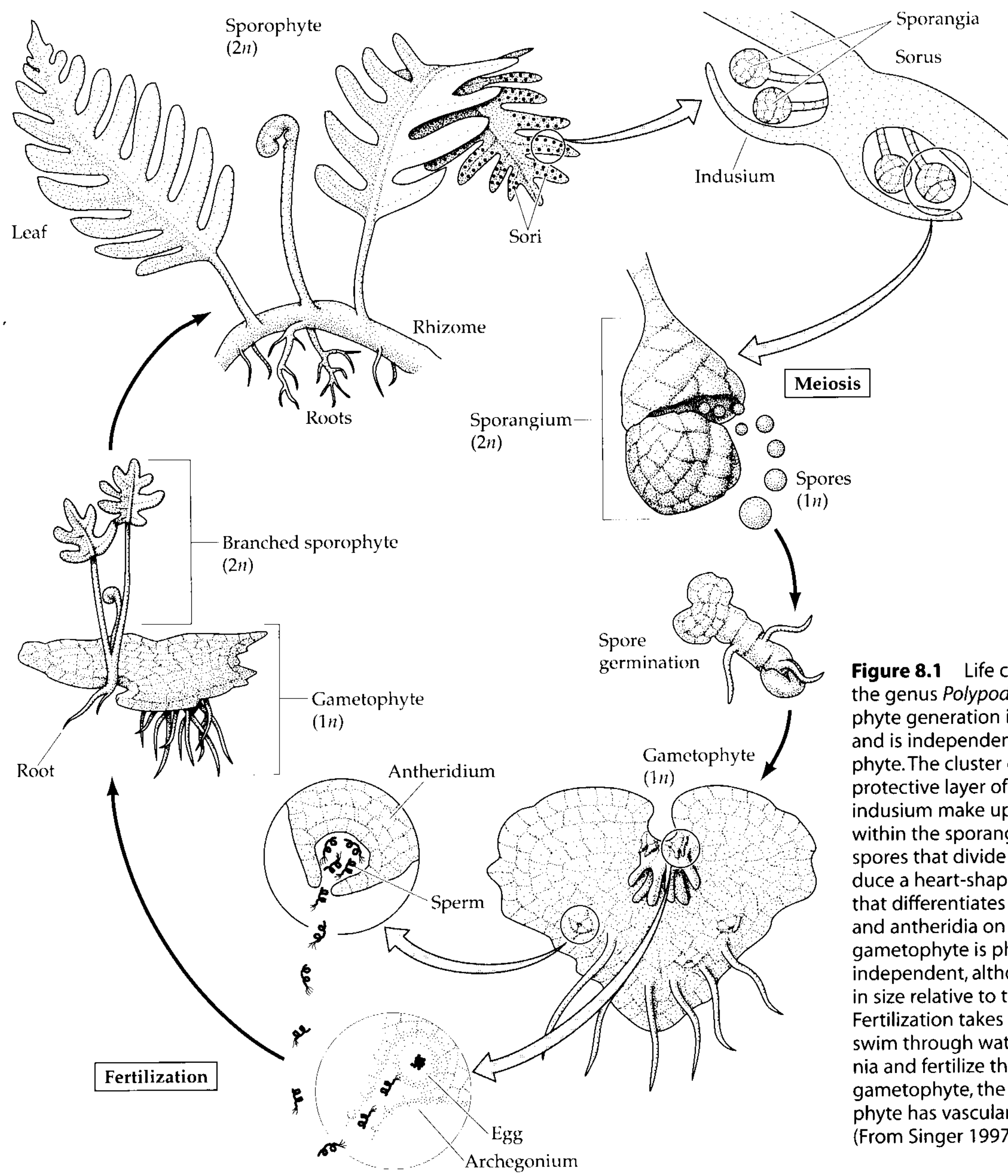

Figure 8.1 Life cycle of a fern of the genus *Polypodium*. The sporophyte generation is photosynthetic and is independent of the gametophyte. The cluster of sporangia plus a protective layer of cells called the indusium make up a sorus. Meiosis within the sporangia yields haploid spores that divide mitotically to produce a heart-shaped gametophyte that differentiates both archegonia and antheridia on one individual. The gametophyte is photosynthetic and independent, although it is reduced in size relative to the sporophyte. Fertilization takes place when sperm swim through water to the archegonia and fertilize the eggs. Unlike the gametophyte, the developing sporophyte has vascular tissue and roots. (From Singer 1997.)

commonly referred to as gymnosperms. In the angiosperms, seeds are enclosed inside one or more carpels.

Phylogenetic relationships among the seed plant lineages are not yet well resolved, although studies, including fossils, do indicate that seed plant lineages with naked seeds are paraphyletic with respect to angiosperms (see Figure 7.12). One possibility is that Gnetales are more closely related to angiosperms than they are to the other extant gymnosperms (the "anthophyte hypothesis"). However, a number of recent studies support the view that the extant gymnosperm lineages form a clade that is sister to the angiosperms.

This chapter covers the major extant lineages of tracheophytes except for the angiosperms, which are covered in detail in Chapter 9. All together there are about 12,000 species of lycophytes, monilophytes, and extant gymnosperms, or about 5% of the total number of flowering plant species. In this chapter and the next, each family treatment includes a description in which useful identifying characters are indicated in *italic print* and synapomorphies (which may also be useful for identification) in **boldface**; a brief summary of distribution and ecology; the estimated number of genera and species (including a listing of major genera); a list of major economic plants and products; and a discussion. The family discussion includes information regarding characters supporting the group's monophyly, a brief overview of phylogenetic relationships within the family, information

Key to Major Groups of Tracheophytes

1. Sperm biflagellate; .... **Lycophytes**
1. Sperm multiflagellate (or sperm without flagella) .... 2 **(Euphyllophytes)**
2. Dispersal by spores; seeds absent .... 3 **(Ferns and their allies)**
2. Dispersal by seeds .... 6 **(Seed plants)**
3. Leaves generally less than 2 cm in length, with an unbranched vein or veinless, not divided into leaflets 4
3. Leaves generally more than 2 cm in length, with a branched vein, divided into leaflets or not 5
4. Leaves whorled, fused at base; branches, if present, whorled; internodes with conspicuous vertical ridges; sporangia clustered on peltate sporangiophores and aggregated in strobili; roots present and irregularly branching .... **Equisetaceae**
4. Leaves spiral, not fused at base; stem without vertical ridges; sporangia sometimes associated with forked or lobed leaves; roots lacking .... **Psilotaceae**
5. Leaves not coiled and unfolding lengthwise when enmerging; sporangia walls more than one cell in thickness, without an annulus, borne on or embedded in a special portion of the leaf (the *sporophore*) .... **Ophioglossaceae**
5. Leaves coiled and unfolding lengthwise when emerging; sporangia walls one-cell thick, mostly with an annulus, mostly clustered in sori on the abaxial leaf surface, less often scattered on the abaxial leaf surface or in sporocarps .... **Leptosporangiate ferns**
6. Carpels and endosperm present .... **Angiosperms**
6. Carpels and endosperm absent .... 7 **(Gymnosperms)**
7. Vessels present; leaves opposite, joined at base .... **Gnetales**
7. Vessels absent; leaves usually spiral, rarely opposite or joined at base 8
8. Sperm not flagellate, transported to ovule by pollen tube; leaves simple, small, and scale-like to larger and linear, with resin canals in most species .... **Conifers**
8. Sperm motile, swimming by means of flagella; leaves either pinnately compound or simple, large, and as broad or broader than long, with resin, if present, not in canals 9
9. Leaves pinnately or twice pinnately compound, persistent; stem mostly short and unbranched or dichotomously branching, sometimes subterranean; ovules borne on the margin of often peltate megasporophylls that are either loosely clustered at the shoot apex or grouped in strobili; outer layer of seeds mostly fleshy but not unpleasant-smelling; microsporangia clustered in sori on the abaxial surface of microsporophylls; mucilage canals present .... **Cycads**
9. Leaves simple, fan-shaped, deciduous; large, freely branching trees; ovules 2 at the end of a long stalk, often only one maturing; outer layer of seeds fleshy, unpleasant-smelling at maturity; microsporangia paired at the end of slender stalk; mucilage canals absent .... **Ginkgoaceae**

regarding pollination biology and seed dispersal (where relevant), and notes on other matters of biological interest. Finally, each family treatment includes a list of references that are useful sources of additional information.

References: Bowe and de Pamphilis 1997; Bowe et al. 2001; Chaw et al. 2000; Donoghue 1994; Doyle et al. 1994; Kenrick 2000; Kenrick and Crane 1997; Mishler et al. 1994; Nickrent et al. 2000; Nixon et al. 1994; Pryer et al. 2001; Renzaglia et al. 2000; Renzaglia et al. 2001; Rothwell 1999; Rydin et al. 2002; Stefanovic et al. 1998; Stewart and Rothwell 1993.

LYCOPHYTES

Arising at least 400 MYA, lycophytes were largest in size in the Carboniferous (345–290 MYA), when arborescent members of this group, some of them over 40 m tall and 2 m in diameter at the base, dominated forests. Almost half of the plant fossils from this time are from this group. There are three families, about five genera, and about 1250 species of extant lycophytes, and they are placed in the Lycopodiales. The remains of these ancient trees are the chief components of commercially important coal

TABLE 8.1 ***Families of tracheophytes as classified in this book.***[a]

LYCOPHYTES

Lycopodiales
- **Lycopodiaceae** (p. 187)
- **Selaginellaceae** (p. 189)
- *Isoetaceae* (p. 187)

FERNS AND THEIR ALLIES (MONILIFORMS)

Psilotales
- **Psilotaceae** (p. 191)

Ophioglossales
- **Ophioglossaceae** (p. 192)
- *Marattiaceae* (p. 190)

Equisetales
- **Equisetaceae** (p. 193)

Polypodiales (leptosporangiate ferns)
- *Dipteridaceae* (p. 195)
- **Osmundaceae** (p. 196)
- **Cyatheaceae** (p. 196)
- *"Dicksoniaceae"* (p. 197)
- *Gleicheniaceae* (p. 195)
- *Hymenophyllaceae* (p. 195)
- *Hymenophyllopsidaceae* (p. 197)
- *Metaxyaceae* (p. 197)
- **Marsileaceae** (p. 197)
- *Matoniaceae* (p. 195)
- *Plagiogyriaceae* (p. 195)
- *Salviniaceae* (p. 197)
- **Polypodiaceae** (including numerous segregates) (p. 198)
- *Schizaeaceae* (p. 194)

SEED PLANTS

Gymnosperms

Cycadales (Cycads)
- **Cycadaceae** (p. 201)
- **Zamiaceae** (p. 201)

Ginkgoales
- **Ginkgoaceae** (Ginkgoales; p. 203)

Coniferales (Conifers)
- **Pinaceae** (p. 205)
- **Cupressaceae** (including "Taxodiaceae") (p. 207)
- *Sciadopityaceae* (p. 209)
- **Podocarpaceae** (p. 209)
- **Araucariaceae** (p. 210)
- **Taxaceae** (p. 211)
- *Cephalotaxaceae* (p. 212)

Gnetales
- **Ephedraceae** (p. 213)
- *Gnetaceae* (p. 213)
- *Welwitschiaceae* (p. 213)

Angiosperms: See Table 9.1

[a]Families receiving full coverage in the text are indicated in **boldface**, while those only briefly characterized are in *italics*. Page numbers (in parentheses) indicate discussion of the family in this chapter.

deposits of Europe and North America. The closest living relatives of the clade to which these ancient trees belonged are thought to be the small grass-like plants of the Isoetaceae, one of the three extant families of lycophytes. Isoetaceae and Selaginellaceae are sister groups.

Lycopodiaceae Mirbel
(Club Moss Family)

Terrestrial or epiphytic plants usually about 5–20 cm tall, with *dichotomously branching* stems. Roots dichotomously branching. Leaves simple (microphylls), 0.2–2 cm long, with 1 unbranched vein, often densely covering the stem; linear and more or less spreading away from the stem or scale-like and appressed to the stem; spiral or opposite. **Sporangia ± kidney-shaped,** ***opening by a transverse slit*** *that divides the sporangium in two; solitary in leaf axils or borne on leaf bases,* sporophylls unmodified or modified and sometimes clustered into strobili. Homosporous; spores subglobose to tetrahedral, with a 3-branched scar. Gemmae (small structures of various sizes and shapes that detach from the plant for vegetative reproduction) present in some species of *Huperzia*. Gametophytes mycorrhizal and wholly subterranean, partly green and on or near the surface of the ground, or initially mycorrhizal and later photosynthetic (Figure 8.2).

Distribution and ecology: Cosmopolitan, rare in arid areas; most diverse in tropical montane and alpine habitats.

Genera/species: ca. 3/380. ***Major genera:*** *Huperzia* (300 spp.), *Lycopodiella* (40), and *Lycopodium* (40).

Economic plants and products: The family is not significant economically. Oily, highly flammable compounds in the spore wall ignite rapidly into a flash of light and were used by magicians and sorcerers in the Middle Ages, as a flash early in photography, and in the first (experimental) photocopying machines. The spores have been used as industrial lubricants and formerly were used to prevent rubber cohesion in condoms and surgical gloves.

Key to Families of Lycophytes

1. Homosporous; leaves nonligulate .... **Lycopodiaceae**
1. Heterosporous; leaves ligulate, with a small projection on the adaxial surface 2
2. Sporangia borne singly in the axils of unmodified or modified leaves; leaves usually under 2 cm long .... **Selaginellaceae**
2. Sporangia at least initially embedded in adaxial face of leaf base; leaves 2–100 cm long .... Isoetaceae

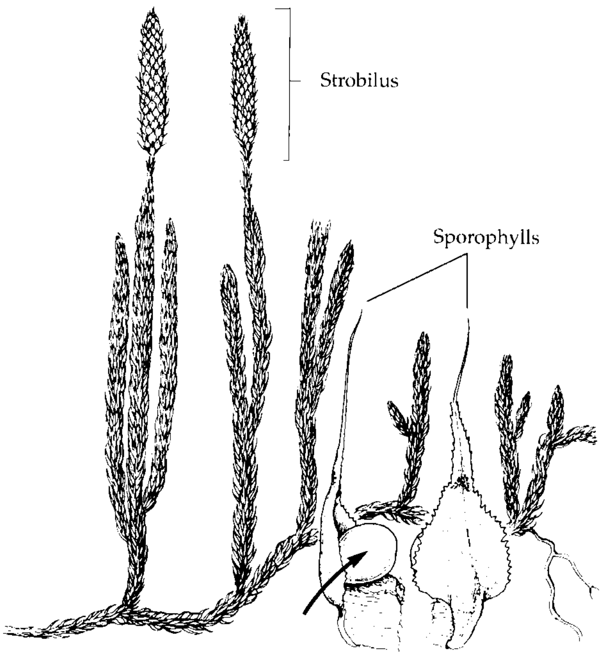

Figure 8.2 Lycopodiaceae. *Lycopodium clavatum*: habit (shown about two-thirds actual size) and sporophylls (× 7); the arrow points to a sporangium. (From Øllgaard 1990.)

Discussion: Taxonomic problems exist at generic and specific levels in the Lycopodiaceae. Traditionally treated as including just one large genus, *Lycopodium*, the family is here considered to contain four genera. Some of these genera contain monophyletic sections that some workers have recognized as genera. DNA sequences from *rbcL* divide the family into a *Huperzia* clade and a *Lycopodiella-Lycopodium* clade. A peculiar species, usually placed in a distinct genus (*Phylloglossum*), consists of plants only about 5 cm tall and highly reduced for arid environments of Australia, New Zealand, and Tasmania. Gametophyte morphology and *rbcL* sequences support inclusion of this species in *Huperzia*. Most members of *Huperzia* are tropical epiphytes with sporangia borne in the axil of the leaves and not collected into strobili. *Huperzia* is divided into to a neotropical and a paleotropical clade, which are thought to evolved after continental drift separated South America and Africa about 80 MYA. The terrestrial habit has apparently evolved at least two times in neotropical mountains. Species delimitation in *Huperzia* is poorly understood, at least in part due to frequent interspecific hybridization.

The *Lycopodiella-Lycopodium* clade is primarily temperate in distribution, and its sporangia are usually borne in conspicuous strobili. Some clades within these two genera have wider geographic distributions than the major neotropical and paleotropical clades in *Huperzia*, and some species, such as *Lycopodium clavatum*, are more or less cosmopolitan.

Lycopodiaceae have an extensive geological history extending back to about 380 MYA, but most of the modern diversity developed after 80–90 MYA, when the formation of forests of broadleaved species shaded the forest floor and favored the evolution of epiphytism in the ancestors of *Huperzia*. One of the reversions to the terrestrial habit is thought to have been in response to the formation of the Andes about 15 MYA.

Members of this family may have somatic chromosome numbers up to about 275. These high numbers may be the result of repeated episodes of polyploidy, or these plants may simply be diploids with numerous chromosomes.

References: DiMichele and Skog 1992; Kenrick and Crane 1997; Lellinger 1985; Øllgaard 1990, 1992; Soltis and Soltis 1988; Tryon and Tryon 1982; Wagner and Beitel 1992, 1993; Wikstrom 1999; Wikstrom and Kenrick 1997; Wikstrom and Kenrick 2000; Whittier and Braggins 2000.

Selaginellaceae Willk.

(Spike Moss Family)

Mostly terrestrial, herbaceous, and perennial plants under 2 cm tall. Roots dichotomously branching; rhizophores usually produced from the stem, dichotomously branching. Stems erect or creeping. *Leaves about 0.5–1 cm long, spirally arranged and often 4-ranked on the secondary and ultimate branches*; ligulate; often dimorphic, those on upper side of stem smaller than those on lower side; with a single, unbranched vein; with a ligule. Heterosporous; **sporangia borne in or near the axils of well-differentiated sporophylls, usually on 4-sided (cylindrical in a few species) strobili**; strobili usually terminating branches, with either or both megasporangia and microsporangia; megasporangia usually with 4 megaspores 200–600 μm in diameter, with distinct ridges and conspicuously patterned with variously shaped projections; microsporangia with more than 100 microspores 20–60 μm in diameter. Megagametophytes partly protruding from the megaspore wall; microgametophytes developing wholly within the microspore, the wall rupturing to release the sperm. (Figure 8.3).

