CHAPTER 8

Phylogenetic Relationships of Angiosperms

The **angiosperms** (or flowering plants) are the dominant group of land plants. The monophyly of this group is strongly supported, as discussed in the previous chapter, and these plants are possibly sister (among extant seed plants) to the gnetopsids (Chase et al. 1993; Crane 1985; Donoghue and Doyle 1989; Doyle 1996; Doyle et al. 1994). The angiosperms have a long fossil record, going back to the upper Jurassic and increasing in abundance as one moves through the Cretaceous (Beck 1973; Sun et al. 1998). The group probably originated during the Jurassic, more than 140 million years ago.

Cladistic analyses based on morphology, rRNA, *rbcL*, and *atpB* sequences do not support the traditional division of angiosperms into **monocots** (plants with a single cotyledon, radicle aborting early in growth with the root system adventitious, stems with scattered vascular bundles and usually lacking secondary growth, leaves with parallel venation, flowers 3-merous, and pollen grains usually monosulcate) and **dicots** (plants with two cotyledons, radicle not aborting and giving rise to mature root system, stems with vascular bundles in a ring and often showing secondary growth, leaves with a network of veins forming a pinnate to palmate pattern, flowers 4- or 5-merous, and pollen grains predominantly tricolpate or modifications thereof) (Chase et al. 1993; Doyle 1996; Doyle et al. 1994; Donoghue and Doyle 1989). In all published cladistic analyses the "dicots" form a paraphyletic complex, and features such as two cotyledons, a persistent radicle, stems with vascular bundles in a ring, secondary growth, and leaves with net venation are plesiomorphic within angiosperms; that is, these features evolved earlier in the phylogenetic history of tracheophytes. In contrast, the monophyly of the monocots is supported by the synapomorphies of leaves with parallel venation, embryo with a single cotyledon, sieve cell plastids with several cuneate protein crystals, stems with scattered vascular bundles, and an adventitious root system, although several of these characters are homoplasious (see page 174). The monophyly of monocots also is supported by 18S rDNA, *atpB* and *rbcL* nucleotide sequences (Bharathan and Zimmer 1995; Chase et al. 1993, 1995a; Soltis et al. 1997, 1998).

Although the "dicots" apparently are nonmonophyletic, a large number of species traditionally considered within this group do constitute a well-supported clade: the tricolpates (or eudicots) (Chase et al. 1993; Donoghue and Doyle 1989; Doyle et al. 1994; Soltis et al. 1997). Synapomorphies of this monophyletic group include tricolpate pollen (or modifications of this basic pollen type), plus *rbcL*, *atpB*, and 18S rDNA nucleotide sequences.

Unfortunately, phylogenetic relationships among the nonmonocot, nontricolpate angiosperms are poorly understood. These families have often been considered to represent a paraphyletic, primitive angiosperm complex, and are treated as the superorder Annonanae by Thorne (1992) and as the subclass Magnoliidae by Cronquist (1981, 1986, 1988) and Takhtajan (1980, 1997). Most have ethereal oils in scattered spherical cells within the parenchymatous tissues and elongate vessel elements with slanted, scalariform perforation plates. Their flowers usually are radially symmetrical; the carpels and stamens are usually distinct and free, and the former have a poorly developed style and an elongate stigmatic region. The pollen is usually monosulcate, and the seeds have a tiny embryo with copious endosperm.

It is convenient to divide the families of this complex into two groups: the magnoliids and the paleoherbs. The magnoliids include Magnoliales, Laurales, and Illiciales. They are woody plants with alternate or opposite, usually pinnately veined, coriaceous leaves, and paracytic stomates. Flowers typically have several to numerous parts, with little or no fusion. Perianth parts are arranged spirally or in whorls of three, and stamens are often laminar. The filament is poorly differentiated from the anther, and the connective tissue is often well developed. Pollen grains of Magnoliales lack a columellar exine structure. The paleoherbs include Aristolochiales, Piperales, Nymphaeales, and Ceratophyllales. They are usually herbaceous (but sometimes secondarily soft-woody) plants that may have adaxial prophylls (lowermost bract of shoot). Leaves are alternate, often more or less palmately veined, thin-textured, and with anomocytic stomates. Flowers have numerous to few parts; those of the perianth and androecium usually are in whorls of three. The filament is well differentiated from the anther, and the connective usually is inconspicuous. Pollen grains usually have a columellar exine.

Note that the monocots share most of the above-listed paleoherb characters. The paleoherb families (or at least some of them) may be closely related to monocots (Chase et al. 1993; Donoghue and Doyle 1989; Doyle et al. 1994). In fact, the monocots often are considered one of the subgroups of paleoherbs, and the other paleoherbs are then referred to as nonmonocot paleoherbs.

Magnoliids traditionally have been considered to retain the greatest number of plesiomorphic features within the

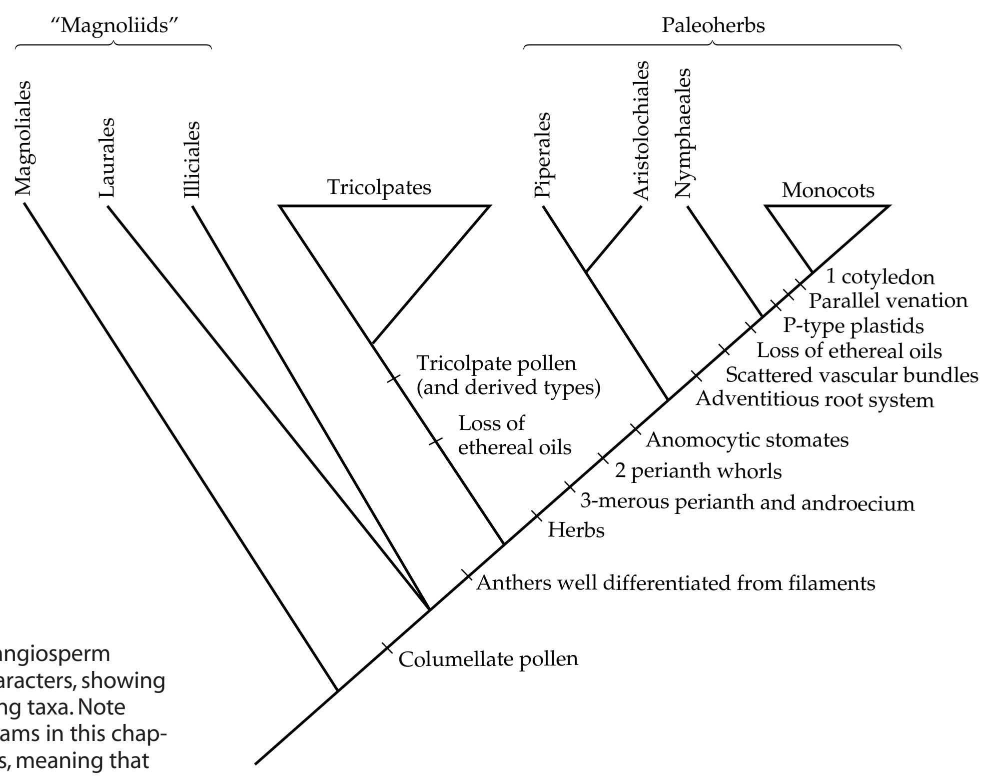


Figure 8.1 Cladogram of major angiosperm groups based on morphological characters, showing Magnoliales as sister to the remaining taxa. Note that in this and subsequent cladograms in this chapter, the use of quotation marks shifts, meaning that whether or not a group is seen as monophyletic can change based on the criteria (morphology, nucleotide sequence, etc.) used to create the cladogram. (Modifed from Donoghue and Doyle 1989.)

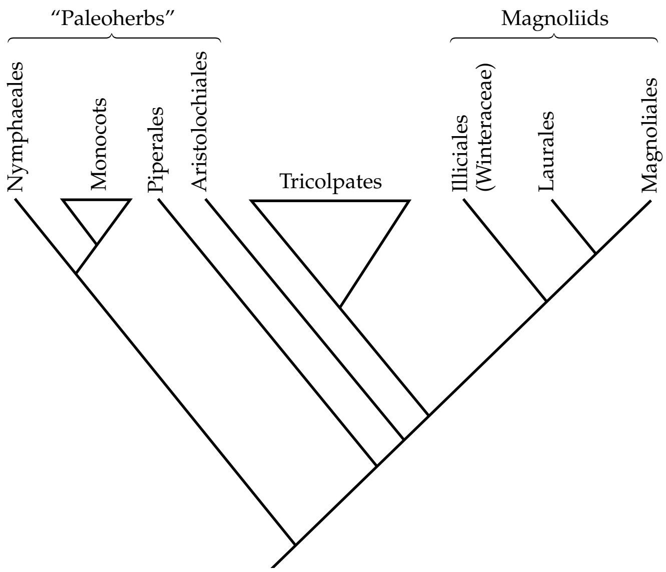


Figure 8.2 Cladogram of major angiosperm groups based on morphological characters, showing Nymphaeales and monocots as sister to the remaining taxa. (Modifed from Doyle et al. 1994.)

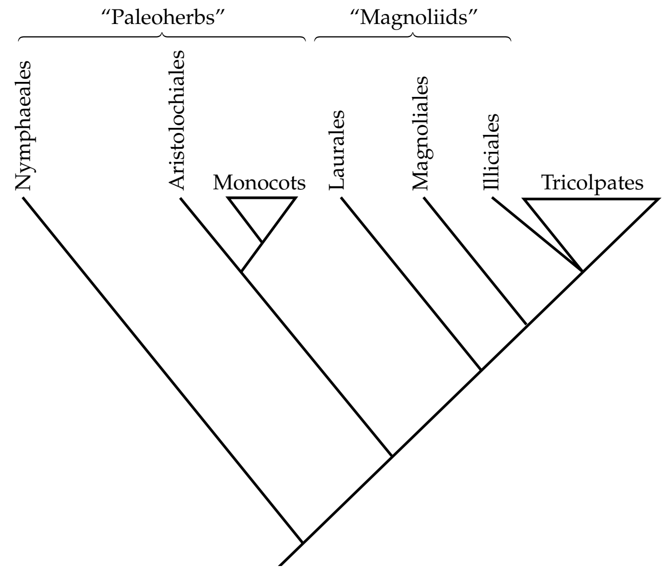


Figure 8.3 Cladogram of major angiosperm groups based on nuclear ribosomal RNA nucleotide sequences. (Modified from Doyle et al. 1994.)

angiosperms (Cronquist 1968, 1981, 1988; Thorne 1974, 1992; Takhtajan 1969, 1980; Dahlgren 1977, 1983). This viewpoint has received some support from morphology-based cladistic analyses (Donoghue and Doyle 1989; Doyle et al. 1994; Loconte and Stevenson 1991). The magnoliids, therefore, may represent a basal paraphyletic complex within the angiosperms, as supported by the possibly retained plesiomorphic feature of laminar anthers (Figure 8.1). The noncolumellate pollen of Magnoliales may also be a retained plesiomorphy.

Several cladistic analyses based on 18S nucleic acid sequences, however, support a rooting of the angiosperm clade within the nonmonocot paleoherbs (Doyle et al. 1994; Zimmer et al. 1989; Hamby and Zimmer 1992; Soltis et al. 1997). The paleoherbs also occupy a basal paraphyletic position in some recent analyses based on either morphology alone or rDNA combined with morphology (Doyle et al. 1994; Figures 8.2, 8.3, and 8.4). Thus, the primitive angiosperm may have been semiherbaceous, with alternate, more or less palmately veined leaves and anomocytic stomates. Its flowers may have been 3-merous, with six tepals (in two whorls of three), and six stamens (also in two whorls of three) that were well differentiated into an anther and filament (see also Taylor and Hickey 1996).

Cladistic analyses based on *rbcL* sequences (Figure 8.5) support placement of most angiosperms in one of two major clades. Taxa with monosulcate pollen (monocots, nonmonocot paleoherbs, and magnoliids) are on one branch and tricolpates on a second (Chase et al. 1993). These analyses also suggest that Ceratophyllaceae may represent the sister group to all other angiosperms. Finally, recent analyses based on 18S rDNA, *rbcL*, and *atpB* nucleotide sequences suggest that a clade containing Nymphaeales and magnolid families such as Illiciaceae and Austrobaileyaceae may be sister to the remaining angiosperms, with Ceratophyllaceae placed as sister to the tricolpate clade (D. Soltis, personal communication; M. Chase, personal communication).

In summary, the rooting of the angiosperm cladogram is equivocal. It is obvious, however, that a simplistic division of the angiosperms into monocots and dicots does

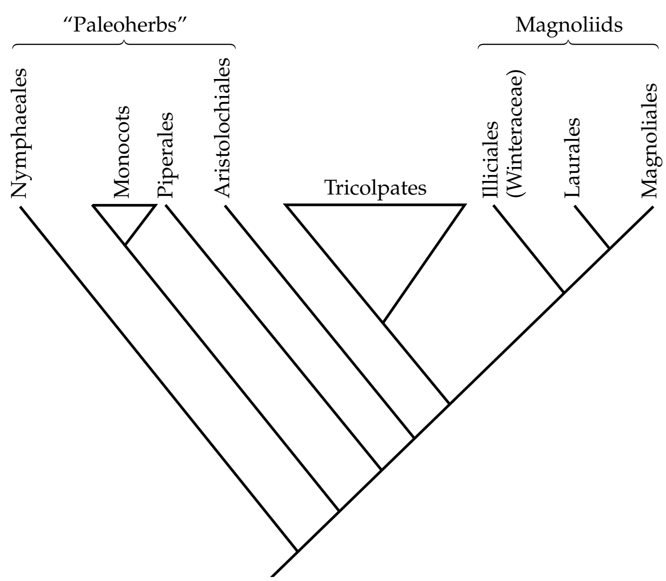


Figure 8.4 Cladogram of major angiosperm groups based on both morphology and nuclear ribosomal RNA. (Modified from Doyle et al. 1994.)

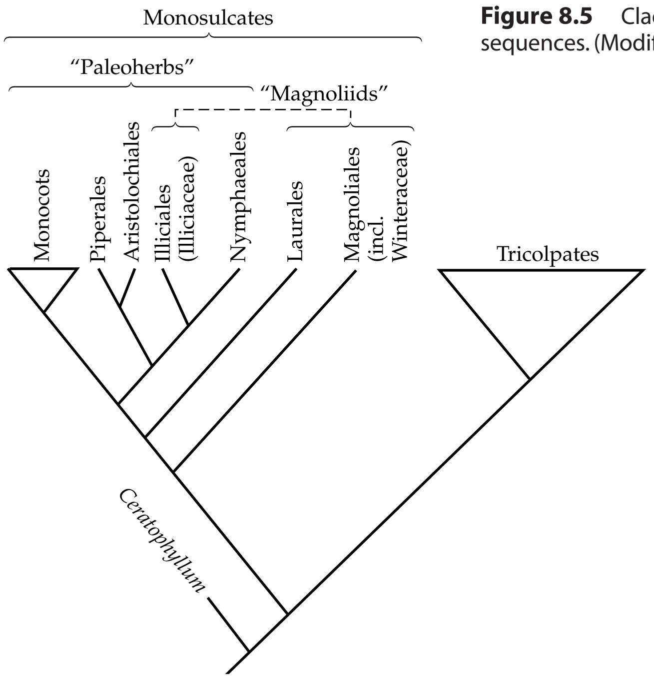


Figure 8.5 Cladogram of major angiosperm groups based on *rbcL* nucleotide sequences. (Modified from Chase et al. 1993.)

not accurately reflect phylogenetic history. At this time, the monophyly of only two major angiosperm clades—the monocots and tricolpates (eudicots)— is well supported. The remaining families form a largely unresolved complex and have retained numerous plesiomorphic characters. Nearly every one of these families has been suggested, at one time or another, as being the most primitive extant angiosperm (see especially Magnoliaceae, Degneriaceae, Winteraceae, Illiciaceae, Calycanthaceae, Chloranthaceae, and Nymphaeaceae). We are a long way from a complete understanding of phylogenetic relationships among angiosperms, and the identity of the early divergent angiosperm clades will continue to generate interest and arguments. It is anticipated, however, that progress will be made most rapidly through analyses combining data from several sources—morphological as well as molecular (especially 18S rDNA, *rbcL*,

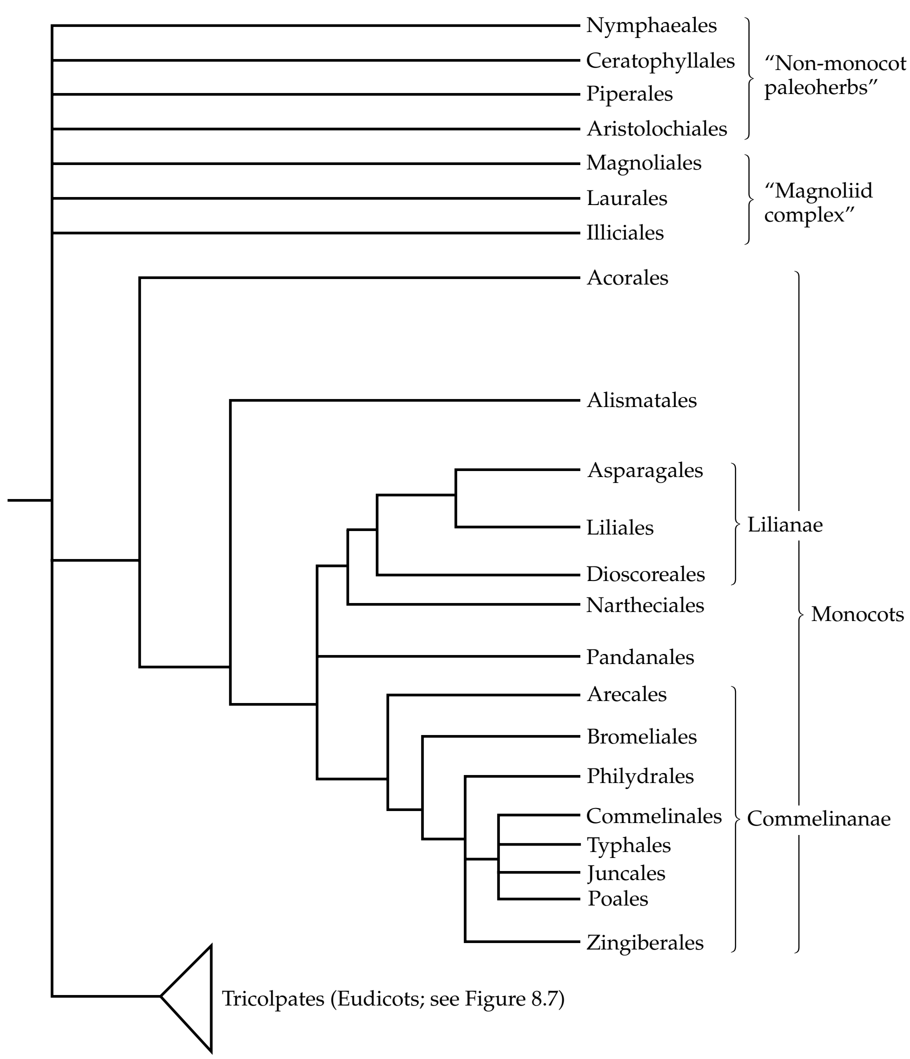


Figure 8.6 Major angiosperm clades reflected in the classification of the Angiosperm Phylogeny Group, based on characters derived from morphology, *rbcL*, *atpB*, and 18S nuclear ribosomal DNA nucleotide sequences. (Modified from Angiosperm Phylogeny Group 1998.)

and *atpB* sequences) (see Soltis et al. 1998). A cladogram presenting a conservative estimate of our knowledge of phylogenetic relationships among angiosperms is presented in Figures 8.6, 8.7, and 8.8; this tree is modified from that of the Angiosperm Phylogeny Group (1998).

The estimated 233,885 angiosperm species in 12,650 genera (Thorne 1992) occur in an extremely wide array of terrestrial habitats and exhibit an amazing diversity of morphological, anatomical, biochemical, and physiological characters. These plants are usually divided into about 400 families—Thorne (1992) recognized 440, Cronquist (1988) 387, Dahlgren (1983) 462, Takhtajan (1980) 589, and the Angiosperm Phylogeny Group (1998) 462.

This text gives detailed treatments of 130 angiosperm families, and an additional 95 families are briefly characterized (Table 8.1). Each family treatment includes a **description** (in which useful identifying characters are indicated in *italic print* and presumed synapomorphies in **boldface**), a **floral formula**, a brief summary of **distribution** (with indication of ecology when the family occurs in only a limited array of plant communities or ecological conditions), a statement regarding estimated **number of genera and species** (including a listing of major genera), a listing 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 regarding pollination biology and fruit dispersal, and notes on other matters of biological interest. Finally, each family treatment includes a list of **references** that are useful sources of additional information.

The family descriptions are necessarily somewhat generalized, and exceptional conditions usually are not indicated. In these descriptions, anthers are assumed to be 2-locular and opening by longitudinal slits, and ovules are assumed to be anatropous, have two integuments, and a thick megasporangium, unless otherwise indicated. Endosperm is considered to be present in the seeds, and the embryo is considered to be straight, unless otherwise noted. The stem of any nonmonocot family is assumed to contain a ring of vascular bundles (eustele), while that of monocots is considered to have scattered bundles; therefore, only divergent conditions are described. Likewise, the embryos of any nonmonocot family are assumed to have two cotyledons, while those of monocots have only a single cotyledon, unless stated otherwise.

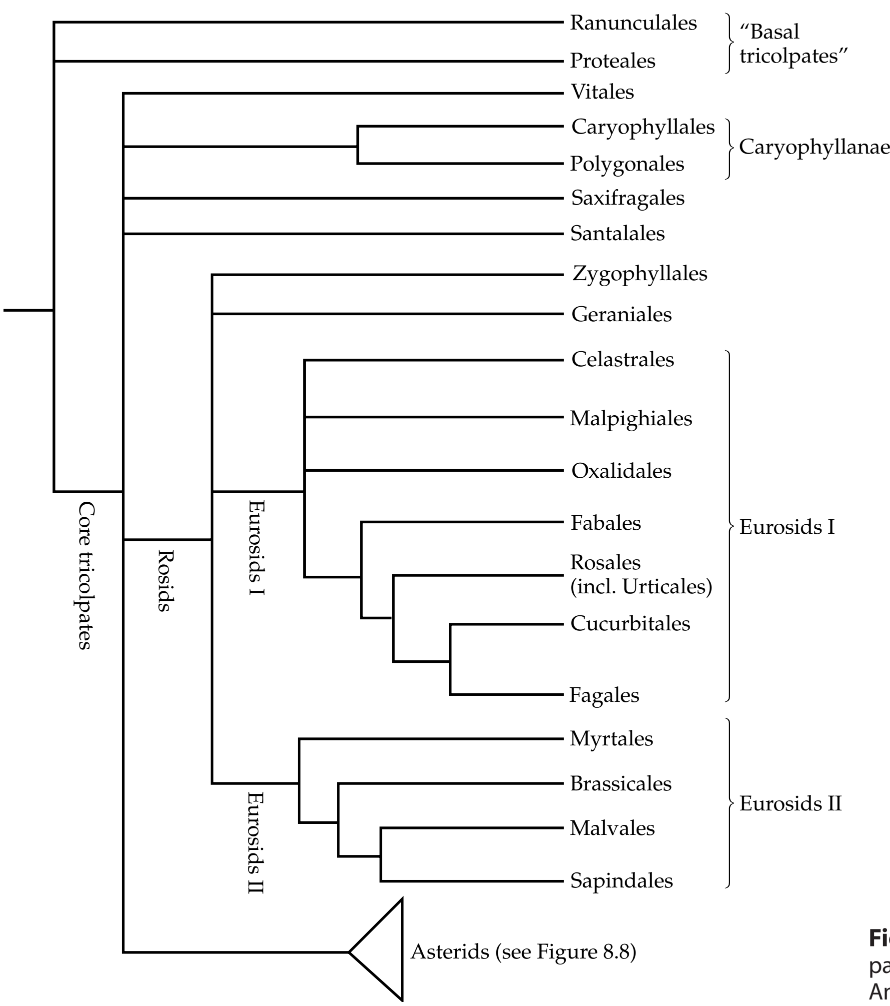


Figure 8.7 Major clades within the tricolpates (= eudicot clade). (Modified from Angiosperm Phylogeny Group 1998.)

TABLE 8.1 ***Major families of angiosperms as classified in this book.***[a]

"NON-MONOCOT PALEOHERBS"

Nymphaeales
- **Nymphaeaceae** (p. 168) (includes Barclayaceae, Cabombaceae)

Ceratophyllales
- **Ceratophyllaceae** (p. 170)

Piperales
- **Piperaceae** (p. 171)
- *Saururaceae* (p. 171)

Aristolochiales
- **Aristolochiaceae** (p. 172)
- *Lactoridaceae* (p. 173)

MONOCOTS

Acorales
- *Acoraceae* (p. 177)

Alismatales
- **Araceae** (p. 175) (includes Lemnaceae)
- **Alismataceae** (p. 177) (includes Limnocharitaceae)
- **Hydrocharitaceae** (p. 179)
- **Potamogetonaceae** (p. 179)
- *Ruppiaceae* (p. 174)
- *Butomaceae* (p. 174)
- *Najadaceae* (p. 174)
- *Zannichelliaceae* (p. 174)
- *Posidoniaceae* (p. 174)
- *Cymodoceaceae* (p. 174)
- *Zosteraceae* (p. 174)
- *Tofieldiaceae* (p. 185)

Nartheciales
- *Nartheciaceae* (p. 185)

Lilianae

Liliales
- **Liliaceae** (p. 181)
- **"Uvulariaceae"** (p. 182)
- **Trilliaceae** (p. 182)
- **Smilacaceae** (p. 183)
- **Melanthiaceae** (p. 183)
- *Alstroemeriaceae* (p. 180)
- *Calochortaceae* (p. 181)
- *Colchicaceae* (p. 182)

Asparagales
- **Convallariaceae** (p. 185) (includes Nolinaceae, Dracaenaceae)
- **Asphodelaceae** (p. 188)
- **Agavaceae** (p. 189)
- **Alliaceae** (p. 189)
- **Amaryllidaceae** (p. 190)
- **Iridaceae** (p. 191)
- **Orchidaceae** (p. 193)
- *Asparagaceae* (p. 185)
- *Hypoxidaceae* (p. 185)
- *Hyacinthaceae* (p. 185)
- *Agapanthaceae* (p. 190)
- *Hemerocallidaceae* (p. 185) (includes Phormiaceae)
- *Themidaceae* (p. 190)

Dioscoreales
- **Dioscoreaceae** (p. 195)
- *Burmanniaceae* (p. 197)
- *Taccaceae* (p. 197)

Commelinanae

Arecales
- **Arecaceae** (p. 197)

Bromeliales
- **Bromeliaceae** (p. 199)

Philydrales
- **Haemodoraceae** (p. 201)
- **Pontederiaceae** (p. 202)
- *Philydraceae* (p. 201)

Commelinales
- **Commelinaceae** [possibly in Philydrales] (p. 204)
- **Eriocaulaceae** (p. 205)
- **Xyridaceae** (p. 206)
- *Mayacaceae* (p. 204)

Typhales
- **Typhaceae** (p. 206) (includes Sparganiaceae)

Juncales
- **Juncaceae** (p. 209)
- **Cyperaceae** (p. 210)

Poales
- **Poaceae** (p. 210)
- *Restionaceae* (p. 216)

Zingiberales
- **Zingiberaceae** (p. 218)
- **Marantaceae** (p. 218)
- **Cannaceae** (p. 220)
- *Muscaceae* (p. 217)
- *Strelitziaceae* (p. 217)
- *Heliconiaceae* (p. 217)
- *Costaceae* (p. 217)

"MAGNOLIID COMPLEX"

Magnoliales
- **Magnoliaceae** (p. 222)
- **Annonaceae** (p. 224)
- *Myristicaceae* (p. 222)
- *Degeneriaceae* (p. 222)

Laurales
- **Lauraceae** (p. 226)
- *Monimiaceae* (p. 226)
- *Chloranthaceae* (p. 226)

Illiciales
- **Winteraceae** [possibly in Magnoliales] (p. 228)
- **Illiciaceae** (p. 228)
- *Schizandraceae* (p. 228)

TRICOLPATES (EUDICOTS)

"BASAL TRICOLPATES"

Ranunculales
- **Ranunculaceae** (p. 230)
- **Berberidaceae** (p. 233)
- **Papaveraceae** (p. 233) (includes Fumariaceae)
- *Menispermaceae* (p. 230)

Proteales[b] and other "basal tricolpates"
- **Platanaceae** (p. 237)
- **Proteaceae** (p. 237)
- *Nelumbonaceae* (p. 236)
- *Trochodendraceae* (p. 237) (includes Tetracentraceae)
- *Buxaceae* (p. 237)

CORE TRICOLPATES (CORE EUDICOTS)

Vitales
- **Vitaceae** (p. 238)
- *Leeaceae* (p. 240)

***Caryophyllanae** (includes Caryophyllales and Polygonales)*

Caryophyllales
- **Caryophyllaceae** (p. 240)
- **Phytolaccaceae** (p. 243)
- **Nyctaginaceae** (p. 243)
- **Amaranthaceae** (p. 245) (includes Chenopodiaceae)
- **Aizoaceae** (p. 246)
- **"Portulacaceae"** (p. 248)
- **Cactaceae** (p. 250)
- *Petiveriaceae* (p. 243)

Polygonales
- **Droseraceae** (p. 253)
- **Polygonaceae** (p. 253)
- *Plumbaginaceae* (p. 252)
- *Nepenthaceae* (p. 252)

Saxifragales
- **Saxifragaceae** (p. 256)
- **Crassulaceae** (p. 258)
- **Hamamelidaceae** (p. 260)
- **Altingiaceae** (p. 262)
- *Grossulariaceae* (p. 256)
- *Haloragaceae* (p. 256)
- *Cercidophyllaceae* (p. 256)
- *Iteaceae* (p. 257)

Santalales
- **Loranthaceae** (p. 263)
- **Viscaceae** (p. 264)
- *"Santalaceae"* (p. 262)
- *"Olacaceae"* (p. 262)
- *Opiliaceae* (p. 262)
- *Misodendraceae* (p. 262)
- *Eremolepidaceae* (p. 262)

[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 the discussion of the family in this chapter.

[b] Proteales include Plantanaceae, Proteaceae, and Nelumbonaceae.

TABLE 8.1 *(continued)*

Rosid clade

- Zygophyllales
  - **Zygophyllaceae** (p. 264)
  - *Krameriaceae* (p. 266)
- Geraniales
  - **Geraniaceae** (p. 268)

Eurosids I

- Celastrales
  - **Celastraceae** (p. 268) (includes Hippocrateaceae)
- Malpighiales
  - **Malpighiaceae** (p. 268)
  - **Euphorbiaceae** (p. 271)
  - **Clusiaceae** (p. 274)
  - **Rhizophoraceae** (p. 275)
  - **Violaceae** (p. 277)
  - **Passifloraceae** (p. 278)
  - **Salicaceae** (p. 279)
  - *Chrysobalanaceae* (p. 268)
  - *"Flacourtiaceae"* (p. 268)
- Oxalidales
  - **Oxalidaceae** (p. 282)
  - *Cephalotaceae* (p. 282)
  - *Cunoniaceae* (p. 282)
- Fabales
  - **Fabaceae** (p. 283)
  - **Polygalaceae** (p. 288)
  - *Suraniaceae* (p. 284)
- Rosales
  - **Rosaceae** (p. 292)
  - **Rhamnaceae** (p. 299)
  - **Ulmaceae** (p. 299)
  - **Celtidaceae** (p. 300)
  - **Moraceae** (p. 302)
  - **Urticaceae** (p. 304)
  - *Cecropiaceae* (p. 290)
  - *Cannabaceae* (p. 290)
- Cucurbitales
  - **Cucurbitaceae** (p. 306)
  - *Begoniaceae* (p. 306)
- Fagales
  - **Fagaceae** (p. 308)
  - **Betulaceae** (p. 309)
  - **Casuarinaceae** (p. 313)
  - **Myricaceae** (p. 314)
  - **Juglandaceae** (p. 315)
  - *Nothofagaceae* (p. 308)
  - *Rhoipteleaceae* (p. 308)

Eurosids II

- Myrtales
  - **Lythraceae** (p. 318) (includes Sonneratiaceae, Trapaceae, Punicaceae)
  - **Onagraceae** (p. 320)
  - **Myrtaceae** (p. 321)
  - **Melastomataceae** (p. 323)
  - **Combretaceae** (p. 325)
  - *Vochysiaceae* (p. 317)
  - *Memecylaceae* (p. 318)
- Brassicales
  - **Brassicaceae** (p. 326) (includes Capparaceae)
  - *Bataceae* (p. 326)
  - *Caricaceae* (p. 326)
  - *Resedaceae* (p. 326)
  - *Moringaceae* (p. 326)
- Malvales
  - **Malvaceae** (p. 329) (includes Tiliaceae, Sterculiaceae, Bombacaceae)
  - **Cistaceae** (p. 333)
  - *Dipterocarpaceae* (p. 329)
  - *Thymelaeaceae* (p. 329)
- Sapindales
  - **Rutaceae** (p. 333)
  - **Meliaceae** (p. 336)
  - **Simaroubaceae** (p. 337)
  - **Anacardiaceae** (p. 338) (includes Julianaceae)
  - **Sapindaceae** (p. 340) (includes Aceraceae, Hippocastanaceae)
  - *Burseraceae* (p. 334)

Asterid Clade (= Sympetalae)

- Cornales
  - **Hydrangeaceae** (p. 343)
  - **Cornaceae** (p. 344) (includes Nyssaceae)
  - *Loasaceae* (p. 343)
- Ericales
  - **Sapotaceae** (p. 346)
  - **Primulaceae** (p. 348)
  - **Myrsinaceae** (p. 348)
  - **Theaceae** (p. 351)
  - **Ericaceae** (p. 351) (includes Pyrolaceae, Monotropaceae, Empetraceae, Epacridaceae)
  - **Sarraceniaceae** (p. 354)
  - **Polemoniaceae** (p. 354)
  - *Ebenaceae* (p. 354)
  - *Styracaceae* (p. 354)
  - *Theophrastaceae* (p. 347)
  - *Ternstroemiaceae* (p. 347)
  - *Clethraceae* (p. 347)
  - *Actinidaceae* (p. 347)
  - *Cyrillaceae* (p. 347)
  - *Lecythidaceae* (p. 347)

Euasterids I

- *Garryales*
  - *Garryaceae* (p. 343)
- Solanales
  - **Solanaceae** (p. 357) (includes Nolanaceae)
  - **Convolvulaceae** (p. 359) (includes Cuscutaceae)
  - **"Hydrophyllaceae"** (p. 360) [placement questionable]
  - **Boraginaceae** (p. 361) [placement questionable]
  - *Lennoaceae* (p. 362) [placement questionable]
- Gentianales
  - **Gentianaceae** (p. 364)
  - **Rubiaceae** (p. 365)
  - **Apocynaceae** (p. 366) (includes Asclepiadaceae)
  - *"Loganiaceae"* (p. 363)
- Lamiales
  - **Oleaceae** (p. 372)
  - **Plantaginaceae** (p. 373) (includes Callitrichiaceae, Scrophulariaceae in part)
  - **Scrophulariaceae** (p. 375)
  - **Orobanchaceae** (p. 375) (includes Scrophulariaceae, parasitic species)
  - **Bignoniaceae** (p. 377)
  - **Acanthaceae** (p. 379) (includes Mendonciaceae)
  - **Gesneriaceae** (p. 379)
  - **Lentibulariaceae** (p. 381)
  - **Verbenaceae** (p. 382)
  - **Lamiaceae** (p. 383) (includes many genera typically treated as Verbenaceae)
  - *Avicenniaceae* (p. 370)
  - *Buddlejaceae* (p. 371)
  - *Myoporaceae* (p. 371)
  - *Phrymaceae* (p. 383)

Euasterids II

- Aquifoliales
  - **Aquifoliaceae** (p. 385)
  - *Helwingiaceae* (p. 387)
- Apiales
  - **Apiaceae** (p. 387) (includes Araliaceae, Hydrocotylaceae)
  - *Pittosporaceae* (p. 387)
- Dipsacales
  - **Caprifoliaceae** (p. 390) (includes Dipsacaceae, Valerianiaceae, Diervillaceae, Linnaeaceae)
  - *Adoxaceae* (p. 391) (includes *Sambucus*, *Viburnum*) [placement questionable]
- Asterales
  - **Campanulaceae** (p. 393) (includes Lobeliaceae)
  - **Asteraceae** (p. 396)
  - *Stylidiaceae* (p. 392)
  - *Calyceraceae* (p. 392)
  - *Menyanthaceae* (p. 392)
  - *Goodeniaceae* (p. 392)

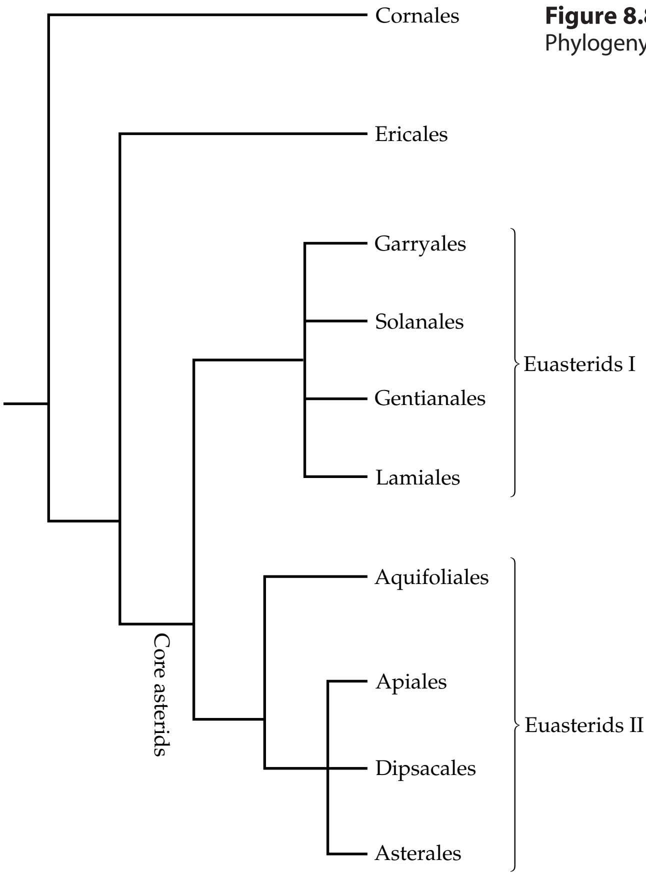


Figure 8.8 Major clades within the asterids. (Modified from Angiosperm Phylogeny Group 1998.)

Many families are provided with illustrations, which were prepared in connection with the Generic Flora of the Southeastern United States Project unless otherwise indicated. Closely related families are treated within orders (i.e., names ending in *-ales*; see Appendix 1). **Ordinal treatments** include an outline of characters supporting the group's monophyly (ordinal synapomorphies) and a brief discussion of phylogenetic relationships of the families within the group. A **key** to all (or at least the most important) families constituting each order is included. Families with formal treatments in this text are indicated in **bold** in these keys. Circumscription of some families (and orders) has been altered from that traditionally used in order to render these groups monophyletic. Occasionally, related orders are grouped into superorders (with names ending in *-anae*). We largely follow the recently published classification of the Angiosperm Phylogeny Group (1998) because this classification is based on published cladistic analyses.