Distribution and ecology: Mainly tropical, with a few species extending into arctic regions of both hemispheres; occupying a wide range of habitats.

Genera/species: 1 (*Selaginella*)/750.

Economic plants and products: The family is not significant economically, although a few species are ornamentals.

Discussion: Fossils of this family are known from tropical wetlands almost 350 MYA. Early in their history, members of Selaginellaceae evolved leaf dimorphism, with smaller leaves on the upper surface of the stem. At about the same time, it appears that closed-canopy forests were established by tree ferns. Leaf dimorphism, which has

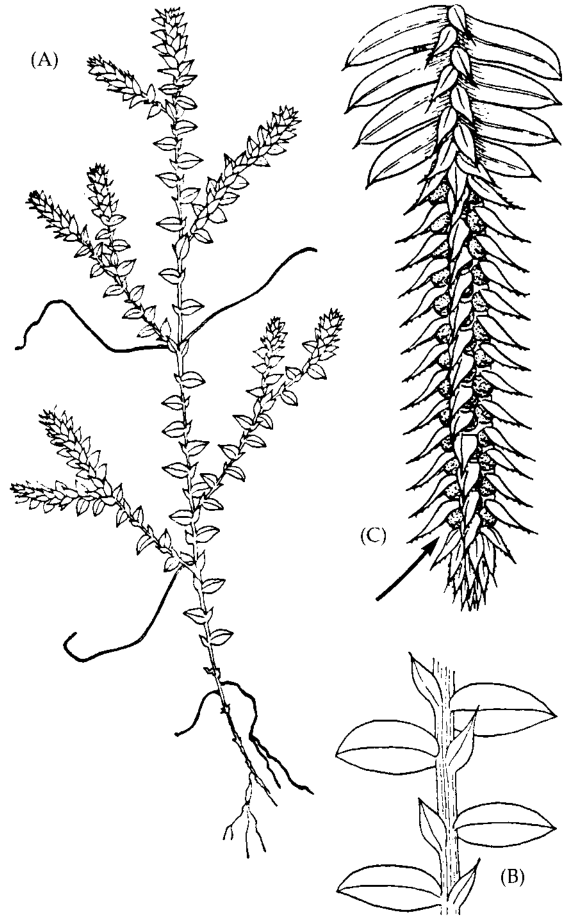

Figure 8.3 Selaginellaceae. (A, B) *Selaginella apoda*: (A) habit (× 1.5); (B) sterile portion of plant (× 12). (C) *S. myosurus*: strobilus and vegetative branch bearing it (× 6); the arrow points to a sporangium. (A, B from Billington 1952; C from Alston 1959.)

been hypothesized to be an adaptation to poor light, may have been important for these early plants of Selaginellaceae and for modern forms as well, which mostly live on forest floors.

The majority of the species of the family occurs in tropical rainforests, but many species are capable of surviving long periods of drought with small leaves covered by a thick cuticle and by curling their branches into a ball. These plants can revive rapidly from apparent death by uncurling their branches, and they are therefore commonly called resurrection plants. The resurrection adaptation has evolved at least three times in the genus.

Although the small leaves and habit make many species of Lycopodiaceae and Selaginellaceae resemble one another, heterospory and ligulate leaves are potential synapomorphies linking Selaginellaceae and Isoetaceae. Isoetaceae are terrestrial or aquatic plants with erect or short cormlike stems and usually long leaves. Sporangia embedded in the adaxial face of the leaf bases are distinctive. The family has a nearly cosmopolitan distribution; the one genus (*Isoetes*) has about 150 species.

References: Jermy 1990a,b; Kenrick and Crane 1997; Korall and Kenrick 2002 (their Figure 3 shows important morphological features); Lellinger 1985; Manhart 1995; Taylor et al. 1993; Tryon and Tryon 1982; Valdespino 1993; Webster 1992.

FERNS AND THEIR ALLIES

The ferns and their allies span a broad range of morphological diversity. The great majority of the members of this clade are plants commonly referred to as ferns. Many ferns have a subterranean stem bearing a clump of leaves that are compound or deeply lobed, many-veined, and comparatively large (up to 7 m or more in length). Fern leaves are sometimes referred to as **fronds** and their petioles as **stipes**. Ferns also include plants with leaves that are simple or resemble those of clovers, tree ferns with stems up to 20 m tall, and aquatics with filiform leaves. Two groups, long referred to as "fern allies"—Psilotaceae and Equisetaceae—have, with few exceptions, rather small leaves with a single or no vein and superficially do not resemble ferns. For over 30 years, however, some workers have suggested that Psilotaceae and Equisetaceae are highly modified ferns, and recent DNA evidence clearly supports this view (see Chapter 7). Ferns and their allies, which are referred to in some works as moniliforms, include about 260 genera and 12,000 species ranging in size from a few cm to 20 m tall.

There are two kinds of sporangia within ferns and their allies: **eusporangiate**, in which the sporangium wall has two or more cell layers, and **leptosporangiate**, in which the sporangium wall is composed of just one cell layer. The eusporangiate condition characterizes Psilotaceae, Ophioglossaceae, Equisetaceae, and Marattiaceae (and lycophytes). The Marattiaceae contain 4–7 genera and about 300 species, most found on the shaded floor of wet tropical forests. This family is not treated in detail in this book.

The great majority of ferns and their allies belong to the leptosporangiate ferns. In addition to sporangium wall thickness, the evolution of leptosporangiate ferns resulted in four other unique structural characteristics: the **annulus** (described later); a sporangial stalk with 4–6 cells in cross-section; a vertical first zygotic division; and primary xylem with scalariform bordered pits. Rearrangements of the chloroplast genome and DNA sequence data also mark the origin of leptosporangiate ferns.

While there is strong morphological and molecular support for the monophyly of leptosporangiate ferns, morphology has not been very helpful in assigning relationships of other fern and allied groups. DNA sequences from three chloroplast genes (*rbcL*, *atpB*, and *rps4*) and the nuclear small subunit rDNA strongly link Ophioglossaceae and Psilotaceae in a clade (Figure 8.4). Relationships of Ophioglossaceae had long been a puzzle. Based on morphology, they appeared to be distantly

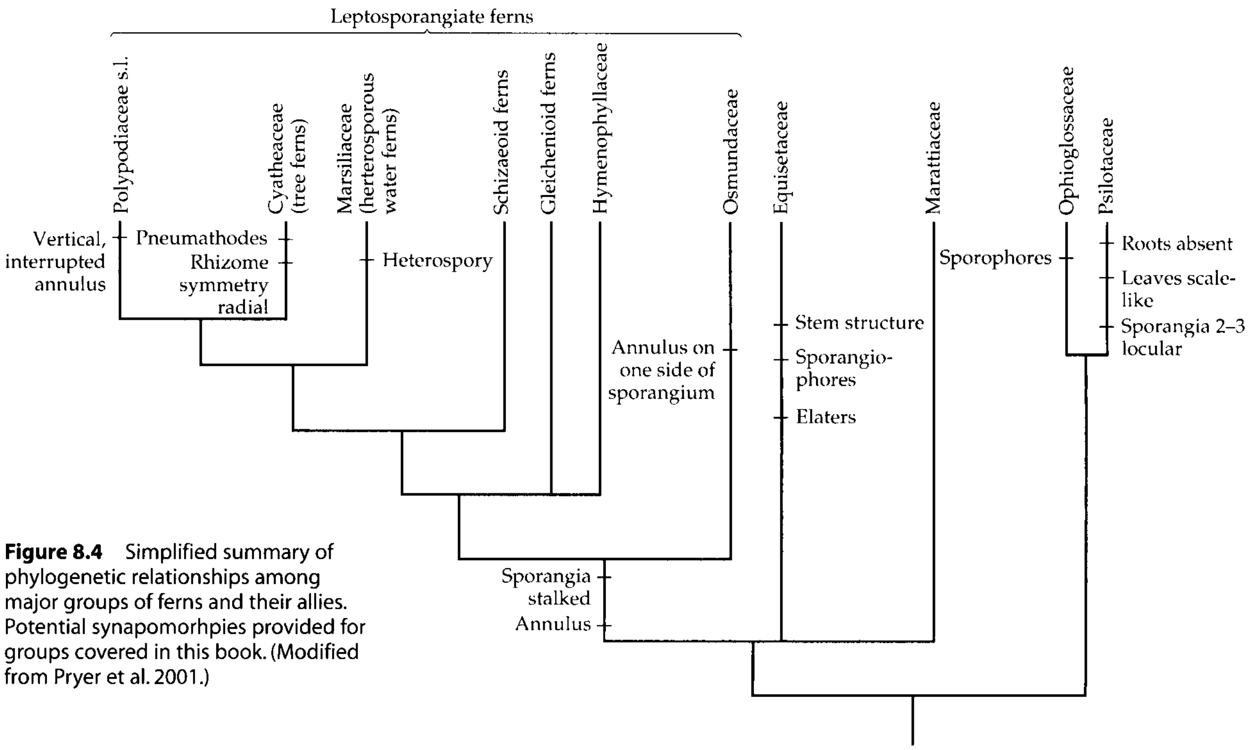

Figure 8.4 Simplified summary of phylogenetic relationships among major groups of ferns and their allies. Potential synapomorhpies provided for groups covered in this book. (Modified from Pryer et al. 2001.)

related to other tracheophytes, or perhaps they had affinities with a long-extinct group of plants called progymnosperms. Relationships of Marattiaceae are also confused. The same DNA evidence that resolved a close relationship of Ophioglossaceae and Psilotaceae place Equisetaceae and Marattiaceae in a clade that is sister to the leptosporangiate ferns (see also Chapter 7). Because support for the Equisetaceae-Marattiaceae is weak, we have not included it in Figure 8.4.

Spore shape, size, symmetry, the shape of a prominent scar—whether straight or three-branched—and the nature of the surface and layers of the spore wall have been taxonomically useful at all levels within the ferns and their allies. Spores of these plants are very small and are produced in great numbers; one estimate is that an individual tree fern in the genus *Cyathea* generates 1,250,000,000,000 spores in its lifetime. Spore dispersal is facilitated by adaptations such as elaters in *Equisetum* and the annulus in most ferns (see below). Because prothalli produced by individual spores of many homosporous ferns can produce zygotes by themselves, they can start a new population. Consequently, long-distance dispersal is probably more common in ferns than in flowering plants.

The gametophytes of ferns and their allies are generally small (less than 1 cm) and variously shaped. Many leptosporangiate ferns have heart-shaped gametophytes, although they may also be elongate, filamentous, or take various other forms. Gametophytes of most ferns are photosynthetic and live above ground. Gametophytes of Psilotaceae are subterranean, lack chlorophyll, and are mycotrophic, depending upon fungal partners for nutrition. Most are homosporous, and their gametophytes are at least potentially bisexual, producing both gametes—eggs (in archegonia) and sperm, also called antherozoids (in antheridia; see Figure 8.1). However, gametophytes producing archegonia may release compounds called antheridiogens that stimulate nearby gametophytes to produce antheridia, thus promoting mating between gametophytes. Marsileaceae (see below) are heterosporous, and their gametophytes are endosporic, being wholly or mostly retained within the spore wall.

Fertilization in ferns and their allies usually requires water through which the flagellate sperm can swim from the antheridium to the archegonium. This requirement for water excludes these plants from some dry habitats. Many ferns and their allies can reproduce asexually (see Figure 8.1) by means of rhizomes, vegetative propagules on the gametophyte called **gemmae** in *Psilotum* and several leptosporangiate ferns, vegetative propagules on the sporophyte, direct outgrowths from gametophytic tissue (called apogamy), and spores that are produced via modified meiotic divisions.

Psilotales

Psilotaceae Kanitz
(Whisk Fern Family)

Herbs, terrestrial but more *often epiphytic*. **Roots absent**, the plant anchored by subterranean stems that may bear gemmae. Aerial stems erect or hanging, glabrous, simple or dichotomously branched. Leaves spirally arranged, 2-

ranked in some species; **scale-like or awl-shaped to lanceolate; simple or once-forked**, one-veined or veinless. **Sporangia 2- or 3-locular and -lobed**, sessile on or above the base of forked sporophylls. Homosporous; **spores bean-shaped**, pale in color. Gametophytes subterranean (Figure 8.5).

Distribution and ecology: Pantropical and warm temperate except in dry areas, with the greatest number of species in Southeast Asia and the South Pacific; primarily at lower elevations, especially as epiphytes on tree fern trunks.

Genera/species: 2/17. ***Major genera:*** *Tmesipteris* (15 spp.) and *Psilotum* (2).

Economic plants and products: The family is not significant economically.

Discussion: Although there is no extensive fossil record of Psilotaceae, they have long been thought to be among the most primitive extant vascular plants due to similarities to ancient and simple fossil plants. Morphological, chemical, DNA sequence data, and detailed features of the architecture of sperm cells, however, support a relationship to eusporangiate "ferns." The distinctive simplicity of these plants—part of the reason they do not resemble "ferns"—is probably reduction associated with mycotrophy. Growth of spores depends upon the presence of endophytic mycorrhizae.

References: Kramer 1990d; Kenrick and Crane 1997; Lellinger 1985; Manhart 1995; Pryer et al. 1995, 2001; Renzaglia et al. 2001; Thieret 1993b; Tryon and Tryon 1982; Wolf 1997; Wolf et al. 1998.

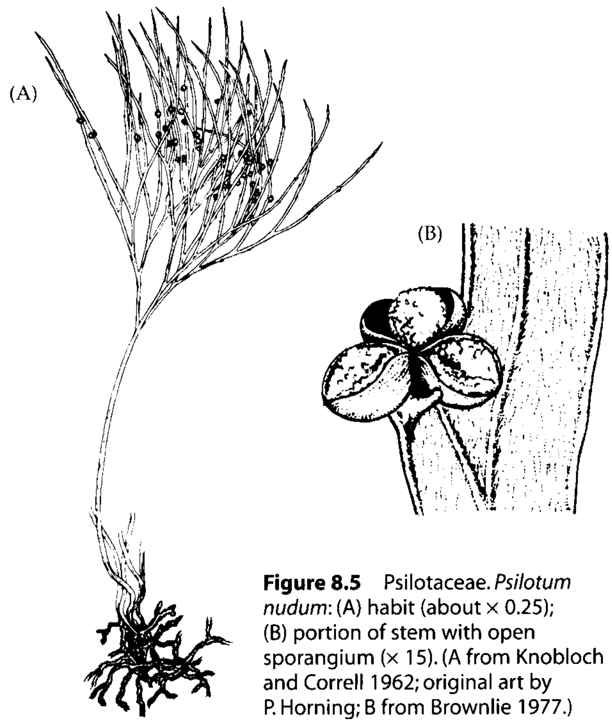

Figure 8.5 Psilotaceae. *Psilotum nudum*: (A) habit (about × 0.25); (B) portion of stem with open sporangium (× 15). (A from Knobloch and Correll 1962; original art by P. Horning; B from Brownlie 1977.)

Ophioglossales

Ophioglossaceae C. Agardh
(Adder's-tongue Family)

Terrestrial or epiphytic. Stems unbranched, short, mostly subterranean. Leaves usually one per stem, with or without a stalk that is expanded at the base into a sheath, usually divided into a photosynthetic, sterile blade and a spore-bearing portion (the ***sporophore***); the blade simple to more or less palmately compound to many times pinnately compound, from a few cm to about 50 cm long, rarely absent, conduplicate before unfolding (not or rarely somewhat circinate). Sporangia thick-walled (eusporangiate), not clustered in sori, separate or joined in synangia, **exposed on branches of the sporophore or embedded in a spike-like sporophore**; annulus absent. Homosporous; spores not green, thousands per sporangium. Gametophytes subterranean, mycorrhizal, not green (Figure 8.6).

Distribution and ecology: Worldwide, especially in temperate regions and the tropics. Members of this family may be associated with disturbance in pastures, old fields, and young second-growth forests, although there is considerable diversity in relatively undisturbed habitats.

Genera/species: 3/70–90. ***Major genera:*** *Botrychium* (45–60 spp.) and *Ophioglossum* (25–30).

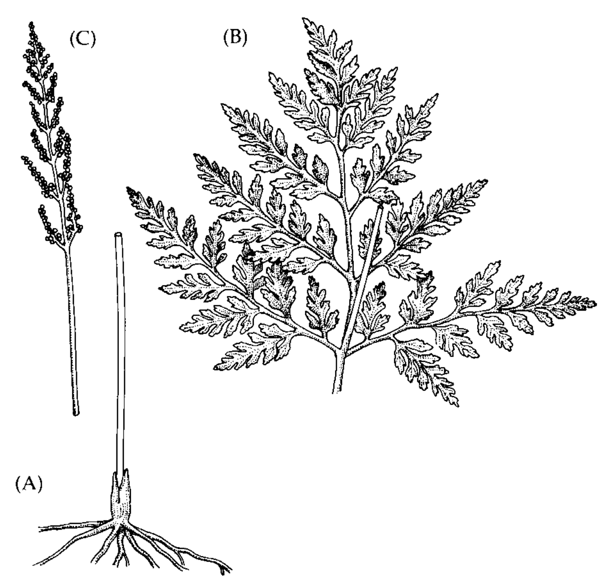

Figure 8.6 Ophioglossaceae. *Botrychium virginianum*: (A) base of plant; (B) portion of a sterile (photosynthetic) leaf; (C) fertile leaf (all × about 0.3). (From Wagner and Wagner 1993.)

Economic plants and products: None.

Discussion: The sporophore, which is assumed to be two basal leaf segments that have fused together, is a likely synapomorphy and the most unusual feature of the family. The family is morphologically distinct relative to other members of the ferns and their allies, and the DNA sequence support for its relationship with Psilotaceae has no obvious support from morphology. Chromosome numbers in *Ophioglossum* of more than $2n$ = 1400 have been reported, the highest of all tracheophytes.

References: Hasebe et al. 1995; Pryer et al. 1995; Pryer et al. 2001; Tryon and Tryon 1982; Wagner 1990; Wagner and Wagner 1993.

Equisetales

Equisetaceae Michx. ex DC.