Families have been chosen for formal treatment on the basis of their number of genera and species, floristic dominance (especially in North America), economic importance, and phylogenetic interest. Table 8.1 lists these angiosperm families in an arrangement reflecting our understanding of their phylogenetic relationships (based on recent cladistic analyses and the classification proposed by the Angiosperm Phylogeny Group in 1998). Families receiving full coverage in the text are indicated in **boldface**, while those only briefly characterized are in *italics*. Because the root of the angiosperm clade may be within either the nonmonocot paleoherbs or the magnoliids, the sequence of orders employed in this chapter is somewhat arbitrary. Indeed any linear sequence is necessarily arbitrary because it cannot reflect the branching pattern expressed in a cladogram.

"NONMONOCOT PALEOHERBS"

Nymphaeales

Nymphaeaceae Salisbury
(Water Lily Family)

Aquatic, **rhizomatous herbs**; stem with vascular bundles usually scattered, *with conspicuous air canals* and usually also **laticifers**; usually with distinct, stellate-branched sclereids projecting into the air canals; often with alkaloids (but not of the benzyl-isoquinoline type). Hairs simple, **usually producing mucilage (slime)**. *Leaves* alternate, opposite, or occasionally whorled, simple, entire to toothed or dissected, short- to *long-petiolate, with blade submerged, floating, or emergent*, with palmate to pinnate venation; stipules present or absent. Inflorescences of solitary flowers. **Flowers** bisexual, radial, **with a long pedecel and usually floating or raised above the surface of the water, with girdling vascular bundles in receptacle**. Tepals 4–12, distinct to connate, imbricate, often petal-like. *Petals* (*petal-like staminodes*) *lacking or 8 to numerous*, inconspicuous to showy, often intergrading with stamens. *Stamens 3 to numerous*, the innermost sometimes represented by staminodes; filaments distinct, free or adnate to petaloid staminodes, slender and well differentiated from anthers to laminar and poorly differentiated from anthers; pollen grains usually monosulcate or lacking apertures. Carpels 3 to numerous, distinct or connate; ovary/ovaries superior to inferior, *if connate then with several locules and* **placentation parietal (the ovules scattered on the partitions)**; *stigmas often elongate and radiating on an expanded circular to marginally lobed and grooved disk*, often surrounding a knob or circular bump. Ovule 1 to numerous, anatropous to orthotropous. Nectaries lacking or sometimes present on the staminodes, although a sweet fluid may also be secreted by the stigma. *Fruit an aggregate of nuts or few-seeded indehiscent pods, a berry, or sometimes an irregularly dehiscent fleshy capsule;* seeds **usually operculate** (opening by a cap), often arillate; endosperm ± lacking, but with abundant perisperm (Figure 8.9).

Floral formula: *, 4–12, 0–∞•, 3–∞, 1–∞; berry, nuts

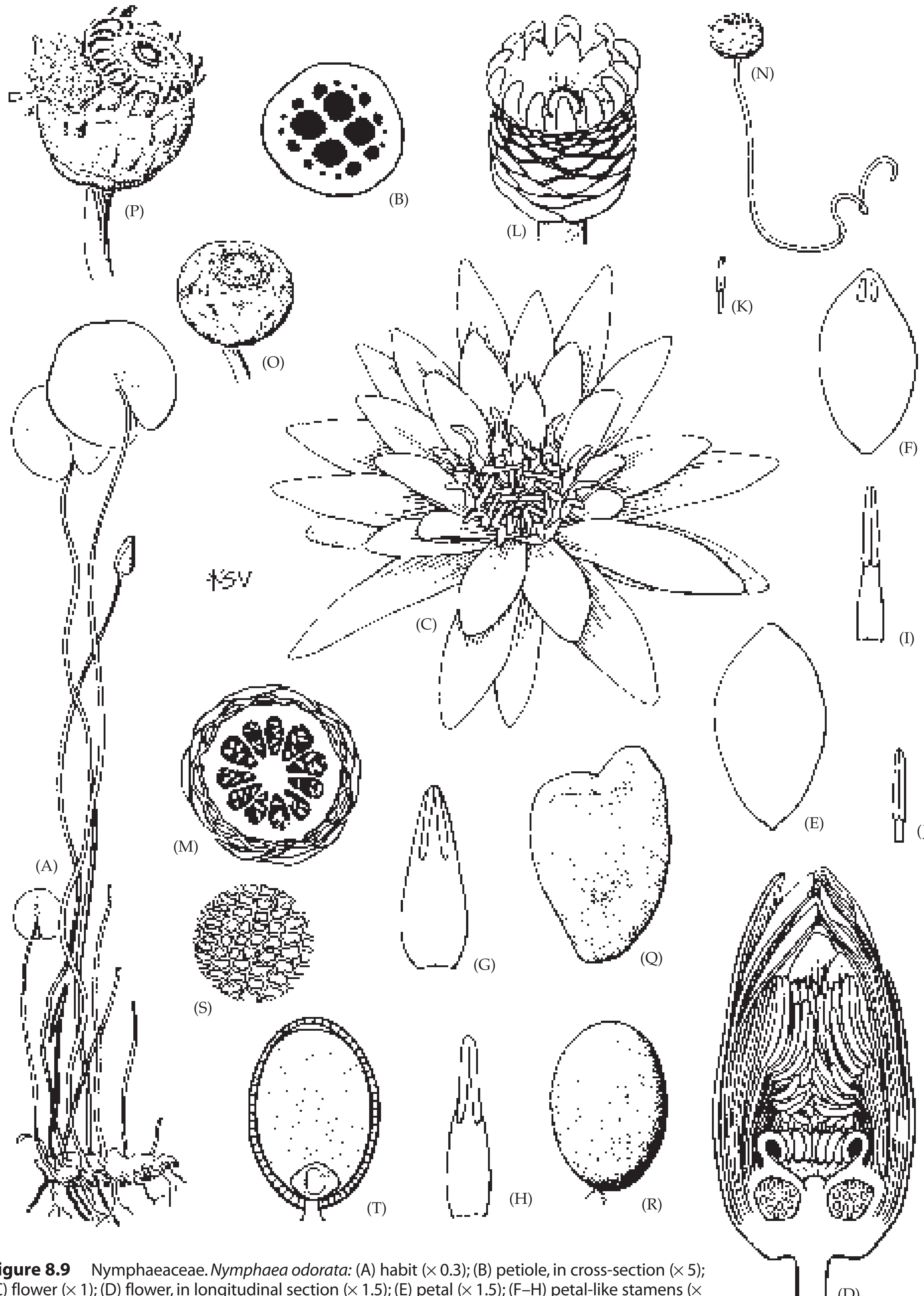


Figure 8.9 Nymphaeaceae. *Nymphaea odorata:* (A) habit (× 0.3); (B) petiole, in cross-section (× 5); (C) flower (× 1); (D) flower, in longitudinal section (× 1.5); (E) petal (× 1.5); (F–H) petal-like stamens (× 1.5); (I–K) inner stamens (× 1.5); (L) gynoecium showing numerous carpels (× 2); (M) gynoecium in cross-section (× 1.5); (N) germinating seed (× 0.5); (O) fruit (× 1); (P) dehiscing fruit (× 1.5); (Q) seed, with gelatinous covering (× 15); (R) seed (× 30); (S) seed coat (greatly magnified); (T) cross-section of seed (× 30). (Original art prepared for the Generic Flora of the Southeast U.S. Project. Used with permission.)

Distribution and ecology: Widespread from tropical to cold temperate regions, occurring in rivers, ponds, lakes, and other freshwater wetlands.

Genera/species: 8/70. ***Major genera:*** *Nymphaea* (40 spp.) and *Nuphar* (15). These genera, along with *Cabomba* and *Brasenia*, occur in the continental United States and Canada.

Economic plants and products: Species of *Nymphaea* (water lily), *Nuphar* (yellow water lily, spatterdock), and *Victoria* (Amazon water lily) provide ornamental plants for pools. *Cabomba* is a popular aquarium plant.

Discussion: The family comprises five subfamilies. Euryaloideae includes *Euryale* and *Victoria*; these share the apomorphy of prickles on the petiole and abaxial leaf surface. Barclayoideae includes only *Barclaya*, which is unique in having connate petals. Cabomboideae includes *Cabomba* and *Brasenia*, which are united by the presence of free-floating stems in addition to the rhizome. They also have distinct carpels, nutlike fruits, and six-tepaled flowers that lack petal-like staminodes. "Nymphaeoideae" are paraphyletic and include *Nymphaea*, *Nuphar*, and *Ondinea*, with *Nymphaea* linked to Euryaloideae by the synapomorphies of four tepals, numerous staminodes, and a partly inferior ovary (Ito 1987; Moseley et al. 1993). Although sometimes divided into several families, the Nymphaeaceae, as here circumscribed, clearly are monophyletic (Donoghue and Doyle 1989; Zimmer et al. 1989; Hamby and Zimmer 1992; Qiu et al. 1993; Chase et al. 1993; Doyle et al. 1994) and there is little reason to subdivide the group.

The family is placed within the paleoherb complex on the basis of its scattered vascular bundles, lack of a vascular cambium, adventitious root system, and lack of ethereal oils. Nelumbonaceae have often been placed in Nymphaeales (or even Nymphaeaceae), but all recent evidence places them within the tricolpate clade (Donoghue and Doyle 1989; Moseley et al. 1993; Chase et al. 1993; Qiu et al. 1993). Although superficially similar to Nymphaeaceae, Nelumbonaceae have numerous carpels that are sunken in pits within an enlarged, funnel-shaped, spongy receptacle. Molecular data suggest that the Illiciaceae may be related to the Nymphaeaceae (Chase et al. 1993).

The fragrant, showy flowers of Nymphaeaceae attract various insects (beetles, flies, and bees), which gather pollen or, less commonly, nectar. However, flowers of *Brasenia* lack nectar glands and are wind-pollinated, having numerous easily shaken anthers. Outcrossing is favored by protogyny. Flowers of *Victoria* and some species of *Nymphaea* attract beetles by providing food bodies (starch-filled carpel appendages) and producing heat along with a strong fruity odor. The flowers open and close daily and trap the beetles. In other species of *Nymphaea*, flies and small bees gather pollen from 2-or 3-day-old flowers. They are then attracted to a pool of sweet stigmatic fluid in young (1-day-old) flowers, in which they frequently drown. Pollen on their bodies becomes suspended in the stigmatic fluid and eventually germinates. The fleshy fruits of many Nymphaeaceae mature underwater and rupture irregularly due to swelling of the mucilaginous aril surrounding the seeds, which are water dispersed. In *Nuphar* the carpel segments separate and float away. Vegetative reproduction commonly occurs through production of rhizomes or specialized shoots/tubers.

References: Chase et al. 1993; Dahlgren and Clifford 1982; Donoghue and Doyle 1989; Doyle et al. 1994; Hamby and Zimmer 1992; Ito 1986, 1987; Les et al. 1991; Orgaard 1991; Osborn et al. 1991; Osborn and Schneider 1988; Qiu et al. 1993; Meeuse and Schneider 1979; Moseley et al. 1993; Schneider and Carlquist 1995; Schneider and Jeter 1982; Schneider and Williamson 1993; Schneider et al. 1995; Taylor and Hickey 1996; Thorne 1974, 1992; Wiersema 1988; Wood 1959a; Zimmer et al. 1989.

Ceratophyllales

Ceratophyllaceae S. F. Gray
(Hornwort Family)

Submersed, aquatic herbs; roots lacking, but often with colorless rootlike branches anchoring the plant; stems with a single vascular strand with central air canal surrounded by elongate starch-containing cells; with tannins. Leaves whorled, simple, often **dichotomously dissected**, entire to serrate, **lacking stomates and a cuticle**; stipules lacking. **Inflorescences of solitary, axillary flowers. Flowers unisexual (plants monoecious)**, *radial, inconspicuous,* **with a whorl of 7 to numerous bracts** (possibly tepals). *Stamens 10 to numerous*, distinct; filaments not clearly differentiated from anthers; anthers with connective prolonged beyond pollen sacs, and forming 2 prominent teeth; **pollen grains lacking apertures, with reduced exine, forming branched pollen tubes. Carpel 1**; ovary superior, **with ± apical placentation**; stigma elongated and extending along one side of style. Ovule 1 per carpel, **orthotropous, with 1 integument**. Nectaries lacking. **Fruit an achene, often with 2 or more projections, along with persistent style; endosperm lacking**.

Floral formula: Staminate: *, -7–∞-, 10–∞, 0
Carpellate: *, -7–∞-, 0, $\underline{1}$; achene

Distribution and ecology: Cosmopolitan; forming floating masses in freshwater habitats.

Genus/species: 1/6. ***Genus:*** *Ceratophyllum*.

Economic plants and products: *Ceratophyllum* is ecologically important in that it provides protection from predation for newly hatched fish; the foliage and fruits are important food items for migratory waterfowl; sometimes it is weedy, choking waterways.

Discussion: This family is clearly monophyletic, showing numerous adaptations to life as a submerged aquatic herb. The group has a fossil record extending back to the Early Cretaceous, and is most likely an ancient and highly modified taxon related to one of the basal angiosperm clades.

The species of *Ceratophyllum* are highly variable and taxonomically difficult. Relationships within the family are based on variation in the leaves and fruits.

The inconspicuous flowers of Ceratophyllaceae are submerged, and pollen is dispersed by water currents, as are the achenes, although dispersal by birds also occurs. The persistent style and variously developed appendages attach the small fruits to vegetation or sediments. Vegetative reproduction by fragmentation is common.

References: Chase et al. 1993; Cronquist 1981; Dahlgren 1989; Dahlgren 1983; Dilcher 1989; Endress 1994a; Les 1988, 1989, 1993; Les et al. 1991; Qiu et al. 1993; Takhtajan 1980; Thorne 1974, 1992; Wood 1959a.

Piperales

Piperaceae C. A. Agardh

(Pepper Family)

Herbs to small trees, sometimes epiphytic; *nodes often ± swollen or jointed*; **vessel elements with usually simple perforations; stem with vascular bundles of more than 1 ring or ± scattered**; *with spherical cells containing ethereal oils*; often with alkaloids. Hairs simple. Leaves usually alternate, simple, entire, with palmate to pinnate venation, *with pellucid dots*; stipules lacking or adnate to petiole (and petiole sometimes sheathing stem). Inflorescences indeterminate, **of thick spikes, densely covered with minute flowers**, terminal or axillary, often displaced to a position opposite the leaf due to development of axillary shoot. **Flowers** bisexual or unisexual (plants monoecious or dioecious), appearing to be radial, **inconspicuous**, each with a broadly triangular to peltate bract. *Perianth lacking*. Stamens 1–10, often 6; filaments usually distinct; pollen grains monosulcate or lacking apertures. **Carpels 1–4, connate**; ovary superior, *with basal placentation*; stigmas 1–4, capitate, lobed, or brushlike. **Ovule 1 per gynoecium**, orthotropous, with 1 or 2 integuments. Nectaries lacking. **Fruit usually a drupe**; endosperm scanty, supplemented by perisperm (Figure 8.10).

Floral formula: *, -0-, 1–10, $\underline{1–4}$; drupe

Distribution and ecology: Widely distributed in tropical and subtropical regions. Species of *Peperomia* are commonly epiphytes in moist broad-leaved forests.

Genera/species: 6/2020. ***Major genera:*** *Peperomia* (1000 spp.) and *Piper* (1000). Both occur within the continental United States.

Economic plants and products: Fruits of *Piper nigrum* provide black and white pepper, one of the oldest and most important spices. Leaves of *Piper betle* (betel pepper) are chewed (along with various spices and fruits of *Areca catechu*, betel nut) and have a mildly stimulating effect. A few species of *Piper* are used medicinally. Several species of *Peperomia* are grown as ornamentals because of their attractive foliage.

Discussion: Piperales are an easily recognized and clearly monophyletic order, comprising only Piperaceae and Saururaceae (a small family of four genera and six species). Synapomorphies of this order include tetracytic stomata, indeterminate, terminal, spicate inflorescences, bilateral floral symmetry, minute pollen grains, orthotropous ovules, and anatomical or developmental details of the flowers and seeds (Donoghue and Doyle 1989; Tucker et al. 1993; Doyle et al. 1994). The monophyly of the order is also supported by cladistic analyses based on 18S nucleic acid sequences (Zimmer et al. 1989; Doyle et al. 1994; Soltis et al. 1997) and *rbcL* sequences (Qiu et al. 1993). Piperales clearly belong within the paleoherbs. Although the exact phylogenetic position of the group is still unclear, these plants may be most closely related to Aristolochiales.

Piperaceae are clearly monophyletic (Tucker et al. 1993). Members of the related family Saururaceae can be easily separated from Piperaceae by their two to ten ovules per carpel and distinct carpels (both plesiomorphies), although Saururaceae probably are monophyletic (Tucker et al. 1993). The Chloranthaceae, which also have inconspicuous flowers, were once included in Piperales (Cronquist 1981), but are here tentatively referred to the Laurales.

Within Piperaceae, *Zippelia* is the sister group to the remaining species, which form a clade on the basis of a reduction to three carpels and capitate stigmas (Tucker et al. 1993). Relationships among the remaining genera are problematic. *Pothomorphe* is distinct due to its axillary, umbel-like clusters of spikes. *Piper* may be most closely related to *Peperomia* on the basis of an unusual development of the female gametophyte. *Peperomia* is the most derived member of this family, and shows numerous apomorphies, such as a single carpel, two unilocular stamens, a 16-nucleate female gametophyte (vs. 8 nuclei in other genera), ovules with a single integument, unusually small pollen grains that lack apertures, herbaceous habit, and succulent leaves.

The tiny flowers of Piperaceae probably are insect-pollinated, but more work on the pollination biology of the family is needed. Outcrossing may predominate due to protogyny. The drupes of *Piper* are mainly dispersed by birds and bats, while those of *Peperomia* are often sticky and may be externally transported by animals.

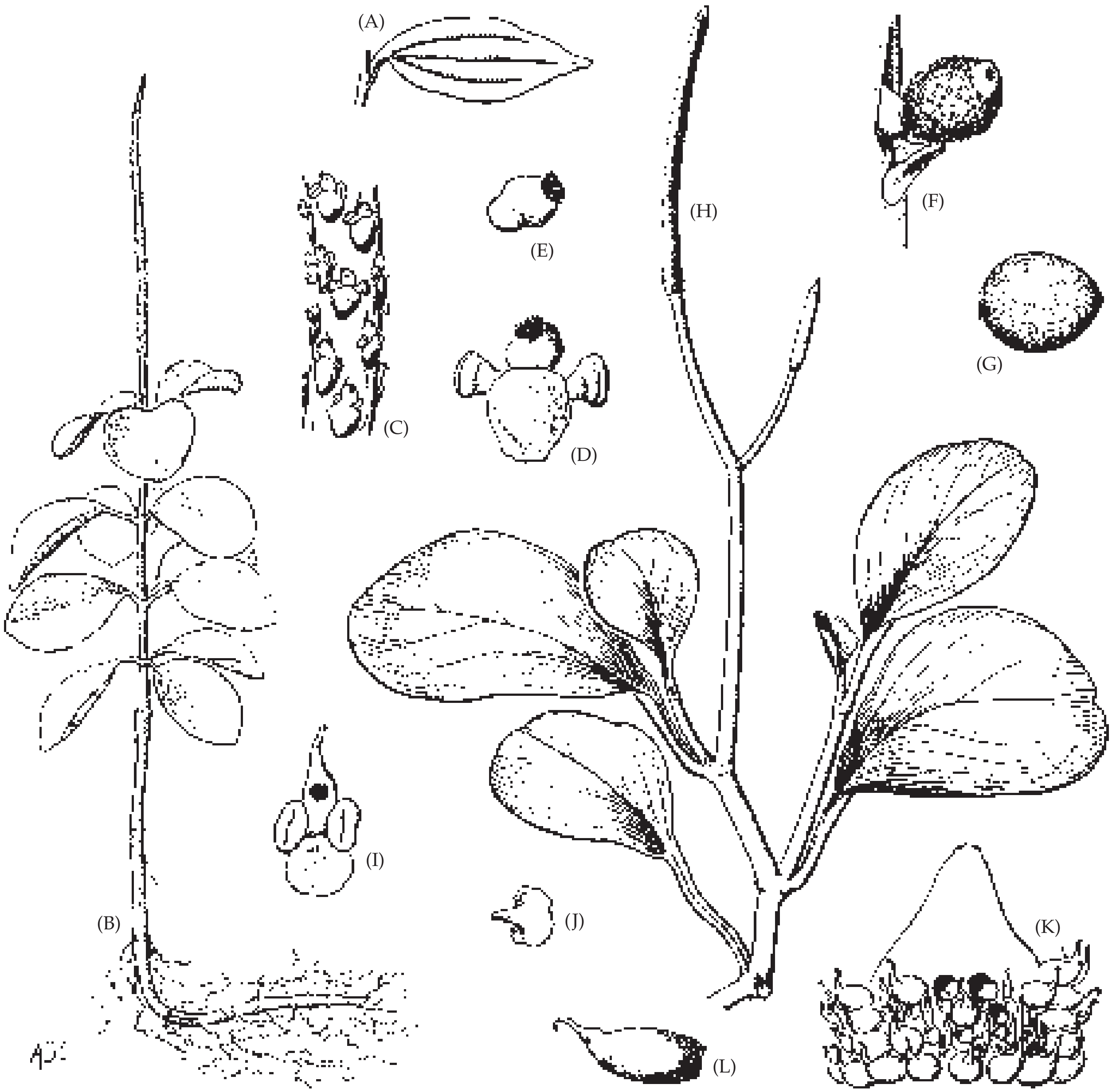


Figure 8.10 Piperaceae. (A) *Peperomia glabella:* leaf (× 0.75). (B–G) *P. humilis:* (B) flowering shoot (× 0.75); (C) portion of inflorescence (× 9); (D) flower with bract, showing gynoecium and two stamens (× 27); (E) gynoecium (× 27); (F) portion of spike with a mature drupe (× 18); (G) pit of drupe (× 27). (H–L) *P. obtusifolia:* (H) flowering shoot (× 0.75); (I) flower with bract, showing gynoecium and two stamens (× 27); (J) bract (× 27); (K) tip of spike with partly mature fruits, three removed to show immersion of base of fruit in tissue of axis, apex of spike with undeveloped flowers shown only in outline (× 9); (L) mature drupe, showing hooked apex and position of stigma (× 18). (From Borstein 1991, *J. Arnold Arbor. Suppl. Ser.* 1, p. 359.)

References: Borstein 1991; Burger 1977; Chase et al. 1993; Donoghue and Doyle 1989; Doyle et al. 1994; Hamby and Zimmer 1992; Qiu et al. 1993; Semple 1974; Soltis et al. 1997; Taylor and Hickey 1992; Tebbs 1993; Thorne 1974, 1992; Tucker et al. 1993; Wood 1971; Zimmer et al. 1989.

Aristolochiales

Aristolochiaceae Lindley

(Dutchman's-Pipe Family)

Herbs, lianas, or occasionally shrubs; with spherical cells containing ethereal oils and terpenoids; **with aristolochic acids (bitter, yellow, nitrogenous compounds)** or alkaloids. Hairs simple. *Leaves alternate*, simple, sometimes lobed, *entire, with palmate venation, with pellucid dots*; stipules usually lacking. Inflorescences various. Flowers bisexual, radial to bilateral. *Sepals 3*, **connate**, *often bilateral, tubular, and S-shaped or pipe-shaped, with spreading 3-lobed to 1-lobed limb*, **showy**, dull red and mottled, valvate, and deciduous. Petals usually lacking or vestigial, but in *Saruma* present and well developed, distinct, yellow, and imbricate. Stamens usually 6–12; filaments distinct, often adnate to style; pollen grains usually lacking apertures (monosulcate in *Saruma*). Carpels 4–6, connate (distinct in *Saruma*), often twisting in development; **ovary/ovaries half-inferior to inferior**, with axile placentation, or parietal with intruded placentas; stigmas 4–6, often lobed and spreading. Ovules numerous. Nectaries often of patches of glandular hairs on calyx tube. *Fruit a septicidal capsule* (cluster of follicles in *Saruma*), often pendulous and opening from the base; seeds flattened, winged, or associated with fleshy tissue (Figure 8.11).

Floral formula: * or X, 3, 3 or 0, 6–12, –4–6–; capsule

Distribution and ecology: Widespread in tropical and temperate regions but absent from Australia.

Genera/species: 7/450. ***Major genera:*** *Aristolochia* (320 spp.), *Asarum* (70), and *Isotrema* (50). *Asarum* and *Aristolochia* occur in the continental United States.

Economic plants and products: Many species of *Asarum* (wild ginger, incl. *Hexastylis*) and *Aristolochia* (Dutchman's-pipe) are cultivated as ornamentals because of their unusual flowers or variegated leaves. Some species of *Aristolochia* are used medicinally.

Discussion: Aristolochiaceae are often placed within (e.g., Thorne 1992) or near (e.g., Cronquist 1981) Magnoliales. However, their 3-merous flowers and monocot-like sieve tube plastids suggest an affinity to the paleoherbs, and especially monocots (Dahlgren and Clifford 1982; Donoghue and Doyle 1989). Ribosomal RNA sequences (Zimmer et al. 1989; Doyle et al. 1994) indicate that Aristolochiaceae may be the sister group to the monocots. Studies using *rbcL* sequences indicate that the family may be paraphyletic, with *Lactoris* (Lactoridaceae) placed within it, but the family here is considered monophyletic on the basis of its usually more or less inferior ovary and synsepalous flowers. The achlorophyllous root-parasitic Hydnoraceae, which have syn-

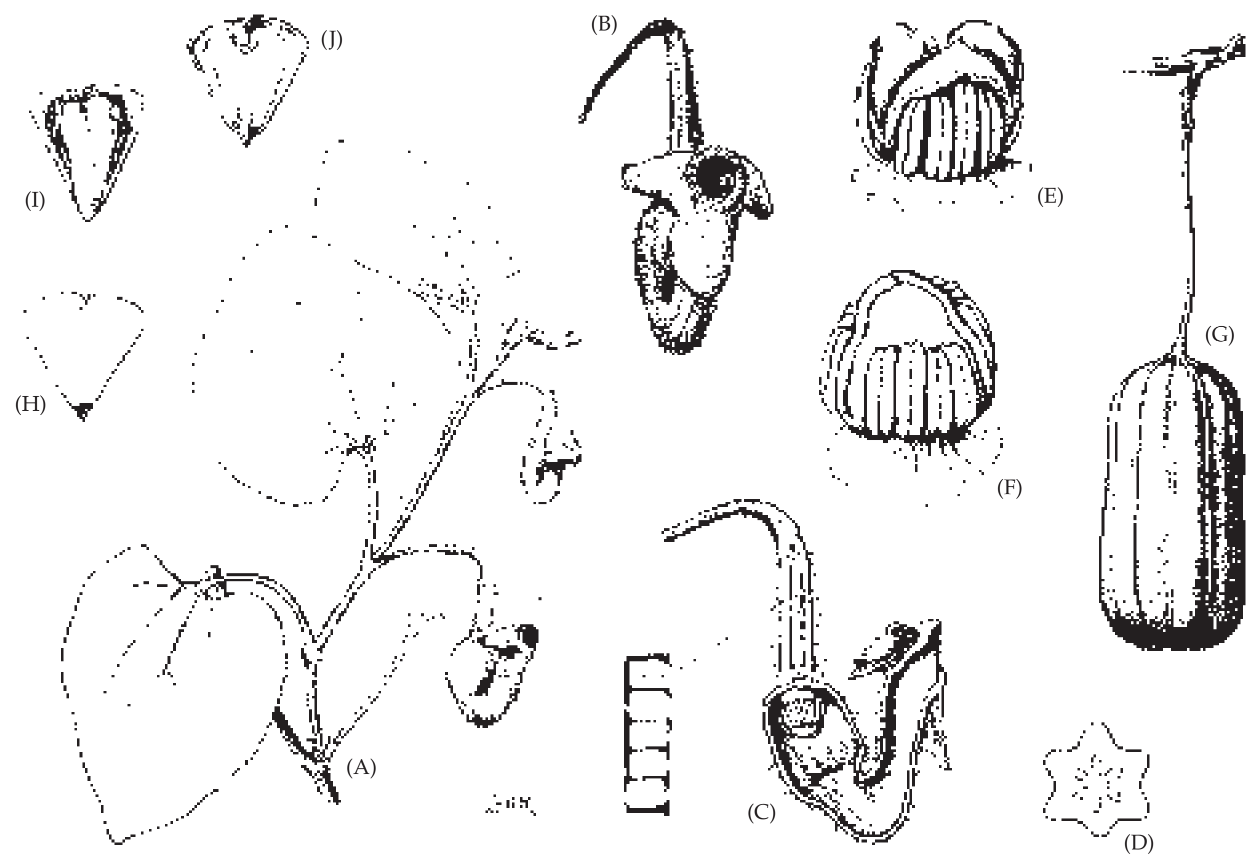


Figure 8.11 Aristolochiaceae. *Aristolochia tomentosa:* (A) branch with flower and bud (× 0.5); (B) flower (× 1); (C) flower with half of perianth and ovary removed, and detail of ovules in a single locule (× 1); (D) ovary in cross-section (× 3); (E) receptive stigmas, at opening of flower (× 4); (F) stigmas at time of shedding of pollen (but adnate anthers shown as closed) now folded inward (× 4); (G) fruit (× 1); (H) seed, upper surface (× 1.5); (I) seed, lower surface, with corky funiculus (× 1.5); (J) seed, lower surface, corky funiculus removed (× 1.5). (From Wood 1974, *A student's atlas of flowering plants*, p. 21.)

tepalous flowers that arise endogenously from roots of the host, may also be related to the Aristolochiaceae.

Thorne (1992) and Huber (1993) divided the family into Asaroideae, including *Asarum* and *Saruma*, which are perennial herbs with radial flowers in which the stamens are free or only very slightly adnate to the gynoecium, and Aristolochioideae, including *Aristolochia*, which are subshrubs to lianas with usually bilateral flowers in which the stamens are strongly adnate to the style.

Flowers of Aristolochiaceae are mainly fly-pollinated. The pollination syndrome is quite specialized in *Aristolochia*, which has elaborate trap flowers with a highly modified calyx. Flies are attracted to these flowers by their dull red and often mottled coloration and odor (which may be fruity to fetid). Nectar, produced by glandular hairs on the calyx tube, functions as a pollinator reward. Pollen-bearing flies become trapped within an inflated portion of the calyx tube, which may be entered only through the constricted opening, which often is provided with downward-pointing hairs. During the first phase of the flower's life, pollen is deposited on the receptive stigmas that crown the gynoecium, projecting over the still unopened anthers. After pollination, the stigmas wither and become erect, thus exposing the dehiscing anthers. The flies become covered with pollen, and are allowed to leave when the downward-pointing hairs and/or the calyx tube wither. The seeds of *Aristolochia*, which are typically flattened, are dispersed by wind from the hanging, parachute-like capsules, although some species are water-dispersed, or have sticky seeds, leading to external transport by animals; a few have fleshy fruits and are vertebrate dispersed. Dispersal of the seeds by ants is common in herbaceous taxa (e.g., *Asarum*); these seeds possess an aril-like structure.

References: Chase et al. 1993; Cronquist 1981; Dahlgren and Clifford 1982; Donoghue and Doyle 1989; Doyle et al. 1994; Faegri and van der Pijl 1980; Huber 1993; Kelly 1997; Qiu et al. 1993; Thorne 1974, 1992; Zimmer et al. 1989.

MONOCOTS

The monocots are considered monophyletic based on their parallel-veined leaves, embryo with a single cotyledon, sieve cell plastids with several cuneate protein crystals, stems with scattered vascular bundles, and adventitious root system. Sieve cell plastids with several protein crystals also occur in some Aristolochiaceae (*Saruma* and *Asarum*), and the feature may actually be a synapomorphy of Aristolochiaceae and monocots. Scattered vascular bundles and adventitious roots also occur in the Nymphaeaceae and some Piperaceae. Several monocots have pinnate to palmate leaves with obviously reticulate venation patterns (see Dahlgren et al. 1985; Chase et al. 1995b), but these are probably reversals associated with life in shaded forest understory habitats. In addition, the leaves of most monocots, even those with a well-developed blade and petiole, are formed almost entirely from the basal end of the leaf primordium, while the leaves of nonmonocots are mainly derived from the apical end of the primordium. Several features often considered to characterize monocots, such as 3-merous flowers with two perianth whorls and herbaceous habit, occur throughout the paleoherbs (and may be synapomorphies of this group). Monocots typically have monosulcate pollen, probably a retention of an ancestral angiosperm feature.

The monophyly of the monocots is supported by 18S rDNA sequences, *rbcL* sequences, and morphology (Bharathan and Zimmer 1995; Chase et al. 1993, 1995a,b; Stevenson and Loconte 1995; Soltis et al. 1997). The taxonomic diversity of monocots is presented by Kubitzki (1998a,b).

Alismatales

Cladistic analyses of *rbcL* sequences (Chase et al. 1993, 1995b; Duvall et al. 1993) support the monophyly of the Alismatales, as does the morphological synapomorphy of stems with small scales or glandular hairs within the sheathing leaf bases at the nodes (see Dahlgren and Rasmussen 1983; Dahlgren et al. 1985; Stevenson and Loconte 1995). The Araceae are sister to the remaining families of the order, which constitute a subclade based on their seeds lacking endosperm and root hair cells shorter than other epidermal cells. All members of this subclade occur in wetland or aquatic habitats. Two major clades are recognized within this aquatic clade. The first contains Alismataceae, Hydrocharitaceae, and Butomaceae, and is supported by the apomorphies of perianth differentiated into sepals and petals, stamens more than six and/or carpels more than three (a secondary increase), and ovules scattered over the inner surface of the locules. Major families constituting the second clade are Potamogetonaceae, Ruppiaceae, Zosteraceae, Posidoniaceae, Zannichelliaceae, Cymodoceaceae, and Najadaceae. This group is diagnosed on the basis of pollen that lacks apertures and more or less lacks an exine (Dahlgren and Rasmussen 1983; Cox and Humphries 1993). Plants of marine habitats evolved within Hydrocharitaceae, and more than twice in the sea grass families (Zosteraceae, Cymodoceaceae, Ruppiaceae, and Posidoniaceae) (Les et al. 1997a). The order probably diverged very early in the evolution of monocots. Alismatales contains 13 families and about 3320 species; major families include **Araceae**, **Alismataceae**, **Hydrocharitaceae**, Butomaceae, **Potamogetonaceae**, Ruppiaceae, Zosteraceae, Posidoniaceae, Zannichelliaceae, Cymodoceaceae, and Najadaceae.

References: Chase et al. 1993, 1995b; Cox and Humphries 1993; Dahlgren and Rasmussen 1983; Dahlgren et al. 1985; Duvall et al. 1993; Les et al. 1997; Stevenson and Loconte 1995.

Key to Major Families of Alismatales

1. Flowers on a thick axis, the spadix, surrounded by or associated with a leaflike bract, the spathe; plants of various habitats .... **Araceae**
1. Flowers not on a spadix; plants aquatic or of wetlands 2
2. Perianth of sepals and petals 3
2. Perianth of tepals or lacking 5
3. Ovary inferior; carpels connate; fruits berries .... **Hydrocharitaceae**
3. Ovary superior; carpels ± distinct; fruits follicles or achenes 4
4. Pollen grains monosulcate; laticifers lacking and sap watery; fruits follicles; embryo straight .... Butomaceae
4. Pollen grains usually 4-multiporate or occasionally lacking apertures; laticifers present and sap milky; fruits achenes or follicles; embryo curved .... **Alismataceae**
5. Pollen grains globose or ellipsoid; plants of fresh, alkaline, or brackish water 6
5. Pollen grains threadlike; plants of marine environments 9
6. Flowers bisexual 7
6. Flowers unisexual 8
7. Stamens 2, each with a small appendage; carpels on long stalks .... Ruppiaceae
7. Stamens 4, each with a large appendage; carpels sessile .... **Potamogetonaceae**
8. Carpel solitary; ovule basal, erect .... Najadaceae
8. Carpels usually 3 or 4; ovule ± apical, pendulous .... Zannichelliaceae
9. Flowers bisexual; stamens 3; carpel 1 .... Posidoniaceae
9. Flowers unisexual; stamens 1 or 2; carpels 2 10
10. Carpels distinct; stamens 2, connate .... Cymodoceaceae
10. Carpels connate; stamen 1 .... Zosteraceae

Araceae A. L. de Jussieu
(Arum Family)

Terrestrial to aquatic herbs, often with rhizomes or corms, vines with aerial roots, epiphytes, or floating aquatics, the latter often very reduced with ± thalloid vegetative body; *raphide crystals of calcium oxalate present, and associated chemicals causing irritation of mouth and throat if eaten;* cyanogenic compounds often present, and sometimes with alkaloids; often with laticifers, mucilage canals, or resin canals, and latex watery to milky. Hairs simple, but often lacking. *Leaves alternate*, sometimes basal, simple, *blade often well developed*, sometimes strongly lobed, pinnately to palmately compound, usually entire, with parallel, pinnate, or palmate venation, sheathing at base; stipules lacking, but glandular hairs or small scales present at the node inside the leaf sheath. **Inflorescences indeterminate**, usually terminal, **forming a spike of numerous small flowers packed onto a fleshy axis (a spadix), which may be lacking flowers toward its apex, which is subtended by a large leaflike to petal-like bract (a spathe)**, but reduced in floating aquatic taxa. Flowers bisexual to unisexual (plants usually monoecious), radial, **lacking individual bracts**. Tepals usually 4–6 or lacking, distinct to connate, inconspicuous and often fleshy, valvate or imbricate. Stamens 1–6 (–12); filaments distinct to connate; anthers sometimes opening by pores, distinct to connate; pollen grains various. Carpels usually 2–3, connate; ovary superior, placentation various; stigma 1, punctate or capitate. Ovules 1 to numerous, anatropous to orthotropous. Nectaries lacking. *Fruit usually a berry*, but occasionally an utricle, drupe, or nutlike; endosperm sometimes lacking (Figure 8.12).

Floral formula: *, 4–6 or -0-, 1–6, $\underline{1–3}$; berry, utricle

Distribution and ecology: Cosmopolitan, but best developed in tropical and subtropical regions; very common in tropical forests and wetlands.