(Horsetail Family)

Terrestrial to aquatic, rhizomatous perennials. Stems to 8 m, but under 1 m in height in most species; swollen (joint-like) nodes; **internodes with alternating vertical ridges and grooves externally and usually hollow, with a central canal and smaller canals under the ridges and valleys internally**; branches none or whorled and structurally similar to the main stem. **Leaves whorled, fused into sheaths at base**, usually much less than 2 cm long, the sheaths sometimes more or less swollen. Sporangia elongate, pendant beneath the expanded apex of sporangiophores; **sporangiophores** peltate, whorled in strobili terminating stems that are green or, in a few species, not green, unbranched, and either ephemeral or becoming green and branched after the spores are shed. Homosporous; spores spherical, green, and with **4–6 straplike elaters** wrapped around the spore that rapidly straighten and assist in moving the spore out of the sporangium. Gametophytes green, growing on the surface of the ground (Figure 8.7).

Distribution and ecology: Cosmopolitan, except for Australia, New Zealand, and Antarctica, with the greatest number of species between 40° and 60° north latitude. These plants are primarily colonizers of unforested areas, lake margins, and wetlands.

Genera/species: 1 (*Equisetum*)/15.

Economic plants and products: The family is not significant economically. Silica in the stems made them useful to early European settlers in North America for scouring cookware, a practice that is apparently the source of another common name, scouring rush.

Discussion: This monogeneric family is morphologically distinct in its grooved and hollowed stem, whorled leaves, and sporangiophores. The genus is divided into two subgenera -- subgen. *Equisetum* (8

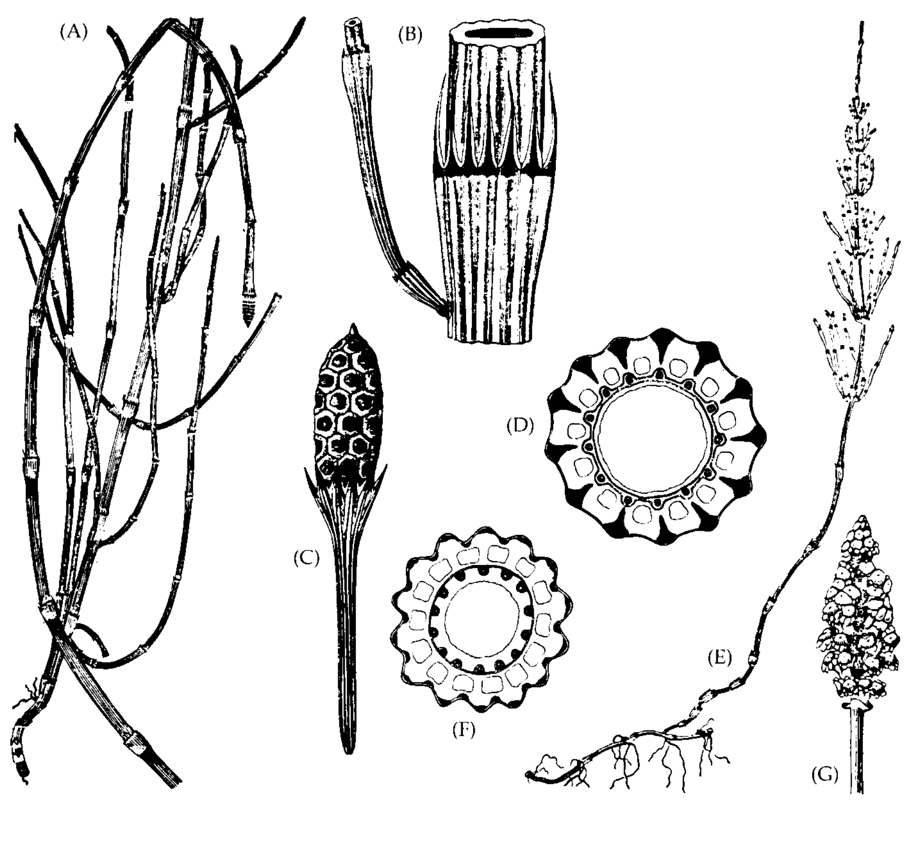

Figure 8.7 Equisetaceae. (A–D) *Equisetum ramosissimum*: (A) habit (× 0.5); (B) node with branch (× 4); (C) strobilius (× 3); (D) cross-section through stem, showing hollow center and more or less circular canals under valley (× 6.5). (E–G) *E. arvense*: (E) habit of sterile plant (× 0.4); (F) cross-section through stem (× 9.5); (G) apex of fertile stem with strobilus (× 0.8). (A–F from Madalski 1954; G from Hauke 1990.)

species; superficial stomates; stems branched) and subgen. *Hippochaete* (7 species; sunken stomates; stems unbranched) -- which have been recognized as distinct genera by some. Hybridization occurs frequently between species of the same subgenus but not between species of the two subgenera. A phylogenetic study of all 15 species, based on a combined analysis of two chloroplast markers, *trnL-F* and *rbcL*, demonstrates robust support for monophyly of the two subgenera. The South American species, *E. bogotense*, however, is not a member of either clade but instead is sister to the other 14 species.

Fossil relatives of Equisetaceae are known since the Devonian (408–360 MYA), and they became most abundant as relatively small (under 1 m tall) plants of the understory of Carboniferous forests. Some members of the clade to which Equisetaceae belongs that grew in the Carboniferous has stems as tall as 20 m, and, like large Carboniferous lycophytes of that time, they went extinct. The first fossils clearly assignable to *Equisetum* are from the Eocene (54–38 MYA), but the genus may extend back into the Permian, more than 300 MYA.

References: Des Marais et al. 2001; Hauke 1990, 1993; Lellinger 1985; Pryer et al. 2001; Stewart and Rothwell 1993; Tryon and Tryon 1982.

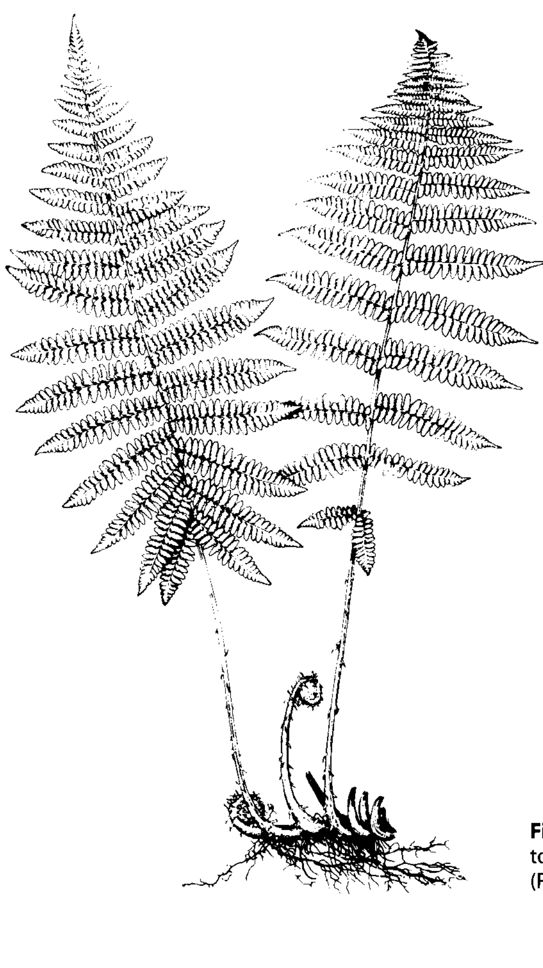

Figure 8.8 Polypodiaceae. *Athyrium filix-femina*: habit (about one-third to one-quarter actual size). Note circinate vernation of developing leaves. (From Taylor 1984; Milwaukee Public Museum, original art by P. Nelson.)

Leptosporangiate Ferns (Polypodiales)

Terrestrial, epiphytic, or aquatic. **Primary xylem with scalarifrom bordered pits.** Stems rhizomatous to treelike and up to 20 m tall. Leaves megaphylls (see Figures 8.8, 8.13, 8.14), often much more than 2 cm long and with numerous and forking veins; mostly divided into separate lobes or separate leaflets, but sometimes simple and unlobed; spirally arranged or sometimes 2-ranked, their bases often persistent and more or less covering the stem or sometimes cleanly abscising; with *circinate vernation* (Figure 8.8)—forming a crozier or "fiddlehead" (i.e., coiled and unfolding lengthwise when emerging); monomorphic or dimorphic (sterile and fertile leaves different). **Sporangia with stalk 4-6 cells in cross-section,** *mostly clustered in sori* on the abaxial leaf surface of normal leaves, or in specialized portions of leaves, or on completely separate fertile leaves (see Figure 8.14), less often scattered on the abaxial leaf surface or in sporocarps; usually with an **annulus**, a cluster or row of cells with thick walls that open the sporangium and catapult the spores into the air; the sporangium wall one cell layer thick at maturity (except in Osmundaceae). Homosporous, sometimes heterosporous; spores mostly not green. Gametophytes exosporic and growing on the surface of the ground or endosporic. **First cell division of the zygote vertical.**

Discussion: Leptosporangiate ferns are distinguished by their usually large leaves that form croziers as they unfold and sporangia that often cluster in sori. The many species in this group display tremendous leaf diversity, from the large, pinnately compound forms of the stereotypic fern (see Figures 8.8, 8.9, and 8.14), to the cloverlike leaves of the water-clover ferns (see Figure 8.11), to the needlelike leaves of curly-grass ferns (Schizaeaceae, not treated here). Habit varies from aquatics (Marsileaceae), to epiphytes with ribbon-shaped leaves, to trees (Cyatheaceae).

Currently between 25 and 35 families of leptosporangiate ferns are recognized. Here we treat four families, chosen to span the evolutionary diversity of this group as currently understood, from one of the first branches within the leptosporangiate fern clade (Osmundaceae) to the derived Polypodiaceae. These four families also display tremendous morphological diversity.

Polypodiaceae are treated broadly here to include many groups that have traditionally been considered separate families. Polypodiaceae plus the tree fern clade (with Cyatheaceae), heterosporous aquatic ferns (including Marsileaceae), and schizaeoid ferns (not treated here) form a tentative clade called by some workers the higher

Key to Selected Families of Leptosporangiate Ferns

1. Plants floating in water or sometimes rooted in mud bordering water leaves divided into 2 or 4 segments or threadlike and undivided; heterosporous, the sporangia lacking an annulus and of two kinds that are borne in the same specialized, hardened and bean- or pea-shaped sporocarp .... **Marsileacae**
1. Plants mostly terrestrial; leaves mostly pinnately compound with numerous segments, at least pinnatifid, infrequently simple; homosporous, the sporangia annulate and usually borne in sori that are exposed on the leaf surface 2
2. Annulus merely a patch of cells on the side of the sporangium; sori absent; spores over 100 to several thousand per sporangium .... **Osmundaceae**
2. Annulus usually a much larger vertical or obliqueband of cells; sori usually present; spores usually 64 or fewer per sporangium 3
3. Stems usually massive and often arborescent, reaching 20 m in height; leaves (0.5–) 2–3 (–5) m long; annulus oblique, not interrupted by stalk of sporangium .... **Cyatheaceae**
3. Stems creeping along the ground or subterranean, usually only tip of stem and leaves evident, or epiphytic; leaves generally less than 2 m long; annulus vertical, interrupted by the sporangium stalk .... **Polypodiaceae s.l.**[a]

[a] The abbreviation "s.l." stands for *sensu lato,* meaning "in the broad sense," or broadly defined; its converse "s.s." stands for *sensu stricto,* "in the narrow sense," or narrowly defined. Both terms are used throughout Chapters 7 and 8.

leptosporangiate ferns (see Figure 8.4). Several families of basal leptosporangiate ferns, such as Dipteridaceae, Gleicheniaceae (the gleichenoid ferns), Hymenophyllaceae, Matoniaceae, Osmundaceae, and Plagiogyriaceae, are also supported, but relationships are in some cases unclear (Figure 8.4). Osmundaceae are probably sister to the remaining families. Recent papers are clarifying phylogenetic relationships of leptosporangiate ferns (Hasebe et al. 1995; Pryer et al. 1995, 2001; Smith 1995; Wolf 1997; Wolf et al. 1998, 1999; Pryer 1999; Vangerow et al. 1999; Smith and Cranfill in press).

The nature of the annulus is critical to the phylogeny of leptosporangiate ferns. In Osmundaceae it is merely a patch of cells on one side of the sporangium (Figure 8.9). Marsileaceae have no annulus, as the sporangia are encased and dispersed in the sporocarp. The annulus of Cyatheaceae (see Figure 8.10) consists of a series of cells that are not vertical in orientation—it does not lie in the same plane as the sporangium stalk—and therefore does

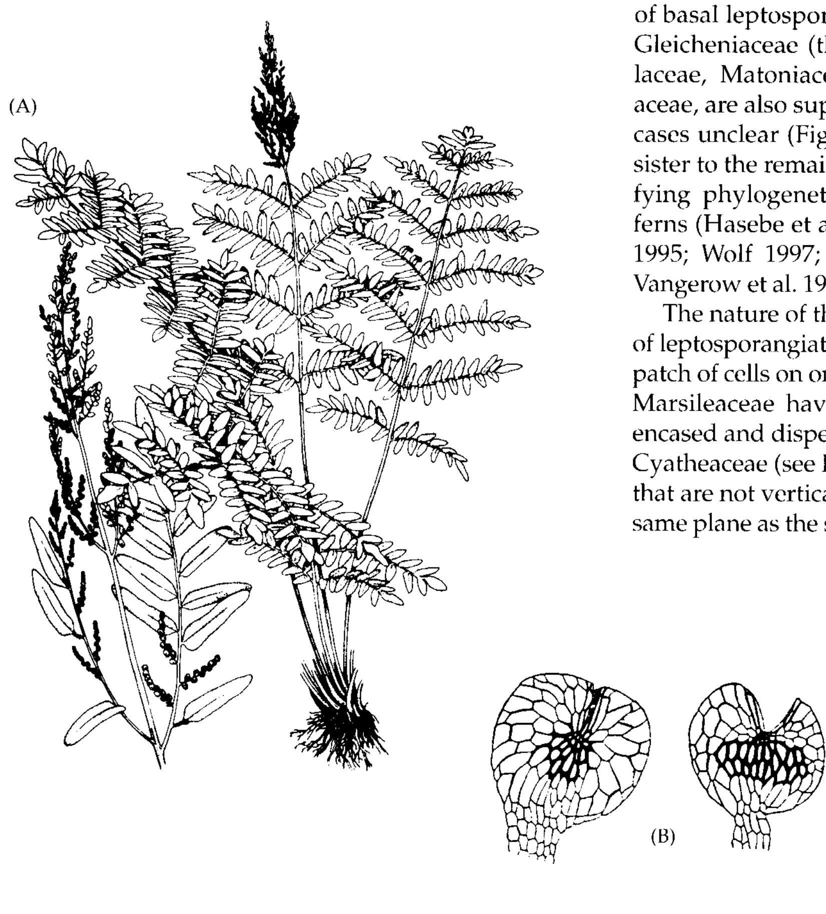

Figure 8.9 Osmundaceae. (A) *Osmunda regalis*: habit (about × 0.1), with an enlarged apical, partially fertile portion of the leaf to the left (about × 0.3). (B) *O. lancea*: sporangia, closed on left and open on right (× 315). Note thickened cell walls of annulus. (A from Taylor 1984; Milwaukee Public Museum, original art by P. Nelson; B from Hewitson 1962.)

not contact the stalk. In Polypodiaceae, the annulus is a line of cells whose vertical orientation puts it in the plane of the stalk, but the annulus stops where it meets the stalk, and hence it is said to be "interrupted" by the stalk (see Figure 8.12).

References: Flora of North America Editorial Committee 1993; Hasebe et al. 1995; Kramer and Green 1990; Lellinger 1985; Pryer et al. 1995, 2001; Smith 1995; Stein et al. 1992; Tryon and Tryon 1982; Vangerow et al. 1999; Wagner and Smith 1993; Wolf 1997; Wolf et al. 1998; Wolf et al. 1999.

Osmundaceae Berchtold and J. Presl
(Royal Fern Family)

Terrestrial. Stems branched, often covered by persistent leaf bases, horizontal to erect and arborescent. Leaves about 0.5–2 m long, once- to thrice-pinnately compound or once-pinnate-pinnatifid (deeply pinnately lobed), with an expanded petiolar base, circinate before unfolding; in some species wholly or partially dimorphic, with separate sporangium-bearing segments or whole leaves; often forming a vase-shaped clump. *Sporangia separate or in loose clusters, not clustered in sori, borne on wholly fertile portions of the leaf or on the abaxial surface of relatively unmodified portions of the leaf, with a short stalk of many rows of cells and a poorly differentiated* **annulus that consists of a group of thickened cells on the side of the sporangium**. Homosporous; spores green, over 100 to several thousand per sporangium. Gametophytes growing on the surface of the ground, heart-shaped to elongate, green (see Figure 8.9).

Distribution and ecology: Worldwide except for very cold and dry climates and Pacific islands. *Osmunda*, the only genus in the Northern Hemisphere, is common in wetlands, such as swamps, swales, and lowland forests.

Genera/species: 3/18. ***Genera:*** *Osmunda* (10 spp.), *Leptopteris* (6), and *Todea* (2).

Economic plants and products: Some species, such as cinnamon fern (*Osmunda cinnamomea*) and royal fern (*O. regalis*), are grown as ornamentals.

Discussion: The numerous spores, rudimentary annulus, sporangium wall more than one-cell thick, lack of a sorus, and *rbcL* DNA sequence data all support Osmundaceae as sister to all other leptosporangiate ferns. This conclusion is consistent with the long fossil record dating to the Permian (286–245 MYA). *Osmunda claytoniana* has apparently lived since the lateTriassic, about 220 MYA.

References: Hasebe et al. 1994, 1995; Kramer 1990c; Lellinger 1985; Phipps et al. 1998; Pryer et al. 1995; Tryon and Tryon 1982; Whetstone and Atkinson 1993.

Cyatheaceae Kaulf.
(Scaly Tree Fern Family)

Stem usually a single, erect, arborescent trunk to 20 m tall, usually massive and unbranched, sometimes creeping along the ground. **Leaves distinctly scaly,** *(0.5–) 2–3 (–5) m long*, pinnately or bipinnately compound, with leaflets deeply pinnately lobed, circinate before unfolding. Sporangia borne in sori on the abaxial leaf surface; the annulus continuous, not interrupted by the sporangium stalk. Indusium (a thin, platelike structure that covers a sorus) below the sorus or absent. Homosporous; spores not green, usually 64 (sometimes only 16) per sporangium. Gametophyte heart-shaped or occasionally elongate, growing on the surface of the ground; green (Figure 8.10).