Genera/species: 108/2830. ***Major genera:*** *Anthurium* (900 spp.), *Philodendron* (500), *Arisaema* (150), *Homalomena* (140), *Amorphophallus* (100), *Schismatoglottis* (100), *Spathiphyllum* (60), *Monstera* (50), *Pothos* (50), *Xanthosoma* (40), *Dieffenbachia* (40), and *Syngonium* (30). Noteworthy genera of the continental United States and/or Canada are *Arisae-*

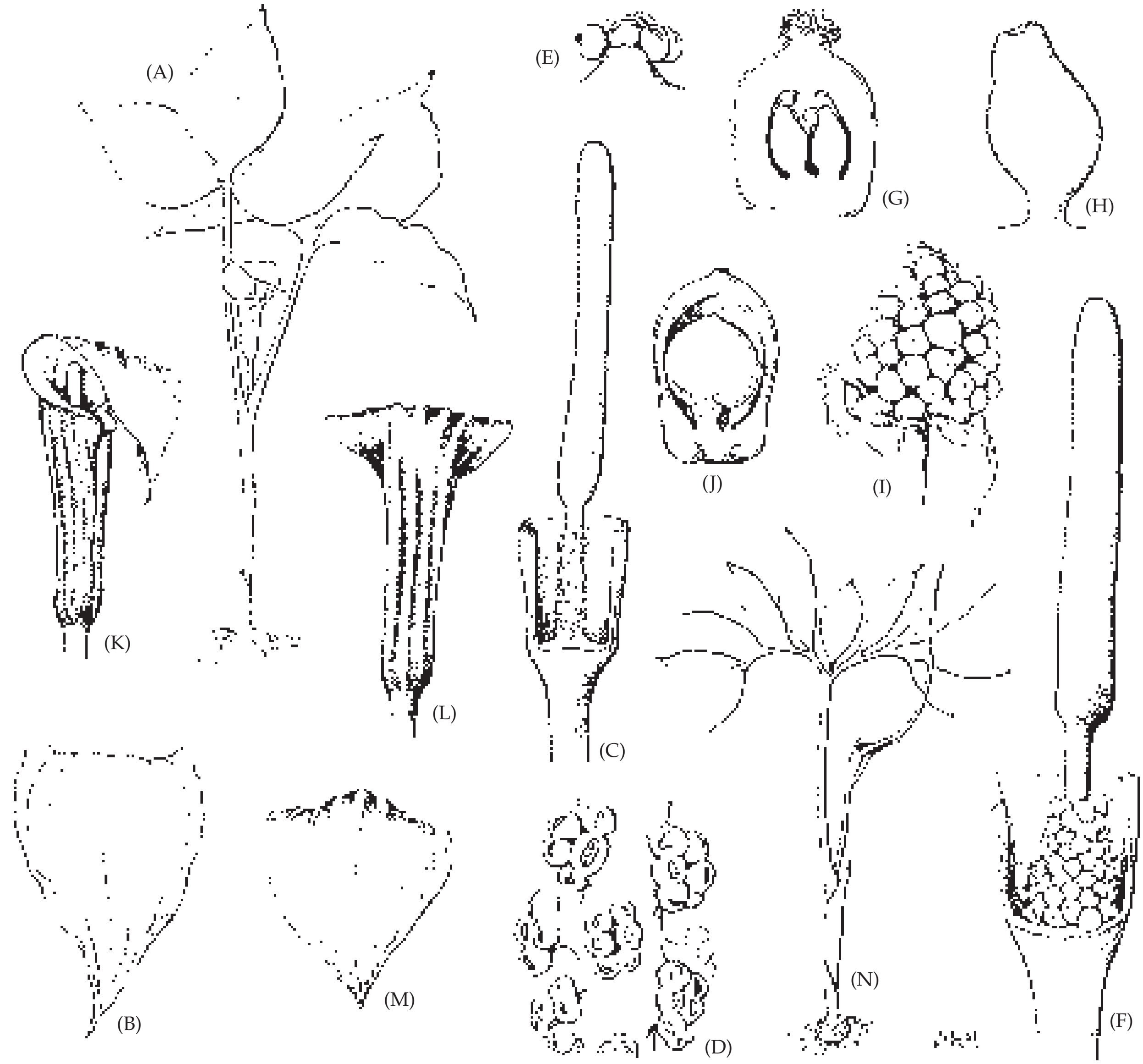


Figure 8.12 Araceae. (A–J) *Arisaema triphyllum:* (A) habit (× 0.2); (B) spathe, apical view (× 0.75); (C) staminate inflorescence, spathe removed (× 1.5); (D) portion of staminate spadix (× 8.75); (E) staminate flower, lateral view (× 11.5); (F) carpellate inflorescence, spathe removed (× 1.5); (G) carpellate flower, longitudinal section, showing ovules (× 11.5); (H) ovule (× 30); (I) fruiting spadix (× 0.75); (J) fruit in longitudinal section, showing seed (× 3). (K–M) *A. triphyllum* var. *stewardsonii:* (K) inflorescence, lateral view (× 0.75); (L) inflorescence, back view (× 0.75); (M) spathe, apical view (× 0.75). (N) *A. dracontium:* habit (× 0.2). (From Wilson 1960a, *J. Arnold Arbor.* 41: p. 59.)

ma, *Lemna*, *Orontium*, *Peltandra*, *Pistia*, *Spirodela*, *Symplocarpus*, and *Wolffia*.

Economic plants and products: The starchy corms of *Alocasia*, *Colocasia* (taro), and *Xanthosoma* (yautia) are eaten (after proper treatment to remove the irritating chemicals). The berries of *Monstera* occasionally are eaten. The family contains numerous ornamentals, including *Philodendron*, *Zantedeschia* (calla lily), *Anthurium*, *Caladium*, *Colocasia*, *Dieffenbachia* (dumbcane), *Epipremnum*, *Monstera*, *Spathiphyllum*, *Syngonium*, *Aglaonema*, *Xanthosoma* (elephant's-ear), *Scindapsus*, *Spathicarpa*, and *Zamioculcus*.

Discussion: Araceae are considered monophyletic based on morphology (Grayum 1990; Mayo et al. 1995) and cpDNA sequences (Chase et al. 1993; French et al. 1995). The family may be a fairly early divergent lineage within monocots and probably is sister to the remaining families of Alismatales (Dahlgren and Rasmussen 1983; Dahlgren et al. 1985; Chase et al. 1995b; Stevenson and Loconte 1995).

Araceae have been divided into several subfamilies based on variation in habit, leaf arrangement and morphology, floral morphology, pollen structure, anatomy, and chromosome number (Grayum 1990). Phylogenetic relationships have also been assessed within Araceae through the use of *rbcL* sequences (French et al. 1995). A few genera of very reduced floating aquatics, including *Spirodela*, *Lemna*, *Wolffia*, and *Wolfiella*, are often segregated as Lemnaceae (see den Hartog 1975; Landolt 1980, 1986; Landolt and Kandeler 1987; Cronquist 1981; Dahlgren et al. 1985). In *Lemna* and *Spirodela* the spathe is represented by a membranous sheath, while it is completely lacking in *Wolffia* and *Wolfiella*. It is reasonably clear that these genera have been derived from less modified members of the subfamily Aroideae (French et al. 1995; Mayo et al. 1995; Stockey et al. 1997). Although *rbcL* sequences support a phylogenetic relationship of these reduced aquatics with the much larger floating aquatic aroid *Pistia*, these genera are not sister taxa (French et al. 1995).

Acorus has been removed from the Araceae and placed in its own family, the Acoraceae (Grayum 1987, 1990; Bogner and Nicolson 1991; Thorne 1992), as suggested by morphology, secondary compounds, and DNA sequence characters. *Acorus* is a wetland herb with narrow, equitant leaves, small bisexual flowers with six tepals, six stamens, and two or three fused carpels, which are borne on a spadix, and berry fruits. Unlike Araceae, Acoraceae contain ethereal oils in specialized spherical cells and lack raphide crystals; anther development is also quite different in the two families. Cladistic analyses based on *rbcL* sequences (Chase et al. 1993, 1995b) suggest that *Acorus* is the sister group to the remaining monocots.

Inflorescences of Araceae are pollinated by several groups of insects, especially beetles, flies, and bees. The inflorescence usually produces a strong odor (sweet to noxious) and often heat. The gynoecium matures before the androecium, and when the flowers are unisexual, the carpellate mature before the staminate, leading to outcrossing. In *Arisaema*, small (generally young) plants are staminate and larger (older) plants are carpellate, again leading to outcrossing. Dispersal of the green to brightly colored berries is presumably by birds or mammals. The utricles of *Lemna* and relatives are water dispersed.

References: Bogner and Nicolson 1991; Chase et al. 1993, 1995b; Croat 1980; Cronquist 1981; Dahlgren and Rasmussen 1983; Dahlgren et al. 1995; den Hartog 1975; French et al. 1995; Grayum 1987, 1990; Landolt 1980, 1986; Landolt and Kandeler 1987; Les et al. 1997b; Maheshwari 1958; Mayo et al. 1995; Ray 1987a,b; Stevenson and Loconte 1995; Stockey et al. 1997; Wilson 1960a.

Alismataceae Vent.
(Water Plantain Family)

Aquatic or wetland, rhizomatous herbs; **laticifers present, the latex white**; tissues ± aerenchymatous. Hairs usually lacking. Leaves alternate, usually ± basal, simple, entire, usually with a well-developed blade, with parallel or palmate venation, sheathing at base; sometimes polymorphic, with submerged, floating, and/or emergent blades; stipules lacking; small scales present at the node inside the leaf sheath. Inflorescences determinate, but often appearing indeterminate, with branches or flowers often ± whorled, terminal, borne at the apex of a scape. Flowers bisexual or unisexual (plants then monoecious), radial, *with perianth differentiated into a calyx and corolla*. *Sepals 3*, distinct, imbricate. *Petals 3*, distinct, imbricate and crumpled, *usually white or pink*. *Stamens usually 6 to numerous*; filaments distinct; **pollen grains usually 2- to polyporate**. *Carpels* (*3*–) *6 to numerous*, distinct, ovaries superior, with ± basal placentation; stigma 1, minute. Ovules few to more commonly 1 per carpel. Nectaries at base of carpels, stamens, or perianth parts. *Fruit a cluster of achenes* (rarely follicles); **embryo strongly curved**; endosperm lacking (Figure 8.13).

Floral formula: *, 3, 3, 6–∞, $\underline{6–\infty}$; achenes

Distribution and ecology: Widely distributed; plants of freshwater marshes, swamps, lakes, rivers, and streams.

Genera/species: 16/100. ***Major genera:*** *Echinodorus* (45 spp.) and *Sagittaria* (35). The family is represented in the continental United States and/or Canada by the above and *Alisma*, *Damasonium*, and *Limnocharis*.

Economic plants and products: *Sagittaria* (arrowhead), *Alisma* (water plantain), *Echinodorus* (bur-heads), and *Hydrocleis* (water poppy) provide pond and/or aquarium ornamentals. The rhizomes of *Sagittaria* may be eaten.

Discussion: Alismataceae are defined broadly (including the Limnocharitaceae; see Pichon 1946; Thorne 1992) and considered monophyletic on the basis of morphological characters (Dahlgren et al. 1985). The genera with achenes and only a single basal ovule per carpel (e.g., *Alisma*, *Sagittaria*, and *Echinodorus*) may form a monophyletic subgroup (Chase et al. 1993, 1995b).

Species are often difficult to identify due to extensive variation in leaf morphology, which correlates with environmental parameters such as light intensity, water depth, water chemistry, and rate of flow (Adams and Godfrey 1961). Submerged leaves are usually linear, while floating or emergent leaves are petiolate with elliptic to ovate blade with an acute to sagittate base. Several different leaf forms may occur on the same plant.

Alistmataceae (and Butomaceae) have often been considered to represent primitive monocots (Cronquist 1981; Hutchinson 1973) due to their numerous, distinct stamens and carpels. However, developmental and anatomical studies have indicated that these numerous stamens are actually due to secondary increase from an ancestral condition of two whorls of three parts.

The showy flowers of Alismataceae are pollinated by various nectar-gathering insects (often bees and flies). In *Alisma* and *Echinodorus* the flowers are bisexual, while they are usually unisexual in *Sagittaria*. The achenes are often dispersed by water; they float due to the presence of spongy tissue and are resinous on the outer surface. They are also eaten (and dispersed) by waterfowl.

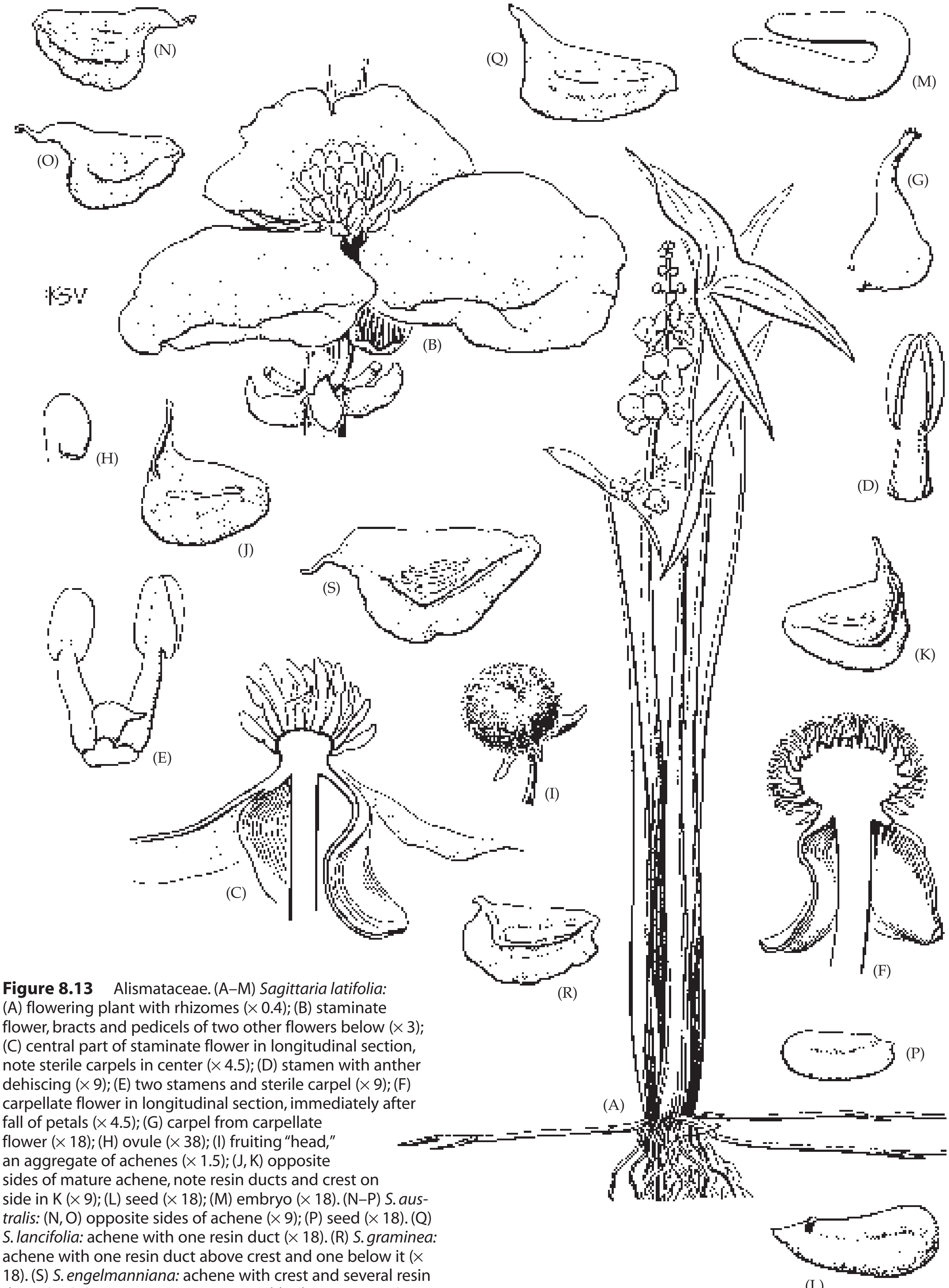


Figure 8.13 Alismataceae. (A–M) *Sagittaria latifolia:* (A) flowering plant with rhizomes (× 0.4); (B) staminate flower, bracts and pedicels of two other flowers below (× 3); (C) central part of staminate flower in longitudinal section, note sterile carpels in center (× 4.5); (D) stamen with anther dehiscing (× 9); (E) two stamens and sterile carpel (× 9); (F) carpellate flower in longitudinal section, immediately after fall of petals (× 4.5); (G) carpel from carpellate flower (× 18); (H) ovule (× 38); (I) fruiting "head," an aggregate of achenes (× 1.5); (J, K) opposite sides of mature achene, note resin ducts and crest on side in K (× 9); (L) seed (× 18); (M) embryo (× 18). (N–P) *S. australis:* (N, O) opposite sides of achene (× 9); (P) seed (× 18). (Q) *S. lancifolia:* achene with one resin duct (× 18). (R) *S. graminea:* achene with one resin duct above crest and one below it (× 18). (S) *S. engelmanniana:* achene with crest and several resin ducts (× 9). (From Rogers 1983, *J. Arnold Arbor.* 64: p. 410.)

References: Adams and Godfrey 1961; Chase et al. 1993, 1995b; Cronquist 1981; Dahlgren et al. 1985; Hutchinson 1973; Pichon 1946; Rogers 1983; Thorne 1992; Tomlinson 1982.

Hydrocharitaceae A. L. de Jussieu
(Frog's-Bit or Tape Grass Family)

Aquatic herbs, completely submerged to partly emergent, and rooted in the substrate or floating and unattached, in freshwater or marine habitats, often rhizomatous; tissues ± aerenchymatous. Hairs unicellular, thick-walled, prickle-like along leaf margins and/or veins. Leaves alternate, opposite, or whorled, along stem or in a basal rosette, simple, entire or serrate, sometimes with a well-developed blade, with parallel or palmate venation, or only midvein evident, sheathing at base; stipules usually lacking; small scales present at the node inside the leaf sheath. Inflorescences determinate, sometimes reduced to a solitary flower, axillary, subtended by 2 often connate bracts. Flowers bisexual or unisexual (plants then monoecious or dioecious), usually radial, *with perianth differentiated into calyx and corolla*. *Sepals 3, distinct*, valvate. *Petals 3, distinct*, usually white, imbricate, *sometimes lacking*. Stamens 2 or 3 to numerous; filaments distinct to connate; pollen grains monosulcate or lacking apertures, in *Thalassia* and *Halophila* united into threadlike chains. *Carpels usually 3–6, connate*; **ovary inferior**, with ovules scattered over surface of locules, the placentae often ± deeply intruded; styles often divided, appearing twice the number of carpels; stigmas elongate and papillose. Ovules numerous. Nectar often secreted from staminodes. **Fruit a berry or fleshy**, irregularly to valvately opening capsule; endosperm lacking.

Floral formula:

Staminate: *, 3, 3, 2–∞, 0

Carpellate: *, 3, 3, 0, $\overline{3–6}$; berry, fleshy capsule

Distribution and ecology: Widely distributed, but most common in tropical and subtropical regions, in freshwater (most genera) and marine habitats (*Euhalus*, *Halophila*, *Thalassia*).

Genera/species: 16/100. ***Major genera:*** *Ottelia* (40 spp.) and *Elodea* (15). *Egeria*, *Elodea*, *Halophila*, *Hydrilla*, *Limnobium*, *Thalassia*, and *Vallisneria* occur in the continental United States and/or Canada.

Economic plants and products: Several genera, including *Hydrilla*, *Egeria*, and *Elodea* (waterweeds), *Vallisneria* (tape grass), and *Limnobium* (frog's-bit), are used as aquarium plants. Species of *Elodea*, *Hydrilla*, and *Lagarosiphon* are pernicious aquatic weeds.

Discussion: Hydrocharitaceae, although monophyletic (Dahlgren and Rasmussen 1983), are morphologically heterogeneous, and have been divided into three to five subfamilies (Dahlgren et al. 1985).

The family shows an interesting array of pollination mechanisms. Several species in *Egeria*, *Limnobium*, *Stratiotes*, and *Blyxa* have showy flowers that are held above the surface of the water and pollinated by various nectar-gathering insects. In *Vallisneria*, *Enhalus*, and *Lagarosiphon*, the staminate flowers become detached and float on the water's surface, where they come into contact with the carpellate flowers (see Chapter 4). In *Elodea* the staminate flowers either detach or remain attached, but have anthers that explode, scattering pollen grains on the water's surface. In *Hydrilla* pollen transport may occur by wind or water. Finally, in *Thalassia* and *Halophila* pollination takes place underwater. Both outcrossing or selfing can occur. The fleshy fruits ripen below the water surface; fruits and/or seeds are either water or animal dispersed. Vegetative reproduction by fragmentation of rhizomes is common.

References: Cox and Humphries 1993; Dahlgren et al. 1985; Dahlgren and Rasmussen 1983; Haynes 1988; Kaul 1968, 1970; Lowden 1982; Tomlinson 1969b.

Potamogetonaceae Dumortier
(Pondweed Family)

Aquatic, rhizomatous herbs. Stems with reduced vascular bundles often in a ring, with air cavities; tannins often present. Hairs lacking. Leaves alternate or opposite, blade sometimes well developed, simple, entire, with parallel venation or with only a single midvein, sheathing at base, the sheath open, **and ± separated from blade so that it appears to be a stipule**, the leaves sometimes heteromorphic, with submerged and floating forms; 2 to several small scales present at the node, inside the leaf sheaths. *Inflorescences* indeterminate, terminal and axillary, *spikelike* and elevated above or lying on water's surface. Flowers bisexual, radial, *not associated with bracts* (*at maturity*). Tepals lacking. **Stamens 4, with well-developed appendages at base of anther that form what appears to be a ± fleshy perianth**; pollen grains without functional aperture, globose to ellipsoid. **Carpels usually 4**, distinct; *ovaries superior, with ± basal to apical placentation*; stigma 1, truncate to capitate. *Ovule 1*, ± anatropous to orthotropous. Nectaries lacking. *Fruit a cluster of achenes or occasionally drupes*; endosperm lacking.

Floral formula:

*, -0-, 4 (appendaged), $\underline{4}$; achenes, drupes

Distribution and ecology: Cosmopolitan; herbs of lakes, rivers, and other wetland habitats.

Genera/species: 4/100. ***Major genera:*** *Potamogeton* (90 spp.) and *Coleogeton* (6); both occur in North America.

Economic plants and products: Although the family is of little direct economic importance, many species provide wildlife food.

Discussion: *Ruppia*, a genus of alkaline, brackish, or occasionally salt water, is often placed here, but its inclusion makes the family biphyletic (Les et al. 1997a). Ruppiaceae are characterized by flowers with two stamens that have minute appendages, pollen slightly elongated, and carpels with long stalks.

In *Potamogeton* and *Coleogeton* the flowers are raised above the surface of the water and wind-pollinated, while flowers of *Ruppia* are held at the water surface and are water-pollinated. The fruits are animal- or water-dispersed.

***References*:** Haynes 1978; Les et al. 1997a.

Lilianae

The closely related Liliales, Asparagales, and Dioscoreales together constitute the Lilianae (Dahlgren et al. 1985; Thorne 1992; Chase et al. 1995b), a group often referred to as the petaloid monocots. This group is characterized by flowers with showy tepals (or petals) and endosperm lacking starch. The monophyly of Lilianae has often been questioned (Goldblatt 1995; Stevenson and Loconte 1995; Chase et al. 1995a), but received some support in a recent cladistic analysis based on both DNA and morphological characters (Chase et al. 1995b). The presence of inferior ovaries may be synapomorphic, but frequent reversals to the superior condition have occurred.

Liliales

The monophyly of Liliales is supported by cladistic analyses based on morphology and *rbcL* sequences (Chase et al. 1995a,b; Stevenson and Loconte 1995; Goldblatt 1995). The order is here circumscribed on the basis of the phylogenetic analyses of Chase et al. (1995b). Synapomorphies supporting this group include nectaries mostly on the base of tepals or filaments, extrorse anthers, and the frequent presence of spots on the tepals. The outer epidermis of the seed coat has a cellular structure and lacks phytomelan (a black crust); the inner part of the seed coat also has cellular structure (both plesiomorphies).

Key to Major Families of Liliales

1. Vines, climbing by paired stipular tendrils at the base of the petiole .... **Smilacaceae**
1. Herbs, not climbing, and lacking tendrils 2
2. Ovary inferior; leaves usually twisted at base .... Alstroemeriaceae
2. Ovary superior; leaves not twisted at base 3
3. Bulbs present........ 4
3. Rhizomes or corms present 6
4. Capsule loculicidal; megagametophyte of *Fritillaria* type (egg, synergids, and one polar nucleus haploid, antipodals and second polar nucleus triploid) .... **Liliaceae**
4. Capsule septicidal or ventricidal; megagametophyte of *Polygonum* type (all cells haploid) 5
5. Capsules with carpel units splitting apart and their ventral margins separating; flowers usually small, tepals not spotted; anther locules confluent .... **Melanthiaceae**
5. Capsules septicidal; flowers large, tepals often with spots or lines; anther locules not confluent........ Calochortaceae
6. Corms present .... Colchicaceae
6. Rhizomes present........ 7
7. Leaves whorled, with parallel to palmate venation and pinnate secondary veins; perianth of sepals and petals........ **Trilliaceae**
7. Leaves alternate, with ± parallel venation; perianth of tepals 8
8. Inflorescences determinate, usually few-flowered and paniculate, with cymose branching, or reduced to paired or solitary flowers; flowers minute to conspicuous; style 1, but sometimes apically 3-branched .... **Uvulariaceae**
8. Inflorescences indeterminate, simple or compound racemes or spikes; flowers ± minute; styles 3 .... **Melanthiaceae**

It is important to note that the order Liliales and family Liliaceae here are quite narrowly delimited, following Dahlgren et al. (1985) and recent cladistic analyses (see references cited above). The families here treated within Dioscoreales, Asparagales, and Liliales were formerly considered within a more broadly circumscribed Liliales (Cronquist 1981; Thorne 1992). Cronquist (1981) placed most petaloid monocots with six-stamened flowers into a very broadly circumscribed—and clearly polyphyletic—Liliaceae. Others have divided the petaloid monocots with six stamens into Liliaceae, including species with a superior ovary, and Amaryllidaceae, including species with an inferior ovary (Lawrence 1951). This separation is also artificial, separating clearly related genera such as *Agave* and *Yucca* (Agavaceae), *Crinum* (Amaryllidaceae) and *Allium* (Alliaceae), as is discussed in the family treatments. The Liliales include 10 families and ca. 1300 species.

References: Chase et al. 1995a,b; Cronquist 1981; Dahlgren et al. 1985; Goldblatt 1995; Lawrence 1951; Stevenson and Loconte 1995; Thorne 1992.

Liliaceae A. L. de Jussieu
(Lily Family)

Herbs usually with **bulbs and contractile roots**; steroidal saponins often present. Hairs simple. *Leaves alternate or whorled, along stem or in a basal rosette*, simple, entire, *with parallel venation*, sheathing at base; stipules lacking. *Inflorescence* usually determinate, sometimes reduced to a single flower, *terminal*. *Flowers* bisexual, radial to slightly bilateral, *conspicuous*. *Tepals 6, distinct*, imbricate, *petaloid, often with spots or lines*. *Stamens 6*; filaments distinct; pollen grains usually monosulcate. *Carpels 3, connate; ovary superior, with axile placentation*; stigma 1, 3-lobed, or 3, ± elongated and extending along inner face of style branches. Ovules numerous, usually with 1 integument and a ± thin megasporangium; **megagametophyte developing from 4 megaspores** (*Fritillaria* type), with some cells haploid and others triploid. **Nectar produced at base of tepals**. *Fruit a loculicidal capsule*, occasionally a berry; seeds usually flat and disk-shaped, *seed coat not black*; endosperm oily, **its cells pentaploid** (Figure 8.14).

Floral formula: *, -6-, 6, $\underline{3}$; capsule, berry

Distribution and ecology: Widely distributed in temperate regions of the Northern Hemisphere; mainly spring-blooming plants of prairies, mountain meadows, and other open communities.

Genera/species: 13/400. ***Major genera:*** *Fritillaria* (100 spp.), *Gagea* (90), *Tulipa* (80), and *Lilium* (80). Only *Erythronium*, *Medeola*, and *Lilium* occur in the continental United States and/or Canada.

Economic plants and products: *Tulipa* (tulips), *Fritillaria* (fritillary), *Lilium* (lilies), and *Erythronium* (trout lilies, adder's-tongue) are important ornamentals.

Discussion: Liliaceae, as here defined (Dahlgren et al. 1985), are probably monophyletic (Chase et al. 1995a,b). *Medeola* is often placed in Uvulariaceae or Trilliaceae (Dahlgren et al. 1985). *Calochortus* (mariposa lily) is often placed here, but this genus has septicidal capsules and the typical (or *Polygonum*) type of megagametophyte. Analyses based on *rbcL* sequences (Chase et al. 1995a) support placement of this genus in the Calochortaceae (Dahlgren et al. 1985).

Figure 8.14 Liliaceae. *Lilium lancifolium:* (A) leaf (× 1); (B) gynoecium (× 1); (C) ovary, in cross-section (× 5); (D) flowering plant (× 0.3). (From Hutchinson 1973, *The families of flowering plants*, 3rd ed., p. 755.)

The showy flowers of this family are insect-pollinated (especially by bees, wasps, butterflies, and moths); nectar and/or pollen are employed as pollinator rewards. The seeds are dispersed by wind or water.

References: Chase et al. 1995a,b; Dahlgren et al. 1985.

"Uvulariaceae" C. S. Kunth
(Bellflower Family)

Herbs with creeping rhizomes. Hairs simple. *Leaves alternate, along stem or in a basal rosette*, simple, entire, *with parallel venation*, and in *Prosartes* and *Tricyrtis* with clearly reticulate venation between the primary veins, sheathing at base; stipules lacking. *Inflorescences* determinate, but sometimes appearing indeterminate, rarely reduced to a single flower, *terminal*. *Flowers* bisexual, radial, *usually not conspicuous*. *Tepals 6, distinct*, imbricate, *petaloid, sometimes spotted*. Stamens 6; filaments distinct to connate; pollen grains monosulcate. *Carpels 3, connate; ovary superior, with axile placentation*; stigmas 3, ± elongated and extending along inner face of style branches. Ovules ± numerous, with usually 1 integument and a ± thin megasporangium. *Nectar produced at base of tepals*. *Fruit a septicidal or loculicidal capsule*, or sometimes a berry; seeds flat and disklike to globose, *not black*.

Floral formula: *, -6-, 6, $\underline{3}$; capsule, berry

Distribution: Widely distributed, mostly in temperate regions of the Northern Hemisphere.

Genera/species: 9/50. ***Major genera:*** *Disporum* (15 spp.), *Tricyrtis* (11), *Clintonia* (6), *Prosartes* (5), *Uvularia* (5), and *Streptopus* (4). The family is represented in the continental United States and/or Canada by *Clintonia*, *Prosartes*, *Scoliopus*, *Streptopus*, and *Uvularia*.

Economic plants and products: Members of genera such as *Tricyrtis* and *Uvularia* are used as ornamentals.

Discussion: "Uvulariaceae," as delimited by Dahlgren et al. (1985), are probably biphyletic (see Chase et al. 1995a). More study is needed before the group can be definitively restructured, but it seems clear that *Uvularia* and *Disporum* are not very closely related to *Prosartes*, *Scoliopus*, *Streptopus*, and *Tricyrtis* (Shinwari et al. 1994). The former are closely allied to Colchicaceae, while the latter are related to Liliaceae (Chase et al. 1995a). *Scoliopus* has sometimes been placed in the Trilliaceae, and the position of *Clintonia* also is problematic. It may eventually be necessary to segregate the taxa with ascending ovules and three-parted stigmas as the Tricyrtidaceae, or to expand the circumscriptions of Liliaceae and Colchicaceae.

Flowers of "Uvulariaceae" are insect-pollinated, with nectar often providing the pollinator reward.

References: Chase et al. 1995a; Dahlgren et al. 1985; Shinwari et al. 1994.

Trilliaceae Lindley
(Trillium Family)

Herbs with slender to thick and tuberlike rhizomes; vascular bundles of stem usually in 3 rings; roots contractile; steroidal saponins present. Hairs simple. **Leaves whorled (and usually the same number as the sepals)**, simple, entire, sessile, **with ± palmate venation, with primary veins converging, secondary veins pinnate, and higher-order veins forming a distinct reticulum**; stipules lacking. **Inflorescences reduced to a single flower**, terminal. Flowers bisexual, radial, conspicuous, **the perianth differentiated into a calyx and corolla**. Sepals and petals usually 3 or 4, distinct, imbricate. Stamens 6 or 8 (rarely numerous); filaments distinct; pollen grains usually lacking apertures. Carpels 3–10, connate; *ovary superior, usually with axile placentation*; stigmas 3, ± elongate. Ovules numerous in each locule; megagametophyte formed from two megaspore nuclei (*Allium* type). Nectar lacking, produced by base of perianth parts, or in septa of ovary. **Fruit a fleshy capsule or berry; seeds usually arillate**, not black (Figure 8.15).

Floral formula:

*, 3–8, 3–8, 6–16, $\underline{3–8}$; fleshy capsule, berry

Distribution and ecology: Widely distributed in temperate regions of the Northern Hemisphere; mainly herbs of shaded forest habitats.

Genera/species: 1/50; *Trillium*.

Economic plants and products: A few species of *Trillium* are used medicinally or as ornamentals.

Discussion: The haploid chromosome set of Trilliaceae consists of five large chromosomes, and this condition may be an additional synapomorphy of the family. The characters that have been used to distinguish *Paris* (and a couple of other segregate genera) from *Trillium* are inconsistent, and their recognition probably would make *Trillium* paraphyletic (Kato et al. 1995b; Zomlefer 1996). Two large subgenera traditionally recognized within *Trillium* are subg. *Trillium*, with pedicellate flowers, and subg. *Phyllantherum*, with sessile flowers. The pedicellate condition is plesiomorphic, calling the monophyly of subg. *Trillium* into question. Cladistic analyses based on cpDNA restriction sites (Kato et al. 1995a) and morphology (Kawano and Kato 1995) also indicate that subg. *Trillium* is paraphyletic and subg. *Phyllantherum* is monophyletic.

The showy flowers are pollinated by various insects (especially flies, beetles, and bees). Floral visitors to some

Figure 8.15 Trilliaceae. *Paris polyphylla:* note whorled and net-veined leaves and terminal flower with sepals (leaflike structures) and petals (elongate structures) (× 0.75). (From Engler 1889, in Engler and Prantl, *Die naturlichen Pflanzenfamilien*, II (5): p. 83.)

species, however, are infrequent. Both selfing and agamospermy have been documented in the group. Dispersal by ants is characteristic of species producing capsules with arillate seeds, while bird dispersal is likely in those with colorful berries.

References: Dahlgren et al. 1985; Kato et al. 1995a,b; Kawano and Kato 1995; Samejima and Samejima 1987; Zomlefer 1996.

Smilacaceae Ventenat
(Catbrier Family)

Vines, *usually climbing by paired tendrils arising from petiole*, or rarely erect herbs, *often with thick, tuberlike rhizomes*; steroidal saponins present. Hairs simple; prickles often present. **Leaves** alternate, simple, entire to spinose-serrate, **differentiated into a petiole and blade**, **with palmate venation, with primary veins converging, and clearly connected by a reticulum of higher-order veins**, *with a pair of tendrils positioned near petiole base*. *Inflorescences* determinate, *usually umbellate*, terminal or axillary. *Flowers usually unisexual* (*plants dioecious*), radial, and inconspicuous. *Tepals 6*, distinct to slightly connate, imbricate. Stamens usually 6; filaments distinct to slightly connate; *anthers usually unilocular* due to confluence of two locules; pollen grains monosulcate or ± lacking apertures. Carpels 3, connate; ovary superior, usually with axile placentation; stigmas 3, ± elongate. **Ovules 1 or 2 in each locule**, anatropous to orthotropous. Nectar produced at base of tepals and stamens. **Fruit a 1–3-seeded berry**; seeds ± globose, not black (Figure 8.16).

Floral formula: Staminate: *, -6-, 6, 0
Carpellate: *, -6-, 0, 3; berry

Distribution: Widespread in tropical to temperate regions.

Genera/species: 2/317. ***Genera:*** *Smilax* (310 spp.) and *Ripogonium* (7). The family is represented in the continental United States and Canada only by *Smilax*.

Economic plants and products: Several species of *Smilax* are used medicinally; the genus was also the source of the flavoring sarsaparilla. Young stems, berries, and tubers are occasionally eaten.

Discussion: The monophyly of Smilacaceae is supported by morphological data and *rbcL* sequences (Chase et al. 1995a; Judd 1998). The family has often been considered to be related to Dioscoreaceae (Dahlgren et al. 1985), which are also vines with net-veined leaves. However, morphology (Conran 1989) and *rbcL* sequences (Chase et al. 1993, 1995a) support a placement in the Liliales. The family is often more broadly defined (Cronquist 1981), including genera such as *Luzuriaga*, *Petermannia*, and *Philesia*, but it is clear that inclusion of these genera renders the family polyphyletic (Chase et al. 1995a). In contrast, the family is restricted to *Smilax* by Thorne (1992).

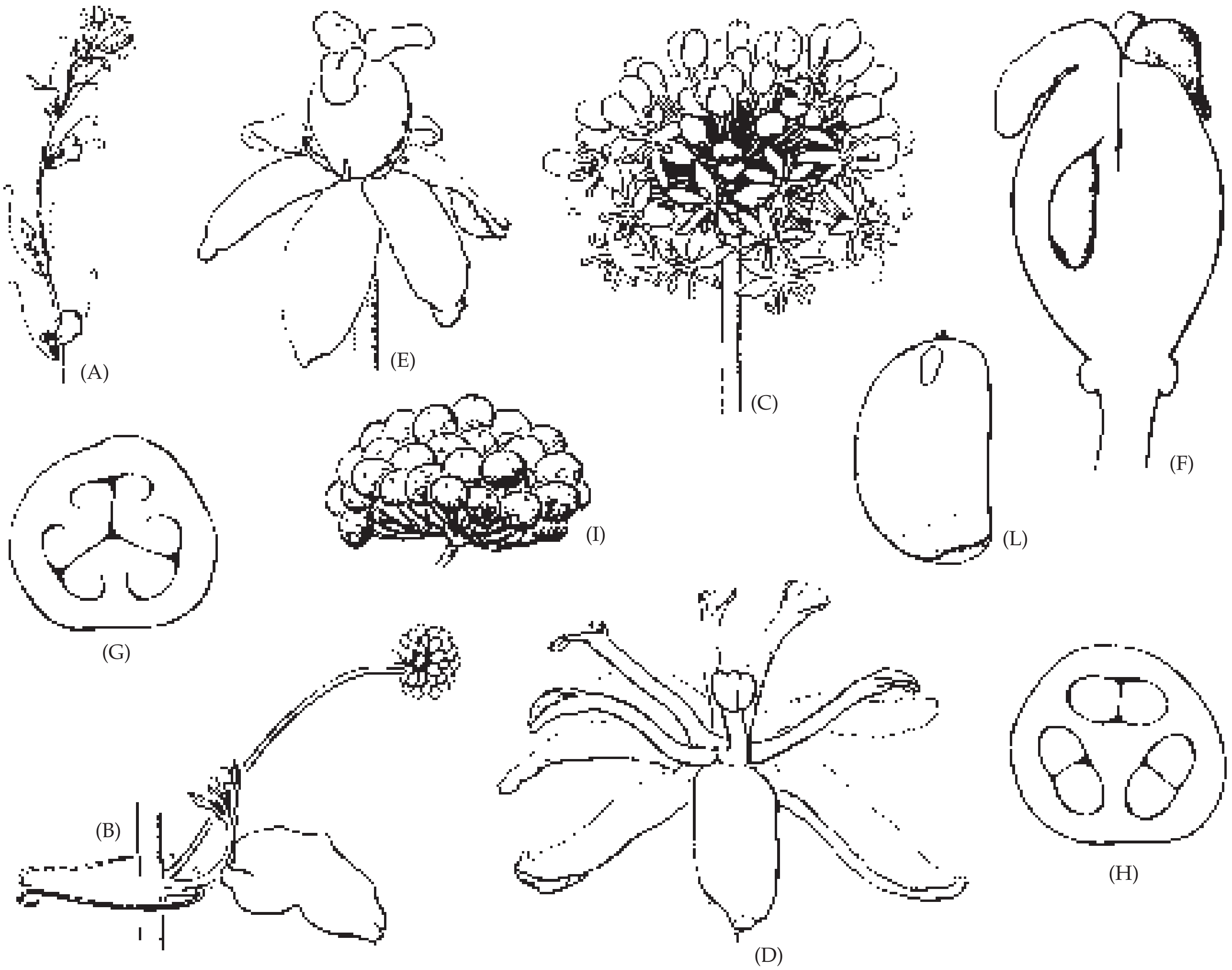
The large genus *Smilax* is clearly monophyletic, as evidenced by the synapomorphies of paired tendrils arising from the petiole, imperfect flowers, anthers with confluent locules, and umbellate inflorescences.