Distribution and ecology: New and Old World tropical wet montane forests and cloud forests. Some species extend into south temperate areas (New Zealand and southern South America) and into north temperate India, China, and Japan. Some species are widely distributed, but local endemics are numerous on oceanic islands and tropical mountains. Many species are early successional on landslides.

Genera/species: ca. 3–6/500. ***Major genera:*** *Alsophila* (230 spp.), *Sphaeropteris* (120), and *Cyathea* (110).

Economic plants and products: Members of this family are sometimes grown as ornamentals, and the fibrous rhizomes are used as a base for epiphytes in greenhouses. Human exploitation has led to extensive destruction of tree fern stands, but most species are now covered by international agreements barring trade in endangered species.

Discussion: Chloroplast DNA restriction site data establish three well-defined lineages: the *Alsophila* clade (including *Nephelea*), the *Cyathea* clade (including

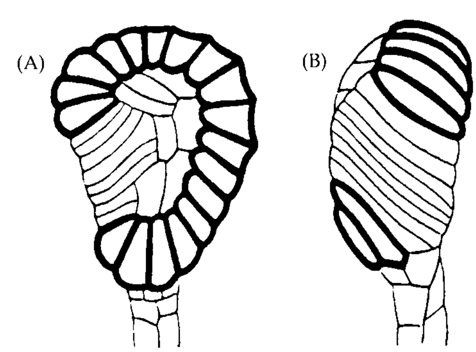

Figure 8.10 Cyatheaceae. *Cyathea capensis*: (A) sporangium, showing interrupted annulus with cells with thicked walls; (B) the same, different view (both × about 100). (From Holttum 1963.)

Trichipteris and *Cnemidaria*), and the *Sphaeropteris* clade. Relationships among these clades are unresolved.

The phylogenetic relationships of this family also are not clear, although it is phylogenetically close to two other tree fern families: the "Dicksoniaceae," which recently has been shown not to be monophyletic, and the Metaxyaceae (two species). Another relative, according to DNA sequence evidence, is Hymenophyllopsidaceae, which is surprising in that members of this family have short-creeping to suberect or erect stems and leaves only 10–30 cm long. The name of the family reflects the similarity of its delicate nature to that of members of the Hymenophyllaceae, the filmy ferns, a family of about 600 species. Hymenophyllopsidaceae, which contain a single genus and about eight species, are the most narrowly distributed fern family, restricted to the Roraima geological formation in Venezuela, Guyana, and northernmost Brazil.

Two potential synapomorphies of the broadly defined tree fern clade are pneumathodes (ventilation lines or patches on the leaf axis or petiole or on the rachis for gas exchange) and radial symmetry of the rhizome. Molecular data tentatively support a sister-group relationship between this tree fern calde and the Polypodiaceae s.l.

Groves of tree ferns, with the crown of large leaves atop the unbranched stems, make some of the most attractive displays in the natural world.

References: Conant et al. 1995; Conant and Stein 2001; Kramer 1990a; Pryer et al. 1995; Tryon and Tryon 1982; Wolfe et al. 1999.

Marsileaceae Mirbel
(Water-Clover Family)

Plants aquatic or rooted in the mud bordering bodies of water. Stems slender, glabrous, and creeping, growing on soil surface or subterranean. *Leaves long-petioled, the blade divided into 2 or 4 leaflets or filiform and not expanded;* circinate before unfolding. Sori **with no indusial opening**, enclosed in bean- or pea-shaped *sporocarps* that are borne on short stalks near or at base of petioles; each sporocarp with at least 2 sori. Heterosporous. Sporangia without an annulus; megasporangia with one megaspore; microsporangia with 16–64 microspores. Gametophytes minute, remaining within spores; megagametophytes **with one archegonium**, protruding from spores; microspores bursting as male gametophytes release sperm (Figure 8.11).

Distribution and ecology: Nearly cosmopolitan in warm temperate and tropical areas; amphibious, growing in water or near water in very wet soil.

Genera/species: 3/76. Major genera: *Marsilea* (50–70 spp.) and *Pilularia* (6).

Economic plants and products: Occasionally planted as a curiosity.

Discussion: The common name refers to the similarity between water-clover (*Marsilea*) leaves and those of clovers (*Trifolium*, Fabaceae). *Pilularia*, which is widely distributed, has filiform leaves. Leaves of *Regnellidium*, a monotypic genus of southern Brazil and adjacent Argentina, have two leaflets. Recent studies show that *Pilularia* and *Regnellidium* are sister taxa and *Marsilea* is the sister of that clade.

Morphological and DNA sequence data show that this family is the sister to the Salviniaceae, which consists of two genera of aquatic, heterosporous ferns, *Azolla* and *Salvinia*. Heterospory, therefore, is hypothesized to have arisen a single time within the leptosporangiate ferns. Salviniaceae are cosmopolitan, with *Azolla* and *Salvinia* each having fewer than 10 species, and contain plants that are floating aquatics bearing flattened sporocarps. The clade of heterosporous ferns is sister to Cyatheaceae plus Polypodiaceae.

The sporocarps of Marsileaceae are highly unusual. They protect spore viability for over 100 years in some species and may be an adaptation for growth in arid regions where rainfall is infrequent. Waterfowl consume

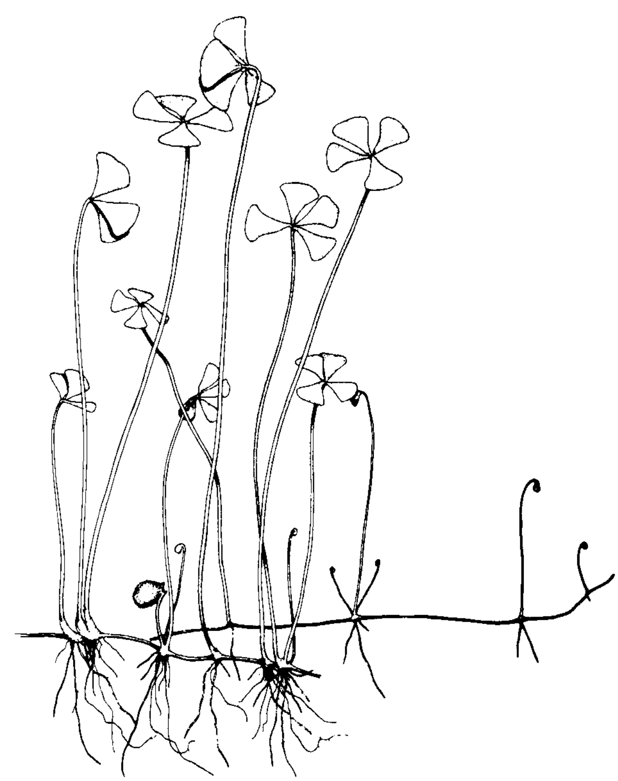

Figure 8.11 Marsileaceae. *Marsilea vestita*: habit (about × 0.7). Note mature, cloverlike leaves; numerous young, circinate leaves and single sporocarp (arrow). (From Taylor 1984; Milwaukee Public Museum, original art by P. Nelson.)

the sporocarps, which pass through the digestive tract and thus disperse the spores.

The fossil record indicates that the genera of this family diversified by the mid-Cretaceous.

References: Johnson 1993a; Kramer 1990b; Lellinger 1985; Lupia et al. 2000; Pryer 1999; Pryer et al. 1995.

Polypodiaceae Berchtold and J. C. Presl s.l.
(Higher Fern or Polypody Family)

Terrestrial, sometimes growing on rocks, sometimes epiphytic or climbing, infrequently aquatic; perennial, rarely annual. Stems subterranean or barely evident at soil surface (except in epiphytes, climbers, and aquatics), sometimes horizontal (rhizomatous) and creeping, reproducing vegetatively; often with epidermal scales of various sizes, shapes, and textures. Leaves mostly pinnately lobed to once, twice, or several times pinnately compound (Figures 8.8, 8.13, 8.14); less often palmately compound, simple, or ribbonlike; usually *circinate*, clustered or separated from one another on an elongate stem; petiole usually well developed, rarely absent; sterile-fertile dimorphism well developed (see Figure 8.14) to absent; with hydathodes; variously hairy, scaly, or glabrous. Sporangia with a well-developed **vertical annulus, interrupted by the sporangium stalk** (Figure 8.12); *usually borne in sori* that may be covered by an indusium; sometimes intermixed with special branched or unbranched hairs (paraphyses). Sori on the abaxial surface or near the margin of the leaf; round to elongate (Figures 8.12, 8.13). Indusium above, beside, or less often below the sorus; round to elongate; sometimes absent, replaced by the recurving leaf margin, or combining with a recurving leaf margin. Homosporous; spores 64, 32, 16, or 8 per sporangium, usually not green, monolete or trilete, the surface smooth or variously sculptured with ridges and spines. Gametophytes growing on the surface of the ground; green, heart-, kidney-, or ribbon-shaped; sometimes with small buds (gemmae) that separate from the gametophyte for asexual reproduction.

Distribution and ecology: Worldwide and in a great range of habitats, from saline and freshwater wetlands to deserts, from tropical lowlands to montane and alpine areas, from the understory of mature forests to early successional sites.

Genera/species: 193–223/7500. ***Major genera:*** *Asplenium* (700 spp.), *Cyclosorus* (600), *Elaphoglossum* (500), *Diplazium* (400), *Grammitis* (400), *Thelypteris* (280), *Dryopteris* (225), *Polystichum* (200), *Pteris* (200), *Blechnum* (175), *Adiantum* (150), *Athyrium* (150), *Cheilanthes* (150), *Ctenitis* (150), *Lindsaea* (150), *Polypodium* (150), *Tectaria* (150), and *Dennstaedtia* (45).

Economic plants and products: Many species, including maidenhair ferns (*Adiantum*), Boston fern (*Nephrolepis*), and brakes (*Pteris*), are grown as ornamentals, either in gardens or as houseplants. *Matteuccia struthiopteris* (Figure 8.14), a robust fern of alluvial woods in

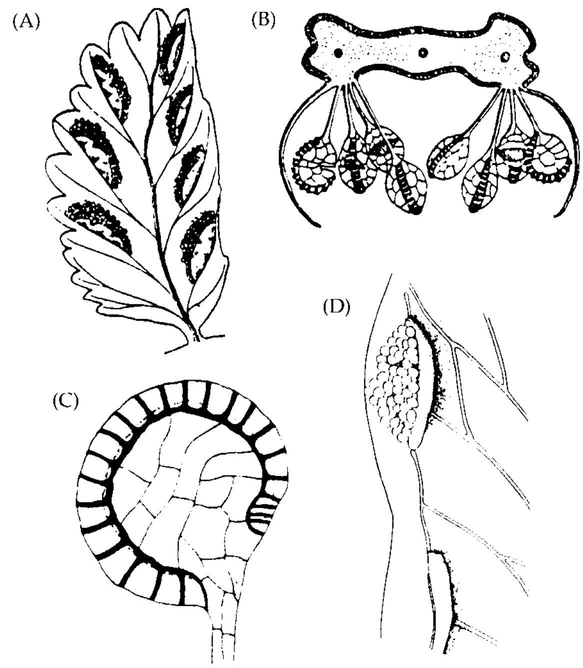

Figure 8.12 Polypodiaceae. (A, B) *Asplenium tripteropus*: (A) portion of underside of leaf, showing sori (× 4); (B) cross-section of fertile leaf, showing two sori and sporangia. (C) *A. nidus*: sporangium, showing interrupted annulus with cells with thickened walls (× 140). (D) *Asplenium* sp.: margin of leaf, with sori (× 8) (A, B from *Flora Tsinlingensis* 1974; C from Haider 1954; D from Pérez Arbeláez 1928.)

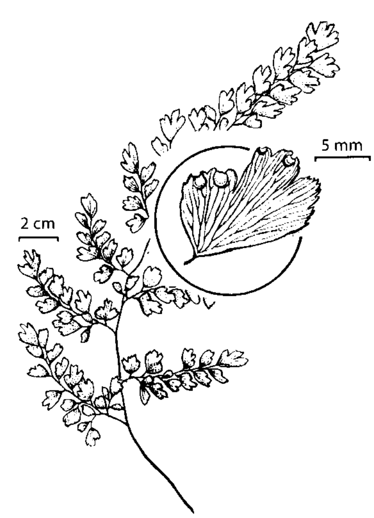

Figure 8.13 Polypodiaceae. *Adiantum capillus-veneris*: portion of leaf; enlarged portion of a leaf segment, showing marginal sporangia. (From Paris 1993.)

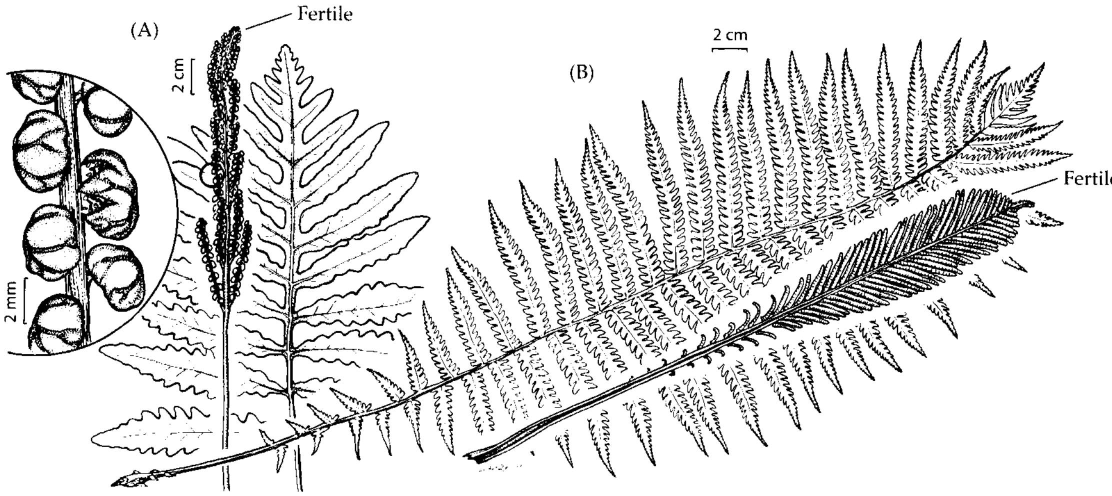

Figure 8.14 Polypodiaceae. (A) *Onoclea sensibilis*: fertile and sterile leaves; enlargement of portion of fertile leaf. (B) *Matteucia struthiopteris*: fertile and sterile leaves. (From Johnson 1993b.)

much of the Northern Hemisphere, is collected in the spring and its young leaves—often referred to as fiddleheads—are consumed fresh or canned. This species is often planted near houses. Some species have been used to dye cloth. *Pteridium aquilinum* is an invasive weed in many parts of the world.

Discussion: The Polypodiaceae are broadly defined here* and include at least 11 families that are currently recognized by some systematists. DNA sequence and morphological data together support monophyly of some of these families, such as the Aspleniaceae (1 genus, 700 species) and Thelypteridaceae (5–25, about 1000), whereas Dennstaedtiaceae (20, 400), Dryopteridaceae (60, 3000), and Polypodiaceae s.s. (40, 500) are clearly shown to be para- or polyphyletic. More intensive taxonomic sampling and new structural and molecular data have greatly improved our understanding of relationships within Polypodiaceae s.l. The broad definition is used here because monophyly of Polypodiaceae s.l. is corroborated by morphological and DNA sequence data.

Features common to many leptosporangiate ferns—large, clumped, pinnately compound leaves and mesic forest habitat—hold for many species in this family. Nevertheless, as its description indicates, the family encompasses tremendous variation in habit, leaf morphology, and reproductive features. For example, aquatics, such as *Ceratopteris*, may have inflated petioles for flotation. Epiphytes, such as *Vittaria*, the shoestring ferns, have long, linear leaves with indistinct petioles.

Characters of sori and indusia vary greatly as well in Polypodiaceae s.l. In some, the sori and indusia are linear, and the indusium is attached beside and covers part or all the sorus. Other species bear round sori that are more or less covered by an indusium. Sori of yet other species are marginal and partially covered by the recurving leaf margin. Sori of still other species are not associated with indusia. In addition to leaf morphology and these reproductive features, scales on the stem and leaves, leaf architecture, habit, number and arrangement of vascular bundles in the petiole, hairs, venation, spore morphology, and chromosome number are taxonomically informative.

Hybridization and polyploidy play prominent roles in the evolution and systematics of *Asplenium*, *Athyrium*, *Ceratopteris*, *Cheilanthes*, *Cystopteris*, *Diplazium*, *Dryopteris*, *Gymnocarpium*, *Pellaea*, *Polypodium*, *Polystichum*, *Pteris*, *Woodsia*, and other genera.

References: Hasebe et al. 1995; Kramer and Green 1990; Lellinger 1985; Pryer et al. 1995; Smith and Cranfill 2002; Tryon and Tryon 1982; Wagner and Smith 1993; Wolf 1997.

GYMNOSPERMS

Living seed plants form a monophyletic group with five major clades: cycads, Ginkgoaceae, conifers, Gnetales, and angiosperms. The first four groups have commonly been called gymnosperms, which means "naked" (*gymno*) "seed" (*sperm*). The seeds are not enclosed in a carpel, as they are in angiosperms (*angio* means "vessel," referring to the carpel), although they may sometimes be enclosed at maturity by fused cone scales or bracts, as in juniper "berries."

*The broad definition of a group is indicated by s.l. and the narrow definition by s.s.; see the footnote to the key on p. 195.