The small flowers of Smilacaceae are pollinated by insects (bees, flies). The fruits are bird-dispersed.

References: Chase et al. 1993, 1995a; Conran 1989; Cronquist 1981; Dahlgren et al. 1985; Judd 1998; Thorne 1992.

Melanthiaceae Batsch
(Death Camas Family)

Herbs **from short to elongate, usually bulblike rhizomes**; steroidal saponins and **various toxic alkaloids present**. Hairs simple. *Leaves* alternate, along stem or in a basal rosette, simple, entire, *with parallel venation*, sheathing at base; stipules lacking. *Inflorescences indeterminate*, terminal. *Flowers* usually bisexual, usually radial, *small*. *Tepals 6*, distinct to slightly connate, imbricate. Stamens 6; filaments distinct; anthers only 2-locular, **the locules usu-**



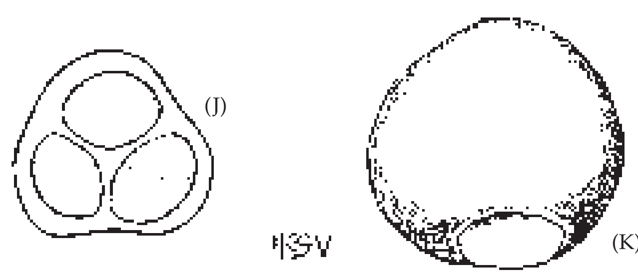


Figure 8.16 Smilacaceae. *Smilax herbacea:* (A) tip of growing stem with developing leaves and inflorescences (× 0.3); (B) node with leaf with two tendrils, young staminate inflorescence, and vegetative shoot (× 0.6); (C) umbellate staminate inflorescence (× 1.25); (D) staminate flower (× 7.5); (E) carpellate flower, note staminodes (× 7.5); (F) gynoecium in longitudinal section (× 15); (G, H) gynoecium in cross-section (× 15); (I) infructescence (× 0.6); (J) berry in cross-section with three seeds, one per locule, the endosperm stippled (× 2.5); (K) seed, showing minute embryo, endosperm stippled (× 6.25). (From Judd 1998, *Harvard Pap. Bot.* 3(2): p. 162.)

ally confluent, opening by a single slit, resulting in a peltate appearance; pollen grains usually monosulcate. Carpels 3, connate; ovary superior to slightly inferior, with axile placentation; *styles 3*; stigmas 3. Ovules 2 to numerous in each locule. Nectaries at base of tepals. **Fruit usually a ventricidal capsule** (carpels splitting apart and their ventral margins separating to release seeds); **seeds flattened, usually winged or appendaged**, not black.

Floral formula: *, 6, 6, $\underline{3}$; capsule

Distribution and ecology: Widely distributed in temperate and/or montane habitats; typically of herb-dominated communities.

Genera/species: 9/100. ***Major genera:*** *Veratrum* (50 spp.), *Zigadenus* (15), *Schoenocaulon* (15), and *Stenanthium* (5). All of the above genera, along with *Xerophyllum*, occur in the continental United States and/or Canada.

Economic plants and products: A few genera, including *Veratrum* and *Zigadenus*, are used as ornamentals; several genera have various medicinal or insecticidal uses (due to their poisonous alkaloids). The leaves of *Xerophyllum* are used for making baskets.

Discussion: The monophyly of Melanthiaceae is problematic; as usually circumscribed (Dahlgren et al. 1985) the group is obviously polyphyletic, as indicated by *rbcL* sequences (Chase et al. 1993, 1995a,b) and morphology (Goldblatt 1995). Phenetic studies confirm the heterogenity of this group (Ambrose 1980). Thus, the family here excludes the tribes Narthecieae and Tofieldieae, which are not at all closely related to the remaining species (Zomlefer 1997a,b,c). Tolfieldiaceae (e.g., *Tofieldia* and *Harperocallis*) are distinct from Melanthiaceae (as here circumscribed) in their 2-ranked, equitant leaves, 2-sulcate pollen, presence of druses in parenchymatous tissues, and stalked ovary. Nartheciaceae (e.g., *Aletris*, *Narthecium*, *Lophiola*) have unusual roots with air spaces in the cortex, a single style, and loculicidal capsules; some also have 2-ranked, equitant leaves. These two families also lack the *Veratrum* alkaloids and flattened to winged seeds characteristic of Melanthiaceae as defined here. *Chionographis*, *Chamaelirium*, and *Xerophyllum* are tentatively included within Melanthiaceae; their inclusion may render the family nonmonophyletic. It is also evident (Chase et al. 1995a) that *Trillium* is closely related to Melanthiaceae, and its treatment as Trilliaceae may make Melanthiaceae paraphyletic.

The small flowers of Melanthiaceae are pollinated by various insects (and possibly also wind). The small seeds are probably wind dispersed.

References: Ambrose 1980; Dahlgren et al. 1985; Chase et al. 1993, 1995a,b; Goldblatt 1995; Zomlefer 1997a,b,c.

Asparagales

The monophyly of Asparagales is supported by cladistic analyses based on morphology, *rbcL*, and *atpB* sequences (Chase et al. 1995a,b; Conran 1989; Rudall et al. 1997; but contrast with Stevenson and Loconte 1995). Supporting characters include their characteristic seeds, which have the outer epidermis of the coat obliterated (in most fleshy-fruited species) or present and with a phytomelan crust (black and carbonaceous) in many dry-fruited species, and with the inner part of the seed coat usually completely collapsed. In contrast, seeds of Liliales always have a well-developed outer epidermis, lack phytomelan, and usually retain a cellular structure in the inner portion of the coat. Asparagales also can be distinguished from Liliales by their usually nonspotted tepals, nectaries in the septa of the ovary (instead of at base of tepals or stamens), and sometimes anomalous secondary growth (vs. lack of secondary growth).

The order consists of about 30 families and about 26,800 species; major families include **Orchidaceae**, Hypoxidaceae, **Iridaceae**, **Amaryllidaceae**, **Alliaceae**, Hyacinthaceae, Lomandraceae, **Agavaceae**, Asparagaceae, **Convallariaceae**, **Asphodelaceae**, and Hemerocallidaceae.

Relationships within the order have been investigated by Dahlgren et al. (1985), Rudall and Cutler (1995), Chase et al. (1995a,b, 1996), Rudall et al. (1997), and Stevenson and Loconte (1995). A paraphyletic basal assemblage, called the "lower" Asparagales, including families such as Orchidaceae, Hypoxidaceae, Iridaceae, Asphodelaceae, and Hemerocallidaceae, is characterized by simultaneous microsporogenesis (the four microspores separate all at once from one another after both meiotic divisions have been completed). In contrast, a specialized clade within the order, called the "higher" Asparagales, including Alliaceae, Amaryllidaceae, Hyacinthaceae, Agavaceae, Asparagaceae, and Convallariaceae, has successive microsporogenesis. In these families a cell plate is laid down immediately after the first meiotic division and another in each of the daughter cells after the second meiotic division (Dahlgren and Clifford 1982).

Within "lower" Asparagales, Orchidaceae are probably related to Hypoxidaceae, while Hemerocallidaceae may be close to Asphodelaceae. Within "higher" Asparagales, Alliaceae, Amaryllidaceae, and Hyacinthaceae may form a clade, based on their bulbous rootstock and scapose inflorescences. Alliaceae and Amaryllidaceae are sister families, and both have umbellate inflorescences. These relationships receive support from *rbcL* sequences. Convallariaceae and Asparagaceae may be related, as evidenced by their indehiscent, usually fleshy fruits; this relationship receives preliminary support from some analyses of *rbcL* sequences (Chase et al. 1995a,b, 1996) but not others (Rudall et al. 1997).

References: Chase et al. 1995a,b, 1996; Conran 1989; Dahlgren et al. 1995; Dahlgren and Clifford 1982; Rudall et al. 1996; Rudall and Cutler 1995; Stevenson and Loconte 1995; Tomlinson and Zimmerman 1969; Zomlefer 1998.

Convallariaceae P. Horaninow

(Lily of the Valley Family)

Rhizomatous herbs to trees; stems sometimes with anomalous secondary growth, sometimes with resin canals; steroidal saponins present. Hairs simple. *Leaves* usually alternate, along stem or in a basal rosette, simple, entire, *with parallel venation*, occasionally petiolate, sheathing at base; stipules lacking. Inflorescences determinate, sometimes reduced to a single flower, terminal or axillary. *Flowers* bisexual, radial, *usually small*. *Tepals* (4) 6, *distinct, or more commonly connate and perianth then urn-shaped to bell-shaped, or wheel-shaped*, petaloid, *not spotted*, imbricate. *Stamens* (4) 6; filaments distinct or occasionally connate, often adnate to tepals; pollen grains monosulcate or lacking an aperture. *Carpels* (2) *3, connate; ovary usually superior, with axile placentation*; stigma 1, capitate to 3-lobed. *Nectaries in septa of ovary*. Ovules 2 to few in each locule, anatropous to orthotropous. *Fruit usually a few-seeded berry*; seeds ± globose, **seed coat** with outer epidermis lacking cellular structure, and **lacking phytomelan** (black crust), and inner layers collapsed (Figure 8.17).

Floral formula:

*, 6, 6, $\underline{3}$; berry, or dry 3-angled and nutlike

Key to Major Families of Asparagales

1. Ovary inferior 2
1. Ovary superior 6
2. Stamens adnate to style, usually only 1 or 2; one perianth member highly modified, forming a lip; seeds lacking endosperm; placentation usually parietal .... **Orchidaceae**
2. Stamens not fused to style, usually 3 or 6; all perianth parts alike or 3 outer ± differentiated from 3 inner; seeds with endosperm; placentation usually axile 3
3. Stamens 3; leaves equitant; seed coat not black, with cellular structure .... **Iridaceae**
3. Stamens 6; leaves not equitant; seed coat with outer epidermis obliterated, or present and with black crust 4
4. Inflorescences scapose, umbellate (or reduced to a solitary flower); plants from a bulb, with contractile roots .... **Amaryllidaceae**
4. Inflorescences paniculate, racemose, fasciculate, or reduced to a solitary flower, usually not scapose; plants from a rhizome or corm, the roots contractile or not 5
5. Plants with fleshy rosettes of fibrous leaves; karyotype dimorphic, of 5 large and 25 small chromosomes; nectaries in the septa of the ovary; roots not contractile .... **Agavaceae** (subfam. Agavoideae)
5. Plants nonsucculent, leaves thin-textured and not strongly fibrous; karyotype not dimorphic; nectaries lacking; roots usually contractile .... Hypoxidaceae
6. Fruit fleshy, a berry 7
6. Fruit dry, hard or leathery, usually a capsule, or triangular and nutlike 8
7. Leaves rudimentary, forming small scales; plants with cylindrical to flattened green cladodes; seeds black .... Asparagaceae
7. Leaves ± large and photosynthetic; stems cylindrical, green to brown, but not the major photosynthetic organ of the plant; seeds not black .... **Convallariaceae** (various herbaceous genera, along with ± woody plants, i.e., subfam. Dracaenoideae)
8. Seeds not black; guard cells rich in oil; fruits dry, triangular, and nutlike .... **Convallariaceae** (subfam. Nolinoideae)
8. Seeds black (with phytomelan); guard cells lacking oil; fruits various, but usually capsules and never as above 9
9. Plants from a bulb; inflorescence scapose (atop an elongate internode) 10
9. Plants from a rhizome; inflorescence usually not scapose 11
10. Inflorescence umbellate; plants usually with an onion or garlic smell .... **Alliaceae**
10. Inflorescence with an axis; plants without an onion or garlic smell .... Hyacinthaceae
11. Plants with woody trunk (or rhizome) and strongly fibrous leaves; anthers small in relation to filaments; chromosomes dimorphic (5 large and 25 small) .... **Agavaceae** (subfam. Yuccoideae)
11. Plants with or without a woody trunk; leaves not strongly fibrous; anthers not small; chromosomes more uniform in size 12
12. Pollen monosulcate; inflorescences indeterminate, forming simple or compound racemes or spikes; seeds usually arillate; leaves usually succulent, often having conspicuous gelatinous central zone, and often with colored sap produced by specialized cells associated with vascular bundles of leaves; filaments free from tepals .... **Asphodelaceae**
12. Pollen trichotomosulcate, with Y-shaped aperture; or if monosulcate then inflorescences determinate, forming scorpioid cymes; seeds not arillate; leaves thin, lacking gelatinous zone and colored sap; filaments ± adnate to tepals .... Hemerocallidaceae [incl. Phormiaceae]

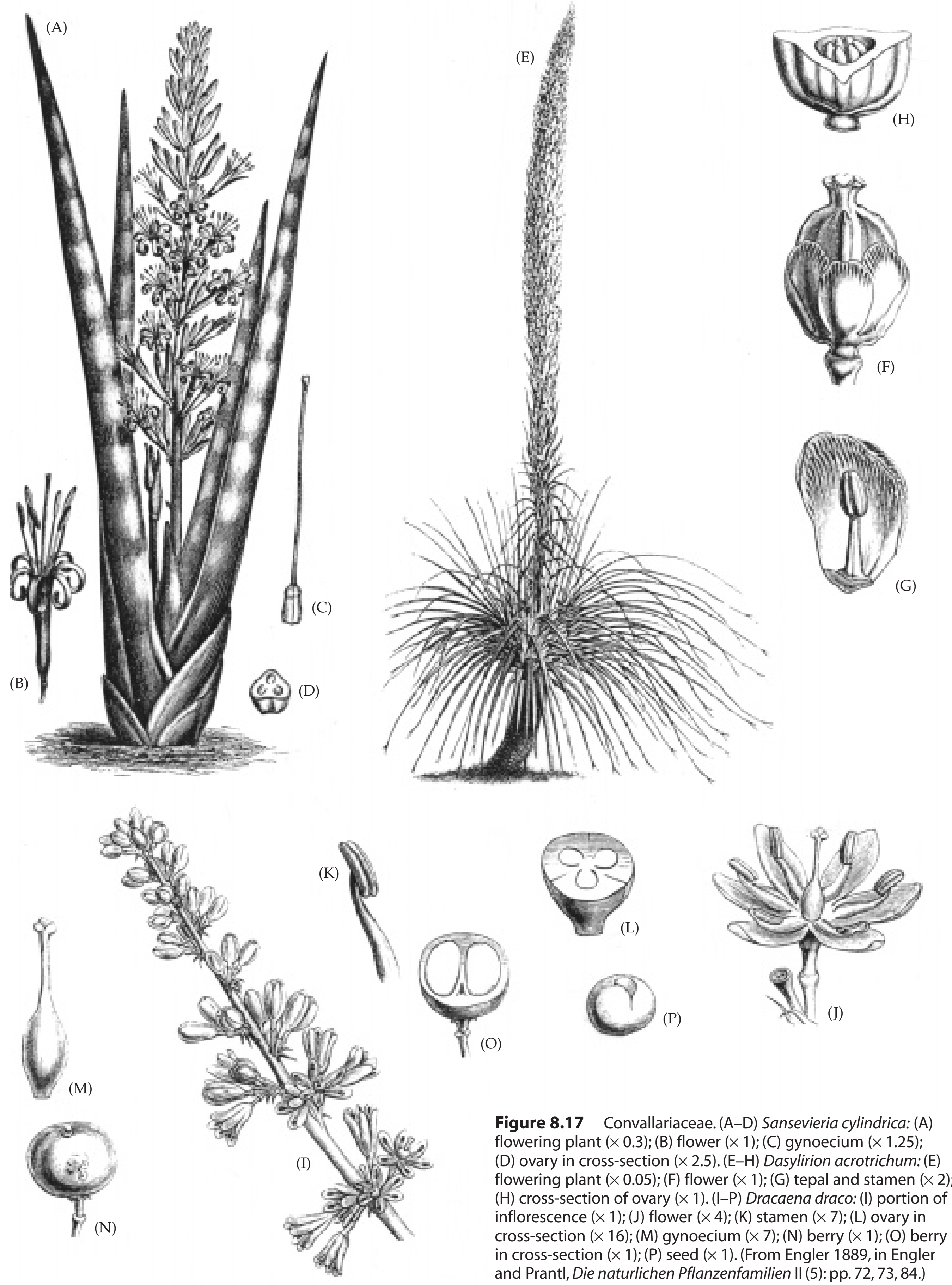


Figure 8.17 Convallariaceae. (A–D) *Sansevieria cylindrica:* (A) flowering plant (× 0.3); (B) flower (× 1); (C) gynoecium (× 1.25); (D) ovary in cross-section (× 2.5). (E–H) *Dasylirion acrotrichum:* (E) flowering plant (× 0.05); (F) flower (× 1); (G) tepal and stamen (× 2); (H) cross-section of ovary (× 1). (I–P) *Dracaena draco:* (I) portion of inflorescence (× 1); (J) flower (× 4); (K) stamen (× 7); (L) ovary in cross-section (× 16); (M) gynoecium (× 7); (N) berry (× 1); (O) berry in cross-section (× 1); (P) seed (× 1). (From Engler 1889, in Engler and Prantl, *Die naturlichen Pflanzenfamilien* II (5): pp. 72, 73, 84.)

Distribution and ecology: Widely distributed from temperate to tropical regions; herbaceous species often understory herbs of moist forests and woody species often of arid regions.

Genera/species: 24/300. ***Major genera:*** *Dracaena* (80 spp.), *Polygonatum* (50), *Sansevieria* (50), *Maianthemum* (33), *Ophiopogon* (30), and *Nolina* (25). The family is represented in the continental United States and/or Canada by *Convallaria*, *Maianthemum*, *Polygonatum*, *Nolina*, *Dasylirion*, and *Sansevieria*.

Economic plants and products: Several genera, including *Aspidistra* (cast-iron plant), *Convallaria* (lily of the valley), *Dracaena* (dragon tree), *Liriope* (border grass), *Maianthemum* (false Solomon's seal), *Polygonatum* (Solomon's seal), *Ophiopogon* (mondo grass), and *Sansevieria* (mother-in-law's tongue) are used as ornamentals.

Discussion: Convallariaceae are broadly circumscribed, including Nolinaceae, Ruscaceae, and Dracaenaceae, as suggested by Chase et al. (1995a, 1996) and Rudall et al. (1997). The monophyly of the family is supported by *rbcL* and ITS sequences (Chase et al. 1995a; Bogler and Simpson 1995, 1996; Rudall et al. 1997) and the lack of phytomelan in their seeds. Convallariaceae s. l. may be sister to Asparagaceae (Chase et al. 1995a, 1996; Bogler and Simpson 1996), the latter comprising the single genus *Asparagus*. These two families can easily be differentiated because the former almost always have foliaceous leaves and seeds lacking phytomelan, while the latter have reduced, scale-like leaves and cylindrical to flattened stems that function as the major photosynthetic organs and seeds with phytomelan. Both families have few-seeded berries, a possible synapomorphy.

Herbaceous members of Convallariaceae form a paraphyletic complex (Conran 1989; Bogler and Simpson 1996; Chase, personal communication) that is closely related to two woody clades, the Nolinoideae (*Nolina*, *Dasylirion*, and *Beaucarnia*) and the Dracaenoideae (*Dracaena* and *Sansevieria*) (Chase et al. 1995a, 1996; Bogler and Simpson 1995, 1996). The monophyly of the *Nolina* group is supported by their dry, three-angled, and nut-like fruits, and by leaves with minute longitudinal ridges and guard cells containing large amounts of oil. The monophyly of the *Dracaena* group is supported by resin canals in their leaves and bark, which thus frequently stain dark red or orange-red.

The small flowers of most Convallariaceae are insect-pollinated, especially by bees and wasps, which gather nectar or pollen. Their colorful berries usually are dispersed by birds. The dry, angular fruits of *Nolina* and relatives are wind-dispersed.

References: Bogler and Simpson 1995, 1996; Chase et al. 1995a, 1996; Conran 1989; Dahlgren et al. 1995; Rudall et al. 1996.

Asphodelaceae A. L. de Jussieu
(Aloe Family)

Rhizomatous herbs to trees or shrubs; stems often with anomalous secondary growth; **anthraquinones present**. Hairs simple. *Leaves* alternate, *in rosettes at base or ends of branches*, simple, *often succulent, entire to spinose-serrate*, with parallel venation; *often with vascular bundles* (*as seen in cross-section*) *arranged in a ring around central mucilaginous parenchyma tissue, with a cap of aloine cells at the phloem pole of most vascular bundles, these containing colored secretions* **and accumulating anthraquinones**, not fibrous; sheathing at base; stipules lacking. Inflorescences indeterminate, terminal, but sometimes appearing lateral. Flowers usually bisexual, radial to bilateral, often showy. *Tepals 6, distinct to strongly connate* (perianth then ± tubular), imbricate, *petaloid, not spotted*. *Stamens 6*; filaments distinct; pollen grains monosulcate. *Carpels 3, connate; ovary superior*, with axile placentation; stigma 1, ± minute to discoid or slightly 3-lobed. Ovules 2 to numerous in each locule, anatropous to nearly orthotropous. *Nectaries in septa of ovary*. *Fruit a loculicidal capsule*; seeds usually with dry aril, often flattened or winged, *the seed coat with phytomelan* (*a black crust*) and inner layers ± collapsed.

Floral formula: * or X, 6, 6, $\underline{3}$; capsule

Distribution and ecology: Distributed in temperate to tropical regions of the Old World, and especially diverse in southern Africa; usually in arid habitats.

Genera/species: 15/750. ***Major genera:*** *Aloe* (380 spp.), *Haworthia* (70), *Kniphofia* (70), and *Bulbine* (60). The family is represented in the continental United States only by two introduced taxa of *Aloe* (in southern Florida and California).

Economic plants and products: Several species of *Aloe* are used medicinally or in cosmetics; members of several genera, including *Aloe*, *Haworthia*, *Gasteria*, *Kniphofia*, and *Bulbine*, are used as ornamentals.

Discussion: The monophyly of Asphodelaceae is supported by *rbcL* sequences (Chase et al. 1995a; de Bruijn et al. 1995), presence of anthraquinones, and possibly the base chromosome number of seven. Asphodelaceae are usually divided into two subfamilies (Dahlgren et al. 1985): the surely paraphyletic "Asphodeloideae" (including genera such as *Bulbine*, *Kniphofia*, and *Asphodelus*) and the specialized and clearly monophyletic Alooideae (including genera such as *Aloe*, *Gasteria*, and *Haworthia*). Synapomorphies for Alooideae include the distinctive leaves with a central gelatinous zone surrounded by vascular bundles associated with aloine cells and distinctive dimorphic karyotype (Smith and Van Wyk 1991).

The colorful flowers of Asphodelaceae are pollinated by various insects as well as birds. The seeds are mainly dispersed by wind.

References: Chase et al. 1995a; Dahlgren et al. 1985; de Bruijn et al. 1995; Judd 1997a; Smith and Van Wyk 1991.

Agavaceae S. L. Endlicher
(Agave Family)

Usually *large rosette herbs, trees, or shrubs*, rhizomatous; stems with **anomalous secondary growth**; raphidelike crystals of calcium oxalate present; steroidal saponins present. Hairs simple. *Leaves* alternate, *in rosettes at base or ends of branches*, simple, succulent, entire to spinose-serrate, and *usually with a sharp spine at apex*, with parallel venation, **the vascular bundles associated with thick and tough fibers**, sheathing at base; stipules lacking. Inflorescences determinate, *usually paniculate*, terminal. Flowers usually bisexual, radial to slightly bilateral, often showy. *Tepals 6, distinct to connate*, and perianth then tubular to bell-shaped, imbricate, *petaloid, not spotted* (*and usually white to yellow*). *Stamens 6*; filaments distinct, sometimes adnate to the perianth; pollen grains monosulcate. *Carpels 3, connate; ovary superior or inferior*, with axile placentation; stigma minute, capitate to 3-lobed. Ovules ± numerous in each locule. *Nectaries in septa of ovary*. *Fruit a loculicidal capsule*, but sometimes fleshy and berrylike; *seeds flat, the seed coat with black crust* (*phytomelan*) and inner layers ± collapsed; **karyotype of 5 large and 25 small chromosomes**.

Floral formula: * or X, 6, 6, $\overline{\underline{3}}$; capsule

Distribution and ecology: Widely distributed in warm temperate to tropical regions of the New World, and especially diverse in Mexico, but introduced in Old World; characteristic of arid and semiarid habitats.

Genera/species: 9/300. ***Major genera:*** *Agave* (250 spp.) and *Yucca* (40). The family is represented in the continental United States and/or Canada by *Agave*, *Furcraea*, *Hesperoaloe*, *Hesperoyucca*, *Manfreda*, and *Yucca*.

Economic plants and products: Several species of *Agave* (sisal hemp), *Furcraea*, and *Yucca* are used as fiber sources, and a few species of *Agave* are fermented to produce tequila and mescal. Both *Agave* and *Yucca* are used in the manufacture of oral contraceptives (due to their steroidal saponins). Finally, several genera, including *Agave* (century plant), *Manfreda*, *Polianthes*, and *Yucca*, are used as ornamentals.

Discussion: Both phenotypic and DNA characters support the family's monophyly (Bogler and Simpson 1995, 1996). *Camassia* and *Chlorogalum* (Hyacinthaceae) and *Hosta* (Hostaceae) are also closely related (Chase et al. 1995a; Bogler and Simpson 1995, 1996). *Hosta* is a genus of rhizomatous herbs with broad-bladed leaves with prominent parallel veins, one-sided racemes of lilylike flowers, and black-seeded capsules. These three genera also have a distinctive bimodal karyotype. All three genera should be transferred to the Agavaceae (Rudall et al. 1997).

Agavaceae usually are divided into the Yuccoideae (e.g., *Yucca*, *Hesperoaloe*, *Hesperoyucca*), with a superior ovary and reduced anthers, and the Agavoideae (e.g., *Agave*, *Furcraea*, *Manfreda*, *Polianthes*), with an inferior ovary and nonreduced anthers (Dahlgren et al. 1985); both are monophyletic (Bogler and Simpson 1995, 1996). The family often is more broadly circumscribed (Cronquist 1981), including genera that are here considered in Convallariaceae (*Nolina*, *Dasylirion*, *Beaucarnia*, *Dracaena*, and *Sansevieria*) and Lomandraceae (*Cordyline*). Such a broadly defined family is morphologically heterogeneous, unified only by the woody habit, and clearly polyphyletic (Dahlgren et al. 1985; Chase et al. 1995a,b; Bolger and Simpson 1995, 1996; Rudall et al. 1997).

The showy flowers of *Yucca* and *Hesperoyucca* are visited by small moths of the genus *Tegeticula* (see Figure 4.23). Other genera of Agavaceae are pollinated by birds (many species of *Beschornea*) or bats (several species of *Agave*). The black seeds are typically dispersed by wind, and fleshy-fruited species are dispersed by animals.

References: Baker 1986; Bogler and Simpson 1995; Chase et al. 1995a,b; Cronquist 1981; Dahlgren et al. 1985; McKelvey and Sax 1933; Rudall et al. 1997.

Alliaceae J. G. Agardh
(Onion Family)

Herbs with a bulb and contractile roots (or in *Tulbaghia*, a rhizome); stems reduced; **vessel elements with simple perforations; laticifers present (and latex ± clear)**; with steroidal saponins; **with onion- or garlic-scented sulfur compounds such as allyl sulphides, propionaldehyde, propionthiol, and vinyl disulphide**. Hairs simple. Leaves alternate, ± basal, simple, terete, angular, or flat, entire, with parallel venation, sheathing at base; stipules lacking. *Inflorescences* determinate, composed of one or more contracted helicoid cymes and *appearing to be an umbel, subtended by a few membranous spathelike bracts, terminal, at the end of a long scape*. Flowers bisexual, radial or bilateral, often showy; **individual flowers not associated with bracts**. *Tepals 6, distinct to connate*, and perianth then bell-shaped to tubular, imbricate, *petaloid, not spotted*; a corona (outgrowth of the perianth) sometimes present. *Stamens 6* (3); filaments distinct to connate, sometimes adnate to tepals, sometimes appendaged; pollen grains monosulcate. *Carpels 3, connate; ovary superior*, with axile placentation; stigma 1, capitate to 3-lobed. Ovules 2 to numerous in each locule, anatropous to campylotropous. *Nectaries in septa of ovary*. *Fruit a loculicidal capsule; seeds* globose to angular, *the seed coat with phytomelan* and inner layers compressed or collapsed; embryo ± curved.

Floral formula: * or X,-6-,6,3; capsule

Distribution and ecology: Widely distributed in temperate to tropical regions; frequently in semiarid habitats.

Genera/species: 19/645. ***Major genera:*** *Allium* (550 spp.), *Ipheion* (25), and *Tulbaghia* (24). The family is represented in the continental United States and/or Canada by *Allium* and *Nothoscordum*.

Economic plants and products: Several species of *Allium* (garlic, onions, shallots, chives, leeks, ramps) are important vegetables or flavorings. Their sap is mildly antiseptic, and several are used medicinally. A few genera, including *Allium*, *Gilliesia*, *Ipheion*, and *Tulbaghia* (society garlic), are used as ornamentals.

Discussion: The monophyly of Alliaceae is supported by morphology, chemistry, and *rbcL* sequences (Fay and Chase 1996). Alliaceae are closely related to Amaryllidaceae. Both families are bulbous herbs with terminal umbellate inflorescences, which are subtended by spathaceous bracts and borne on a conspicuous scape; all of these features are probably synapomorphic. Cladistic analyses support the sister group relationship of these two families (Chase et al. 1995a,b; Fay and Chase 1996; Rudall et al. 1996). Alliaceae sometimes have been included within Amaryllidaceae (Hutchinson 1934, 1973).

The Themidaceae, which are herbs from corms and include *Dichellostema*, *Triteleia*, and *Brodiaea*, are usually placed within Alliaceae. Recent cladistic analyses have indicated that these genera are more closely related to Hyacinthaceae than to typical Alliaceae (Chase et al. 1995a; Fay and Chase 1996; Rudall et al. 1997). Embryological characters do not support a close relationship between Alliaceae and Themidaceae (Berg 1996). *Agapanthus* also has traditionally been included here, but it lacks the sulfur-containing compounds, and *rbcL* sequences do not support its placement in Alliaceae (Chase et al. 1995a). It is best placed in its own family, Agapanthaceae.

The showy flowers of Alliaceae are pollinated by a variety of insects (especially bees and wasps). The seeds are predominantly wind- or water-dispersed. A few species produce bulblets in the inflorescence.

References: Berg 1996; Chase et al. 1995a,b; Dahlgren et al. 1985; Fay and Chase 1996; Hutchinson 1934, 1973; Mann 1959; Rudall et al. 1997.

Amaryllidaceae J. St. Hilaire
(Amaryllis or Daffodil Family)

Herbs from a bulb with contractile roots; stems reduced; vessel elements with scalariform perforations; **characteristic "amaryllis" alkaloids present**. Hairs simple. Leaves alternate, ± basal, simple, flat, entire, with parallel venation, sometimes differentiated into a blade and petiole, sheathing at base; stipules lacking. *Inflorescences* determinate, composed of one or more contracted helicoid cymes, and *appearing to be an umbel*, sometimes reduced to a single flower, *subtended by a few membranous spathe-like bracts, terminal, on a long scape*. *Flowers* bisexual, radial to bilateral, *showy, each associated with a filiform bract*. *Tepals 6, distinct to connate*, imbricate, *petaloid, not spotted*; a corona (outgrowth of the perianth) sometimes present. *Stamens 6*; filaments distinct to connate, sometimes adnate to the perianth, sometimes appendaged (and forming a staminal corona); pollen grains monosulcate or bisulcate. *Carpels 3, connate;* **ovary inferior**, with axile placentation; stigma 1, minute to capitate or 3-lobed. Ovules ± numerous in each locule, sometimes with 1 integument. *Nectaries usually in septa of ovary*. *Fruit a loculicidal capsule* or occasionally a berry; seeds dry to fleshy, flattened to globose, and sometimes winged, *the seed coat usually with black or blue crust*, phytomelan sometimes lacking and outer epidermis then lacking cellular structure, inner layers also ± collapsed; embryo sometimes curved (Figure 8.18).

Floral formula: * or X,-6-,6,$\overline{3}$; capsule

Distribution: Widely distributed from temperate to tropical regions, and especially diverse in South Africa, Andean South America, and the Mediterranean region.

Genera/species: 50/870. ***Major genera:*** *Crinum* (130 spp.), *Hippeastrum* (70), *Zephyranthes* (60), *Hymenocallis* (50), *Cyrtanthus* (50), *Haemanthus* (40), and *Narcissus* (30). Common genera of the continental United States and/or Canada include *Crinum*, *Hymenocallis*, *Narcissus*, and *Zephyranthes*.

Economic plants and products: The family includes numerous ornamental genera: *Crinum* (crinum lily), *Eucharis* (Amazon lily), *Galanthus* (snowdrops), *Haemanthus* (blood lily), *Hippeastrum* (amaryllis), *Hymenocallis* (spider lily), *Narcissus* (daffodil, jonquil), *Zephyranthes* (rain lily, zephyr lily), *Cyrtanthus* (kaffir lily), *Amaryllis* (Cape belladonna), and *Nerine* (Guernsey lily).

Discussion: The monophyly of Amaryllidaceae is supported by secondary chemistry (amaryllid alkaloids), the inferior ovary, and *rbcL* sequences (Chase et al. 1995a). Tribal characterizations within the family are provided by Meerow (1995), Dahlgren et al. (1985), and Traub (1957, 1963).

The showy flowers of Amaryllidaceae are pollinated by bees, wasps, butterflies, moths, and birds; most are outcrossing, but selfing also occurs. The seeds are usually wind- or water-dispersed, but some taxa, such as *Eucharis* subg. *Eucharis*, have blue seeds that contrast

Figure 8.18 Amaryllidaceae. *Crinum kirkii:* (A) habit (× 0.2); (B) flower (× 0.5). (From Pax and Hoffman 1930, in Engler and Prantl, *Die naturlichen Pflanzenfamilien,* 2nd ed., p. 408.)

with bright orange capsules, leading to dispersal by birds. Large, fleshy seeds lacking phytomelan have evolved several times within the family.

References: Chase et al. 1995a; Dahlgren et al. 1985; Meerow 1995; Traub 1957, 1963.

Iridaceae A. L. de Jussieu
(Iris Family)

Herbs with rhizomes, corms, or bulbs, rarely (achlorophyllous; **styloids (large prismatic crystals) of calcium oxalate usually present in sheaths of vascular bundles**; tannins and/or various terpenoids often present. Hairs simple. *Leaves alternate, 2-ranked*, **usually equitant (oriented edgewise to the stem), and with a unifacial blade**, along the stem to basal, simple, entire, with parallel venation, sheathing at base; stipules lacking. **Inflorescences determinate, a scorpioid cyme, often highly modified**, sometimes reduced to a single flower, terminal. Flowers bisexual, radial to bilateral, conspicuous, subtended individually by 1 or 2 bracts. *Tepals 6*, the outer sometimes differentiated from the inner, distinct or connate, imbricate, *petaloid, sometimes spotted*. **Stamens** (2) **3**; filaments distinct or connate, sometimes adnate to the perianth; anthers sometimes sticking to style branches; pollen grains usually monosulcate. *Carpels 3, connate; ovary usually inferior, with axile placentation*; style branches sometimes expanded and petaloid; stigmas (2) 3, terminal or on abaxial surface of style branches. Ovules few to numerous in each locule, anatropous or campylotropous. Nectaries in septa of ovary, on the tepals, or lacking. *Fruit a loculicidal capsule*; seeds sometimes arillate or with fleshy *seed coat*, the coat usually with cellular structure and *brown* (*black crust lacking*) (Figure 8.19).

Floral formula: * or X, 6, 3, $\overline{3}$; capsule

Distribution: Widely distributed.