Monophyly of gymnosperms has been highly controversial. For many years they were not considered to form a monophyletic group (Crane 1988; Doyle 1998; Doyle et al. 1994; Nixon et al. 1994; Price 1996; Stefanovic et al. 1998). When fossils such as the extinct seed ferns (which had naked seeds) are considered, groups with naked seeds do not represent a clade. The status of gymnosperms also depends upon the location of the root of the seed plants. If, for example, the root places cycads with angiosperms, then gymnosperms are paraphyletic. More recent, molecular data sets conflict about monophyly of extant gymnosperms (Bowe and de Pamphilis 1997, Bowe et al. 2000; Chaw et al. 2000; Goremykin et al. 1996; Rydin et al. 2002). Analyses of Bowe et al. (2000) and Chaw et al. (2000) combine sequences from all three plant genomes. Bowe et al. (2000) used two mitochondrial genes, *cox*1 and *atp*A, plastid *rbcL* and nuclear 18S rDNA, and Chaw et al. (2000) used mitochondrial small subunit rRNA, plastid *rbcL*, and nuclear small subunit rRNA. Both studies strongly support gymnosperm monophyly and, surprisingly, a close relationship of Gnetales and conifers. The nuclear data in both studies have Gnetales and conifers as sister taxa, whereas the mitochondrial and plastid genes resolve a sister group relationship between Gnetales and Pinaceae. Under this so-called "gnepine" hypothesis, conifers are not monophyletic and Gnetales become extremely divergent conifers. A relationship between Gnetales and Pinaceae is unexpected given the many morphological differences between the two groups and a major genomic difference. Pinaceae and other conifers, but not Gnetales, have lost the inverted repeat from the plastid genome.

Rydin et al.'s (2002) analyses of plastid *atpB* plus *rbcL* and nuclear 18S rDNA plus 26S rDNA confirmed monophyly of conifers and rejected the gnepine hypothesis. Resolution of relationships of seed plants awaits further studies, and here we treat conifers as monophyletic and sister to Gnetales.

Together cycads, Ginkgoaceae, conifers, and Gnetales represent only about 15 families, 75–80 genera, and about 820 species. The evolutionary success of angiosperms relative to other seed plants may be attributed to vessels and reproductive features. All gymnosperms except Gnetales have only tracheids in their xylem. Angiosperms and Gnetales also have vessels, which are more efficient than tracheids in water transport, although more likely to suffer irreparable damage during drought. Angiosperm carpels make possible stigmatic germination of pollen and are variously adapted for protection of the young ovule and seed dispersal. Gymnosperms are slow to reproduce; up to a year may pass between pollination and fertilization, and seed maturation may require 3 years. Angiosperms, in contrast, usually reproduce far more rapidly, going from a seed to a seed in weeks in some annuals. With the exception of the cycads and some Gnetales, gymnosperms are pollinated by wind. Angiosperms have adapted in numerous ways to animal pollination, and they are thus able to reproduce in habitats where there is little wind, such as the forest floor. The highly specific nature of animal pollination may promote speciation (see Chapter 6). Furthermore, gymnosperms are rarely polyploid and have not undergone extensive allopolyploid speciation.

Gymnosperms are all woody—being trees, shrubs, or lianas—and include no true aquatics and few epiphytes. These plants grow throughout most of the world, from 72 north to 55 south, and they are the dominant vegetation in many colder and arctic regions. Pines, spruces, hemlocks, firs, yews, cedars, and related groups are familiar as ornamentals and supply high-quality wood. They include the tallest, the most massive, and the longest-living individual plants. We will consider 8 of the 15 families of gymnosperms, which together account for the great majority of species. Phylogenetic relationships among the extant groups of seed plants are not well resolved.

References: Beck 1988; Bowe and de Pamphilis 1997; Bowe et al. 2000; Chaw et al. 2000; Crane 1988; Doyle et al. 1994; Friis et al. 1987; Gifford and Foster 1988; Goremykin et al. 1996; Kubitzki 1990; Nimsch 1995; Nixon et al. 1994; Price 1996; Rydin et al. 2002; Singh 1978; Sporne 1974; Stefanovic et al. 1998; Stewart and Rothwell 1993; Taylor and Taylor 1993.

Cycadales (Cycads)

The cycads are an ancient group that has retained clearly primitive features, such as motile sperm. Cycads evolved in the Carboniferous or early Permian, about 280 million years ago and reached their peak abundance and diversity in the Mesozoic era. Now cycads are mostly Southern Hemisphere relicts, and many of the species are endangered or threatened by extinction.

The group is monophyletic, as judged by synapomorphies in structural features, such as girdling leaf traces, a specialized (omega) pattern of vascular bundles in the petiole, the presence of mucilage canals, and distinctive meristems, as well as poisonous glycosides called **cycasins**. Cycasins and other toxic compounds may have been important in the evolution of cycads as defenses against bacteria and fungi. Cycad toxins have been responsible for partial or total paralysis of the hind limbs of livestock.

Cycads are often palmlike, with an unbranched upright stem up to 18-20 m tall and large compound leaves crowded toward the stem apex, or fernlike, with a subterranean stem and compound leaves. Most cycads bear **cataphylls**, scale-like leaves that occur among the normal leaves and often serve a protective function. Cycads are slow-growing, with stems reaching as little as 1 m in height in 500 years.

Cycad reproductive structures occur in strobili that consist of an axis and megasporophylls (ovule-bearing leaves) or microsporophylls (pollen-bearing leaves). These simple structures contrast with the complex seed cones of conifers (see below). All cycads have pollen

Key to Families of Cycads

1. Leaflets circinate when young, with a midvein and no lateral veins; megasporophylls leaflike, loosely clustered near stem apex and not forming a strobilus, pinnately lobed or toothed above the ovules, with 2–8 ovules attached laterally to the basal portion .... **Cycadaceae**
1. Leaflets flat or conduplicate when young, with or without a midvein but with numerous, ± parallel veins or midvein present, with numerous, dichotomously branched or simple lateral veins; megasporophylls greatly reduced, valvate or imbricate, forming a strobilus with 2 reflexed ovules .... **Zamiaceae**

strobili, and all except *Cycas* have ovulate strobili. Although cycads produce abundant, powdery pollen that suggests wind pollination, insects are the primary vectors of pollen. Beetles and bees are either the sole pollen vector or move pollen to the ovule after wind has carried it to the ovulate strobilus from another plant. Pollination and fertilization may be separated by up to 7 months, during which time a pollen tube forms.

Cycad seeds often have a brightly colored (pink, orange, or red) and fleshy outer layer and are commonly dispersed by birds, bats, opossums, turtles, and many other animals. Some cycads attract dispersers with brightly colored megasporophylls. Ocean currents transport cycads whose seeds are buoyant due to a spongy outer layer, while gravity disperses the seeds of others.

Dioecy, which characterizes all cycads, may be governed by sex chromosomes. Chromosome number varies considerably among, but usually not within, cycad genera, and is taxonomically useful.

All cycad species bear special roots, called **coralloid roots** because of their similarity in appearance to marine coral. These roots host cyanobacteria that carry out nitrogen fixation, like that of bacteria in legumes. The cyanobacteria convert gaseous atmospheric nitrogen, which cycads cannot use, into a form they can use, providing a source of nitrogen that promotes growth in the nutrient-poor soils cycads frequently occupy.

The cycad clade consists of 2 families, 10–11 genera, and about 130 species. Cycadaceae contains only *Cycas*; Zamiaceae comprises the remaining 9–10 genera, including *Stangeria* (which has often been placed in the monogeneric Stangeriaceae).

References: Bogler et al. 2001; Crane 1988; Johnson and Wilson 1990; Jones 1993; Norstog and Nicholls 1997; Landry 1993; Norstog and Fawcett 1989; Rai et al. 2001; Stevenson 1990, 1991, 1992.

Cycadaceae Pers.

(Cycad Family)

Palmlike plants, with an unbranched to sparsely branched, woody stem covered with old remnants of leaf bases and living foliage near the apex of the stem; or *fernlike* with a subterranean stem. Leaves persistent, spiral, *pinnately compound;* **leaflets circinate when young and unfolding, with one midvein and no lateral veins**, entire, lower leaflets often spinelike. Microsporophylls aggregated into compact strobili; pollen nonsaccate, with a single furrow. *Megasporophylls grouped at the stem apex, somewhat leaflike and not clustered into a strobilus;* ovules 2–8 on the megasporophyll margin. Seeds large, *slightly flattened,* and covered by a *brightly colored, fleshy outer layer.*

Distribution and ecology: Madagascar, possibly Africa, Southeast Asia, Malesia, Australia, and Polynesia. In forests and savannas. Many species tolerate fire because the apical meristem is protected underground or by persistent leaf bases.

Genera/species: 1 (*Cycas*)/ca. 20.

Economic plants and products: Several species are popular as ornamentals in warm climates and as houseplants. The stem is a source of starch (called sago), especially in times of food shortage. Seeds may contain 20–30% starch, which is edible after removal of toxins.

Discussion: This family is distinct because its megasporophylls have a well-developed and toothed to pinnately dissected blade and are not compactly clustered into a strobilus. *Cycas* is probably the sister genus to the remainder of the cycads, and its fossil record extends back to the Permian, at least 250 million years ago. It is currently the most widely distributed genus of cycads.

Reference: Bogler and Francisco-Ortega, in press; Johnson and Wilson 1990.

Zamiaceae Horianow

(Coontie Family)

Fernlike with subterranean stem or *palmlike* with aerial, unbranched stem to 18 m tall and large, pinnately compound leaves clustered near stem apex. Stem covered with persistent dead leaf bases or naked. Leaves pinnately (rarely twice pinnately) compound, spiral, persistent, leathery, with or without stout spines on the petiole and rachis; *leaflets flat when young and unfolding, with numerous ± parallel veins* (with a midvein and dichotomously branching secondary veins in *Stangeria*), entire, dentate, or with sharp spines. Microsporophylls aggregated into compact strobili, with numerous small microsporangia that are often clustered; pollen nonsaccate, with a single furrow. **Megasporangiate strobili** 1 to several per plant, more or less globose to ovoid or cylindrical, disintegrating at maturity; **megasporophylls** densely crowded, symmetrically to asymmetrically peltate, valvate or imbricate, **each with 2 ovules**. Seeds large (1–2 or more cm long), **± round in cross-section**, with an *often brightly colored and fleshy outer layer* and a hard inner layer; cotyledons 2 (Figure 8.15).

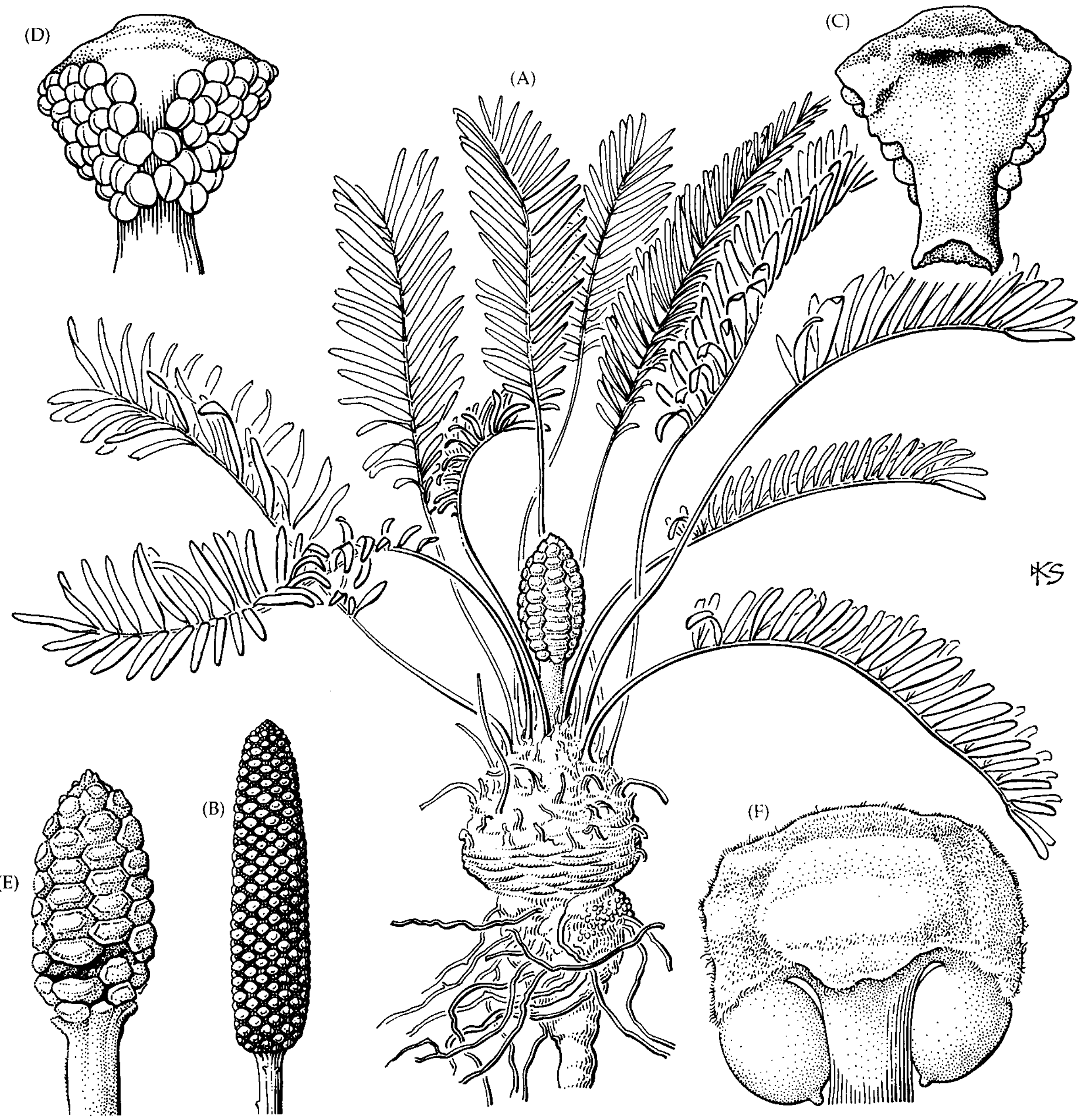

Figure 8.15 Zamiaceae. *Zamia floridana*: (A) habit of ovulate plant (some leaves removed) with strobilus at time of pollination; note large fleshy taproot with small lateral roots and coralloid roots (at right, near stem–root juncture) (× 0.75); (B) microsporangiate strobilus during pollen shedding (× 0.5); (C) adaxial surface of microsporophyll (× 4.5); (D) abaxial surface of microsporophyll, with microsporangia (× 4.5); (E) ovulate strobilus at time of pollination; note separation of megasporophylls in lower portion of strobilus, allowing entry of pollinators and pollen (× 0.75); (F) adaxial view of megasporophyll with two ovules, each with micropyle directed toward axis at bottom (× 4.5). (From Stevenson 1991, *J. Arnold Arbor.* Suppl. Series 1: pp. 367–384.)

Distribution and ecology: Tropical to warm temperate regions of the New World, Africa, and Australia. From poor, dry soils of grasslands and woodlands to dense, tropical forests. The only native cycad of the United States is a *Zamia* in Florida and southern Georgia.

Genera/species: 9–10/111. ***Major genera:*** *Encephalartos* (35 spp.), *Zamia* (35), *Macrozamia* (14), *Ceratozamia* (10), and *Dioon* (10).

Economic plants and products: Many species are grown as ornamentals in warm climates and as houseplants. The stem and seeds have been used as a source of starch (called sago). Removal of the toxic glycosides cycasin and macrozamin by boiling and washing is required before consumption.

Discussion: The seed strobili of this family are among the heaviest and largest of seed plant reproductive structures, weighing up to 40 kg and measuring 60 cm in length and 30 cm in diameter. The seeds are also quite large, up to 4 cm long. *Zamia* is unusual in having species with several different chromosome numbers, and species delimitation is very difficult in this genus. Stevenson (1992) divided the family into two subfamilies, each with two tribes. *Dioon*, which is distinct in having strongly asymmetrically peltate megasporophylls with stalked ovules, is strongly supported as the sister to the remaining genera. Like other cycad genera, *Dioon* was formerly much more widespread and is known as fossils from the Eocene in Alaska.

Bowenia, which has two or three species confined to tropical regions of northeastern Australia, is unique among cycads in its bipinnately compound leaves. This genus has been placed in its own family or united with *Stangeria*, which grows naturally only in southern Africa and contains only one species, in the Stangeriaceae. *Stangeria* is exceptional in the Zamiaceae in its leaf venation (see family description). Molecular data analyzed to date clearly place these two genera within the Zamiaceae, do not show a close relationship between them, but otherwise do not resolve their affinities with other members of the Zamiaceae.

Encephalartos (Africa), *Lepidozamia* (Australia), and *Macrozamia* (Australia) form a clade based on molecular data. *Lepidozamia* was in the past merged into *Macrozamia*, but molecular data actually show that *Lepidozamia* and *Encephalartos* are sister taxa.

Zamia is wide-ranging, morphologically diverse, and has numerous species, although there are differences in the recognition of species by different workers. Pollen-eating beetles are responsible for pollinating *Zamia* in Florida. Release of oil of wintergreen apparently draws the beetles to microsporangiate strobili, which provide an egg-laying site and food for adult and larval beetles. Adult beetles eat pollen and are covered by it. Pollination occurs when pollen-covered adults go to megasporangiate strobili where the beetles neither feed for lay eggs.

References: Bogler and Francisco-Ortega, in press; Johnson and Wilson 1990; Landry 1993; Norstog and Fawcett 1989; Norstog and Nicholls 1997; Stevenson 1991, 1992.

Ginkgoales

Ginkgoaceae Engler

(Ginkgo or Maidenhair Tree Family)

Trees to 30 m, with a more or less asymmetrical crown and furrowed, gray bark. Resin canals absent. Leaves simple, spiral, and widely spaced on long shoots near the tips of branches, often *closely packed on stubby short shoots on older growth;* **fan-shaped**, apically notched (the leaf then bilobed) or entire; **deciduous** and bright yellow in the fall; **dichotomously veined**. Dioecious. Pollen strobili borne on spur shoots, long and pendant; pollen not winged. **Ovules paired on a long stalk from spur shoots**; seeds frequently 1 per stalk, ca. 2.5 cm in diameter, with a juicy, unpleasant-smelling outer coat and hard inner coat; cotyledons 2–3.

Distribution and ecology: Limited to remote mountain valleys of China; possibly extinct in the wild. Little is known about the ecology of this species.

Genera/species: 1 (*Ginkgo*)/1 (*G. biloba*).

Economic plants and products: The maidenhair tree has been grown as an ornamental near religious institutions in eastern Asia for centuries. Individuals live for over a thousand years, and these old trees are probably the source of plantings in many parts of the world, where ginkgo is commonly used as ornamentals for shade and for their interesting and attractive foliage. Staminate individuals, which do not produce the unpleasant-smelling seeds, are commonly planted. The gametophyte and embryo, when boiled, fried, or roasted, are a delicacy in some Chinese dishes.