Genera/species: 78/1750. ***Major genera:*** *Gladiolus* (255 spp.), *Iris* (250), *Moraea* (125), *Sisyrinchium* (100), *Romulea* (90), *Crocus* (80), *Geissorhiza* (80), *Babiana* (65), and *Hesperantha* (65). Noteworthy genera occurring in the continen-

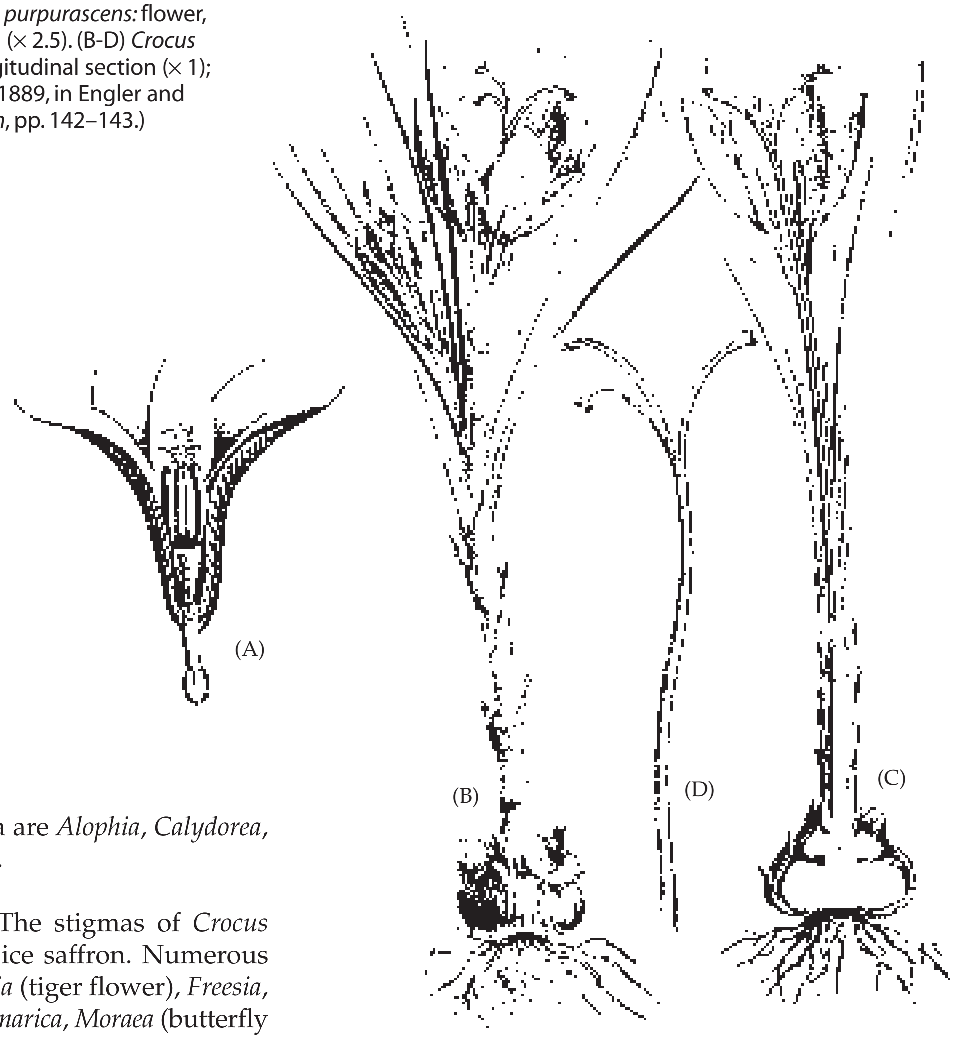


Figure 8.19 Iridaceae. (A) *Romulea purpurascens:* flower, note inferior ovary and three stamens (× 2.5). (B-D) *Crocus sativus:* (B) habit (× 1); (C) plant in longitudinal section (× 1); (D) style and stigmas (× 2). (From Pax 1889, in Engler and Prantl, *Die naturlichen Pflanzenfamilien*, pp. 142–143.)

tal United States and/or Canada are *Alophia*, *Calydorea*, *Iris*, *Nemastylis*, and *Sisyrinchium*.

Economic plants and products: The stigmas of *Crocus sativus* are the source of the spice saffron. Numerous genera, including *Crocus*, *Tigridia* (tiger flower), *Freesia*, *Iris*, *Ixia* (corn lily), *Romulea*, *Neomarica*, *Moraea* (butterfly lily), *Nemastylis*, *Belamcanda*, *Sisyrinchium* (blue-eyed grass), *Gladiolus*, *Crocosmia*, and *Trimezia*, are used as ornamentals.

Discussion: Cladistic analyses based on morphology and *rbcL* sequences support the monophyly of Iridaceae (Goldblatt 1990; Rudall 1994; Chase et al. 1995a). The phylogenetic position of Iridaceae is somewhat uncertain. Morphological characters (Stevenson and Loconte 1995; Chase et al. 1995b) place the family within Liliales, while *rbcL* sequences place it within Asparagales (Chase et al. 1995a). Chloroplast DNA and morphology together placed the family within Asparagales, and therefore we tentatively consider the family to be a fairly basal member of this order.

Several major clades (often recognized as subfamilies) are evident within Iridaceae (Goldblatt 1990; Rudall 1994). The Isophysidoideae, including only *Isophysis*, is distinguished by a superior ovary. The Nivenioideae (including *Aristea* and relatives) share the apomorphy of blue flowers; some members of this subfamily are shrubby. Iridoideae have flowers that last only a single day; they can be recognized by the presence of nectaries on the tepals and by their very long style branches, divided below the level of the anthers, with conduplicate margins so that each branch is stigmatic only apically. The group also contains the free amino acids meta-carboxyphenylalanine and glycine. Several subclades are evident within Iridoideae, including the Sisyrincheae (style branches alternating with stamens vs. opposite them in other members of subfamily; *Sisyrinchium* and relatives) and a clade comprising Irideae, Mariceae, and Tigrideae (tepals differentiated into a limb and claw, upper apices of the style branches with petaloid appendages; e.g., *Iris*, *Belamcanda*, *Moraea*, *Nemastylis*, *Trimezia*, and *Tigridia*). Finally, Ixioideae (e.g., *Ixia*, *Crocosmia*, *Geissorhiza*, *Crocus*, *Romulea*, *Freesia*, *Gladiolus*, and *Hesperantha*) are hypothesized to be monophyletic based on their connate tepals, corms, sessile flowers, operculate pollen with micropunctate exine, and closed leaf sheaths. This group retains the ancestral feature of septal nectaries.

The showy flowers of Iridaceae are mainly insect-pollinated (especially by bees and flies), but some species are pollinated by birds. The seeds usually are dispersed by wind or water, but biotic dispersal also occurs.

References: Chase et al. 1995a,b; Dahlgren et al. 1985; Goldblatt 1990; Rudall 1994; Stevenson and Loconte 1995.

Orchidaceae A. L. de Jussieu
(Orchid Family)

Terrestrial or epiphytic herbs, or occasionally vines, *with rhizomes, corms, or root-tubers*, occasionally mycoparasitic; *stems often basally thickened and forming pseudobulbs; roots strongly mycorrhizal, often with spongy, water-absorbing epidermis composed of dead cells* (*velamen*). Hairs various. Leaves usually alternate, often plicate, basal or along the stem, sometimes reduced, simple, entire, with usually parallel venation, sheathing at base; stipules lacking. Inflorescences indeterminate, sometimes reduced to a single flower, terminal or axillary. Flowers usually bisexual, **bilateral, usually resupinate (twisted 180° during development)**, often conspicuous, the perianth ± differentiated into a calyx and corolla. Sepals 3, distinct to connate, usually petaloid, imbricate. Petals 3, distinct, sometimes spotted or variously colored, **the median petal clearly differentiated from the 2 laterals, forming a lip (labellum)**, often with fleshy bumps or ridges and of an unusual shape or color pattern, the 2 lateral petals often similar to the sepals. **Stamens usually 1 or 2 (very rarely 3), adnate to style and stigma, forming a column**; pollen usually *grouped into soft or hard masses* (*pollinia*). Carpels 3, connate; *ovary inferior, usually with parietal placentation*, but occasionally axile; style and stigma highly modified, with portion of the latter usually nonreceptive (rostellum), a portion of which may form a sticky pad (viscidium) attached to the pollinia. Ovules numerous, with a thin megasporangium (Figure 8.20). Nectar produced in a lip-spur, by sepal apices, or in septal nectaries, but often lacking. *Fruit a capsule opening by* (1–) *3 or 6 longitudinal slits; seeds minute*, the seed coat crustose or membranous, **lacking phytomelan**, with only the outer layer persisting, the inner tissues collapsed; **embryo very minute; endosperm lacking** (Figure 8.21.)

Floral formula: X, 5+1, 1 or 2, 3; capsule

Distribution and ecology: Widely distributed, but most diverse in tropical regions (where frequently epiphytic).

Genera/species: 775/19,500. ***Major genera:*** *Pleurothallis* (1120 spp.), *Bulbophyllum* (1000), *Dendrobium* (900), *Epidendrum* (800), *Habenaria* (600), *Eria* (500), *Lepanthes* (460), *Maxillaria* (420), *Oncidium* (420), *Masdevallia* (380), *Stelis* (370), *Liparis* (350), *Malaxis* (300), *Oberonia* (300), *Encyclia* (235), *Eulophia* (200), *Angraecum* (200), *Taeniophyllum* (170), *Phreatia* (160), *Polystachya* (150), *Calanthe* (150), *Vanilla* (100), and *Catasetum* (100). The family is represented in the continental United States and/or Canada by numerous genera; some of the more noteworthy include *Bletia*, *Calopogon*, *Calypso*, *Cleistes*, *Corallorhiza*, *Cypripedium*, *Encyclia*, *Epidendrum*, *Goodyera*, *Habenaria*, *Harrisella*, *Hexalectris*, *Liparis*, *Listera*, *Malaxis*, *Oncidium*, *Orchis*, *Platanthera*, *Pogonia*, *Ponthieva*, *Spiranthes*, *Tipularia*, *Triphora*, and *Zeuxine*.

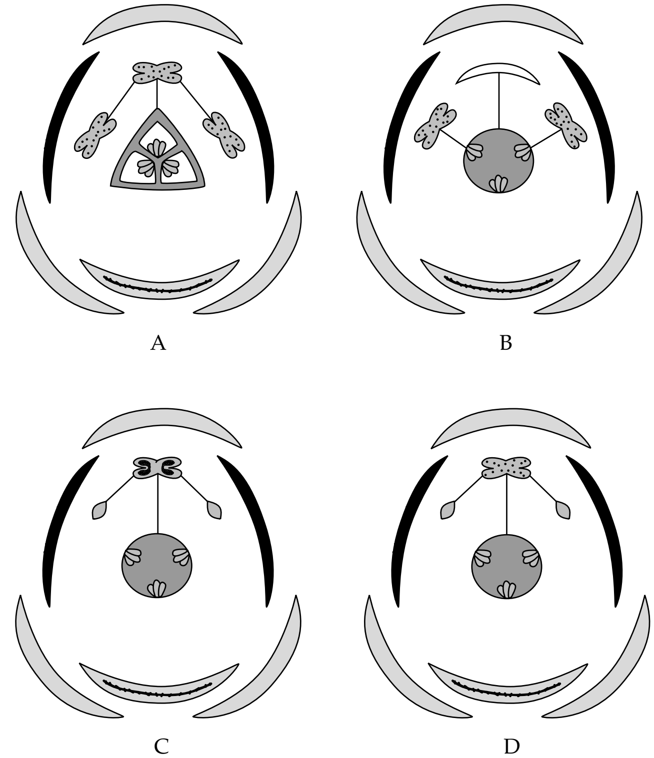


Figure 8.20 Floral diagrams of major groups of Orchidaceae. (A) Apostasioideae. (B) Cypripedioideae. (C) Orchidoideae and Epidendroideae. (D) Vanilloideae. Gray crescents = sepals; black crescents = uppermost petals; bicolored crescents = labellum (or lip petal); stamens are indicated by four-lobed structures, with dots indicating pollen not in pollinia and solid black indicating pollen shed in pollinia. Staminodes indicated by small, open crescent or elliptical structures near stamen(s). Gynoecium indicated by circle or triangle showing placentation type; adnation and connation shown by lines connecting structures. (Modified from Endress 1994 and Dahlgren et al. 1985.)

Economic plants and products: Vanilla flavoring is extracted from the fruits of *Vanilla planifolia*. The family is economically important because of its numerous ornamentals, including *Cattleya* (corsage orchid), *Dendrobium*, *Epidendrum*, *Paphiopedilum* (slipper orchid), *Phalaenopsis*, *Vanda*, *Brassia*, *Cymbidium*, *Laelia*, *Miltonia*, *Oncidium*, *Encyclia*, and *Coelogyne*.

Discussion: The monophyly of Orchidaceae is supported by morphology and *rbcL* sequences (Dressler 1981, 1993; Dressler and Chase 1995; Dahlgren et al. 1985; Burns-Balogh and Funk 1986; Judd et al. 1993). Phylogenetic relationships within the family have been addressed by several cladistic analyses (Burns-Balogh and Funk 1986; Dressler 1986, 1993; Judd et al. 1993; Dressler and Chase 1995; Cameron et. al. 1999; Freudenstein and Rasmussen 1999) although delimitation of some groups is still unclear. *Apostasia* and *Neuwiedia* (subfamily Apostasioideae) are considered to be sister to the remaining orchids (Dressler 1993; Judd et al. 1993; Dressler and Chase 1995; Neyland

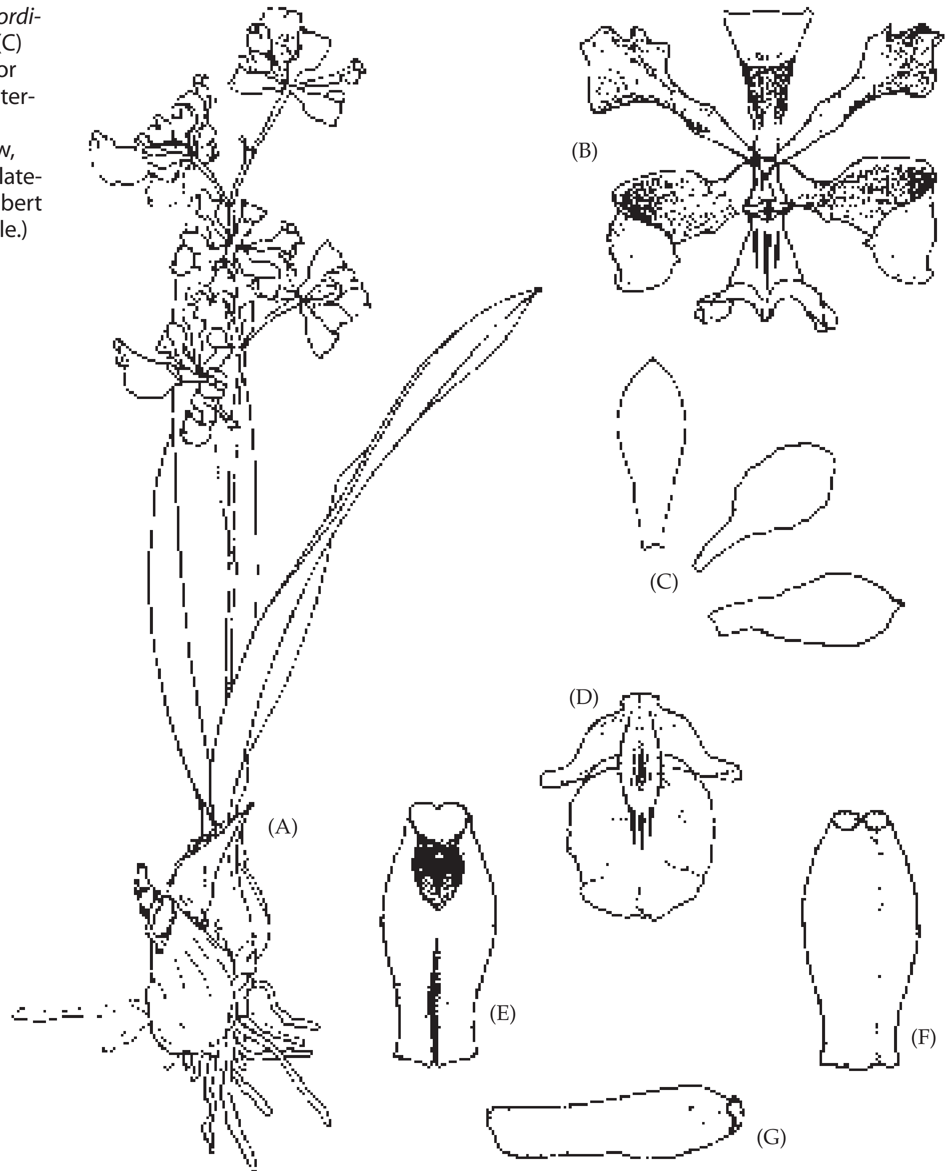


Figure 8.21 Orchidaceae. *Encyclia cordigera:* (A) habit (× 0.75); (B) flower (× 2); (C) sepals and petals (× 1.5); (D) labellum (or lip) (× 4); (E) column, ventral view, note terminal anther and stigma (in darkened depression (× 4); (F) column, dorsal view, note terminal anther (× 4); (G) column, laterial view (× 4). (Original drawings by Robert Dressler, University of Florida, Gainesville.)

and Urbatsch 1996; Cameron et. al. 1999; Freudenstein and Rasmussen 1999). The monophyly of Apostasioideae is supported by their vessel elements with simple perforation plates and distinctive seed type. These two genera, and especially *Neuwiedia*, have retained many ancestral features, such as flowers with two (*Apostasia*) or three (*Neuwiedia*) stamens that are only slightly adnate to the style, axile placentation, and pollen released as single grains. The remaining orchids all have sticky (or fused) pollen and a broad, asymmetrical stigma (with all lobes facing the center of the flower). Within this sticky-pollen clade, Cypripedioideae and Vanilloideae are discernible as more or less basal lineages. Cypripedioideae (e.g., *Cypripedium* and *Paphiopedilum*) are clearly monophyletic, as supported by their saccate (slipperlike) lip petal and median anther modified into a shieldlike staminode (see Figure 8.20); they have two functional stamens and lack pollinia. Vanilloideae (i.e., *Vanilla*, *Pogonia*, *Cleistes*) form a clade based on *rbcL* sequence data (Dressler and Chase 1995). This group is distinctive in that its flowers have only a single functional stamen and lack pollinia. Many Vanilloideae are vines with net-veined leaves; their ovaries are sometimes 3-locular. The remaining, more specialized genera of the sticky-pollen clade are linked by pollinia and a complete fusion of filament and style (Dahlgren et al. 1985; Burns-Balogh and Funk 1986; Judd et al. 1993; see Figure 8.20). This pollinia-forming clade, like the Vanilloideae, has flowers with only a single functional stamen (monandry; the two lateral stamens are represented by slender staminodes or are entirely lacking). Molecular analyses support the view that the reduction to a single functional stamen probably has occurred twice within orchids (Cameron et. al. 1999), while morphological analyses more strongly support the hypothesis that the monandrous orchids are monophyletic (Freudenstein and Rasmussen 1999). Most systematists divide this large and variable family into several subfamilies (Dressler 1981, 1986, 1993) based on characteristics of the column. Two large subfamilies, the Epidendroideae and the Orchidoideae (incl. Spiranthoideae), are recognized here. Epidendroideae share the apomorphies of a beaked and incumbent anther (i.e., anther bent over apex of column), while Orchidoideae share the apomorphies of acute anther apex, soft stems, leaves convolute but not plicate, and lack of silica bodies (see also Stern et al. 1993; Dressler 1993). Epidendroideae contain numerous tropical epiphytes; representative genera include *Bulbophyllum*, *Catasetum*, *Dendrobium*, *Epidendrum*, *Encyclia*, *Maxillaria*, *Oncidium*, *Pleurothallis*, and *Vanda*. Representative members of the Orchidoideae include *Cynorkis*, *Diuris*, *Goodyera*, *Habenaria*, *Orchis*, *Platanthera*, *Spiranthes*, and *Zeuxine*.

Orchid flowers are extremely varied in form and attract a wide array of insects (bees, wasps, moths, butterflies, flies) as well as birds (see Chapter 4). Some attract generalist visitors, but many are quite specialized, attracting only one or a few species as pollinators. Pollen, nectar, or floral fragrances may be employed as pollinator rewards, although some flowers (e.g., *Cypripedium*) manipulate their pollinators and provide no reward, and some species of *Ophrys* and *Cryptostylis* mimic the form and scent of female bees, and are pollinated when the male bees attempt to mate with the flower (pseudocopulation, see Figure 4.12). Generally, the lip functions as a landing platform and provides visual or tactile cues orienting the pollinator. The pollinia become attached to the pollinator's body, and often are deposited in the stigma (usually a depression in the underside of the column) of the next flower visited. In some species pollination is a fairly uncommon event, and the flowers may remain functional (and showy) for many days, with wilting of the perianth occurring rapidly after fertilization. Most species are outcrossing, but selfing is known to occur. The tiny, dustlike seeds are dispersed by wind and require nutrients supplied by a mycorrhizal fungus for germination.

References: Burns-Balogh and Funk 1986; Cameron et. al. 1999; Cox et al. 1997; Dahlgren et al. 1985; Dressler 1961, 1981, 1986, 1993; Dressler and Chase 1995; Freudenstein and Rasmussen 1999; Judd et al. 1993; Neyland and Urbatsch 1995; Stern et al. 1993; van der Pijl and Dodson 1966.

Dioscoreales

Dioscoreaceae R. Brown
(Yam Family)

Twining vines *with thick rhizomes or a large tuberlike swelling; stem with vascular bundles in 1 or 2 rings;* steroidal sapogenins and alkaloids commonly present. Hairs simple to stellate; prickles sometimes present. *Leaves* usually alternate, simple, but sometimes palmately lobed or compound, entire, *differentiated into a petiole and blade, with palmate venation, the major veins converging and connected by a network of higher-order veins; the petiole usually with an upper and lower pulvinus*, sometimes with stipule-like flanges, not sheathing; bulbils sometimes present in leaf axils. Inflorescences determinate, but sometimes appearing indeterminate, axillary. *Flowers usually unisexual* (plants dioecious), radial. *Tepals 6*, distinct to slightly connate, imbricate. *Stamens 6* (3); filaments distinct to slightly connate, adnate to the base of the tepals; pollen grains monosulcate to variously porate. *Carpels 3, connate; ovary inferior, with axile placentation*; stigmas 3, minute to slightly bilobed. Ovules 2 to numerous in each locule. Nectaries in septa of ovary or base of tepals. *Fruit usually a triangular and 3-winged, loculicidal capsule*, but sometimes a berry or samara; **seeds usually flattened or winged**, the coat with yellow-brown to red pigments **and crystals**; embryo sometimes with 2 cotyledons (Figure 8.22).

Floral formula:

Staminate: *, -6-, 6, 0

Carpellate: *, -6-, 0, $\overline{3}$; winged loculicidal capsule, samara, berry

Distribution: Widely distributed in the tropics and subtropics, with a few in temperate regions.

Genera/species: 5/625. ***Major genera:*** *Dioscorea* (600 spp.) and *Rajania* (20); both occur in the continental United States.

Economic plants and products: The starchy "tubers" of many species of *Dioscorea* (yams) are edible; these "tubers" should not to be confused with those of *Ipomoea batatas* (Convolvulaceae), which are also called yams. Other species are medicinally valuable due to the presence of alkaloids or steroidal sapogenins; the latter are used in anti-inflammatory medications and oral contraceptives.

Discussion: Dioscoreaceae are placed in Dioscoreales, an order characterized by vines with net-veined leaves and, as circumscribed by Dahlgren et al. (1985), also containing Trilliaceae, Stemonaceae, Taccaceae, Smilacaceae, and a few other families. Morphology (Conran 1989; Stevenson and Loconte 1995; Chase et al. 1995b) and *rbcL* sequences (Chase et al. 1993, 1995a) suggest that the order is not monophyletic. In this text, Trilliaceae and Smilacaceae are referred to the Liliales and Stemonaceae to the Pandanales, while the mycoparasitic Burmanniaceae are included here. Dioscoreales, as here circumscribed, may be monophyletic (Chase et al. 1995b) and are considered to be most closely related to Liliales and Asparagales. Dioscoreales frequently have been considered to represent primitive monocots (Dahlgren et al. 1985; Stevenson and Loconte 1995), a position not supported by cladistic analyses based on *rbcL* sequences or combined *rbcL* sequences and morphology (Chase et al. 1995a,b).

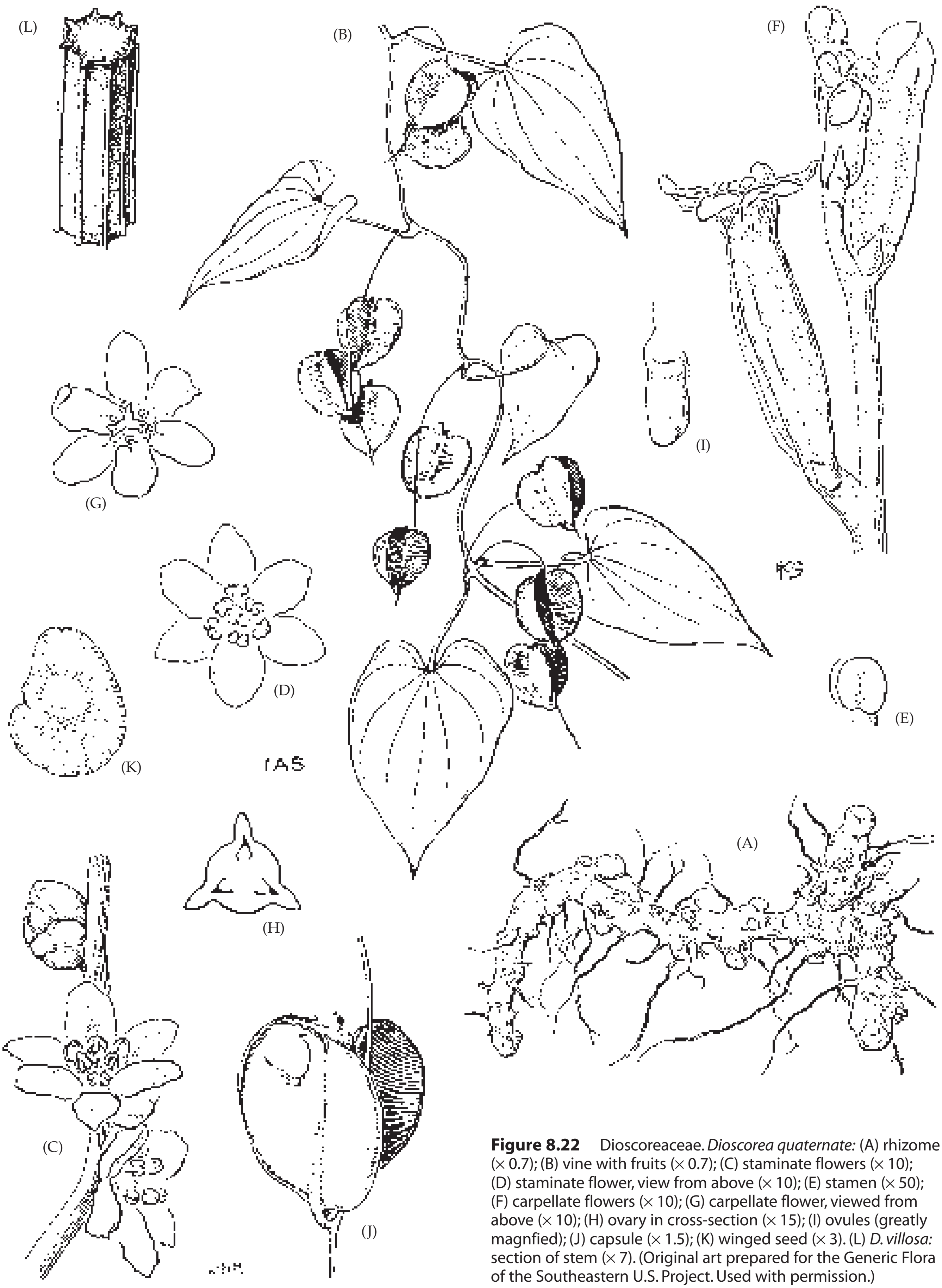


Figure 8.22 Dioscoreaceae. *Dioscorea quaternate:* (A) rhizome (× 0.7); (B) vine with fruits (× 0.7); (C) staminate flowers (× 10); (D) staminate flower, view from above (× 10); (E) stamen (× 50); (F) carpellate flowers (× 10); (G) carpellate flower, viewed from above (× 10); (H) ovary in cross-section (× 15); (I) ovules (greatly magnfied); (J) capsule (× 1.5); (K) winged seed (× 3). (L) *D. villosa:* section of stem (× 7). (Original art prepared for the Generic Flora of the Southeastern U.S. Project. Used with permission.)

Dioscoreaceae are easily differentiated from the closely related Taccaceae by their viny habit and usually unisexual flowers, axile (vs. parietal) placentation, and lack of filamentous bracts within the inflorescence. They may be distinguished from the phenetically similar Stemonaceae by 3-merous (vs. 2-merous) flowers and the consistently inferior ovary. Finally, Dioscoreaceae are easily separated from Burmanniaceae, a family of mycoparasitic herbs with scale-like leaves. Smilacaceae are also vines with net-veined leaves, but can easily be distinguished by their superior ovaries, few-seeded berries, and leaves with paired stipular tendrils.

The small genus *Stenomeris* is probably sister to the remaining taxa, which form a clade supported by the putative synapomorphies of underground root-tubers, unisexual flowers, and three-winged fruits.

The inconspicuous flowers of Dioscoreaceae are insect-pollinated (mainly by flies). Dispersal is usually by wind, as indicated by the specialized fruits: three-winged capsules with flattened and/or winged seeds (as in *Dioscorea*) or samaras (as in *Rajania*).

References: Al-Shehbaz and Schubert 1989; Bouman 1995; Chase et al. 1995a,b; Conran 1989; Dahlgren et al. 1985; Stevenson and Loconte 1995.

Commelinanae

The Commelinanae constitute a monophyletic group supported by *rbcL* sequences (Chase et al. 1993, 1995b; Duvall et al. 1993), *rbcL* and *atpB* sequences (Chase, personal communication), and morphology (Dahlgren and Rasmussen 1983). Putative synapomorphies include *Strelitzia*-type epicuticular wax (Figure 4.34), endosperm with copious starch, and UV-fluorescent compounds in the cell walls (Dahlgren et al. 1985; Harley and Ferguson 1990; Barthlott and Fröhlich 1983; Harris and Hartley 1980). Arecaceae (Palmae) have nonstarchy endosperm; Dahlgren et al. (1985) have suggested that this may represent an evolutionary loss. Analyses using *rbcL* sequences (Chase et al. 1993, 1995b) suggest that palms are the sister group to the remaining members of Commelinanae: Bromeliales, Poales, Juncales, Typhales, Commelinales, Philydrales, and Zingiberales, so starchy endosperm may be synapomorphy of this group.

Arecales

Arecaceae C. H. Schultz-Schultzenstein (= Palmae A. L. de Jussieu) (Palm Family)

Trees or shrubs with unbranched or rarely branched trunks, occasionally rhizomatous; **apex of stem with a large apical meristem**; tannins and polyphenols often present. Hairs various, and plants sometimes spiny due to modified leaf segments, exposed fibers, sharp-pointed roots, or petiole outgrowths. *Leaves* alternate, *often crowded in a terminal crown*, but sometimes well separated, simple and entire, *but usually splitting in a pinnate to palmate fashion as the leaf expands, and at maturity appearing palmately lobed* (*with segments radiating from a single point*), *costapalmately lobed* (± *palmate segments diverging from a short central axis, or costa*), *pinnately lobed or compound* (*with well-developed central axis bearing pinnate segments*), or rarely twice pinnately compound, differentiated into a petiole and blade, **the latter plicate**, and the segments either induplicate (V-shaped in cross-section) or reduplicate (Λ-shaped in cross-section; each segment with veins ± parallel to divergent, the petiole often with a flap (hastula), its base sheathing, with soft tissues often decaying to reveal various fiber patterns; stipules lacking. *Inflorescences* determinate, often *appearing compound-spicate*, axillary or terminal, with small to large, and deciduous to persistent bracts. *Flowers* bisexual or unisexual (and plants then monoecious to dioecious), radial, *usually sessile, with perianth usually differentiated into calyx and corolla*. Sepals 3, distinct to connate, usually imbricate. Petals usually 3, distinct to connate, imbricate to valvate. Stamens 3 or 6 to numerous; filaments distinct to connate, free or adnate to petals; pollen grains usually monosulcate. Carpels usually 3, but occasionally as many as 10, sometimes appearing to have a single carpel, distinct to connate; *ovary superior*, usually with axile placentation; stigmas various. **Ovules 1 in each locule**, anatropous to orthotropous. Nectaries in septa of ovary or lacking. **Fruit a drupe**, often fibrous, or rarely a berry; endosperm with oils or carbohydrates, sometimes ruminate (Figure 8.23).

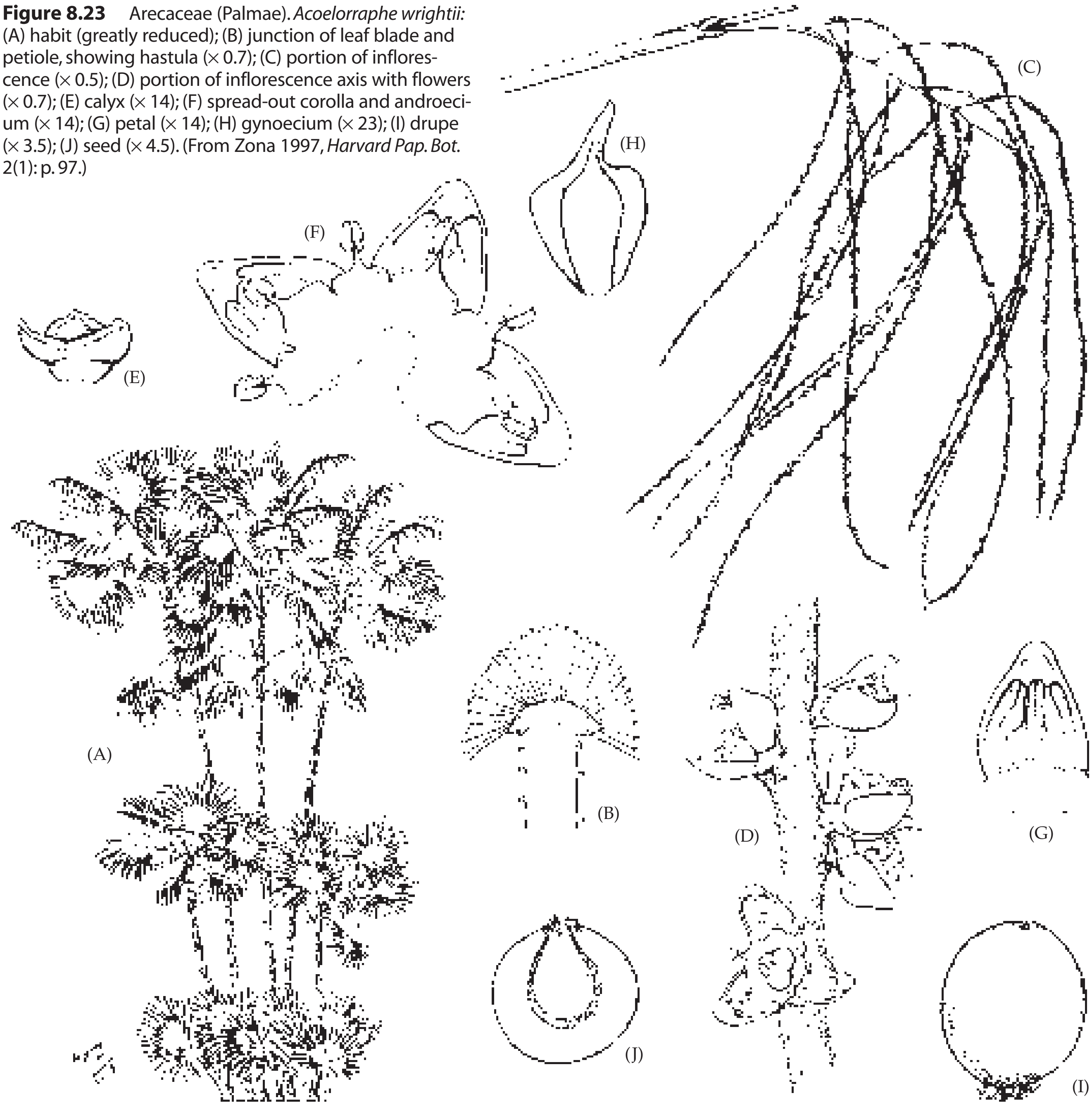
Floral formula: *, 3, 3, 6–∞, $\underline{3}$; drupe, berry

Distribution: Widespread in tropical to warm temperate regions.

Genera/species: 200/2780. ***Major genera:*** *Calamus* (370 spp.), *Bactris* (200), *Daemonorops* (115), *Licuala* (100), and *Chamaedorea* (100). The family is represented in the continental United States by *Coccothrinax*, *Pseudophoenix*, *Raphidophyllum*, *Roystonia*, *Sabal*, *Serenoa*, *Thrinax*, *Washingtonia*, and a few naturalized genera.

Economic plants and products: Food plants come from *Areca* (betel nut), *Attalea* (American oil palm), *Bactris* (peach palm), *Cocos* (coconut), *Elaeis* (African oil palm), *Metroxylon* (sago palm), and *Phoenix* (date palm); a great many genera have an edible apical bud (palm cabbage). Other economically important palms include *Calamus* (rattan), *Copernicia* (carnuba wax), *Phytelephas* (vegetable ivory), *Raphia* (raffia), and many genera that provide thatch. Finally, the family includes a large number of ornamentals: *Caryota* (fishtail palm), *Chamaerops* (European fan palm), *Livistona* (Chinese fan palm), *Roystonea* (royal palm), *Sabal* (cabbage palm), *Syagrus* (queen palm), *Washingtonia* (California fan palm), *Chamaedorea* (parlor palm), *Raphidophyllum* (needle palm), *Thrinax* (thatch palm), *Coccothrinax* (thatch palm), *Licuala*,

Figure 8.23 Arecaceae (Palmae). *Acoelorraphe wrightii:* (A) habit (greatly reduced); (B) junction of leaf blade and petiole, showing hastula (× 0.7); (C) portion of inflorescence (× 0.5); (D) portion of inflorescence axis with flowers (× 0.7); (E) calyx (× 14); (F) spread-out corolla and androecium (× 14); (G) petal (× 14); (H) gynoecium (× 23); (I) drupe (× 3.5); (J) seed (× 4.5). (From Zona 1997, *Harvard Pap. Bot.* 2(1): p. 97.)



Veitchia, *Acoelorraphe* (paurotis palm), *Butia* (jelly palm), *Copernicia*, *Dypsis*, and *Wodyetia* (foxtail palm).

Discussion: Arecaceae (or Palmae) are distinct, easily recognized, and monophyletic. Cladistic analysis of the family (Uhl et al. 1995) using morphology and cpDNA restriction sites supports placement of *Nypa* (a distinctive genus of Asian and western Pacific mangrove communities) as sister to the remaining palms. *Nypa* (Nypoideae) has a dichotomously branching prostrate stem and erect, pinnate, reduplicate leaves. A perianth of sepals and petals may be synapomorphic for the remaining palms. Those genera with usually pinnate and reduplicate leaves probably form a paraphyletic complex, while those with usually costapalmate or palmate and induplicate leaves—the Coryphoideae—probably form a monophyletic group (Uhl et al. 1995).

Major clades of reduplicate-leaved palms (excluding *Nypa*) include the following: The Calamoideae (the lepidocaryoid palms) have pinnate to palmate leaves and distinctive fruits that are covered with reflexed, imbricate scales. Noteworthy genera are *Raphia*, *Mauritia*, *Lepidocaryum*, *Metroxylon*, and *Calamus*. Hyophorbeae (Chamaedoreoid palms; e.g., *Chamaedorea*, *Hyophorbe*) have pinnate leaves and imperfect flowers in lines. Arecoideae have pinnate leaves and flowers in groups of three (triads), with one carpellate flower surrounded by two staminate flowers (a likely synapomorphy). Within the Arecoideae, a few clearly defined monophyletic groups are evident. Cocoseae (cocosoid palms) have the inflorescence associated with a large, persistent, woody bract, and fruits with bony, three-pored endocarps, and include genera such as *Elaeis*, *Cocos*, *Syagrus*, *Attalea*, *Bactris*, *Desmoncus*, and *Jubaea*. Iriarteae (iriartoid palms; e.g., *Iriartea*, *Socratea*) have stilt roots, and leaf segments with blunt apices and diverging veins. Most Arecoideae are placed within a heterogeneous and definitely paraphyletic Areceae; representative genera include *Areca*, *Roystonea*, *Prestoea*, *Dypsis*, *Wodyetia*, *Veitchia*, *Ptychosperma*, and *Dictyosperma*. These palms sometimes have a crownshaft, a structure formed from a series of broad, overlapping leaf bases, which appears to be a vertical extension of the stem.

The Caryoteae (caryotoid or fishtail palms; e.g., *Caryota* and *Arenga*) form a distinctive clade that is usually placed within the Arecoideae because of their floral triads. This group has induplicate, blunt leaf segments with diverging veins.

Coryphoideae are traditionally divided into three tribes. The monogeneric Phoeniceae (*Phoenix*, the date palms) have distinctive pinnate leaves in which the basal segments are spinelike. Borasseae (the borassoid palms; e.g., *Latania*, *Borassus*, *Lodoicea*, and *Hyphaene*) have staminate flowers embedded in thickened inflorescence axes. Most genera of Coryphoideae are placed in a third tribe—the heterogeneous and clearly paraphyletic "Corypheae" (coryphoid palms). Noteworthy genera include *Chamaerops*, *Raphis*, *Coccothrinax*, *Licuala*, *Copernicia*, *Corypha*, *Washingtonia*, *Sabal*, *Serenoa*, *Livistona*, *Thrinax*, *Rhapidophyllum*, and *Acoelorraphe*.

Flowers of palms usually are insect-pollinated (especially by beetles, bees, and flies); nectar is often employed as a pollinator reward (Henderson 1986). Palm fruits are usually fleshy and dispersed by a wide variety of mammals and birds, although some (e.g., *Nypa* and *Cocos*) are water dispersed and float in ocean currents (Zona and Henderson 1989).

References: Dransfield 1986; Henderson 1986, 1995; Henderson et al. 1995; Moore 1973; Moore and Uhl 1982; Tomlinson 1990; Uhl and Dransfield 1987; Uhl et al. 1995; Zona 1997; Zona and Henderson 1989.

Bromeliales

Bromeliaceae A. L. de Jussieu
(Bromeliad Family)

Herbs, usually epiphytic; silica bodies usually associated with epidermal cells. **Hairs water-absorbing peltate scales, occasionally merely stellate**. *Leaves* alternate, *often forming a tanklike basal rosette that holds water*, simple, entire to sharply serrate, with parallel venation, **containing water storage tissue** and air canals (often with stellate cells); sheathing at base; stipules lacking. Inflorescences indeterminate, terminal. *Flowers* usually bisexual, radial, **with perianth differentiated into a calyx and corolla**, *borne in the axils of brightly colored bracts*. *Sepals 3*, distinct to connate, imbricate. *Petals 3*, distinct to connate, often with a pair of appendages at the base, imbricate. *Stamens 6*; filaments distinct to connate, sometimes adnate to petals; pollen grains monosulcate or disulcate, or with 2 to several pores. *Carpels 3, connate*; ovary superior to inferior, with axile placentation; stigmas 3, **usually spirally twisted**. Ovules numerous. Nectaries usually in septa of ovary. *Fruit a septicidal capsule or berry; seeds often winged or with tuft*(*s*) *of hairs* (Figure 8.24).

Floral formula: $*, 3, 3, 6, \overline{\underline{3}}$; capsule, berry

Distribution and ecology: Tropical to warm temperate regions of the Americas (but one species of *Pitcairnia* in tropical Africa). An important group of epiphytes of moist montane forests; also occurring in xerophytic habitats.

Genera/species: 51/1520. ***Major genera:*** *Tillandsia* (450 spp.), *Pitcairnia* (250), *Vriesia* (200), *Aechmea* (150), *Puya* (150), and *Guzmania* (120). The family is represented in the continental United States by *Tillandsia*, *Catopsis*, and *Guzmania*.

Economic plants and products: The berries of *Ananas comosus* (pineapple) are important as an edible fruit. The dried stems and leaves of *Tillandsia usneoides* (Spanish moss) are used as stuffing material. Several genera, including *Aechmea*, *Bilbergia*, *Bromelia*, *Guzmania*, *Neoregelia*, *Pitcairnia*, *Tillandsia*, and *Vriesea*, provide ornamentals.

Discussion: The monophyly of Bromeliaceae is supported by cpDNA restriction sites, *rbcL* sequences (Ranker et al. 1990; Chase et al. 1993, 1995a), and morphology (Dahlgren et al. 1985; Gilmartin and Brown 1987; Varadarajan and Gilmartin 1988). The family probably represents an early divergent clade within the superorder (Dahlgren et al. 1985; Linder and Kellogg 1995; Chase et al. 1993, 1995b).

Bromeliaceae are divided into three subfamilies: Pitcairnioideae, Bromelioideae, and Tillandsioideae. Tillandsioideae are considered monophyletic on the basis of their entire leaf margins, hair-tufted seeds, and distinctive peltate scales that have several rings of isodiametric cells in the center of the scale and a fringe of 32 or 64 radiating cells. This clade has usually superior ovaries and capsular fruits. Bromelioideae are considered monophyletic due to their inferior ovaries and berry fruits; the subfamily has retained serrate leaves (a plesiomorphy). The monophyly of Pitcairnioideae is questionable; this group has serrate leaf margins, superior ovaries, and capsular fruits with winged seeds (all probable plesiomorphies). Analyses of *ndh*F sequences support the monophyly of Tillandsioideae and Bromelioideae, and the paraphyly of Pitcairnoideae (Terry et al. 1997a,b). The epiphytic habit

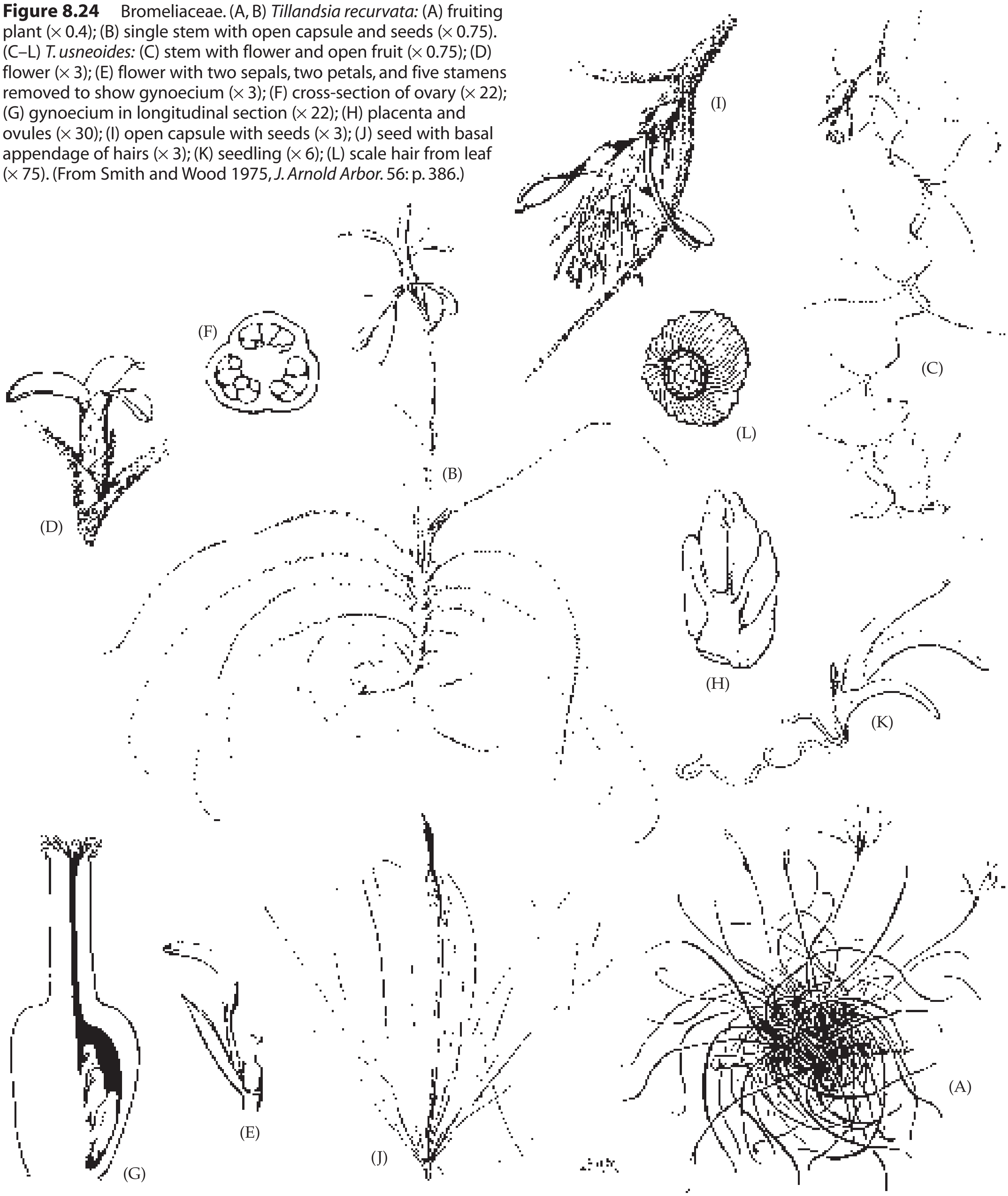


Figure 8.24 Bromeliaceae. (A, B) *Tillandsia recurvata:* (A) fruiting plant (× 0.4); (B) single stem with open capsule and seeds (× 0.75). (C–L) *T. usneoides:* (C) stem with flower and open fruit (× 0.75); (D) flower (× 3); (E) flower with two sepals, two petals, and five stamens removed to show gynoecium (× 3); (F) cross-section of ovary (× 22); (G) gynoecium in longitudinal section (× 22); (H) placenta and ovules (× 30); (I) open capsule with seeds (× 3); (J) seed with basal appendage of hairs (× 3); (K) seedling (× 6); (L) scale hair from leaf (× 75). (From Smith and Wood 1975, *J. Arnold Arbor.* 56: p. 386.)

evolved separately in Tillandsioideae and Bromelioideae.

Bromeliaceae show several adaptations to xerophytic and epiphytic conditions. The elongate, more or less concave leaves are typically clustered at the base of the plant, and their expanded bases form a water-retaining tank. The leaf surface is covered with water-absorbing peltate scales; each scale has a uniseriate stalk (of living cells), while the radiating cells of the scale are dead at maturity. The dead cells expand when wetted, drawing water into (and under) the scale, where it is osmotically taken into the leaf by the stalk cells. Water loss is reduced by location of stomates in furrows and a thick cuticle. Some hold water in a central "tank" while others directly absorb water held by elaborate scales. The plant's adventitious roots function mainly in holding it in place.

The showy flowers are pollinated by various insects, birds, or occasionally bats. The berries of members of the Bromelioideae are dispersed by birds or mammals, while the winged seeds of Pitcairnioideae and hair-tufted seeds of Tillandsioideae are wind dispersed.

References: Benzing 1980; Benzing et al. 1978; Brown and Gilmartin 1989; Chase et al. 1993, 1995b; Dahlgren et al. 1985; Gilmartin and Brown 1987; Linder and Kellogg 1995; Ranker et al. 1990; Smith and Wood 1975; Terry et al. 1997a,b; Varadarajan and Gilmartin 1988.

Philydrales

The Haemodoraceae, Pontederiaceae, Philydraceae, and possibly also Commelinaceae, form the Philydrales. These families have an amoeboid tapetum—the innermost layer of the anther tapetum shows early breakdown of inner and radial cell walls, with the nuclei and cytoplasm moving into the anther cavity (Dahlgren and Clifford 1982). The monophyly of this group is also supported by *rbcL* sequences and morphology (Chase et al. 1993; Duvall et al. 1993; Linder and Kellogg 1995). Additional morphological synapomorphies may include the presence of sclerids in the placentas and spatial separation of the stigmas and anthers within a flower (Graham and Barrett 1995). Pontederiaceae share with Haemodoraceae nontectate-columellate exine structure, while Philydraceae, like the Haemodoraceae, have unifacial leaves (Simpson 1990; Dahlgren et al. 1985).

The placement of Commelinaceae is still problematic. Morphology places this family with Eriocaulaceae and Mayacaceae, in the Commelinales, as traditionally delimited (Stevenson and Loconte 1995), while *rbcL* sequences place it with the Haemodoraceae, Pontederiaceae, and Philydraceae (Linder and Kellogg 1995). In this text, Commelinaceae are tentatively associated with Xyridaceae and Eriocaulaceae (see the immediately following order) because they have flowers with sepals and petals and moniliform hairs. As considered here, the Philydrales comprise 3 families and about 140 species.

References: Chase et al. 1993; Duvall et al. 1993; Dahlgren and Clifford 1982; Dahlgren et al. 1985; Graham and Barrett 1995; Linder and Kellogg 1995; Simpson 1990; Stevenson and Loconte 1995.

Haemodoraceae R. Brown

(Bloodwort or Blood Lily Family)

Herbs, with rhizomes, corms, and roots often with orange-red pigment, **containing various phenalones, i.e., polyphenolic compounds**. *Hairs simple to dendritic or stellate, and usually densely covering inflorescence axes, bracts, and outer perianth parts*. *Leaves* alternate, *2-ranked, equitant, unifacial*, those of upper portion of stem reduced, simple, entire, with parallel venation, sheathing at base; stipules lacking. **Inflorescences determinate, consisting of a series of helicoid cymes**, but sometimes appearing indeterminate, terminal. Flowers bisexual, radial to bilateral. *Tepals 6*, showy, distinct to connate, the perianth tube (when present), sometimes with a slit along upper surface, imbricate or valvate. Stamens 3 or 6, sometimes reduced to 1, occasionally dimorphic; filaments free or adnate to the tepals; pollen grains monosulcate or 2–7-porate. *Carpels 3, connate;* **ovary** superior or **inferior**, with axile placentation; stigma 1, capitate to 3-lobed. Ovules 1 to numerous in each locule, anatropous to orthotropous. Nectaries in septa of ovary, but often poorly developed. *Fruit a loculicidal capsule;* seeds often winged.

Floral formula: * or X, 6, 6 or 3, $\overline{\underline{3}}$; capsule

Distribution and ecology: Widespread in Australia, southern Africa, and northern South America, but a few in North America; often wetland plants.

Genera/species: 13/100. ***Major genera:*** *Conostylis* (30 spp.), *Haemodorum* (20), *Anigozanthos* (11). The family is represented in the United States by *Lachnanthes*.

Key to Families of Philydrales

1. Leaves with distinct petiole and expanded, bifacial blade (i.e., the adaxial surface anatomically differentiated from the abaxial) .... **Pontederiaceae**
1. Leaves equitant, unifacial (i.e., adaxial and abaxial surfaces identical); petiole lacking 2
2. Stamen solitary; tepals 4 and distinct; flowers lacking septal nectaries; arylphenalenones absent, the roots never reddish .... Philydraceae
2. Stamens 3 or 6; tepals 6 and distinct to connate; flowers with septal nectaries, but these sometimes poorly developed; arylphenalenones (often reddish polyphenolics) present, often giving an orange-red to purple color to the rhizomes and roots .... **Haemodoraceae**

Economic plants and products: Genera such as *Anigozanthos* (kangaroo paw), *Conostylis*, and *Lachnanthes* (blood lily, redroot) are used as ornamentals.

Discussion: Haemodoraceae are considered monophyletic due to the presence of arylphenalenones; they are the only vascular plants to possess these pigments, which produce the orange-red to purple coloration characteristic of the roots and rhizomes of many genera (Simpson 1990). Morphology supports recognition of two major clades: Haemodoreae and Conostylideae (Simpson 1990). The monophyly of Haemodoreae (e.g., *Haemodorum*, *Lachnanthes*, and *Xiphidium*) is supported by a reddish coloration in the roots and rhizomes, lack of sclereids in the placentas, and discoid seeds that are pubescent or marginally winged. Synapomorphies of Conostylideae (e.g., *Anigozanthos*) are multiseriate, branched hairs; six fertile stamens; pollen with rugulate (wrinkled) wall sculpturing and porate apertures; a nondeflexed style; and a base chromosome number of seven. The perianth of *Anigozanthos* has a dorsal slit, and bilateral flowers have evolved within both tribes.

The eastern North American *Lophiola* resembles Haemodoraceae in its unifacial leaves, inflorescence of helicoid cymes, and densely hairy flowers, but differs in pollen ultrastructure, hair morphology, and stem anatomy. *Lophiola* lacks the arylphenalenones so characteristic of Haemodoraceae, as well as the UV-fluorescent cell-wall-bound compounds that are present in Haemodoraceae (and all other Commelinanae). *Lophiola* is now placed within Melanthiaceae (Ambrose 1985) or Nartheciaceae (Zomlefer 1997a,b,c and this text).

The variously colored flowers of Haemodoraceae are usually pollinated by insects (especially bees and butterflies), but bird pollination is characteristic of *Anigozanthos*. Nectar usually provides the pollinator reward, but *Xiphidium* is pollinated by pollen-gathering bees. Many species probably are dispersed by wind; the seeds are often small, flattened, hairy, or winged.

References: Ambrose 1985; Anderberg and Eldenäs 1991; Dahlgren et al. 1985; Robertson 1976; Simpson 1990, 1993; Zomlefer 1997a,b,c.

Pontederiaceae

(Water Hyacinth Family)

Herbs, rhizomatous, floating to emergent aquatics; stems spongy. Hairs simple, only on reproductive parts. Leaves usually alternate, along stem or ± basal, ± differentiated into a petiole and blade, simple, entire, with parallel to palmate venation, sheathing at base; stipules lacking. Inflorescences determinate, but often appearing to be racemes or spikes, sometimes reduced to a single flower, terminal, but often appearing lateral, subtended by a bract. *Flowers* bisexual, radial to bilateral, *often tristylous*. *Tepals 6, showy*, **variably connate**, imbricate, *adaxial tepal of inner whorl often differentiated*. *Stamens usually 6*; **filaments adnate to the perianth tube**, *often unequal in length*; pollen grains with 1 or 2 furrows. Carpels 3, connate; ovary superior, with axile to occasionally intruded parietal placentation, sometimes with 2 locules sterile; stigma 1, capitate to 3-lobed. Ovules numerous to 1 in each locule. Nectaries often present in septa of ovary. *Fruit a loculicidal capsule or nut*, **surrounded by persistent basal portion of perianth tube** (Figure 8.25).

Floral formula: * or X, -6-, 6, $\underline{3}$; capsule, nut

Distribution and ecology: Widespread in tropical and subtropical regions, with a few temperate species; plants of aquatic and wetland habitats.

Genera/species: 4/35. ***Genera*:** *Heteranthera* (15 spp.), *Eichhornia* (7), *Monochoria* (7), and *Pontederia* (6). The family is represented in the continental United States and/or Canada by *Eichhornia*, *Heteranthera*, and *Pontederia*.

Economic plants and products: *Pontederia* (pickerel weed) and *Eichhornia* (water hyacinth) are used as aquatic ornamentals; the latter is also a problem weed.

Discussion: The monophyly of Pontederiaceae has been supported by morphology (Eckenwalder and Barrett 1986) and *rbcL* sequences (Graham and Barrett 1995). The family contains two major monophyletic groups. *Pontederia* and *Eichhornia* form a clade on the basis of a long-lived, perennial habit, a curved inflorescence axis, and bilateral, tristylous flowers, while *Heteranthera* and possibly *Monochoria* form a clade diagnosed by dimorphic stamens (fertile stamens and stamens providing food for insects) with basified anthers (Eckenwalder and Barrett 1986). *Pontederia* is distinct due to the apomorphies of a gynoecium with two locules aborting and the third containing only a single ovule, indehiscent fruits (nuts) surrounded by a ribbed to toothed persistent basal portion of the perianth, and relatively large seeds. *Eichhornia* is not monophyletic.

Pontederiaceae is the only monocot family showing tristyly, which probably evolved just once within the group and then was lost several times. Only Oxalidaceae and Lythraceae also have tristylous species (Vuilleumier 1967).

The showy flowers of Pontederiaceae are pollinated by various insects (especially bees, flies, and butterflies). Outcrossing is characteristic of heterostylous species, but self-pollination, as in *Heteranthera*, is also common. The warty nuts of *Pontederia* are water dispersed, as are the small seeds of capsular fruited species. Asexual reproduction by fragmentation of the rhizome system is common in some species.

References: Dahlgren et al. 1985; Eckenwalder and Barrett 1986; Graham and Barrett 1995; Lowden 1973; Ornduff 1966; Price and Barrett 1982; Rosatti 1987; Vuilleumier 1967.

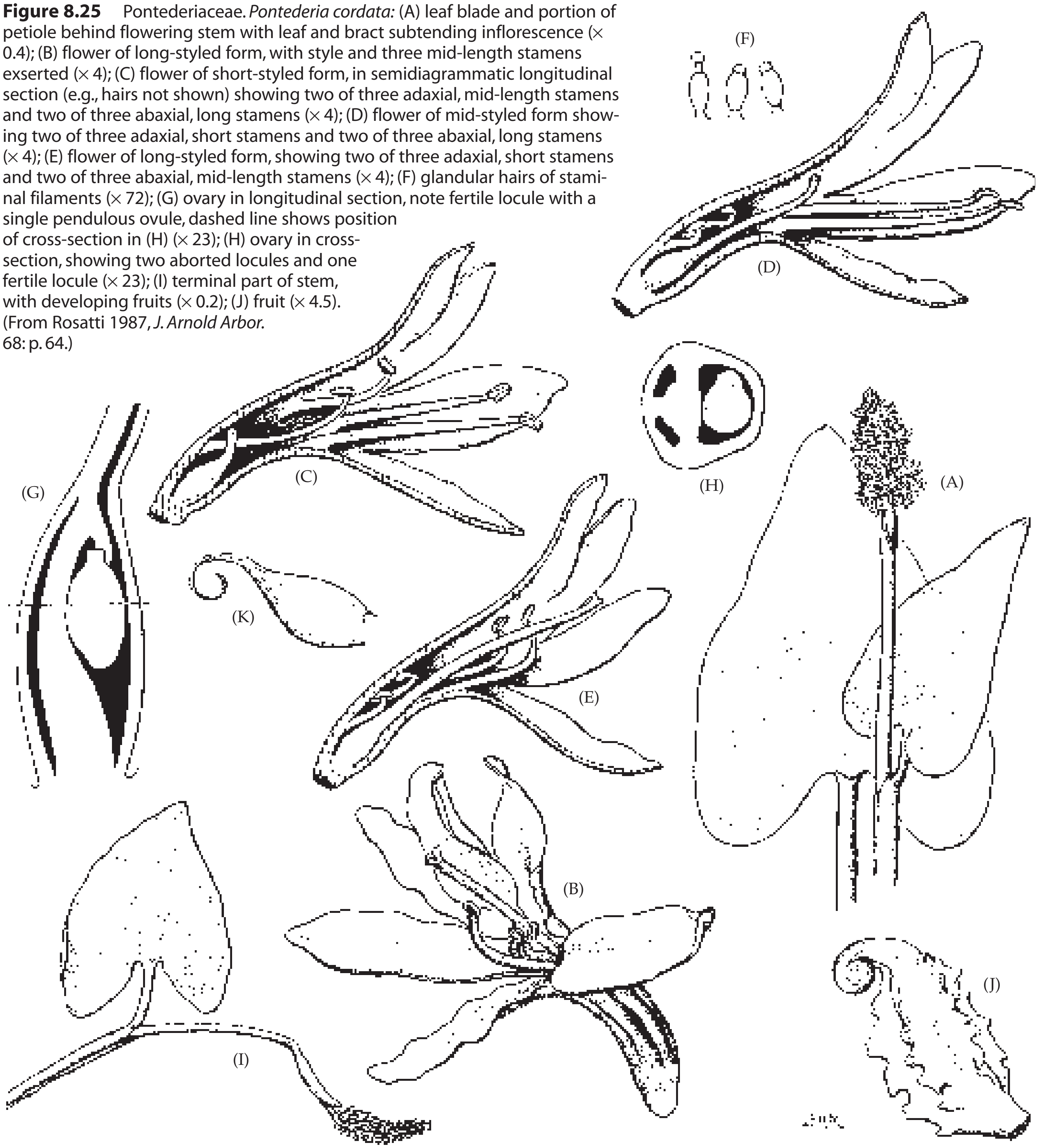


Figure 8.25 Pontederiaceae. *Pontederia cordata:* (A) leaf blade and portion of petiole behind flowering stem with leaf and bract subtending inflorescence (× 0.4); (B) flower of long-styled form, with style and three mid-length stamens exserted (× 4); (C) flower of short-styled form, in semidiagrammatic longitudinal section (e.g., hairs not shown) showing two of three adaxial, mid-length stamens and two of three abaxial, long stamens (× 4); (D) flower of mid-styled form showing two of three adaxial, short stamens and two of three abaxial, long stamens (× 4); (E) flower of long-styled form, showing two of three adaxial, short stamens and two of three abaxial, mid-length stamens (× 4); (F) glandular hairs of staminal filaments (× 72); (G) ovary in longitudinal section, note fertile locule with a single pendulous ovule, dashed line shows position of cross-section in (H) (× 23); (H) ovary in cross-section, showing two aborted locules and one fertile locule (× 23); (I) terminal part of stem, with developing fruits (× 0.2); (J) fruit (× 4.5). (From Rosatti 1987, *J. Arnold Arbor.* 68: p. 64.)

Commelinales

Commelinales are tentatively considered to be monophyletic due to their perianth of sepals and petals, with the latter ephemeral, and uniseriate hairs with a single basal cell (Dahlgren et al. 1985). The monophyly of the order has been supported in morphology-based cladistic analyses (Dahlgren and Rasmussen 1983; Stevenson and Loconte 1995; Linder and Kellogg 1995) but not in analyses of *rbcL* sequences (Chase et al. 1993) or morphology and *rbcL* sequences (Chase et al. 1995b; Linder and Kellogg 1995). In the combined-data analysis of Chase et al. (1995b), the Commelinaceae, Xyridaceae, and Mayacaceae form a clade related to Pontederiaceae and Haemodoraceae, while Eriocaulaceae are placed with Cyperaceae, Juncaceae, and Poaceae (among other families). In the combined-data analysis of Linder and Kellogg (1995), only Commelinaceae are placed near Pontederiaceae and Haemodoraceae, while Xyridaceae and Eriocaulaceae

Key to Major Families of Commelinales

1. Leaf sheath distinct and closed; raphide crystals present; seed with conical cap .... **Commelinaceae**
1. Leaf sheath indistinct to distinct, always open; raphide crystals lacking; seeds lacking conical cap 2
2. Leaves evenly distributed along stem; flowers solitary .... Mayacaceae
2. Leaves ± basal; flowers in heads or conelike spikes borne at apex of long scape 3
3. Flowers unisexual, in involucrate heads with numerous flowers open at one time; ovules 1 per locule .... **Eriocaulaceae**
3. Flowers bisexual, in conelike spikes, with only 1 or 2 flowers open at one time; ovules numerous on each placenta .... **Xyridaceae**

form a clade that is sister to a clade that contains Cyperaceae, Juncaceae, and Poaceae.

Morphological features suggest that Commelinaceae are the sister group to a clade containing Xyridaceae, Eriocaulaceae, and Mayacaceae, diagnosed by lack of raphide crystals and silica bodies, origin of lateral roots opposite the phloem, and ovules with a thin megasporangium wall (Dahlgren and Rasmussen 1983; Linder and Kellogg 1995; Stevenson and Loconte 1995). DNA sequence data suggest that these families are most closely related to Typhales, Juncales, and Poales.

The order contains 5 families and about 2140 species; major families include **Commelinaceae**, Mayacaceae, **Eriocaulaceae**, and **Xyridaceae**.

References: Chase et al. 1993, 1995b; Dahlgren et al. 1985; Dahlgren and Rasmussen 1983; Linder and Kellogg 1995; Stevenson and Loconte 1995.

Commelinaceae
(Spiderwort Family)

Herbs, sometimes succulent, with well-developed stems that are ± swollen at the nodes, or stems sometimes short; often with mucilage cells or canals containing raphides. Hairs simple, uniseriate or unicellular. Leaves alternate, scattered along stem, simple, narrow or somewhat expanded, flat to sharply folded (V-shaped in cross-section) **and with the opposite halves rolled separately against the midrib in bud**, entire, with parallel venation, **with closed basal sheath**; **stomata tetracytic**; stipules lacking. Inflorescences determinate, composed of few to several helicoid cymes, sometimes reduced to a solitary flower, terminal or axillary, often subtended by a folded, leafy bract. *Flowers* usually bisexual, radial to bilateral, *with perianth differentiated into a calyx and corolla*. *Sepals 3*, usually distinct, imbricate or with open aestivation. *Petals 3*, distinct and usually clawed to connate, and corolla then with a short to elongate tube and flaring lobes, *quickly self-digesting*, 1 petal sometimes differently colored and/or reduced, imbricate and crumpled in bud. Stamens 6, or 3 and then often with 3 staminodes; *filaments* slender, distinct to slightly connate, sometimes adnate to petals, *often with conspicuous moniliform* (*beadlike*) *hairs*; anthers occasionally with apical pores; pollen grains usually monosulcate. Carpels 3, connate; *ovary superior, with axile placentation*; stigma 1, capitate, fringed, or 3-lobed. Ovules 1 to several in each locule, anatropous to orthotropous. Nectaries lacking. *Fruit usually a loculicidal capsule* (occasionally a berry); **seeds with a conspicuous conical cap** (Figure 8.26.).

Floral formula: *, 3, 3, 3 or 6, $\underline{3}$; capsule

Distribution: Widespread in tropical to temperate regions.

Genera/species: 40/640. ***Major genera:*** *Commelina* (230 spp.), *Tradescantia* (60), *Aneilema* (60), *Murdannia* (45), and *Callisia* (20). *Callisia*, *Commelina*, *Gibasis*, *Murdannia*, and *Tradescantia* occur in the United States and/or Canada.

Discussion: Most genera of Commelinaceae belong to one of two large tribes (Faden and Hunt 1991): Tradescantieae (25 genera, e.g., *Callisia*, *Tradescantia*, and *Gibasis*) and Commelineae (13 genera, e.g., *Commelina*, *Murdannia*, and *Aneilema*). The former group is characterized by spineless pollen grains, medium to large chromosomes, radial flowers, and filament hairs (when present) moniliform; the latter has spiny pollen, small chromosomes, radial to bilateral flowers, and filament hairs (when present) usually not moniliform.

Flowers of Commelinaceae function for only a day at most. Pollination is usually accomplished by bees or wasps that gather pollen. The moniliform hairs often present on the filaments of members of the Tradescantieae may delude bees into scraping them, as if gathering pollen. Self-pollination is common in some species.

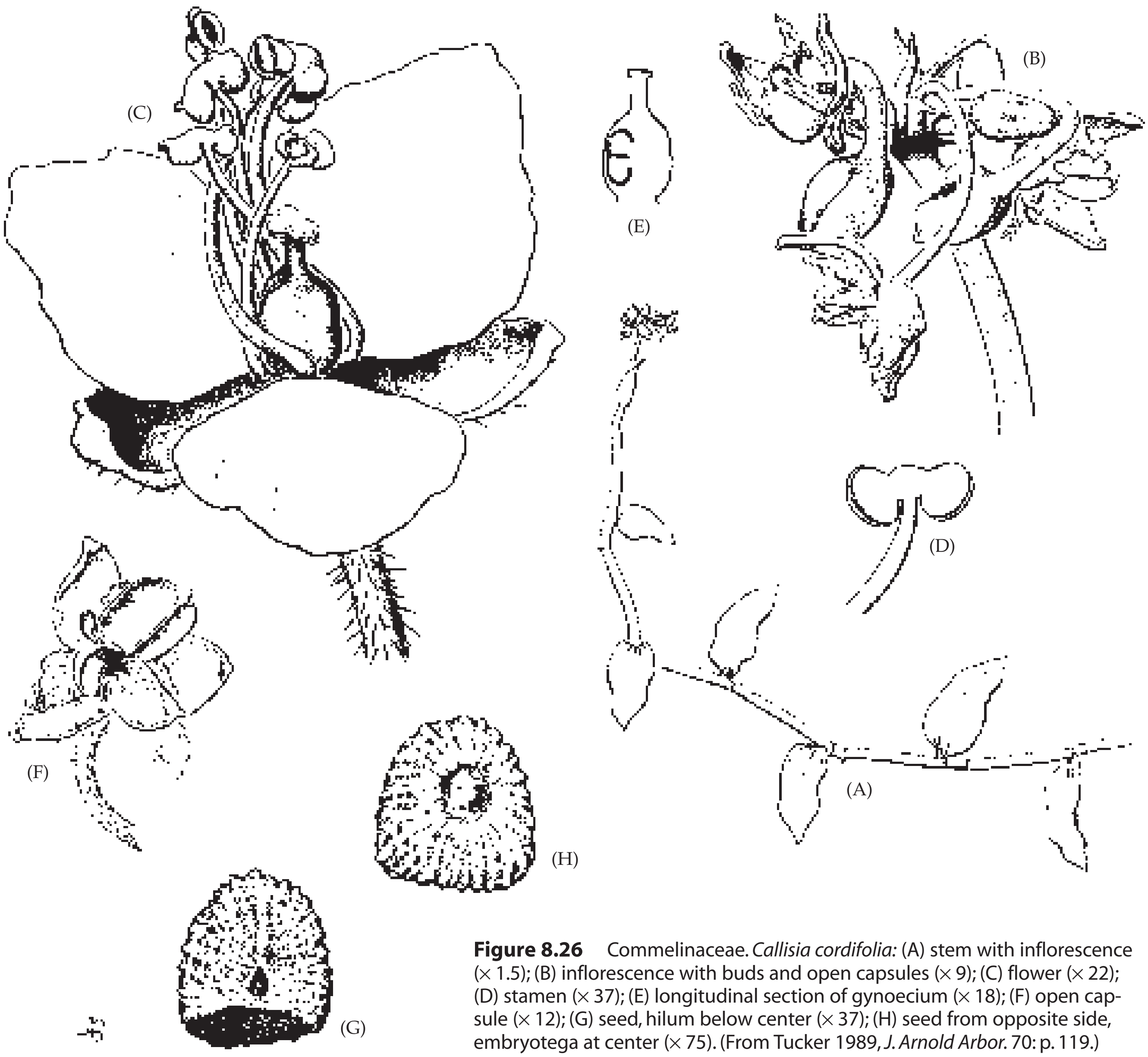


Figure 8.26 Commelinaceae. *Callisia cordifolia:* (A) stem with inflorescence (× 1.5); (B) inflorescence with buds and open capsules (× 9); (C) flower (× 22); (D) stamen (× 37); (E) longitudinal section of gynoecium (× 18); (F) open capsule (× 12); (G) seed, hilum below center (× 37); (H) seed from opposite side, embryotega at center (× 75). (From Tucker 1989, *J. Arnold Arbor.* 70: p. 119.)

References: Brenan 1966; Dahlgren et al. 1985; Faden and Hunt 1991; Tucker 1989.

Eriocaulaceae Desvaux
(Pipewort Family)

Herbs with shortened, cormlike stems or rhizomes; stems with vascular bundles in 1 or 2 rings. Hairs simple and uniseriate, or T-shaped. *Leaves* alternate, *usually in basal rosettes, or in tufts along branching stems*, simple, *narrow and grasslike*, entire, with parallel venation, sheathing at base; stipules lacking. **Inflorescences** indeterminate, **forming a head subtended by an involucre of stiff papery bracts**, *terminal, on a long scape*; scapes 1 to several, basally enclosed by a sheathing bract. **Flowers unisexual** (plants usually monoecious), radial to bilateral, *individually inconspicuous, with the perianth differentiated into a calyx and corolla, and often fringed with hairs*, usually in the axil of a papery bract. *Sepals* 2 or 3, distinct or connate, usually valvate. *Petals* 2 or 3, distinct (in carpellate flowers) or *connate* (*in staminate flowers*), sometimes with nectar-producing glands near the apex, sometimes reduced (in carpellate flowers), usually valvate. Stamens 2–6, often unequal; filaments can be distinct or connate, **adnate to the petals**, sometimes arising from a stalk (formed by fused petals and filaments); anthers 1- or 2-locular; **pollen grains with an elongated and spiral or convoluted germination furrow**. Carpels 2 or 3, connate; *ovary superior, usually borne on a stalk, with axile placentation*; stigmas 2 or 3, minute. Ovules 1 in each locule, orthotropous, with a thin megasporangium. *Fruit a loculicidal capsule*.

Floral formula:

Staminate: * or X, 2–3, 2–3, 2–6, 0

Carpellate: *, 2–3, 2–3, 0, 2–3; capsule

Distribution and ecology: Widespread in tropical and subtropical regions, with a few extending into temperate habitats; usually in wetland habitats.

Genera/species: 9/1175. ***Major genera:*** *Paepalanthus* (500 spp.), *Eriocaulon* (400), *Syngonanthus* (200), and *Leiothrix* (65). The family is represented in the continental United States and/or Canada by *Eriocaulon*, *Lachnocaulon*, and *Syngonanthus*.

Economic plants and products: Dried inflorescences of *Syngonanthus* and *Eriocaulon* (pipeworts) are used in floral arrangements.

Discussion: Eriocaulaceae are distinctive, clearly monophyletic, and easily recognized by their involucrate heads of minute flowers. They are therefore often referred to as the "Compositae of the monocots." Two subfamilies are typically recognized: the Eriocauloideae (e.g., *Eriocaulon*), which have twice as many stamens as petals and an apical nectar gland on the petals, and the Paepalanthoideae (e.g., *Paepalanthus*, *Leiothrix*, *Syngonanthus*, and *Lachnocaulon*), which have as many stamens as petals and lack nectar glands.

Flowers of Eriocaulaceae, which have anthers and styles clearly exserted, may be wind-pollinated, although nectaries on the flowers of *Eriocaulon* suggest that insect pollination also occurs. Floral visitors appear to be infrequent, and self-pollination is probably common. The seeds are presumably dispersed by wind or water.

References: Dahlgren et al. 1985; Kral 1966a, 1989.

Xyridaceae C. A. Agardh
(Yellow-Eyed Grass Family)

Herbs, with cormlike or bulblike stems, or occasionally rhizomes. Hairs simple or branched. *Leaves* alternate, *usually 2-ranked, often equitant and unifacial, those of the upper portion of stem reduced*, simple, flat to cylindrical, entire, with parallel venation, sheathing at base; stipules lacking. *Inflorescences* usually indeterminate and *forming a conelike head or spike, with spirally arranged, imbricate, persistent bracts, terminal, on a long scape*; scapes 1 to several, arising from axils of bracts or inner leaves. *Flowers* bisexual, **slightly bilateral**, *with perianth differentiated into a calyx and corolla*, each in the axil of a stiff, papery to leathery bract. Sepals 3, distinct and **dimorphic, the inner one membranous and wrapped around the corolla, falling as the flower opens, and the 2 lateral ones subopposite, stiff and papery, usually keeled, and persistent**. *Petals 3, distinct and clawed to connate, and then forming corolla with a narrow tube and distinctly 3-lobed, flaring limb*, imbricate, usually yellow or white, quickly wilting. **Stamens 3, opposite the petals and usually alternating with 3 staminodes**; filaments short and adnate to the petals; **staminodes apically 3-branched**, *densely covered with moniliform hairs*; pollen grains monosulcate or lacking an aperture. Carpels 3, connate; *ovary superior, with parietal to free-central or axile placentation*; stigmas 3, ± capitate. Ovules usually numerous on each placenta, anatropous to orthotropous, with a thick to thin megasporangium. **Nectaries lacking**. *Fruit usually a loculicidal capsule*, surrounded by the persistent, dried corolla tube and clasped by the 2 lateral sepals; seeds minute, usually longitudinally ridged (Figure 8.27).