Discussion: The first representatives of this group appear in the Permian, and plants nearly identical to *Ginkgo biloba* extend back nearly 200 million years in the fossil record. During the early Jurassic, extinct relatives of *Ginkgo* were widespread and diverse, consisting perhaps of three families. Now, ironically, although rare or possibly extinct in the wild, *Ginkgo* does well as a shade tree in urban situations.

The broad, deciduous leaves of *Ginkgo* are unlike those of nearly all other gymnosperms. Sperm motility, known elsewhere in seed plants only in the cycads, is clearly a primitive feature, as is the lack of pollen tubes. Ginkgoaceae are not closely related to any extant groups.

Ginkgo is one of the few plants with sex chromosomes. Ovulate plants bear two X chromosomes, and staminate individuals are XY. Pollination occurs by wind in the spring, but fertilization is delayed for 4–7 months, after the ovules have fallen to the ground. The juiciness and odor of the seed suggest animal dispersal, but the dispersing taxa are unknown and may now be extinct.

References: Page 1990b; Whetstone 1993.

Coniferales (Conifers)

Conifers are the largest and most ecologically and economically important group of gymnosperms. Pines, spruces, firs, hemlocks, cedars, cypresses, redwoods, and giant sequoias are familiar, valued, and revered trees. Members of this group are called conifers because most bear their seeds in specialized structures called **cones** (see Figure 8.17P). Cones protect ovules and seeds and also facilitate pollination and dispersal. These structures consist of an axis bearing highly modified short shoots, the ovuliferous scales. These scales are subtended by bracts, which are either large and conspicuous (as in some Pinaceae), very small (as in other Pinaceae), or small to large and more or less fused to the scale (as in Cupressaceae). Seeds are associated with the scales. Cone scales of most members of Pinaceae and Cupressaceae are woody or leathery. The junipers (*Juniperus*) have cone scales that are more or less juicy and brightly colored, making the cones berrylike (see Figure 8.18 H,P,Q) and animal-dispersed. In Podocarpaceae cones are often reduced, with highly modified, juicy, brightly colored scales and just one ovule. Taxaceae bear solitary seeds partially or completely surrounded by a juicy aril.

Conifers date back to the Carboniferous, some 300 million years ago. Many current families developed by the late Triassic or early Jurassic, and some contemporary genera appeared in the middle Jurassic. Today conifers remain important in colder regions, such as the boreal forests of North America and Asia, where species of pine, spruce, and fir make up the dominant vegetation over large regions. Other conifers—particularly Araucariaceae, Cupressaceae, and Podocarpaceae—are prominent in cooler regions of the Southern Hemisphere. Conifers are valuable ornamentals, and their wood is used for paper production, building construction, and many other purposes. They are often referred to as "evergreens" because of the persistent foliage in most species, or as "softwoods" because their wood is softer than that of many angiosperm trees.

Pollination is by wind. Most conifers, like most nonangiosperm seed plants, use a pollination droplet, a sticky fluid extruded from the ovule at pollination, to catch airborne pollen. Pollen grains of most Pinaceae bear two **saccae**: small, winglike appendages that may serve to float the pollen grains upward in the pollination droplet toward the ovule or to orient the grains properly for germination. Alternatively, the pollen may be trapped on more or less sticky structures in the vicinity of the ovule. The pollen then germinates and grows via a pollen tube to the ovule (the sperm lack flagella).

Key to Selected Families of Conifers

1\. Seeds in woody (fleshy only in *Juniperus*) cones, mostly hidden by cone scales, a few to many per cone; plants highly resinous 2

1\. Seeds partially to wholly enclosed or subtended by fleshy, often brightly colored structures, usually solitary: plants slightly resinous 4

2\. Seeds 1 per cone scale .... **Araucariaceae**

2\. Seeds usually more than 1 per cone scale 3

2\. Leaves scale-like or needle-like, spiral, opposite, or whorled, persistent on branches after dying (but most branches shed with age); pollen nonsaccate; cone scales valvate or imbricate (and then leaves scalelike and opposite), flat or peltate, fused to bract, juicy in *Juniperus*; seeds with 2 or 3 lateral wings (infrequently wingless), 1–20 per scale .... **Cupressaceae**

3\. Leaves linear to needle-like, spiral, shed from branches (or as short-shoots in *Pinus*); pollen often saccate; cone scales imbricate, flat, distinct from bract; seeds terminally winged (or rarely wingless), 2 per scale .... **Pinaceae**

4\. Seeds more or less surrounded by a specialized cone scale (the epimatium), not an aril, and usually associated with colored, juicy bracts; pollen mostly saccate; pollen strobili with 2 sporangia per microsporophyll .... **Podocarpaceae**

4\. Seeds more or less surrounded by an aril, an outgrowth of the axis below the ovule; pollen nonsaccate; pollen strobili with 2–9 sporangia per microsporophyll .... **Taxaceae**

Conifer trees are often monopodial with a dominant central shoot or trunk. With age, the crown may branch irregularly. Branches are often whorled, at least when the plant is young.

The conifers comprise 7 families, 60–65 genera, and over 600 species. Relationships among the major groups of conifers are shown in Figure 8.16. The five families treated here include all but a few conifer species.

References: Brunsfeld et al. 1994; Eckenwalder 1976; Farjon 1990; Hart 1987; Kelch 1997; Page 1990a,c–f; Price et al. 1987; Price and Lowenstein 1989; Richardson 1998; Singh 1978; Sporne 1974; Stefanovic et al. 1998; Thieret 1993a; Watson and Eckenwalder 1993.

Pinaceae Adanson
(Pine Family)

Trees (occasionally shrubs), often emitting strong fragrances from bark and/or leaves; *resin canals present in wood and leaves*. Branches whorled or opposite (rarely alternate). Leaves simple, *linear to needlelike* (rarely narrowly ovate), spiral but often appearing 2-ranked by twisting of leaf base to bring most of the leaves into one plane, clustered or fascicled in groups of 2 to 5 in *Pinus*, sessile or short-petioled, on long shoots or tightly clustered on short shoots, persistent (deciduous in *Larix* and *Pseudolarix*). *Monoecious*. Microsporangiate strobili with spirally arranged, bilaterally symmetrical microsporophylls; microsporangia 2 on the abaxial microsporophyll surface; pollen grains with 2 saccae (saccae absent in *Larix*, *Pseudotsuga*, and all but two species of *Tsuga*) and 2 prothallial cells. *Cones with spirally arranged, flattened bract-scale complexes*; scales persistent (deciduous in *Abies*, *Cedrus*, and *Pseudolarix*), *bracts free from the scale*, longer than the cone scale to much shorter than the cone scale; maturing in 2 (3) years; *ovules 2*, **inverted** (micropyle directed toward the cone axis), on the adaxial cone scale surface; archegonia few per ovule, not clustered. **Seeds with a long, terminal wing** derived from tissue of the cone scale (wing reduced or absent in some species of *Pinus*); embryo straight, cotyledons 2–18 (Figure 8.17).

Distribution and ecology: Pinaceae are almost entirely limited to the Northern Hemisphere. Three or four genera grow only in eastern Asia; one (*Cedrus*) is confined to North Africa, the Near East, Cyprus, and the Himalayas; and the remaining six genera (the major genera) all occur widely in the Northern Hemisphere. The family ranges from warm temperate climates to the limit of tree growth above the Arctic Circle, from permanently water-saturated soils to well-drained soils, and from sea level to alpine habitats up to 4800 m above sea level in eastern Tibet. The seeds of pines are primary components of the diets of many species of birds, squirrels, chipmunks, and other rodents. Members of the family provide cover for many wildlife species and are important in watershed protection.

Genera/species: 10/220. ***Major genera:*** *Pinus* (100 spp.), *Abies* (40), *Picea* (40), *Larix* (10), *Tsuga* (10), and *Pseudotsuga* (ca. 5).

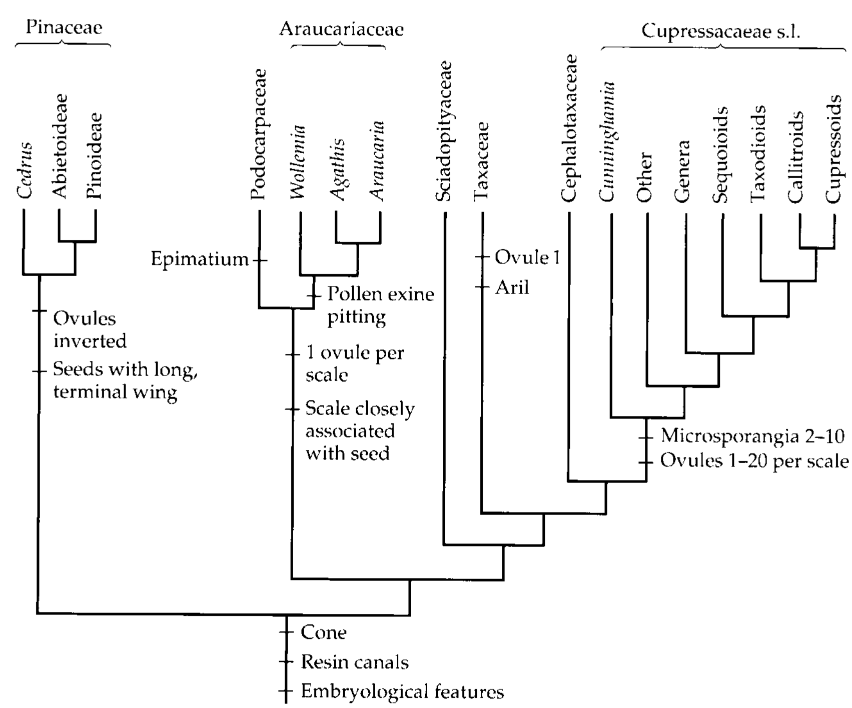

Figure 8.16 Relationships among major groups of conifers, with potential synapomorphies for the families covered in this book. (Based on Kelch 1998; Setogouchi et al. 1998; Stefanovic et al. 1998; and Wang et al. 2000.)

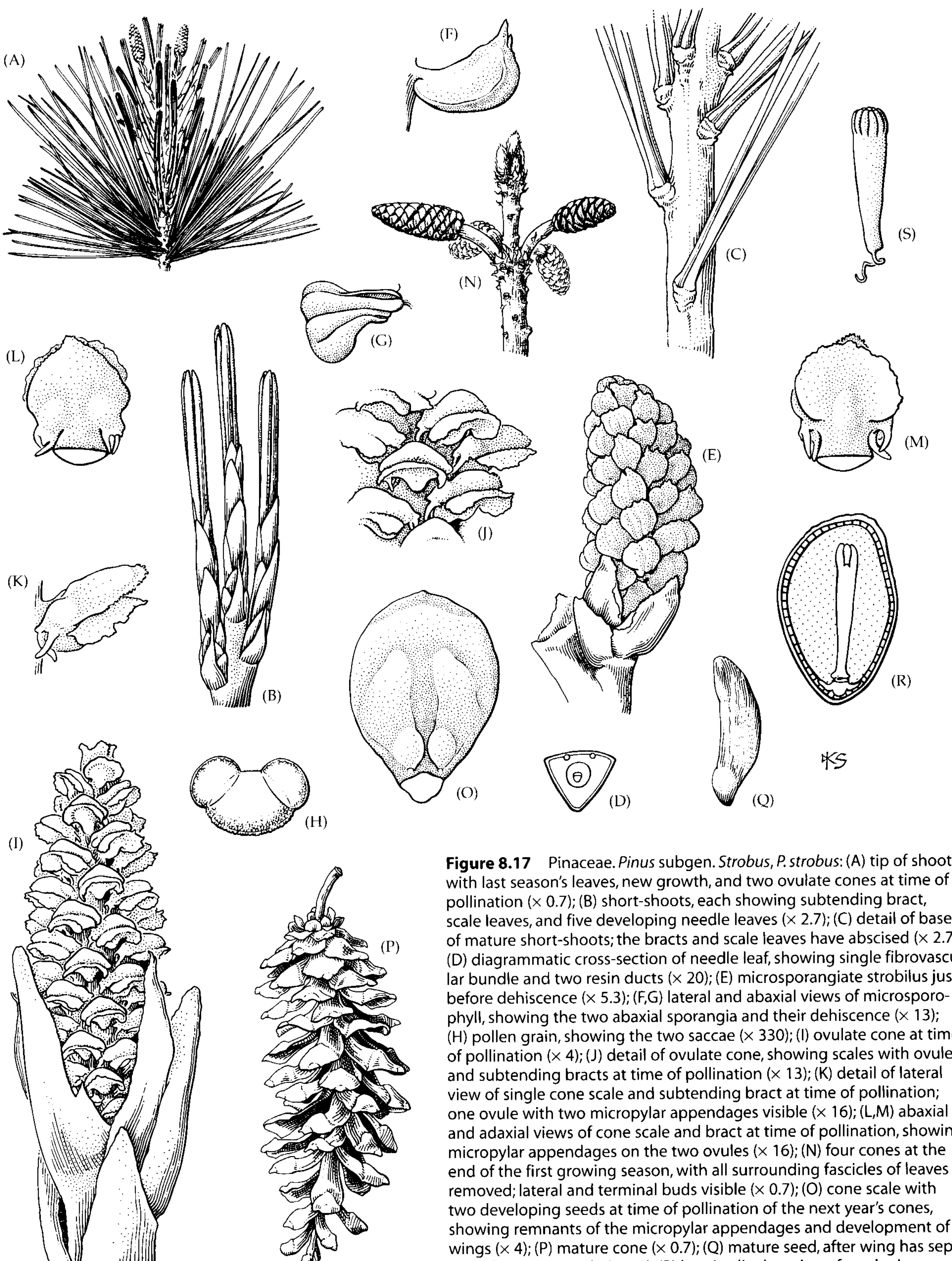

Figure 8.17 Pinaceae. *Pinus* subgen. *Strobus*, *P. strobus*: (A) tip of shoot with last season's leaves, new growth, and two ovulate cones at time of pollination (× 0.7); (B) short-shoots, each showing subtending bract, scale leaves, and five developing needle leaves (× 2.7); (C) detail of bases of mature short-shoots; the bracts and scale leaves have abscised (× 2.7); (D) diagrammatic cross-section of needle leaf, showing single fibrovascular bundle and two resin ducts (× 20); (E) microsporangiate strobilus just before dehiscence (× 5.3); (F,G) lateral and abaxial views of microsporophyll, showing the two abaxial sporangia and their dehiscence (× 13); (H) pollen grain, showing the two saccae (× 330); (I) ovulate cone at time of pollination (× 4); (J) detail of ovulate cone, showing scales with ovules and subtending bracts at time of pollination (× 13); (K) detail of lateral view of single cone scale and subtending bract at time of pollination; one ovule with two micropylar appendages visible (× 16); (L,M) abaxial and adaxial views of cone scale and bract at time of pollination, showing micropylar appendages on the two ovules (× 16); (N) four cones at the end of the first growing season, with all surrounding fascicles of leaves removed; lateral and terminal buds visible (× 0.7); (O) cone scale with two developing seeds at time of pollination of the next year's cones, showing remnants of the micropylar appendages and development of wings (× 4); (P) mature cone (× 0.7); (Q) mature seed, after wing has separated from cone scale (× 1.3); (R) longitudinal section of seed, wing removed, showing embryo surrounded by tissue of megagametophyte (stippled), micropyle facing base (× 7); (S) embryo, showing numerous cotyledons (× 8). (From Price 1989, *J. Arnold Arbor.* 70: pp. 247–305.)

Economic plants and products: Pinaceae are one of the leading sources of timber in the world. The wood of pines (*Pinus*), Douglas firs (*Pseudotsuga*), spruces (*Picea*), hemlocks (*Tsuga*), larches (*Larix*), and firs (*Abies*) is used extensively for construction, pulp for paper production, fenceposts, telephone poles, furniture, interior trim for houses, musical instruments, woodenware, and numerous other purposes. Pines, spruces, hemlocks, cedars (*Cedrus*), Douglas firs, and firs are used extensively as ornamentals, and hundreds of cultivars have been developed in many of the species of these genera. Pine "nuts," the more or less wingless seeds of pinon pines of southwestern North America, were a staple of native North Americans. These seeds and those of some Old World groups of pines are now a gourmet food. Rosin and turpentine are extracted from various species of pines.

Discussion: Pinaceae are the largest and both economically and ecologically the most important family of conifers. Species in the three largest genera—*Abies*, *Picea*, and *Pinus*—are the primary components of many forests in cooler and colder regions of the Northern Hemisphere. *Pinus* often dominates fire-maintained forests in warmer regions, such as the southeastern United States.

Numerous features—ovule inversion, prominent terminal seed wing, pattern of proembryogeny, protein-type sieve cell plastids, and the absence of biflavonoid compounds—establish the monophyly of Pinaceae. The family is not phylogenetically close to other extant conifer groups and is probably the sister group to the remaining conifers (see Figure 8.16).

Strongly congruent structural and seed protein immunological data divide Pinaceae into two subfamilies, Abietoideae and Pinoideae. Abietoideae include *Abies*, *Cedrus*, *Keteleeria*, *Pseudolarix*, and *Tsuga*, while *Cathaya*, *Larix*, *Picea*, *Pinus*, and *Pseudotsuga* make up Pinoideae. Phylogenetic analysis of three genes—*matK* from the chloroplast, mitochondrial *nad5*, and nuclear *4CL*—agree with this fundamental partition of the family except that *Cedrus* is sister to the remainder of the family. The Pinoideae are supported by several synapomorphies (absence of resin canals in the seed coat, absence of a narrowed, pedicillate base of the cone scales, and presence of two resin canals in the vascular cylinder of the young taproot) and contain two clades, *Pseudotsuga* plus *Larix*, and *Cathaya*, *Picea*, plus*Pinus*. Abietoideae in the molecular phylogeny has two sets of sister taxa, *Abies* plus *Keteleeria* and *Pseudolarix* plus *Tsuga*. The monotypic genus *Nothotsuga* is very closely related to *Tsuga* and is best treated as a species of *Tsuga*.

Pinus is highly distinct in its leaves, which are clustered in groups of usually two to five, and its cone scales, which are apically thickened and often armed with a prickle. This genus also has the longest fossil record of extant Pinaceae, extending back to the Jurassic or early Cretaceous. By the late Cretaceous, two monophyletic subgenera—*Pinus* and *Strobus*—had differentiated. Members of subgenus *Pinus* are called hard pines because their wood is harder than that of subgenus *Strobus* species, which are commonly called soft pines. The two subgenera differ in other wood anatomical features and in the number of vascular bundles in each leaf, two in hard pines and one in soft pines. The leaf clusters are surrounded at the base by a sheath, which is persistent in hard pines and deciduous in soft pines. About 65 *Pinus* species are native to North America, with high concentrations of species in Mexico, California, and the southeastern United States.

Pinaceae include the longest-lived trees: intermountain bristlecone pine (*Pinus longaeva*), an alpine species of the southwestern United States, lives over 5000 years. While not matching the Cupressaceae in height and massiveness, the pine family does have some huge trees. Douglas fir (*Pseudotsuga menziesii*), for instance, grows to over 80 m in height, and many pines and spruces exceed 60 m.

References: Farjon 1990; Farjon and Styles 1997; Page 1990c; Price 1989; Richardson 1998; Stefanovic et al. 1998; Thieret 1993a; Vining 1999. Wang et al. 2000.

Cupressaceae Bartlett

(Cypress or Redwood Family)

Trees or shrubs; wood and foliage often aromatic. Bark of trunks often fibrous, shredding in long strings on mature trees or forming blocks. Leaves persistent (deciduous in three genera), simple, spiral or basally twisted to appear 2-ranked, opposite, or whorled, *scale-like, tightly appressed and as short as 1 mm to linear and up to about 3 cm long*, with resin canals, shed with the lateral branches; adult leaves appressed or spreading, sometimes spreading and linear on leading branches and appressed and scale-like on lateral branches; scale-like leaves often dimorphic, the lateral leaves keeled and folded around the branch and the leaves on the top and bottom of the branch flat. *Monoecious* (dioecious in *Juniperus*). Microsporangiate strobili with spirally arranged or opposite microsporophylls; **microsporangia 2–10 on the abaxial microsporophyll surface**; pollen nonsaccate, **without prothallial cells**. Cone maturing in 1–3 years; **scales peltate or basally attached and flattened**, juicy in *Juniperus*, fused to bracts, persistent (deciduous in *Taxodium*); **ovules 1–20, on adaxial scale surface**, erect (micropyle facing away from the cone axis; in some the ovules may eventually be inverted); archegonia quite variable in number per ovule, clustered. Seeds with 2 (3) short lateral wings (wings absent in some genera); embryo straight, cotyledons 2–15 (Figure 8.18).

Distribution and ecology: This is a cosmopolitan family of warm to cold temperate climates. About three-quarters of the species occur in the Northern Hemisphere. About 16 genera contain only one species, and many of these have narrow distributions. Members of this family

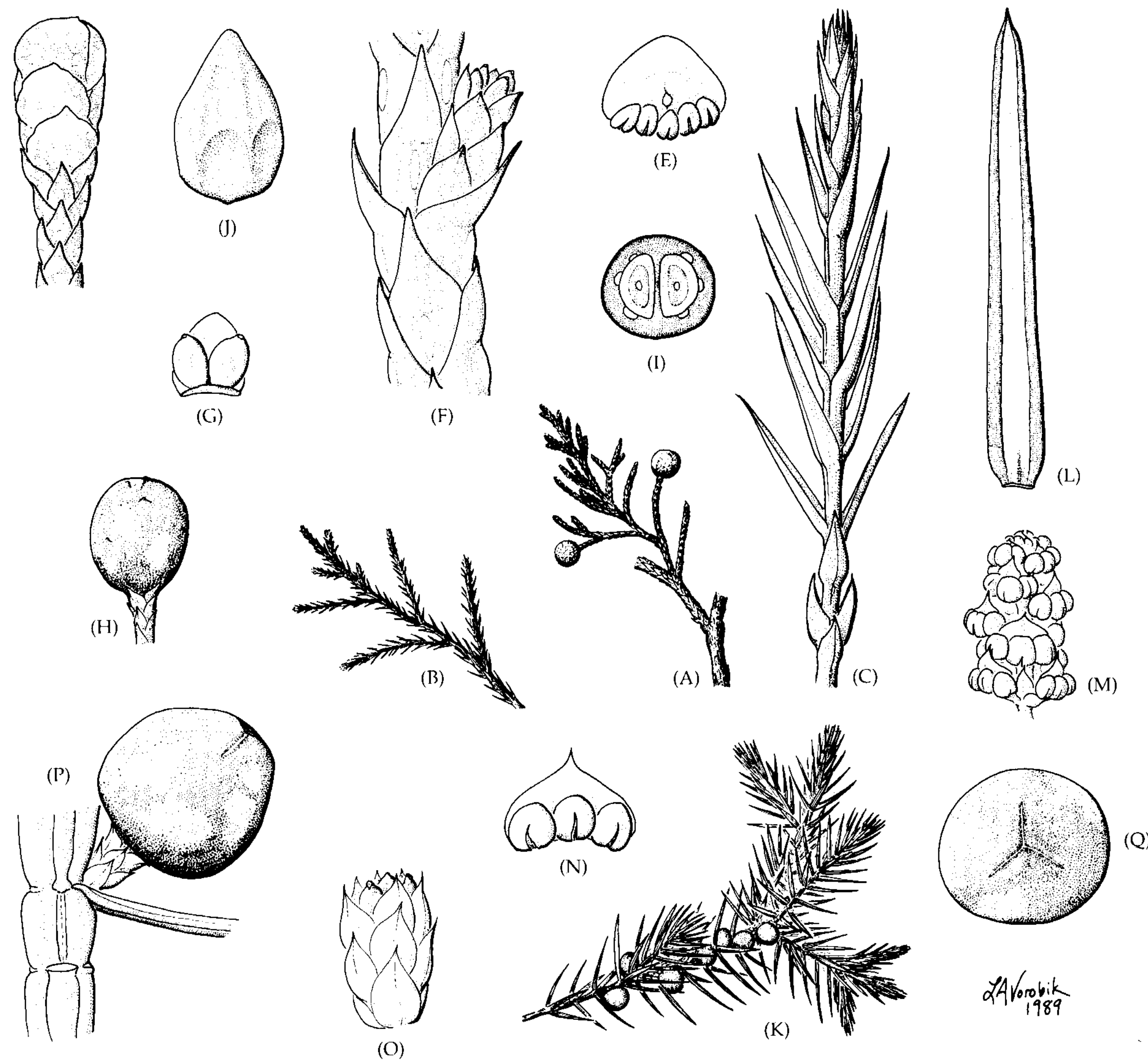

Figure 8.18 Cupressaceae. (A–J) *Juniperus virginiana*: (A) branchlets with only scale leaves, bearing mature ovulate cones (× 0.9); (B) branchlet with scale and needle leaves (× 0.9); (C) detail of branchlet with needle leaves, showing decurrent leaf bases (× 6.2); (D) microsporangiate strobilus before shedding of pollen, subtended by numerous scale leaves (× 6.2); (E) microsporophyll (abaxial view), showing dehisced sporangia (× 12); (F) branchlet with ovulate cone near time of pollination (× 9); (G) cone scale (adaxial view) with 2 erect ovules near time of pollination (× 12); (H) mature ovulate cone with fused cone scales (× 3.7); (I) cross-section of mature cone, only two seeds maturing (note resin vesicles outside seeds) (× 3.7); (J) seed, showing pits and ridges (× 6.2). (K–Q) *J. communis*: (K) branch, showing ternate leaves and axillary ovulate cones (× 0.9); (L) details of abscised portion of leaf in adaxial view, showing broad, white stomatal band (× 6.2); (M) microsporangiate strobilus after shedding of pollen (× 6.2); (N) microsporophyll, abaxial view; (O) axillary shoot with young ovulate cones at apex, showing three ovules near time of pollination (× 12); (P) portion of branchlet with mature ovulate cone; note remnant leaf bases fused to larger stem (× 3.7); (Q) apical views of ovulate cone, showing suture lines between three fused cone scales (× 3.7). (From Hart and Price 1990, *J. Arnold Arbor.* 71: pp. 275–322.)

grow in diverse habitats, from wetlands to dry soils, and from sea level to high elevations in mountainous regions. The two species of *Taxodium* in the southeastern United States often grow in standing water.

Genera/species: 29–32/110–130. Major genera: *Juniperus* (ca. 68 spp.), *Callitris* (15), *Cupressus* (14), *Chamaecyparis* (7), *Thuja* (5), *Taxodium* (3), *Sequoia* (1), and *Sequoiadendron* (1).

Economic plants and products: The family produces highly valuable wood. *Cryptomeria*, *Chamaecyparis*, *Juniperus*, *Sequoia*, *Taxodium*, *Thuja*, and several other genera are suited for house construction, siding, decking, caskets, shingles, boat construction, paneling, wooden pencils, and many other purposes. Many woods from this family are naturally fragrant and have been used as a natural moth-proofing for closets and chests and in the manufacture of perfumes. *Juniperus communis* cones are used to flavor gin. *Juniperus* pollen contains one of the most potent airborne allergens, and the tremendous amount of pollen produced by *Juniperus* species is highly correlated with nasal, sinus, and pulmonary allergies in humans and domestic animals. *Chamaecyparis, Cupressus, Juniperus, Platycladus, Thuja,* and other genera are grown extensively as ornamentals.

Discussion: This family was long split into Cupressaceae s.s. and Taxodiaceae on the basis of differences in the leaves. Cupressaceae s.s. leaves are either opposite and scale-like or whorled and linear, whereas those of Taxodiaceae are mostly spiral and linear. Leaves of *Metasequoia* (Taxodiaceae), however, are opposite, and those of *Athrotaxis* (Taxodiaceae) may be scale-like. There are numerous similarities (and potential synapomorphies) uniting these families: fusion of cone scale and bract; lateral wings on the seeds derived from the seed coat; microsporangia two or more per microsporophyll; more than two seeds per cone scale; shedding of small branches; clustered archegonia; wingless pollen grains that lack prothallial cells; peltate cone scales in many genera, and DNA sequence characters (Brunsfeld et al. 1994; Eckenwalder 1976; Hart 1987; Stefanovic et al. 1998; Tsumura et al. 1995; Watson and Eckenwalder 1993). An immunological study has shown high similarity among genera of Cupressaceae s.s. and Taxodiaceae, and much greater distance to taxa outside this group. Results of phylogenetic analysis of *rbcL* sequences are fully consistent with the immunological study. Finally, Cupressaceae s.s. are monophyletic and probably arose out of a paraphyletic assemblage, the "Taxodiaceae." Hence the evidence comes down decisively on the side of merging the two families.

Both immunology and DNA sequences from five chloroplast genes or regions identify similar groups of genera within the Cupressaceae s.l. Cupressaceae s.s. divide into two well-supported clades, the cupressoid clade with all Northern Hemisphere groups and the callitroid clade with all taxa from the Southern Hemisphere (see Figure 8.16). Cupressaceae s.s. are the sister group of the well supported taxodioid clade of three genera: *Taxodium, Glyptostrobus,* and *Cryptomeria. Taxodium* grows in the eastern United States and Mexico and, like its sister genus *Glyptostrobus* (southern and central China), is deciduous. *Cryptomeria* is wide-ranging in China and Japan. Another well supported trio of genera that diverged early in the evolution of Cupressaceae is the sequoioid clade, with *Metasequoia, Sequoia,* and *Sequoiadendron. Metasequoia* was widely distributed and one of the most common genera of Cupressaceae in the Northern Hemisphere from the late Cretaceous to the Miocene. Its native range is now restricted to an isolated region of west central China, and it was known outside its native range only as a fossil until 1944. Its deciduous habit must have evolved in parallel to that of *Taxodium* and *Glyptostrobus. Sequoia* and *Sequoiadendron,* like *Metasequoia* and several other genera, contain just one species and are very geographically limited. *Sequoia* is restricted to coastal regions of northern California and southern Oregon and *Sequoiadendron* to the mountains of central California. *Cunninghamia,* a genus of about three species of southeast Asia, is the sister to the remainder of the family.

Juniperus is a member of the cupressoid clade and the second largest genus of conifers after *Pinus.* Junipers are mostly confined to the Northern Hemisphere, with centers of diversity in the deserts of Mexico and the southwestern United States, the Mediterranean, and central Asia-China. *Juniperus* species range from sea level to above treeline and from deserts to marches. Some species in this genus are weedy and have invaded millions of acres of rangeland and farmland.

Chamaecyparis nootkatensis, the Nootka cypress (also called the Alaska cedar and yellow cedar), has been difficult to place taxonomically because of its distinctive morphology. This important timber species of northwestern North America had been placed in *Cupressus,* and it does hybridize in cultivation with two species of *Cupressus,* an observation that has led some workers to unite these two genera. Molecular data find a better solution: return *Chamaecyparis nootkatensis* to *Cupressus.*

Sciadopitys, which is commonly called umbrella pine, was traditionally placed in "Taxodiaceae." The leaves in this genus are unusual in that they are fused in pairs so that what is actually a shoot appears to be a leaf. Numerous morphological, molecular, and other differences argue for separate family status (Stefanovic et al. 1998), i.e., Sciadopityaceae.

Cupressaceae include the tallest (*Sequoia sempervirens,* redwood, almost 112 m tall and 6.7 m in diameter) and most massive (*Sequoiadendron giganteum,* giant sequoia, 106 m tall and 11.4 m in diameter) plants on earth. Some species live 2000–3500 years or more.

The juicy cones of *Juniperus* are consumed by birds and small mammals, and long-distance dispersal by birds is suspected to have transported the genus to Atlantic islands such as the Azores, Bermuda, and the Canary Islands.

References: Adams 1993; Brunsfeld et al. 1994; Eckenwalder 1976; Gadek et al. 2000; Hart 1987; Kusumi et al. 2000; Page 1990a; Price and Lowenstein 1989; Stefanovic et al. 1998; Tsumura et al. 1995; Watson and Eckenwalder 1993.

Podocarpaceae Endlicher
(Podocarp Family)

Shrubs or trees to 60 m tall, slightly resinous. Leaves simple, entire, varying greatly in shape (broadly linear and up to 30 cm long and 5 cm wide to scale-like), persistent, alternate. *Dioecious* (rarely monoecious). Microsporangiate strobili cylindrical, with numerous spirally arranged microsporophylls each with 2 microsporangia;

pollen with 2 (0 or 3) saccae. Cones with 1 to many ovulate scales, each with 1 ovule and more or less reduced and fused to ovule, modified into a juicy structure (**epimatium**), and therefore *drupelike*, rarely resembling a cone. Cotyledons 2.

Distribution and ecology: Podocarpaceae are tropical and subtropical (less often cool temperate), especially in the Southern Hemisphere in the Old World. The family extends northward to Japan, Central America, and the Caribbean. Podocarps grow primarily in mesic forests.

Genera/species: 17/170 or more. ***Major genera:*** *Podocarpus* and *Dacrydium*; (the number of species recognized in these genus, neither of which is monophyletic, depends upon how they are subdivided).

Economic plants and products: *Dacrydium*, *Podocarpus*, and other members of the family have valuable timber. *Podocarpus macrophyllus* is widely planted as an ornamental in mild climates.

Discussion: Podocarpaceae are a distinct, Southern Hemisphere family. 28S rRNA gene sequences strongly support a sister-group relationship of Podocarpaceae and Araucariaceae (see Figure 8.16), sharing the following synapomorphies: one ovule per ovulate scale, ovulate scale closely associated with the seed, and possibly bract fused to scale. All but two of genera of Podocarpaceae bear an epimatium, which is generally interpreted as a modified cone scale that partially folds around the ovule and is juicy at maturity. Podocarps also have an unusual (possibly synapomorphic) binucleate cellular stage early in embryogeny, and are unusual among conifer families in their diversity of cone structure and chromosome number. The family may have been long isolated from other conifers in the Southern Hemisphere. Morphology and 18S rDNA sequence data show that neither *Dacrydium* nor *Podocarpus* is monophyletic, and some workers recognize numerous segregate genera.

References: Axsmith et al. 1998; Kelch 1997, 1998; Page 1990d; Stefanovic et al. 1998; Tomlinson 1992.

Araucariaceae Henkel et Hochstetter (Norfolk Island Pine Family)

Long-lived trees to 65 m tall and 6 m in diameter at the base, highly resinous, usually very symmetrical and conical in growth form. Leaves simple, entire, varying in shape (awl-like, scale-like, linear, oblong, or elliptic) sometimes on the same individual, persistent, sharp-pointed in some species of *Araucaria*, spiral or opposite. Dioecious or monoecious. Microsporangiate strobili cylindrical, with numerous spirally arranged microsporophylls each with 4–20 microsporangia; pollen without saccae, the **exine pitted**. *Cones solitary, more or less erect, heavy*, maturing in 2–3 years and eventually disintegrating on the tree; *ovulate scales each with 1 ovule*, numerous, spirally arranged, flattened, linear to peltate, the bract more or less longer than and fused to the scale; *seeds large*, with or without marginal wings,. Cotyledons 2, sometimes deeply divided and appearing like 4 (Figure 8.19).

Distribution and ecology: Araucariaceae are nearly restricted to the Southern Hemisphere, ranging from southeast Asia to Australia, New Zealand, and southern South America. Members of this family usually grow in tropical and subtropical rainforests as well as more temperate areas. The family is most diverse in New Caledonia, where 5 species of *Agathis* and 13 species of *Araucaria* are endemic. The New Caledonia species of each genus form a monophyletic subgroup according to *rbcL* analyses, and there is little genetic diversification of these species within each genus. This suggests a relatively recent radiation of the genera on the unusual (ultramafic) soils of New Caledonia. In some species of *Araucaria*, sharp-pointed leaves, ability to regenerate branches, and protection of the growing apex by surrounding branches in young plants suggest adaptation against now-extinct herbivores.

Genera/species: 3/32. ***Major genera:*** *Agathis* (13 spp.) and *Araucaria* (18).

Economic plants and products: Both of the major genera produce valuable timber. Larger individuals, such as those of *Agathis australis* of New Zealand, that reach 65 m in height and over 6 m in diameter, contain large amounts of high-quality wood. The Norfolk Island pine (*Araucaria hetrerophylla*) and the monkey puzzle tree (*A. araucana*) of Chile are prized ornamentals, either as landscape plants or house plants (Norfolk Island pine).