Floral formula: X, 1+2, 3, 3+3•, 3; capsule

Distribution and ecology: Widespread in tropical and subtropical regions, with a few extending into temperate habitats; characteristic of wetlands.

Genera/species: 5/270. ***Major genus:*** *Xyris* (260 spp.). The family is represented in the continental United States and Canada only by *Xyris*.

Economic plants and products: A few species of *Xyris* (yellow-eyed grass) are cultivated as ornamentals (especially in aquaria).

Discussion: The morphology of the boat-shaped sepals provides important diagnostic characters for species, most of which belong to *Xyris*.

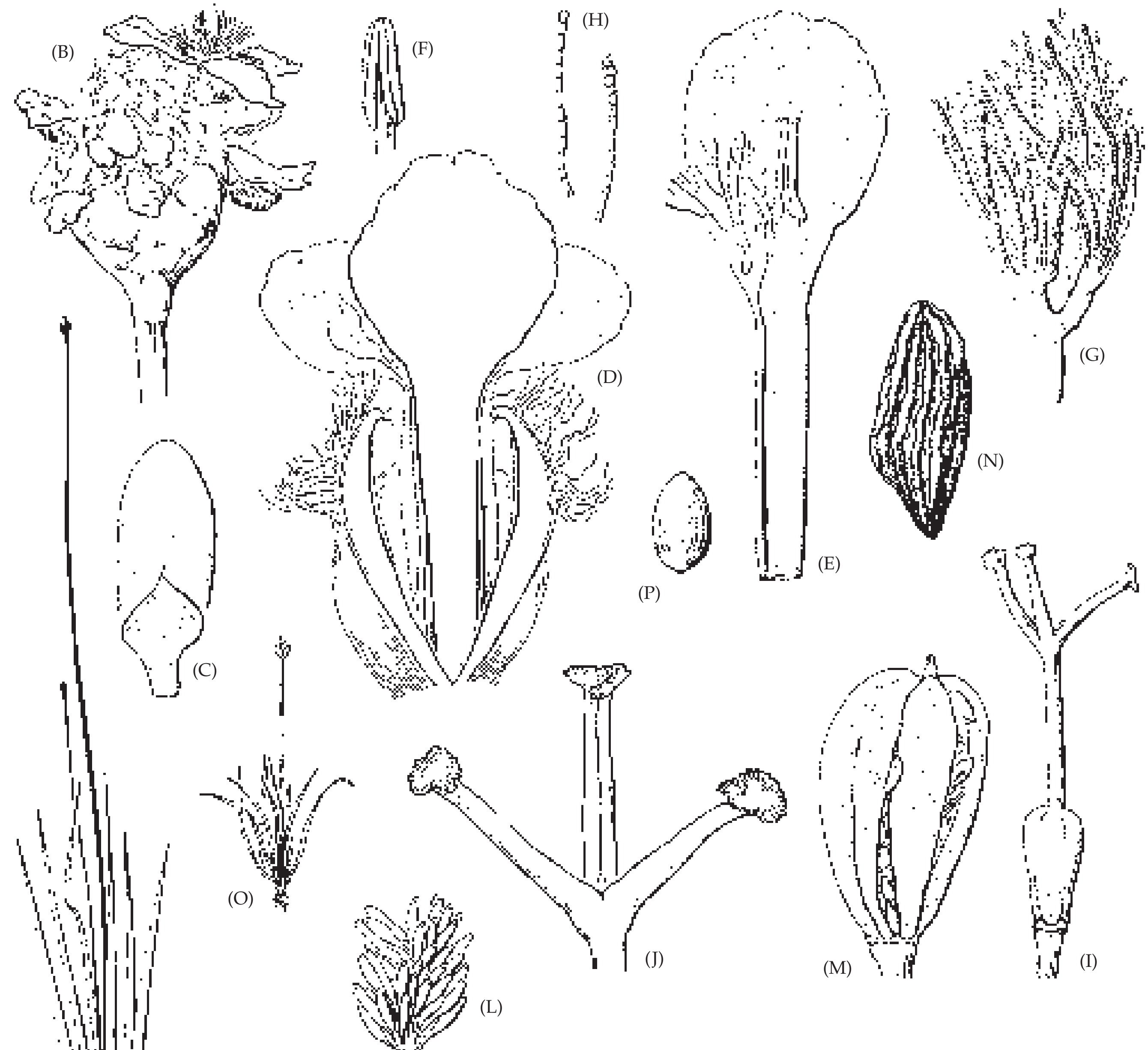
The showy flowers of *Xyris* are ephemeral, and the corollas usually are expanded for no more than a few hours. Usually only one or two flowers per head are open at once. Flowers of sympatric species often open at different times of day. Nectaries are consistently lacking, and pollination may be predominantly accomplished by pollen-gathering bees. The staminodes, with their tufts of moniliform hairs, may facilitate pollination by gathering pollen and presenting it to bees, or may delude bees into scraping them as if gathering pollen. The minute seeds are dispersed by wind and/or water.

References: Dahlgren et al. 1985; Kral 1966b, 1983, 1992.

Typhales

Typhaceae A. L. de Jussieu
(Cattail Family)

Rhizomatous herbs, aquatic or wetland, with leaves and stems distally floating or emergent. Hairs simple. *Leaves* alternate, *2-ranked*, simple, *linear*, entire, with parallel venation, *often spongy, with air canals and partitions containing stellate cells*, sheathing at base; stipules lacking. *Inflorescences* determinate, terminal, highly modified *with numerous*



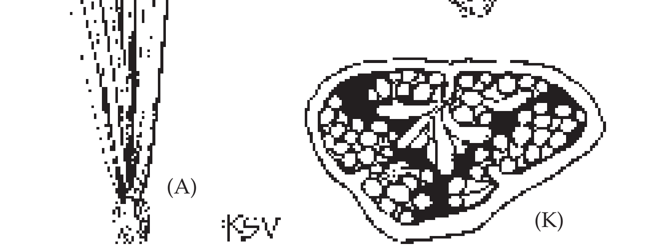


Figure 8.27 Xyridaceae. (A–N) *Xyris fimbriata:* (A) habit (× 0.2); (B) inflorescence (× 3); (C) inner sepal (× 9); (D) flower, showing the two persistent fimbriate lateral sepals and the subtending bract (behind flower) (× 7); (E) petal with filament of fertile anther adnate to claw, and staminode with free filament and much branched tip (× 9); (F) anther (× 9); (G) tip of staminode (× 18); (H) moniliform hairs of staminode (× 37); (I) gynoecium (× 7.5); (J) tip of three-parted style with stigmas (× 18); (K) ovary in cross-section, showing numerous ovules (most sectioned) (× 30); (L) adaxial side of placenta with ovules (× 18); (M) dehiscing capsule (× 9); (N) seed (× 60). (O, P) *X. brevifolia:* (O) habit (× 0.75); (P) seed (× 60). (From Kral 1983, *J. Arnold Arbor.* 64: p. 425.)

densely clustered flowers and appearing to be elongate/cylindrical spikes or globose clusters, the staminate flowers positioned above the carpellate, often subtended by a linear bract. **Flowers unisexual (plants monoecious)**, radial. **Tepals 1–6 and bractlike, numerous and bristle-like, or scale-like**, distinct. Stamens 1–8; filaments distinct or basally connate; anthers with connective sometimes expanded; pollen grains uniporate, in monads or tetrads. **Carpels** 3, connate, **usually only 1 functional**; ovary superior, with **apical placentation (and usually 1 locule)**, often on a stalk; stigma 1, extending along one side of style. **Ovule 1**. **Nectaries lacking**. *Fruit a drupe with dry-spongy "flesh" or an achenelike follicle;* seed or pit containing a pore, through which the embryo emerges (Figure 8.28).

Floral formula:

Staminate: *, (1–∞), 1–8, 0

Carpellate: *, 3–∞, 0, $\underline{1}$; drupe, achene-like follicle

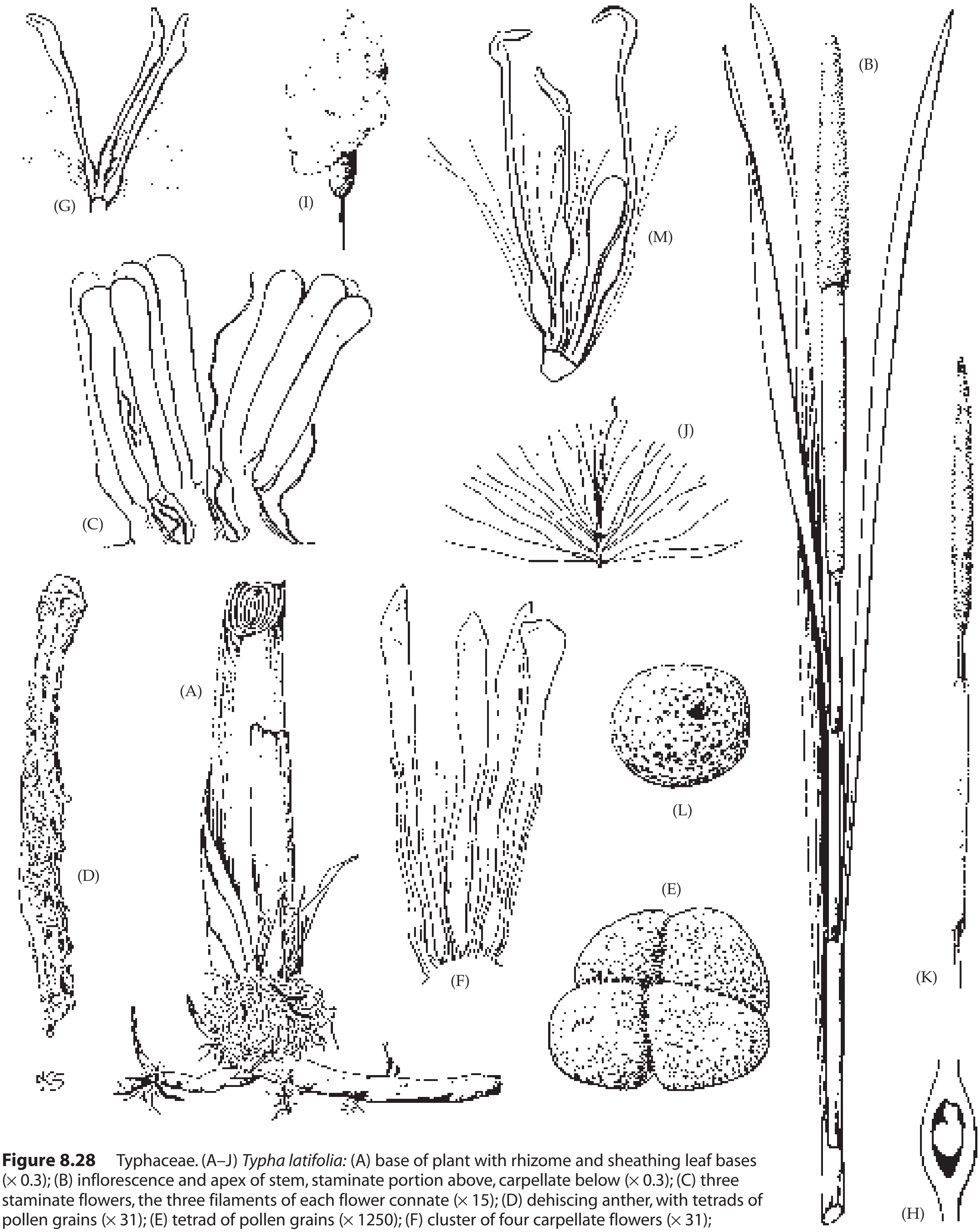


Figure 8.28 Typhaceae. (A–J) *Typha latifolia:* (A) base of plant with rhizome and sheathing leaf bases (× 0.3); (B) inflorescence and apex of stem, staminate portion above, carpellate below (× 0.3); (C) three staminate flowers, the three filaments of each flower connate (× 15); (D) dehiscing anther, with tetrads of pollen grains (× 31); (E) tetrad of pollen grains (× 1250); (F) cluster of four carpellate flowers (× 31); (G) cluster of three carpellate flowers with many trichomes omitted to show stalked ovaries (× 15); (H) ovary in longitudinal section to show single apical ovule (× 31); (I) infructescence shedding fruits (× 0.3); (J) mature fruit, a stalked, achenelike follicle, with numerous hairs on the stalk (× 3.75). (K–M) *T. angustifolia:* (K) inflorescence, showing gap between staminate and carpellate portions (× 0.3); (L) pollen grain (× 1250); (M) portion of carpellate inflorescence to show three flowers, simple and glandular hairs, and spatulate sterile flower (× 15). (From Thieret and Luken 1996, *Harvard Pap. Bot.* 1(8): p. 32.)

Distribution and ecology: Widely distributed, especially in the Northern Hemisphere; characteristic of aquatic and wetland habitats, especially marshes.

Genera/species: 2/28. ***Genera*:** *Sparganium* (15 spp.) and *Typha* (13). Both occur in the continental United States and Canada.

Economic plants and products: *Typha* (cattails) and *Sparganium* (bur reeds) are occasionally used as ornamentals; the leaves of *Typha* are used as weaving material, and the starchy rhizomes, young staminate inflorescences, and pollen of both genera can be eaten.

Discussion: Analyses using *rbcL* sequences (Chase et al. 1993, 1995b; Duvall et al. 1993) and morphology (Dahlgren et al. 1985; Stevenson and Loconte 1995) both support the monophyly of Typhaceae (incl. Sparganiaceae).

Typhaceae are wind-pollinated. The persistent perianth bristles of *Typha* lead to wind dispersal of the achenelike fruits (which after dispersal split open, releasing the single seed). The dry-spongy drupes of *Sparganium* may be dispersed by birds, mammals, or water.

References: Dahlgren et al. 1985; Duvall et al. 1993; Chase et al. 1993, 1995b; Stevenson and Loconte 1995; Thieret 1982; Thieret and Luken 1996.

Juncales

Juncales are certainly monophyletic, based on morphology and *rbcL* sequences (Plunkett et al. 1995; Simpson 1995). Morphological synapomorphies include solid stems, 3-ranked leaves, loss of calcium oxalate raphides, pollen in tetrads (reduced in Cyperaceae), chromosomes with diffuse centromeres, and details of embryo and pollen development. The genus *Prionium* (sometimes placed in Juncaceae, but here considered in Prioniaceae) may be sister to the Cyperaceae/Juncaceae clade (Munro and Linder 1998). All evidence points to Cyperaceae being monophyletic, although *Oxychloe* (Juncaceae) may be embedded within it (based on *rbcL* sequences). Even if *Oxychloe* and *Prionium* are excluded from Juncaceae, its monophyly is not clear; both morphological and *rbcL* sequence data are ambiguous. The order probably is most closely related to Poales and Typhales.

Members of this order are wind-pollinated, superficially grasslike, and often confused with grasses. A common mnemonic is the following rhyme (origin uncertain): "Sedges have edges, and rushes are round, and grasses are hollow right to the ground." This rhyme refers to the sharply triangular stems of some (but not all) sedges (Cyperaceae), and the hollow stems of some (but not all) grasses (Poaceae, in the order Poales). Rushes (Juncaceae) are indeed round-stemmed and solid, but the rhyme's characterization of sedges and grasses is an oversimplification.

The order consists of 4 families, **Juncaceae**, **Cyperaceae**, Thurniaceae, and Prioniaceae, comprising about 4900 species.

References: Munro and Linder 1998; Plunkett et al. 1995; Simpson 1995.

Juncaceae A. L. de Jussieu
(Rush Family)

Herbs, often with rhizomes; silica bodies absent; *stems round and solid*. *Leaves* alternate, *3-ranked*, basal or along lower portion of stem, *composed of a sheath and blade, the sheath usually open*; the blade simple, entire, with parallel venation, linear, flat or cylindrical; ligule and stipules lacking. Inflorescences basically determinate, terminal, highly branched, but often condensed and headlike. *Flowers usually bisexual*, but occasionally unisexual (plants dioecious), radial, inconspicuous. *Tepals 6, distinct*, imbricate, generally dull colored (green, red-brown, black), but sometimes white or yellowish. *Stamens* (*3–*)*6*; filaments distinct; pollen monoporate, in obvious tetrads. *Carpels 3, connate; ovary superior*, with axile or parietal (occasionally basal) placentation; ovules numerous (rarely 3); stigmas 3, usually elongate. Nectaries lacking. *Fruit a loculicidal capsule*, with 3 to many seeds.

Floral formula: *, -6-, (3–)6,$\underline{3}$; capsule

Distribution and ecology: Worldwide, mostly temperate and/or montane. Often in damp habitats, but with notable exceptions, such as the weedy *Juncus trifidus*.

Genera/species: 6/400. ***Major genera:*** *Juncus* (300 spp.), *Luzula* (80). Both occur in the United States and Canada.

Economic plants and products: *Juncus effusus* (soft rush) and *J. squarrosus* (heath rush) are used to produce split rushes for baskets and chair bottoms. A few *Juncus* and *Luzula* species are used as ornamentals.

Key to Major Families of Juncales

1. Perianth of 6 tepals; ovules 3–numerous; fruit a capsule .... **Juncaceae**
1. Perianth lacking or reduced to scales, bristles, or hairs; ovule 1; fruit an achene (nutlet) ..... **Cyperaceae**

Discussion: Juncaceae may be nonmonophyletic as currently circumscribed (see discussion of order). It is not clear which, if any, of the family characteristics are synapomorphic; most are generalized features of monocotyledons.

Many members of this family look superficially like grasses, but the 3-ranked leaves, flowers with obvious tepals, and capsular fruit all make the distinction clear.

In some species of *Juncus*, the large bract subtending the inflorescence is borne upright so that it looks like a continuation of the stem, and the inflorescence appears lateral.

Cyperaceae A. L. de Jussieu
(Sedge Family)

Herbs, generally rhizomatous; **stems usually ± triangular in cross-section**, often leafless above the base. *Leaves alternate, 3-ranked*, **with conical silica bodies**; *composed of a sheath and blade*, **the sheath closed**, the blade simple, entire to minutely serrate, with parallel venation, linear, flattened; stipules lacking; *ligule generally lacking*. *Inflorescence a complex arrangement of small spikes* (*spikelets*), often subtended by bracts. *Flowers* bisexual or unisexual (plants then usually monoecious), *each subtended by a bract*. *Tepals lacking or reduced to usually 3–6 scales, bristles, or hairs*. **Stamens 1–3** (–6); filaments distinct; anthers not sagittate; **pollen** usually uniporate, **in pseudomonads (3 microspores degenerate and form part of the pollen wall)**. Carpels 2–3, connate; ovary superior, **with basal placentation**; **ovule 1**; styles 3, elongated. Nectaries lacking. **Fruit an achene (nutlet)**, often associated with persistent perianth bristles (Figure 8.29).

Floral formula: *, -0–6-, 1–3 (–6), $\underline{3}$; achene

Distribution and ecology: Worldwide; often, but not exclusively, in damp sites.

Genera/species: 122/4500. ***Major genera:*** *Carex* (2000 spp.), *Cyperus* (600), *Fimbristylis* (300), *Scirpus* (300), *Rhynchospora* (200), *Scleria* (200), and *Eleocharis* (200). All of the above occur in North America; other common genera include *Cladium*, *Bulbostylis*, *Bulboschoenus*, *Eriophorum*, *Fuirena*, *Kyllinga*, *Schoenoplectus*, and *Trichophorum*.

Economic plants and products: *Cyperus papyrus* was used for making paper by ancient Egyptians and is also commonly planted as an ornamental. *Cyperus rotundus* (nut sedge) is an agricultural weed. *Cyperus esculentus* (nut sedge, chufa, tigernut) has edible underground storage organs, as do *Mariscus umbellatus*, *Scirpus tuberosus*, and *Eleocharis dulcis;* the latter provides commercial "water chestnuts." Weaving materials are provided by stems and leaves of a few species of *Cyperus*, *Carex*, *Eleocharis*, *Lepironia*, and *Scirpus*. Roots of *Cyperus longus* (galingale) and *C. articulatus* are sweet-scented and used in perfumery. Roots of *Scirpus grossus* and *S. articulatus* are used in Hindu medicine. Various species of *Carex* are used as packing materials, hay, or straw.

Discussion: Cyperaceae contain unique conical silica bodies, which distinguish them from all other monocots. The family is apparently monophyletic (but see above for discussion of the *rbcL* sequence of *Oxychloe*). In a comprehensive morphological study of the family, Bruhl (1995) recognized two subfamilies and ten tribes. The tribes represent groups that appear in both phenetic and cladistic analyses of the family, although only four of the ten have clear synapomorphies. The most common tribe in North America is the Cariceae, in which the spikelet prophyll forms a sac (the perigynium) enclosing the flower.

Like Juncaceae, Cyperaceae are often mistaken for grasses. They are distinguished by the ± triangular stems, 3-ranked leaves, usual lack of a ligule, and closed sheaths. (The latter two characteristics occur in a few grasses, but not together.) Cyperaceae flowers are subtended by a single bract or, in *Carex*, bract plus prophyll, whereas most grass flowers are associated with two bracts (lemma and palea).

References: Bruhl 1995; Tucker 1987.

Poales

Poaceae Barnhart
(= Gramineae A. L. de Jussieu)
(Grass Family)

Herbs, often rhizomatous, but trees in tropical bamboos; *stems jointed, round to elliptical in cross-section*; with silica bodies. *Leaves* alternate, *2-ranked*, **consisting of sheath, ligule, and blade**; *sheaths tightly encircling the stem, the margins overlapping but not fused* or, occasionally, united to form a tube; ligule a membranous flange or fringe of hairs at adaxial apex of sheath; blades simple, usually linear, usually with parallel venation, flat or sometimes rolled into a tube, continuous with the sheath or petiolate. Inflorescence a spike, panicle, cyme, or raceme of **spikelets**. *Spikelet composed of an axis bearing 2-ranked and closely overlapping basal bracts* (*glumes*) *and florets*; breaking up above the glumes or remaining intact at maturity; compressed parallel or perpendicular to the plane of arrangement of glumes and florets. **Glumes** usually 2, equal in size or unequal. **Florets** 1 to numerous per spikelet, made up of a bract (the **lemma**) subtending a flower and another bract (the **palea**, a prophyll) lying between the flower and the spikelet axis. Lemmas sometimes with 1 or more needle-like, straight or bent awns. Palea often translucent, smaller than, and partially enclosed by the lemma. Flowers small, bisexual or unisexual (plants then monoecious or dioecious), usually wind-pollinated, greatly reduced in size and number of floral parts. Lodicules (= perianth parts) mostly 2, translucent. Stamens (1–) 3 (–6, or numerous); anthers usually sagittate; pollen monoporate. Carpels 3, but often appearing as 2, connate; stigmas 2 (–3), plumose, papillae multicellular; ovary superior, with 1

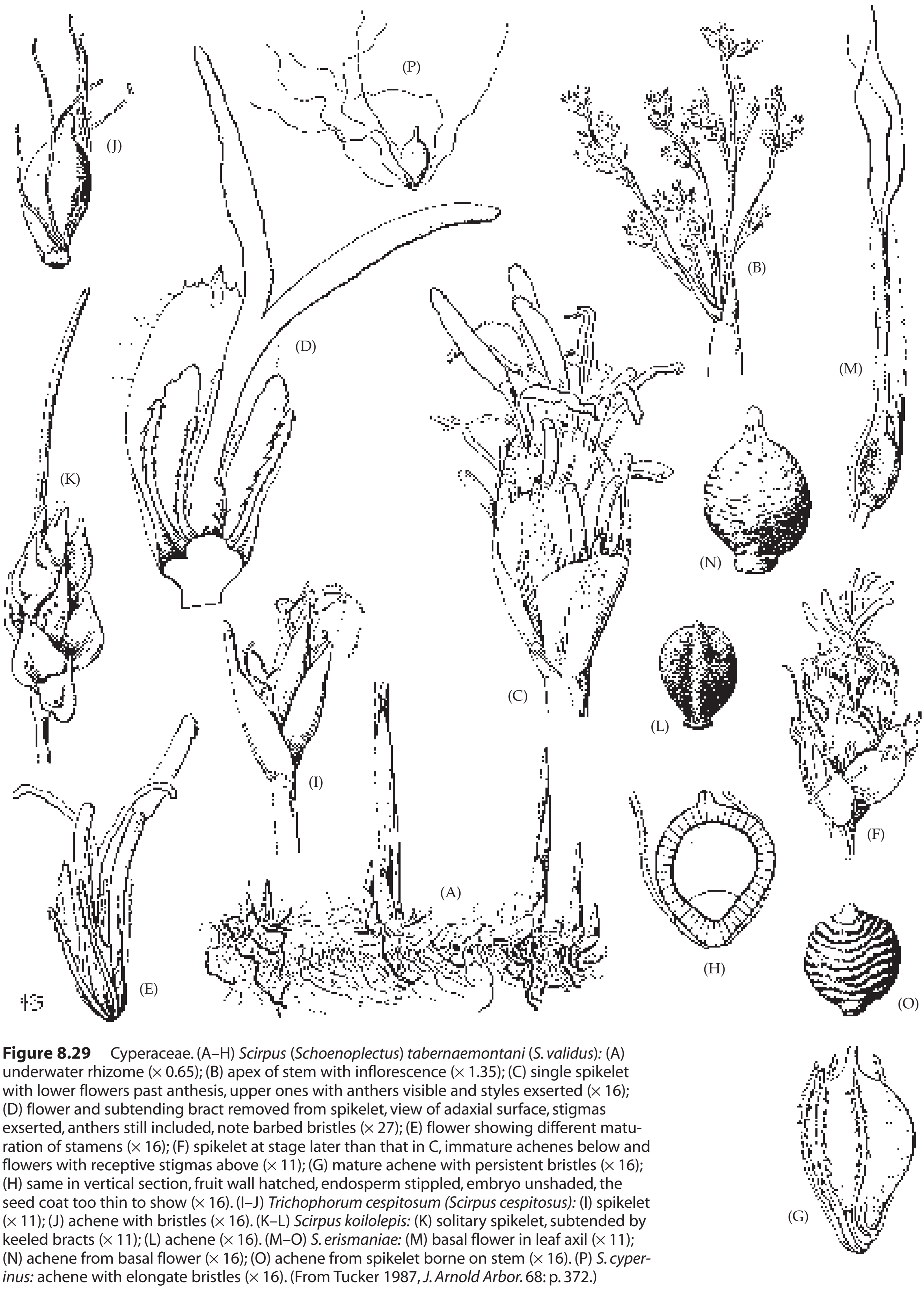


Figure 8.29 Cyperaceae. (A–H) *Scirpus* (*Schoenoplectus*) *tabernaemontani* (*S. validus*): (A) underwater rhizome (× 0.65); (B) apex of stem with inflorescence (× 1.35); (C) single spikelet with lower flowers past anthesis, upper ones with anthers visible and styles exserted (× 16); (D) flower and subtending bract removed from spikelet, view of adaxial surface, stigmas exserted, anthers still included, note barbed bristles (× 27); (E) flower showing different maturation of stamens (× 16); (F) spikelet at stage later than that in C, immature achenes below and flowers with receptive stigmas above (× 11); (G) mature achene with persistent bristles (× 16); (H) same in vertical section, fruit wall hatched, endosperm stippled, embryo unshaded, the seed coat too thin to show (× 16). (I–J) *Trichophorum cespitosum (Scirpus cespitosus):* (I) spikelet (× 11); (J) achene with bristles (× 16). (K–L) *Scirpus koilolepis:* (K) solitary spikelet, subtended by keeled bracts (× 11); (L) achene (× 16). (M–O) *S. erismaniae:* (M) basal flower in leaf axil (× 11); (N) achene from basal flower (× 16); (O) achene from spikelet borne on stem (× 16). (P) *S. cyperinus:* achene with elongate bristles (× 16). (From Tucker 1987, *J. Arnold Arbor.* 68: p. 372.)

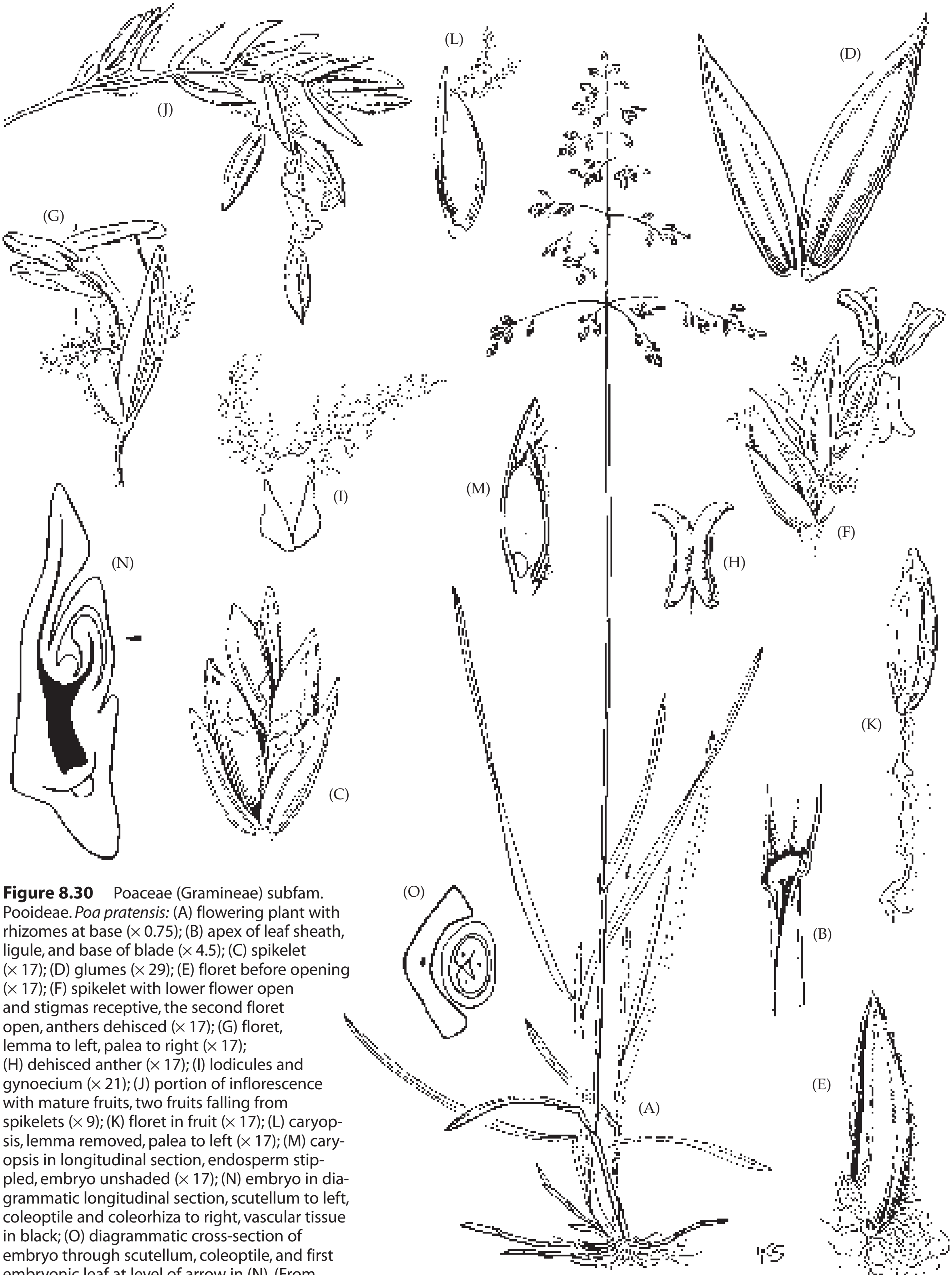


Figure 8.30 Poaceae (Gramineae) subfam. Pooideae. *Poa pratensis:* (A) flowering plant with rhizomes at base (× 0.75); (B) apex of leaf sheath, ligule, and base of blade (× 4.5); (C) spikelet (× 17); (D) glumes (× 29); (E) floret before opening (× 17); (F) spikelet with lower flower open and stigmas receptive, the second floret open, anthers dehisced (× 17); (G) floret, lemma to left, palea to right (× 17); (H) dehisced anther (× 17); (I) lodicules and gynoecium (× 21); (J) portion of inflorescence with mature fruits, two fruits falling from spikelets (× 9); (K) floret in fruit (× 17); (L) caryopsis, lemma removed, palea to left (× 17); (M) caryopsis in longitudinal section, endosperm stippled, embryo unshaded (× 17); (N) embryo in diagrammatic longitudinal section, scutellum to left, coleoptile and coleorhiza to right, vascular tissue in black; (O) diagrammatic cross-section of embryo through scutellum, coleoptile, and first embryonic leaf at level of arrow in (N). (From Campbell 1985, *J. Arnold Arbor.* 66: p. 155.)

locule and 1, subapical to nearly basal ovule. **Fruit a single-seeded caryopsis (grain)** with fruit wall fused to the seed (or less often fruit wall free from the seed, and an achene, utricle, or berry); often associated with parts of the spikelet for dispersal. **Embryo with a highly modified cotyledon (scutellum), lateral in position** (Figures 8.30 and 8.31).

Floral formula: *, -2-, (1–)3(–6), $\underline{2–3}$; caryopsis

(Note: Useful in identification are features of the spikelet, including size, plane of compression, presence or absence of glumes, number of florets, presence of sterile or incomplete florets, number of veins on glumes and lem-

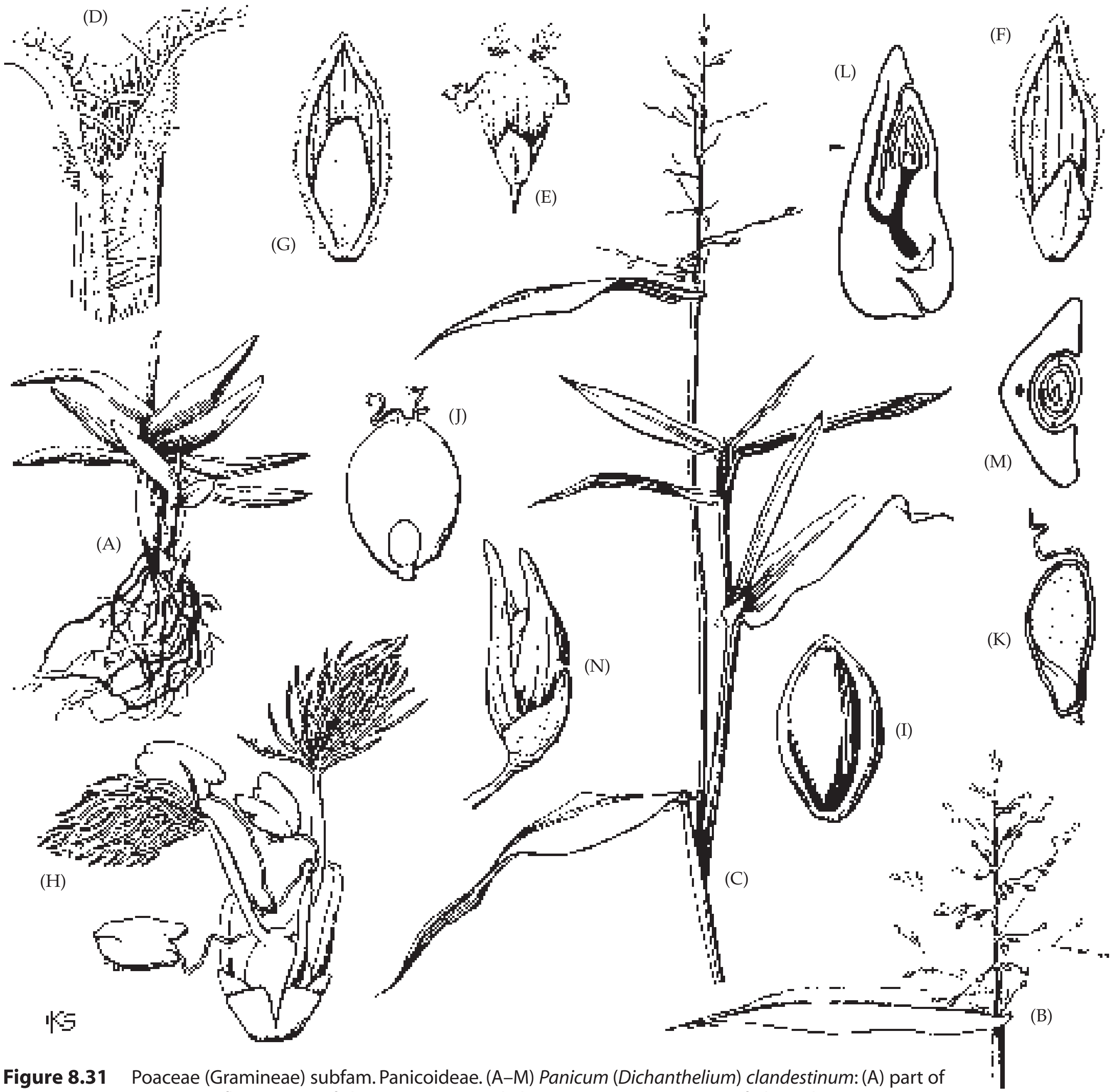


Figure 8.31 Poaceae (Gramineae) subfam. Panicoideae. (A–M) *Panicum* (*Dichanthelium*) *clandestinum*: (A) part of winter rosette (× 0.7); (B) inflorescence of chasmogamous spikelets (× 0.7); (C) upper part of plant, chasmogamous spikelets in fruit or shed from inflorescence, inflorescence of cleistogamous spikelets below (× 0.7); (D) upper part of leaf sheath, base of blade, and ligule (× 8); (E) chasmogamous spikelet at anthesis (× 8); (F) small first and larger second glume (× 14); (G) sterile lemma (pubescent) and sterile palea (× 14); (H) flower of cleistogamous spikelet (× 27); (I) fertile lemma (behind) and palea enclosing mature caryopsis (× 14); (J) mature caryopsis (× 14); (K) longitudinal section of caryopsis, embryo to left, endosperm stippled (× 16); (L) embryo in diagrammatic longitudinal section, scutellum to left, coleoptile and coleorhiza to right, vascular tissue in black, note mesocotyl above trace to scutellum (× 16); (M) diagrammatic cross-section of embryo through scutellum, coleoptile, and first embryonic leaf, at level of arrow in (L) (× 16). (N) *P. anceps:* spikelet in fruit (× 14). (From Campbell 1985, *J. Arnold Arbor.* 66: p. 172.)

mas, presence or absence of awns, and aggregation of spikelets in secondary inflorescences.)