Discussion: Araucariaceae, like Podocarpaceae, are a distinct, almost exclusively Southern Hemisphere family. The fossil record of the Araucariaceae, and *Araucaria*, extends back into the Jurassic.

Agathis and *Araucaria* differ from one another strongly in foliar and reproductive structures. The leaves of *Agathis* are opposite and broad, whereas *Araucaria* leaves are spiral and linear to broad. *Agathis* is monoecious with ovules free from the cone scale and winged seeds. *Araucaria* is dioecious, with ovules that are fused to the cone scale and usually wingless seeds. DNA sequences from *rbcL* also support monophyly of the two genera. The *rbcL* data also agree with the division of the genus into four sections based on nonmolecular characters such as the number of cotyledons, position of microsporangiate cones, and cellular features of the leaf epidermis.

Wollemia nobilis, the Wollemi pine, was found in 1994 in the Wolllemi National Park north of Sydney, Australia by National Park and Wildlife Service officer David Noble. Known to science before 1994 only as a fossil

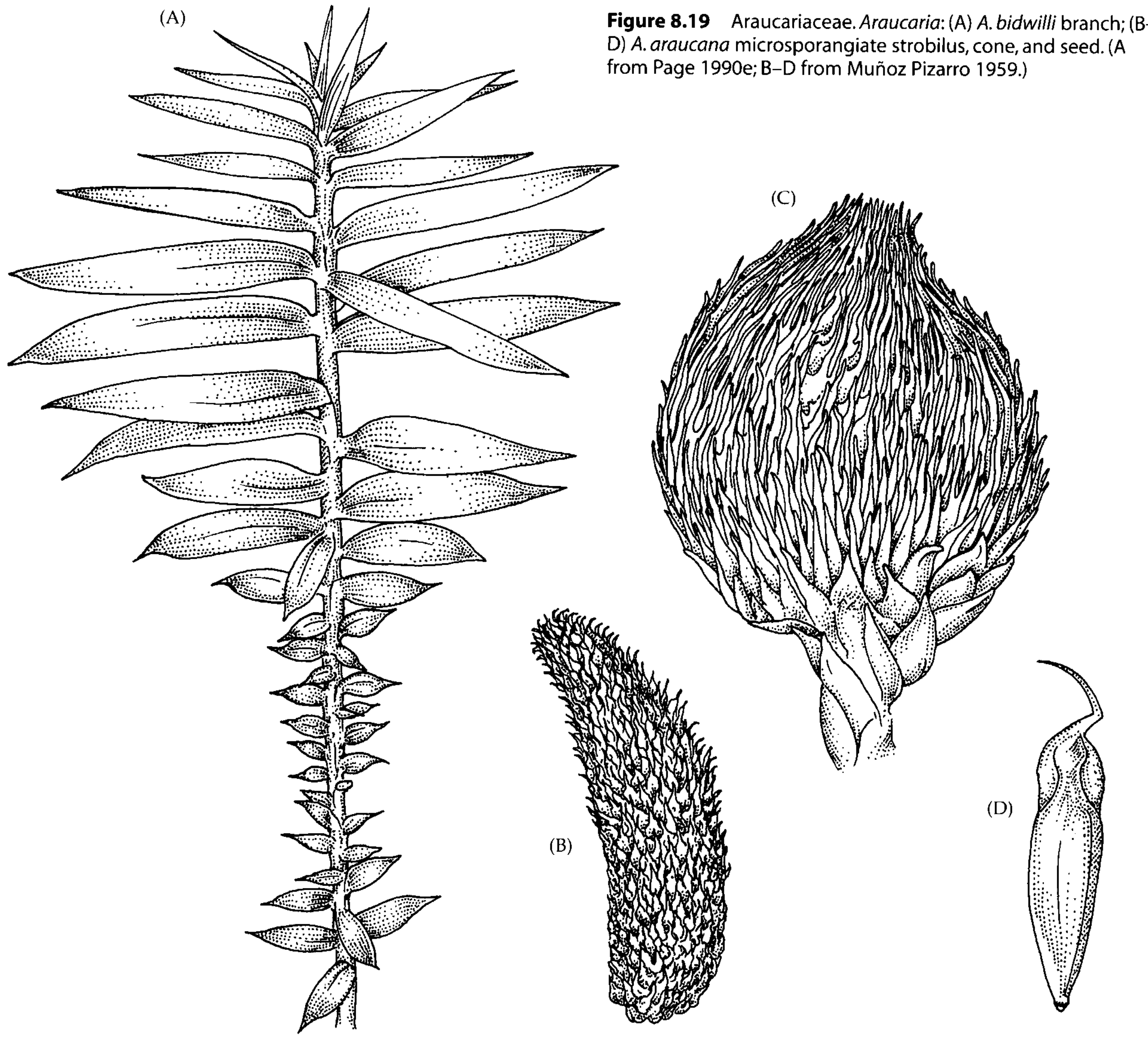

Figure 8.19 Araucariaceae. *Araucaria*: (A) *A. bidwilli* branch; (B–D) *A. araucana* microsporangiate strobilus, cone, and seed. (A from Page 1990e; B–D from Muñoz Pizarro 1959.)

extending back to 150 MYA, this is one of the world's rarest trees, with only about 43 adults in two populations 1.5 km apart. The trees, some of which are 500 to 1000 years old, have an unusual bark, described as "bubbling chocolate." Phylogenetic analyses of *rbcL* sequences show that this genus is the sister to the remainder of the family.

One of the largest and longest-lived trees in this family is *Agathis australis*, commonly called Kauri. One particular individual in northern New Zealand was 51.5 m tall and 13.8 m in circumference and about 2000 years old at the beginning of 2001. The Maori name for this individual is Tane Mahuta, which translates as "god of the forest."

References: Gilmore and Hill 1997; Page 1990e; Setoguchi et al. 1998; Stefanovic et al. 1998; http://www.rbgsyd.gov.au/html/wollemi.html.

Taxaceae Gray
(Yew Family)

Small to moderately sized trees or shrubs, usually not resinous or only slightly resinous; fragrant or not. Wood without resin canals. Leaves simple, persistent for several years, shed singly, spiral (opposite in one species), often twisted so as to appear 2-ranked, *linear, flattened, entire, acute at apex*, with 0–1 resin canals. Dioecious (rarely monoecious). Microsporangiate strobili with 6–14 microsporophylls; microsporangia 2–9 per microsporophyll, radially arranged around the microsporophyll or limited to its abaxial surface; pollen nonsaccate. **Ovules solitary** *and cones lacking*; **seeds with a hard outer layer, associated with a fleshy, usually brightly colored aril**; cotyledons 2 (occasionally 1 or 3) (Figure 8.20).

Distribution and ecology: Mostly Northern Hemisphere, extending south to Guatemala and Java, with one

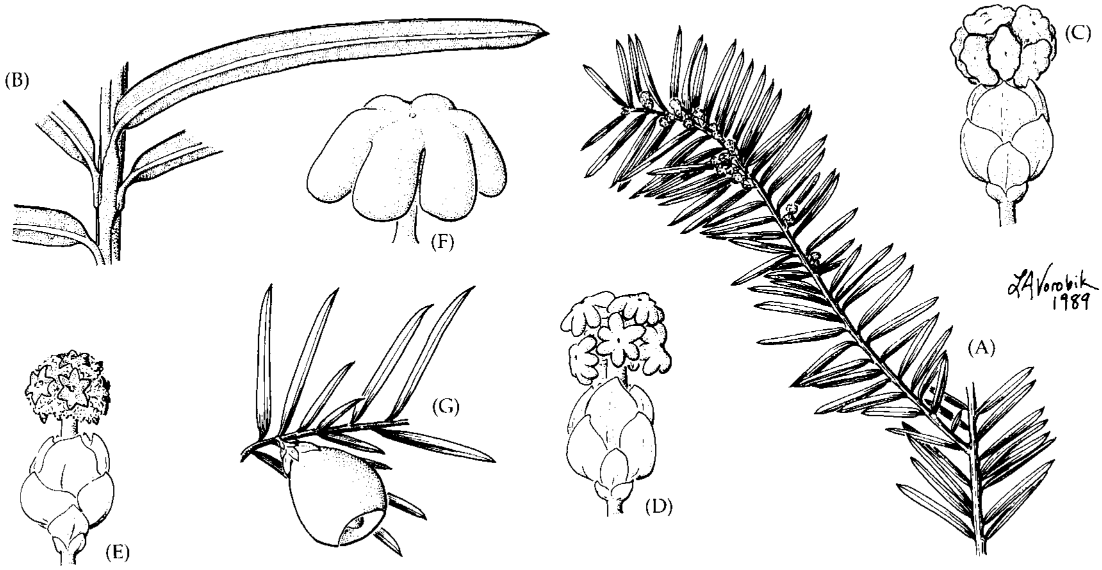

Figure 8.20 Taxaceae. *Taxus floridana:* (A) leafy shoot with microsporangiate strobili at time of pollen release (× 0.7); (B) detail of abaxial surface of leaf (× 3.3); (C–E) microsporangiate strobili before, during, and after shedding of pollen (× 6.5); (F) detail of microsporophyll (× 27); (G) shoot with arillate ovule (× 2). (From Price 1990, *J. Arnold Arbor.* 71: pp. 69–91.)

endemic genus of New Caledonia. Taxaceae tend to grow in damp valley bottom sites where leaf litter accumulates.

Genera/species: 5/20. ***Major genera:*** *Taxus* (10 spp.) and *Torreya* (4).

Economic plants and products: *Taxus* is widely grown as an ornamental in North America and Europe. *Torreya* is less important as an ornamental, but its wood, edible seed, and seed oil are valued in Asia. *Taxus* contains taxol, one of several highly poisonous alkaloids in the leaves, stems, and seeds. Taxol's potent antimitotic activity makes it of potential use as an anticancer chemotherapeutic compound.

Discussion: Taxaceae are unique among the conifers in that their solitary seed is not associated with cone scales. The aril is an outgrowth of the axis below the seed. Some systematists have removed Taxaceae from the conifers because of this lack of a cone, but embryology, wood anatomy, chemistry, and leaf and pollen morphology unquestionably tie this family to other conifers. The cone is thought to be lost, and the solitary seed with an aril is therefore derived feature.

Diverse data from *rbcL* DNA sequences, morphology, anatomy, and alkaloid chemistry divide the family into two clades, one including *Taxus*, *Austrotaxus*, and *Pseudotaxus*, and the other comprising *Torreya* and *Amentotaxus*. The family is apparently most closely related to the Cephalotaxaceae, an East Asian monogeneric family characterized by paired ovules along a cone axis in association with a small outgrowth considered to be a reduced cone scale. Usually only one or two seeds mature, and these develop a juicy outer layer that resembles, but is not homologous with, the aril of Taxaceae. The solitary, drupelike seeds of many Podocarpaceae also resemble the arillate seeds of Taxaceae, but DNA sequence data indicate this fleshiness arose more than once (Stefanovic et al. 1998).

References: Hils 1993; Page 1990f; Price 1990; Stefanovic et al. 1998.

Gnetales

The Gnetales are of particular interest in plant evolution because they show features of conifers—seeds not enclosed in an ovary—and of angiosperms—vessels in the wood, somewhat flowerlike structures, and double fertilization. Together with angiosperms, Gnetales are sometimes referred to as anthophytes because of the presence of flowerlike structures or flowers, compound strobili with at least the rudiments of both megasporangia and microsporangia. Recent molecular phylogenetic studies (Bowe et al. 2000; Chaw et al. 2000) do not support anthophytes as a clade and instead link Gnetales with conifers, but some doubt the molecular resolution of relationships among these plants and continue to support a link with angiosperms (Doyle 1998) or at least do not rule out this relationship (Rydin et al. 2002). Gnetales show several possible synapomorphies: presence of enveloping bracts around the ovules and microsporangia and a micropylar projection of the integument that produces a pollination droplet. The Gnetales consist of three genera—*Gnetum*, *Welwitschia*, and *Ephedra*—each of which is morphologically highly distinct. *Gnetum* (Gnetaceae) contains about 40 species of mostly tropical, dioecious lianas (less often trees or shrubs) with opposite, simple, broad leaves and seeds enclosed in a fleshy, brightly colored envelope. There is one species of *Welwitschia* (Welwitschiaceae), a bizarre plant of southwestern African deserts with a massive and short stem and two enormous, straplike leaves that live for the entire life of the individual (up to 2000 years). *Ephedra* (Ephedraceae) is treated below.

References: Kubitzki 1990; Price 1996; Rydin et al. 2002.

Ephedraceae Dumortier
(Mormon Tea or Joint Fir Family)

Mostly shrubs, less often clambering vines, and rarely small trees; often spreading by rhizomes. Wood with vessels. *Branches numerous, whorled or clustered, longitudinally grooved; usually green and photosynthetic.* Leaves opposite or whorled, **scale-like, fused basally into a sheath, often shed soon after developing**; resin canals absent. Mostly dioecious. Pollen strobili in whorls of 1–10, each consisting of 2–8 series of opposite or whorled bracts, the apical bracts each subtending a stalk with 2–10(–15) microsporangia. Pollen furrowed, not winged. Ovulate strobili of 2–10 series of opposite or whorled bracts, those toward the apex subtending a pair of fused bracts forming a casing around the single ovule. Seeds 1–2(–3) per strobilus, yellow to dark brown; cotyledons 2 (Figure 8.21).

Distribution and ecology: Temperate regions worldwide except Australia. Ephedraceae often grow in dry, sunny habitats, such as deserts and steppes, and can occur as high as 4000 m in the Andes and Himalayas.

Genera/species: 1(*Ephedra*)/ca. 50.

Economic plants and products: *Ephedra* has long been used for a variety of medicinal purposes, such as cough and circulatory weakness. Its primary use today is for the alkaloid ephedrine, which functions as a vessel constrictant.

Discussion: The photosynthetic stem and small leaves make these plants superficially resemble equisetophytes. Pollination is by wind, less often by insects that are attracted by nectar produced by the ovulate strobili. Dispersal is either by wind, promoted by keeled wings on the bracts of the seed strobilus, or by birds, which are attracted to the bright yellow, orange, or red, juicy, outer bracts.

References: Kubitzki 1990; Price 1996; Stevenson 1993.

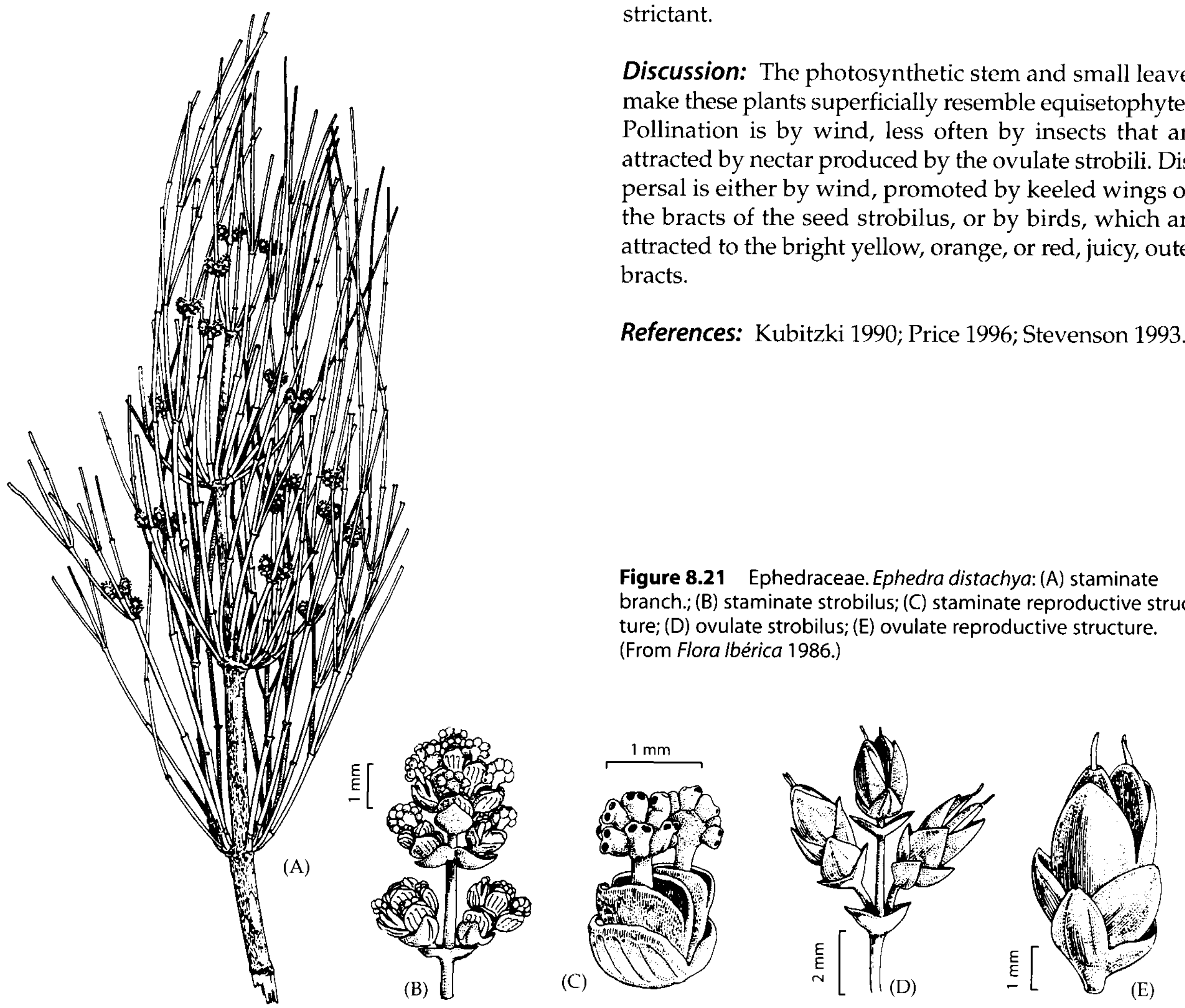

Figure 8.21 Ephedraceae. *Ephedra distachya*: (A) staminate branch.; (B) staminate strobilus; (C) staminate reproductive structure; (D) ovulate strobilus; (E) ovulate reproductive structure. (From *Flora Ibérica* 1986.)