Distribution and ecology: Cosmopolitan; in desert to freshwater and marine habitats, and at all but the highest elevations. Native grasslands develop where there are periodic droughts, level to gently rolling topography, frequent fires, and in some instances grazing and certain soil conditions. Communities dominated by grasses, such as the North American prairie and plains, South American pampas, African veldt, and Eurasian steppes, account for about 24% of the Earth's vegetation. Woody bamboos play important roles in forest ecology in tropical and temperate Asia.

Genera/species: ca. 650/8700. Important genera are listed below under the major subgroups.

Economic plants and products: The economic importance of grasses lies in their paramount role as food: about 70% of the world's farmland is planted in crop grasses, and over 50% of humanity's calories come from grasses. People have cultivated cereals for at least 10,000 years. From the beginning of their domestication, wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), and oats (*Avena sativa*) in the Near East, sorghum (*Sorghum bicolor*) and pearl millet (*Pennisetum americanum*) in Africa, rice (*Oryza sativa*) in southeastern Asia, and maize or corn (*Zea mays*) in Meso-America have made possible the rise of civilization. In terms of global production, the first four crops are grasses: sugarcane (*Saccharum officinale*), wheat, rice, and maize. Barley and sorghum are in the top twelve. Grasses are also used for livestock food, erosion control, turf production, and as a sugar source for the fermentation of alcoholic beverages, such as beer and whiskey. Bamboos are economically important in many tropical areas for their edible young shoots, fiber for paper, pulp for rayon, and strong stems for construction.

Subfamilial phylogenetic relationships: Grasses are easily recognized, and their monophyly has been supported by morphological and DNA characters. Traditionally the family has been subdivided into about five subfamilies and 60 tribes. Within the family, embryological and DNA data strongly support a large clade consisting of three subfamilies: "Arundinoideae," Chloridoideae, and Panicoideae (often called the PACC clade; see Figure 8.32; Clark et al. 1995; Soreng and Davis 1998), characterized by embryological features. The remainder of the family is usually divided into subfamilies Bambusoideae s. s., Oryzoideae, and Pooideae. "Arundinoideae" are clearly not monophyletic as generally defined; their

Key to Major Clades of Poaceae

1. Specialized cells, called arm and/or fusoid cells, within the leaves of most members; stamens often more than 3 2
1. Arm and fusoid cells absent; stamens 3 or fewer 3
2. Stigmas 3; mostly trees .... Bambusoideae
2. Stigmas 2; herbs .... Oryzoideae
3. Spikelets compressed perpendicular to plane of arrangement of glumes and florets, not breaking at maturity into separate florets but falling as a unit, with 1 caryopsis-bearing floret .... Panicoideae
3. Spikelets not compressed, or compressed parallel to plane of arrangement of glumes and florets, breaking up at maturity above the glumes, mostly with more than 1 caryopsis-bearing floret 4
4. Veins in leaves separated by more than 4 cells; bundle sheaths with few chloroplasts, appearing clear in cross-section (C_3 leaf anatomy); bicellular microhairs present or lacking in leaf epidermis 5
4. Veins in leaves separated by 2–4 cells; bundle sheaths with numerous chloroplasts, appearing distinctly green in cross-section (C_4 anatomy); bicellular microhairs present in leaf epidermis 6
5. Bicellular microhairs absent in leaf epidermis; subsidiary cells parallel-sided; plants variable in habit, but mostly less than 1 m tall .... Pooideae
5. Bicellular microhairs present in leaf epidermis; subsidiary cells dome-shaped, plants generally over 1 m tall .... *Phragmites* and relatives
6. Bicellular microhairs generally bulbous; awns, if present, unbranched .... Chloridoideae
6. Bicellular microhairs ± linear, awns divided into 3 parts .... *Aristida* and relatives

members (e.g., *Aristida*, *Chasmanthium*, *Micraira*, *Phragmites*, and *Danthonia*) are spread over much of the PACC clade (Figure 8.32; Barker et al. 1995). Chloridoideae and Panicoideae are generally found to be monophyletic, depending upon the taxa that are included. Similarly, there is structural and DNA support for recognition of Pooideae, Oryzoideae, and Bambusoideae, at least when narrowly defined.

For each of the four major subfamilies—Bambusoideae, Chloridoideae, Panicoideae, and Pooideae—geographic distribution, internal phylogenetic and systematic structure, and important genera are presented. Characters distinguishing the major subfamilies are given in the accompanying key; note that the best structural characters distinguishing subfamilies are anatomical, but morphological characters are used whenever possible.

Bambusoideae, as defined here, are mainly woody plants, and are almost exclusively tropical in distribution. The woody bamboos, with stems up to 40 m in height, certainly do not resemble the turf in lawns. Flowering in many woody bamboos is also unusual, occurring in cycles of up to 120 years. Even though individual stems live for only one or a few decades, some form of "clock" directs stems to flower all at once throughout the range of a species. Important genera of woody bamboos are *Bambusa* (120 spp.), *Chusquea* (100), *Arundinaria* (50), *Sasa* (50), and *Phyllostachys* (45).

Several other kinds of grasses are often associated with Bambusoideae s. s. Two small subfamilies, Anomochlooideae (including *Anomochloa* and *Streptochaeta*) and Pharoideae (including *Pharus*), are herbaceous and have morphologically unique spikelets that are difficult to interpret. They appear to be the basal lineages within the family (see Figure 8.32; Clark et al. 1985; Soreng and Davis 1998). Another group, the oryzoid grasses (i.e., subfam. Oryzoideae), are aquatic or wetland herbs. The most widely known oryzoids are the commercially important Asian rice (*Oryza sativa*) and North American wild rice (*Zizania aquatica*).

Pooideae are largely temperate in distribution, especially in the Northern Hemisphere. Important genera include several cereals (wheat, barley, oats; see above under economic plants and products) as well as rye (*Secale cereale*), turf grasses (e.g., bluegrasses, *Poa*, 500 spp.), fescues (*Festuca*, 450), pasture grasses (e.g., *Phleum*, *Dactylis*), and some weeds (e.g., *Agrostis*, 220, and *Poa*). Other important grasses of this subfamily are *Stipa* (300), *Calamagrostis* (270), *Bromus* (150), and *Elymus* (150).

Chloridoideae bear distinctive and probably apomorphic bicellular hairs on the leaf epidermis and uniformly show C_4 photosynthesis. The subfamily is best developed in arid and semiarid tropical regions, where its C_4 photosynthesis is presumably advantageous. Centers of distribution in Africa and Australia suggest a Southern Hemisphere origin. Some important genera are *Eragrostis* (350 spp.), *Muhlenbergia* (160), *Sporobolus* (160), *Chloris* (55), *Spartina* (15), and *Eustachys* (10).

Panicoideae have long been recognized taxonomically because of their distinctive spikelets (see key to Poaceae). The subfamily is primarily tropical and contains two large tribes, Andropogoneae and Paniceae, along with a number of smaller groups. Andropogoneae are relatively easy to recognize because the spikelets are often paired and grouped into a linear inflorescence. Paniceae are not as homogeneous as Andropogoneae.

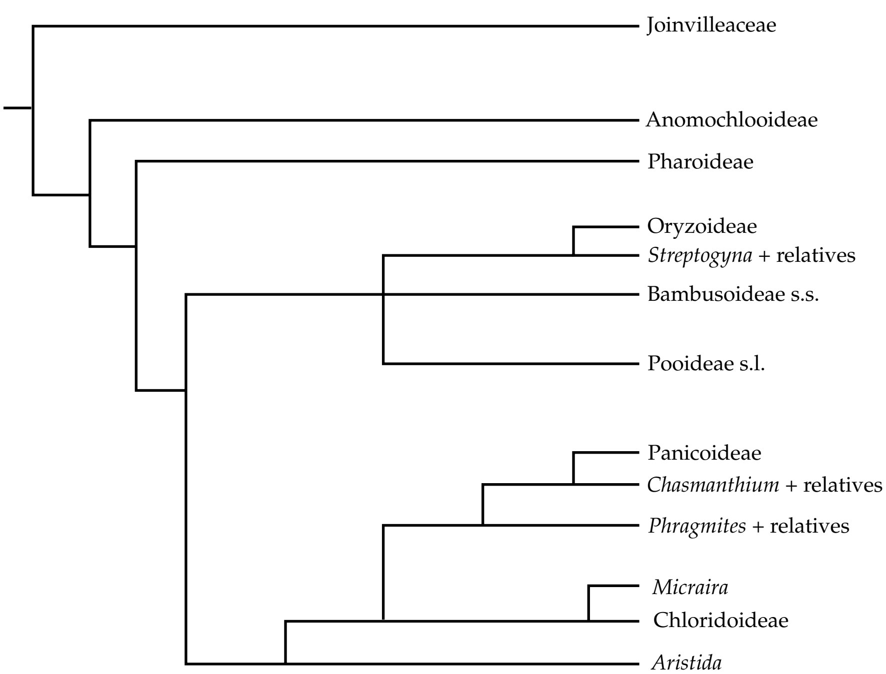


Figure 8.32 A phylogeny of Poaceae. Panicoideae, *Chasmanthium* + relatives, *Phragmites* + relatives, *Micraira*, Chloridoideae, and *Aristida* make up the PACC clade. (Modified from Clark et al. 1995.)

Important genera include *Panicum* (470 spp.), *Paspalum* (330), *Andropogon* (100), *Setaria* (100), *Sorghum* (20), and *Zea* (4).

The so-called arundinoid grasses occur mostly in the Southern Hemisphere. There is considerable structural and genetic diversity among these grasses, which range from small desert species (*Aristida*, 250 spp.) to giant wetland reeds (*Phragmites*). It is clear that they are not monophyletic.

Discussion: Poaceae rank behind Asteraceae, Orchidaceae, and Fabaceae in number of species, but are first in global economic importance and unsurpassed among angiosperms in land surface area dominated. The family's monophyly is strongly supported by phenotypic characters (presence of lodicules, spikelets with glumes and florets made up of a lemma and palea, fruit a caryopsis, and embryo and pollen wall features) as well as *rbcL* and *ndhF* sequences. Similarities to sedges (Cyperaceae) in habit and spikelets represent convergent evolution. Sedges are more closely related to rushes (Juncaceae), and Poaceae belong to Poales, other members of which are small families of herbs growing in the Southern Hemisphere and especially the Pacific Ocean region. The largest family other than Poaceae in Poales is Restionaceae, which grow mostly in South Africa and Australia, and the closest extant relative of Poaceae is Joinvilleaceae of the Pacific region. The monophyly of Poales is supported by both morphological and DNA characters; morphological synapomorphies include the presence of silica bodies, orthotropous ovules, nuclear endosperm development, spikelet composition, fruit, and scutellum characters (Kellogg and Linder 1995; Soreng and Davis 1998).

Grasses have been successful ecologically and have diversified extensively due to several key adaptations. The grass spikelet protects the flowers while permitting pollination when the lodicules open the spikelet. Spikelets have various adaptations for fruit dispersal. Versatility in breeding systems, including inbreeding and agamospermy, helps make some grasses successful colonizers. C_3 and C_4 leaf anatomy adapt grasses to a wide range of habitats. Meristems are located at the bases of the internodes, leaf blades, and sheaths. As a result, grasses tolerate fire and grazing better than many other plants. Development of grasslands during the Miocene epoch (from around 25 to 5 million years ago) may have fostered the evolution of large herbivores, an important food source and stimulus for the evolution of *Homo sapiens*.

The economic and ecological importance of the family has motivated considerable systematic study. Early in the nineteenth century, differences between the spikelets of pooids and panicoids led to division of the family into these two groups. Early in the twentieth century, leaf epidermal characters and chromosome number forged the separation of chloridoid grasses from the pooids. In the middle of the twentieth century, internal leaf anatomy and embryological features set up the recognition of five to eight subfamilies. Differences in leaf anatomy are associated with different photosynthetic pathways. The C_3 pathway is more efficient in regions of cool and cold climate, whereas C_4 photosynthesis is advantageous in regions of high temperatures and low soil moisture. C_3 anatomy is the plesiomorphic state in the family and is found in all Bambusoideae and Pooideae, a majority of "Arundinoideae," and a minority of Panicoideae. Almost all Chloridoideae are C_4.

Phylogenetic studies based on *rbcL* and *ndh*F sequences agree with many phylogenetic relationships inferred from structural data. The arundinoid-Chloridoideae-Panicoideae clade is supported by the embryological feature of a long mesocotyl internode (see Figure 8.31L), and this clade emerges strongly in analyses of *rbcL* and *ndh*F and almost all other molecules. The general picture of grass phylogeny is that (1) the basalmost clades are broad-leaved tropical forest grasses, such as Anomochlooideae and Pharoideae, (2) there is support for four large subfamilies (Bambusoideae s. s., Chloridoideae, Panicoideae, and Pooideae), and (3) bambusoid relatives and arundinoid grasses are spread over the phylogenetic tree (see Figure 8.32).

References: Barker et al. 1995; Campbell 1985; Clark et al. 1995; Clark and Judziewicz 1996; Clayton and Renvoize 1986; Kellogg and Linder 1995; Kellogg and Watson 1993; Soderstrom et al. 1987; Soreng and Davis 1998; Tucker 1996; Watson and Dallwitz 1992.

Zingiberales

The monophyly of Zingiberales is supported by morphology (Dahlgren and Rasmussen 1983; Kress 1990, 1995; Stevenson and Loconte 1995), *rbcL* sequences (Chase et al. 1993, 1995b; Duvall et al. 1993; Smith et al. 1993), *rbcL* and *atpB* sequences (Chase, personal communication), and 18S rDNA sequences (Soltis et al. 1997). Putative synapomorphies include large herbs with vessels more or less limited to the roots; presence of silica cells; leaves clearly differentiated into a petiole and blade, with pinnate venation, often tearing between the secondary veins, with the blade rolled into a tube in bud, and the petiole (and midvein) with enlarged air canals, flowers bilateral (or, in more specialized taxa, lacking a plane of symmetry); pollen usually lacking an exine; ovary inferior; and the seeds with variably developed perisperm (Figure 8.33A). The monophyly of the order also was supported by Tomlinson's (1962) morphological and anatomical study.

Phylogenetic relationships within core Zingiberales are fairly well understood due to careful morphological and cpDNA analyses (Dahlgren and Rasmussen 1983; Kress 1990, 1995; Tomlinson 1962, 1969a). Cannaceae, Marantaceae, Zingiberaceae, and Costaceae form a clade based on reduction of the androecium to only a

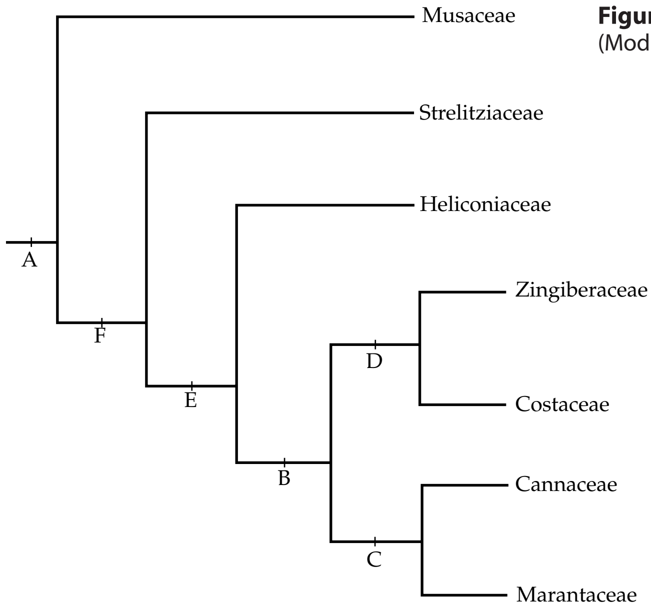


Figure 8.33 A phylogeny of Zingiberales, as discussed in the text. (Modified from Kress 1990, 1995.)

single functional stamen, presence of showy staminodes, seeds with more perisperm than endosperm, lack of raphide crystals in vegetative tissues, and leaves that are not easily torn (Figure 8.33B). Within this clade, Marantaceae and Cannaceae are hypothesized to be sister taxa, as evidenced by their flowers that lack a plane of symmetry, androecium with only half of one stamen fertile (with the other half of this stamen expanded and staminodial), and presence of only one row of ovules per locule (Figure 8.33C). Zingiberaceae and Costaceae constitute a clade that is supported by the unusual feature of the single functional stamen more or less grasping the style, a ligule at the apex of the leaf sheath, connate sepals, fused staminodes, and reduction of two of the three stigmas (Figure 8.33D). Heliconiaceae, Stre-

Key to Major Families of Zingiberales

1. Functional stamens 5 or rarely 6 and staminodes lacking or inconspicuous; raphide crystals lacking; leaf blades typically tearing between the secondary veins 2
1. Functional stamens 1 or 1/2 and staminodes conspicuous, showy; raphide crystals present; leaf blades usually not tearing between the secondary veins 4
2. Leaves spirally arranged, the petiole with 1 row of air canals; latex-producing cells present; fruits berries or fleshy capsules; perianth of tepals, 5 connate and 1 member of the inner whorl distinct .... Musaceae
2. Leaves 2-ranked, the petiole (in cross-section) with 2 rows of air canals; latex-producing cells lacking; fruits dry capsules, opening to reveal arillate seeds, or fleshy schizocarps; perianth of sepals and petals, or tepals, but not as above 3
3. Ovules numerous in each locule; fruit a capsule; seeds with a colorful aril; flowers with a calyx and corolla, the sepals differing in color from the petals, which are dimorphic .... Strelitziaceae
3. Ovules 1 in each locule; fruit a schizocarp, splitting into usually 3 drupelike segments; flowers with tepals, 5 connate and 1 member of the outer whorl distinct .... Heliconiaceae
4. Androecium represented by a single functional stamen; flowers bilaterally symmetrical; sepals connate; leaf sheath associated with a ligule 5
4. Androecium represented by 1/2 functional stamen; flowers without a plane of symmetry; sepals distinct; leaf sheath lacking a ligule 6
5. Leaves 2-ranked, sheath usually open; plants with ethereal oils (spicy fragrant); at least 2 staminodes connate, forming a liplike structure; pollen exine very reduced .... **Zingiberaceae**
5. Leaves 1-ranked, and spiral, sheath closed, at least initially; plants lacking ethereal oils; staminodes not connate; pollen with a well developed exine .... Costaceae
6. Ovule solitary in a single locule or in each of the 3 locules of the ovary; leaves petiolate, with an upper pulvinus; flowers in mirror-image pairs, the style held under pressure by modified and hooded staminode, released during pollination; fruit not warty .... **Marantaceae**
6. Ovules ± numerous in each of the 3 locules of the ovary; leaves ± lacking a petiole and upper pulvinus; flowers not in mirror-image pairs, the style not held under pressure or forcefully moving during pollination; fruit warty .... **Cannaceae**

litziaceae, and Muscaceae constitute a paraphyletic complex. The Heliconiaceae are probably the sister taxon to the Cannaceae-Marantaceae-Zingiberaceae-Costaceae clade, as supported by the putative synapomorphies of a sterile outer median stamen, connate petals, and details of the root anatomy (Figure 8.33E). Strelitziaceae are hypothesized to be sister to the clade containing all of the above-listed families, all having 2-ranked leaves and arillate seeds (Figure 8.33F). Musaceae (banana family) probably represent the sister group to a clade containing the remaining families of the order; this family has retained the plesiomorphic condition of spirally arranged leaves.

Zingiberales contain 8 families and about 1980 species; major families include **Cannaceae**, **Marantaceae**, **Zingiberaceae**, Costaceae, Heliconiaceae, Strelitziaceae, and Musaceae.

References: Chase et al. 1993, 1995b; Dahlgren and Rasmussen 1983; Duvall et al. 1993; Kress 1990, 1995; Smith et al. 1993; Soltis et al. 1997; Tomlinson 1962, 1969a.

Zingiberaceae Lindley
(Ginger Family)

Small to large, **spicy-aromatic herbs, scattered secretory cells containing ethereal oils, various terpenes, and phenyl-propanoid compounds**. Hairs simple. *Leaves* alternate, *2-ranked*, simple, entire, usually petiolate, *with a well-developed blade, pinnate venation*, sheathing base, *and a ligule*; petiole with air canals, these separated into segments by diaphragms composed of stellate-shaped cells; stipules lacking. Inflorescences determinate, but often appearing indeterminate, the cymose units in the axils of usually conspicuous bracts. *Flowers* bisexual, *bilateral*, usually lasting for only 1 day. *Sepals 3, connate*, imbricate. *Petals 3, connate, with one lobe often larger than the others*, imbricate. *Stamen 1, grooved, grasping the style*; staminodes usually 4, **2 large, connate, and forming a liplike structure (labellum)**, *and 2 smaller, these distinct or connate with the 2 larger staminodes*; pollen grains monosulcate or lacking apertures, exine very reduced. Carpels 3, connate; *ovary inferior*, with usually axile placentation; style enveloped in groove between pollen sacs of the anther; stigma 1, funnel-shaped. Ovules ± numerous. **Nectaries 2, positioned atop the ovary. Fruit a fleshy capsule or berry**; seeds usually arillate; endosperm and perisperm present (Figure 8.34).

Floral formula:

X, 3, 2+1, 2•+2• + 1, 3; fleshy capsule, berry

Distribution and ecology: Widespread in tropical regions; chiefly in shaded to semi-shaded forest understory habitats; occasionally in wetlands. Asexual reproduction occurs in some species of *Globba*.

Genera/species: 50/1000. ***Major genera:*** *Alpinia* (150 spp.), *Amomum* (120), *Zingiber* (90), *Globba* (70), *Curcuma* (60), *Kaempferia* (60), and *Hedychium* (50). The family is represented in the continental United States by *Alpinia*, *Curcuma*, *Hedychium*, and *Zingiber* (all rarely naturalized).

Economic plants and products: The family contains several important spices, including *Zingiber* (ginger), *Curcuma* (turmeric), and *Amomum* and *Elettaria* (cardamon). The rhizomes of several species of *Curcuma* are used as a starch source. *Alpinia* (shell ginger), *Curcuma* (hidden lily), *Hedychium* (garland lily), *Globba*, *Nicolaia* (torch ginger), *Renealmia*, and *Zingiber* (ginger) contain ornamental species.

Discussion: The monophyly of the Zingiberaceae has been supported by DNA (Smith et al. 1993; Kress 1995) and morphology (Kress 1990). The family is closely related to the Costaceae, which often is included within Zingiberaceae as a subfamily (see Rogers 1984).

Flowers of Zingiberaceae are diverse in color and form and are mainly pollinated by bees, moths, butterflies, and birds. Many species are outcrossing, but self-pollination and vegetative reproduction also occur. Birds are the most common dispersal agents; the fleshy capsules are usually colorful and often contrast with the brightly colored arillate seeds.

References: Burtt and Smith 1972; Dahlgren et al. 1985; Rogers 1984; Kress 1990, 1995; Smith et al. 1993.

Marantaceae Peterson
(Prayer Plant Family)

Herbs, with erect stem and short, tuberlike, starchy rhizomes. Hairs simple and surrounded by inflated epidermal cells. *Leaves* alternate, *usually 2-ranked*, simple, entire, petiolate, **with an upper pulvinus**, *a well-developed blade* **that folds upward at night**, *and pinnate venation* **with sigmoid secondary veins and evenly spaced cross-veins**, sheathing at base, lacking a ligule; petiole with air canals, these separated into segments by diaphragms composed of stellate-shaped cells; stipules lacking. Inflorescences determinate, but often appearing indeterminate, terminal. *Flowers* bisexual, *lacking a plane of symmetry* **but arranged in mirror-image pairs**. *Sepals 3, distinct*, imbricate. *Petals 3, connate*, imbricate. *Stamen 1, partly fertile and partly staminodial*; filament connate with staminodes and adnate to corolla; *anther unilocular* (*i.e., a half-anther, the other half expanded and sterile*), **depositing pollen onto the style before the flower opens**; *staminodes usually 3 or 4, petaloid and varying in shape*, basally connate and adnate to corolla, **1 from the inner androecial whorl forming a hooded structure with 1 or 2 small appendages (i.e., the hooded or cucullate staminode that holds the curved style under tension before the flower is triggered by a floral visitor), the second from**

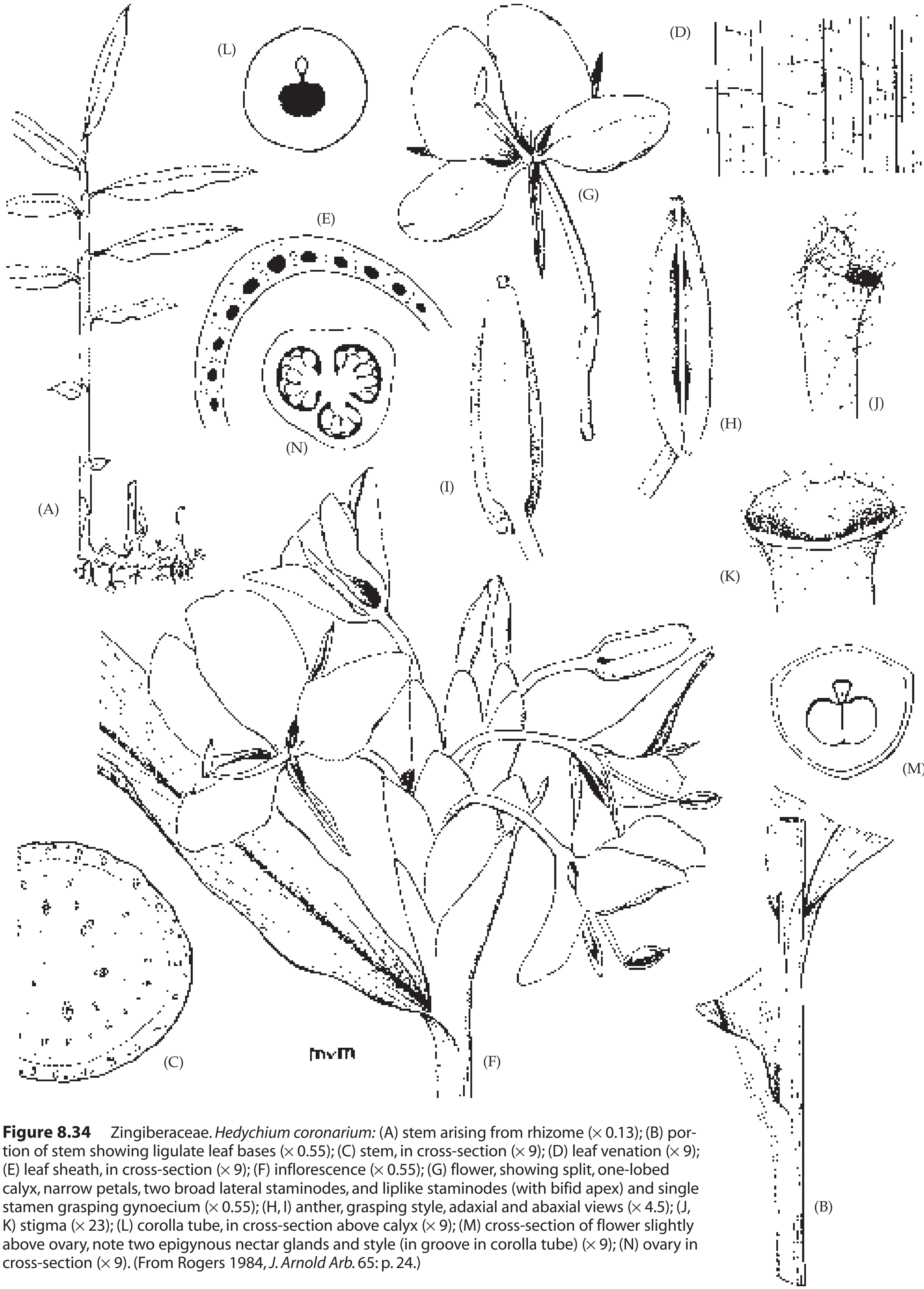


Figure 8.34 Zingiberaceae. *Hedychium coronarium:* (A) stem arising from rhizome (× 0.13); (B) portion of stem showing ligulate leaf bases (× 0.55); (C) stem, in cross-section (× 9); (D) leaf venation (× 9); (E) leaf sheath, in cross-section (× 9); (F) inflorescence (× 0.55); (G) flower, showing split, one-lobed calyx, narrow petals, two broad lateral staminodes, and liplike staminodes (with bifid apex) and single stamen grasping gynoecium (× 0.55); (H, I) anther, grasping style, adaxial and abaxial views (× 4.5); (J, K) stigma (× 23); (L) corolla tube, in cross-section above calyx (× 9); (M) cross-section of flower slightly above ovary, note two epigynous nectar glands and style (in groove in corolla tube) (× 9); (N) ovary in cross-section (× 9). (From Rogers 1984, *J. Arnold Arb.* 65: p. 24.)

the inner androecial whorl forming a callose thickened structure, "the callose staminode," which often serves as a landing platform for insect visitors and helps to brace the hooded staminode, and 1 or 2 from the outer androecial whorl ± petal-like; pollen grains lacking apertures, exine very reduced. Carpels 3, connate; *ovary inferior*, with axile placentation, but 2 carpels often sterile and ± reduced; **style curved, held under tension by the hooded staminode that, when triggered by an insect, releases the style, which then elastically curves downward, scraping pollen from the insect's body and dusting it with pollen (held in a small cavity below the stigma)**; stigma 1, in depression between 3-lobed apex of style. **Ovules 1 in each locule, or solitary in the single functional carpel**. Nectaries in septa of ovary. *Fruit a loculicidal capsule or berry*; seeds usually arillate; embryo usually curved; endosperm and perisperm present.

Floral formula:

$, 3, 3, 1• or 2•+2• + ½ + ½•, $\overline{3}$; capsule, berry

Distribution and ecology: Widely distributed in tropical and subtropical regions. Most occur in tropical rain forest margins and clearings or in wetlands.

Genera/species: 30/450. ***Major genus:*** *Calathea* (250 spp.). The family is represented in the continental United States only by *Thalia* (native) and *Maranta* (rarely naturalized).

Economic plants and products: West Indian arrowroot starch is obtained from the rhizomes of *Maranta arundinacea*. *Calathea*, *Ctenanthe*, *Maranta* (arrowroot, prayer plant), and *Thalia* are cultivated because of their decorative leaves.

Discussion: The monophyly of Marantaceae is supported by DNA and morphology (Kress 1990, 1995; Smith et al. 1993). Phylogenetic relationships within the family are poorly understood, but genera with only a single functional carpel (e.g., *Ischnosiphon*, *Maranta*, and *Thalia*) may form a clade (Maranteae). Genera with 3-locular ovaries (e.g., *Calathea*) are placed in the Phrynieae, which is probably paraphyletic.

The complex flowers of Marantaceae are mainly bee-pollinated and outcrossing; nectar provides the pollinator reward. The arils associated with the seeds of Marantaceae are often brightly colored and contain deposits of lipids, suggesting dispersal by birds or ants. Fruits of *Thalia* are water dispersed.

Some have deep red abaxial leaf surfaces, a possible adaptation for efficient usage of light.

References: Andersson 1981; Classen-Bockhoff 1991; Dahlgren et al. 1985; Kress 1990, 1995; Rogers 1984; Smith et al. 1993.

Cannaceae A. L. de Jussieu
(Canna Family)

Rhizomatous herbs; **mucilage canals present in rhizome and erect stem**. Plants glabrous. *Leaves* alternate, *spirally arranged*, simple, entire, ± *lacking a petiole, with a well-developed blade, the midvein of which possesses air canals, with pinnate venation*, sheathing at base, lacking a ligule, pulvinus, and stipules. Inflorescences determinate or indeterminate, terminal, *the main axis triangular in cross-section, with 3-ranked bracts*, each bract usually associated with reduced, 2- or 1-flowered cymes. *Flowers* bisexual, *lacking a plane of symmetry, often lasting only 1 day*. *Sepals 3, distinct*, imbricate. *Petals 3, connate*, imbricate. *Stamen 1*; filament connate with staminodes and adnate to corolla; *anther unilocular* (*i.e., a half-anther, the other half expanded and sterile*); *staminodes usually 3 or 4, petaloid, 1 larger than the others and recurved*, all basally connate and adnate to corolla; pollen grains lacking apertures, exine very reduced. Carpels 3, connate; *ovary inferior*, **externally papillate**, with axile placentation; **style flattened and ± petaloid**; stigma 1, extending along one edge of the style. Ovules ± numerous in each locule. Nectaries in septa of ovary. **Fruit a warty capsule**, usually splitting irregularly by disintegration of the fruit wall; *seeds spherical, black, associated with a tuft of hairs* (*modified aril*); endosperm and perisperm present (Figure 8.35).

Floral formula:

$, 3, 3, 1• or 2•+ 2• + ½ + ½•, $\overline{3}$; warty capsule

Distribution and ecology: Occurring in tropical and subtropical regions of the Americas; some species naturalized in the Old World; plants of moist openings in tropical forests, along rivers, or in wetlands.

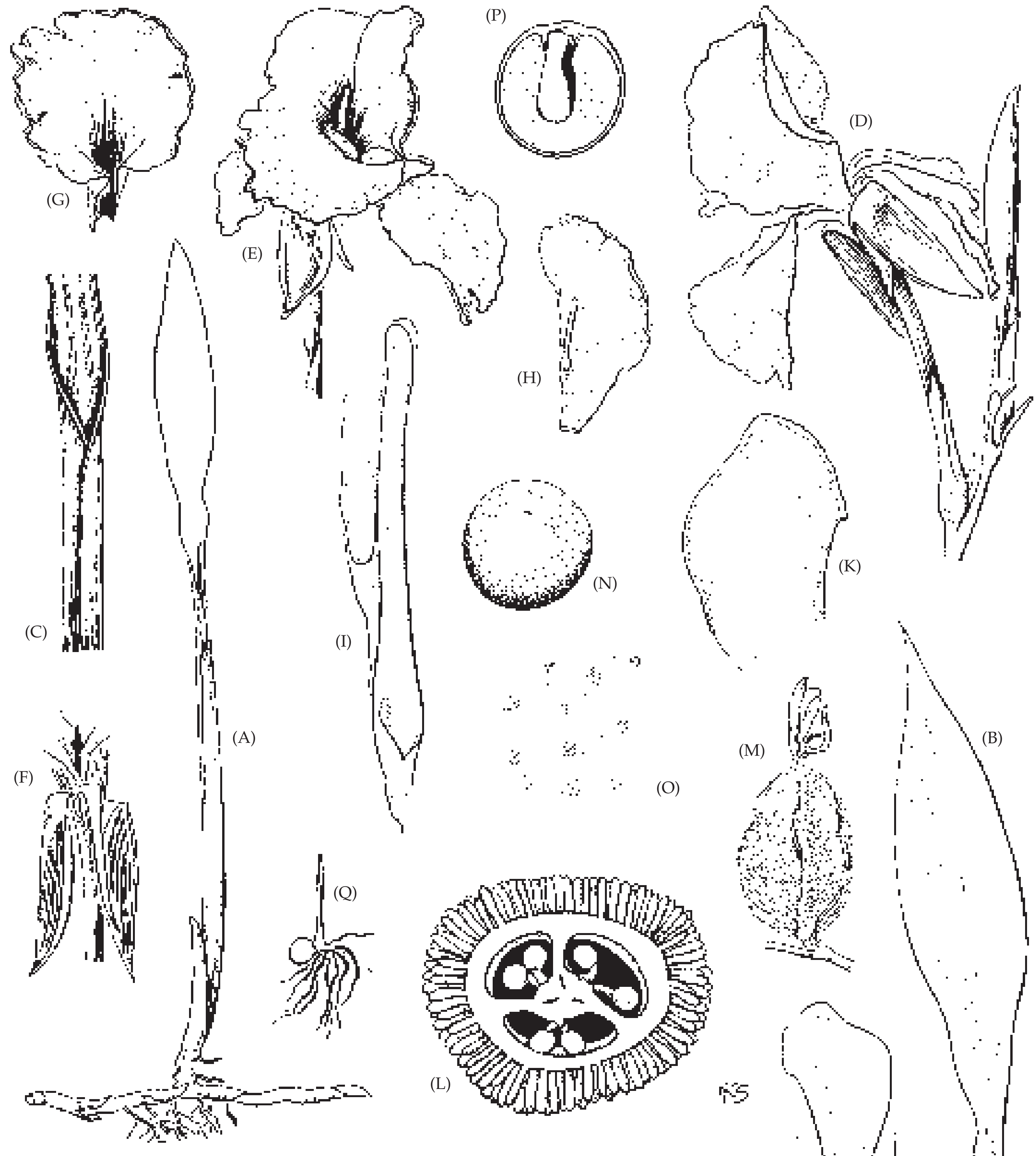
Genera/species: 1/9. ***Genus:*** *Canna*. The family is represented in the continental United States by a few species of *Canna*.

Economic plants and products: The rhizomes of *Canna edulis* (Queensland arrowroot) are used as a starch source. Several species and various hybrids (e.g., *C.* x*generalis*) are used as ornamentals.

Discussion: The monophyly of the Cannaceae has been supported by DNA and morphology (Kress 1990, 1995; Smith et al. 1993).

The pollen is deposited on the style before the flower opens, either directly onto or somewhat below the stigma. Most species are selfing. Pollination biology has been poorly studied, but nectar-gathering bees, butterflies, and moths may be the most frequent pollinators. The seeds are often water dispersed and long-lived.

References: Dahlgren et al. 1985; Kress 1990, 1995; Rogers 1984; Smith et al. 1993.



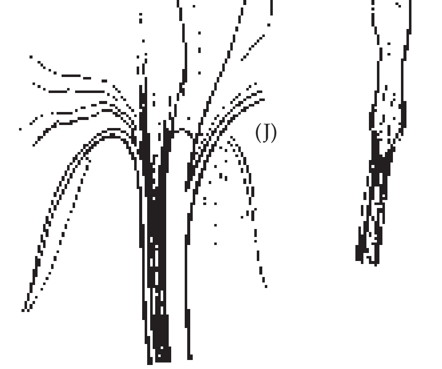


Figure 8.35 Cannaceae. *Canna flaccida:* (A) young shoot from rhizome (× 0.6); (B) blade and portion of petiole (× 0.6); (C) detail of upper part of sheathing petiole (× 1.15); (D) inflorescence, with open flower and flower bud, on open flower note sepals, reflexed petals, and five petaloid staminodes (× 0.75); (E) open flower, the fertile half-anther and tip of stigma visible in center (× 0.75); (F) detail of flower to show reflexed petals (× 0.75); (G) expanded staminode (× 0.75); (H) fertile stamen with half-anther attached to left margin (× 0.75); (I) detail of half anther after dehiscence (× 4.5); (J) longitudinal section near center of flower to show petals, staminodes, and style adnate to floral tube (× 1.5); (K) tip of style showing stigmatic line, near margin (× 3); (L) ovary, in cross-section, the wall papillate (× 7.5); (M) capsule (× 0.75); (N) seed (× 4.5); (O) detail of seed coat (× 37); (P) seed in section, endosperm stippled (× 4.5); (Q) seedling (× 0.75). (From Rogers 1984, *J. Arnold Arb.* 65: p. 30.)

"MAGNOLIID COMPLEX"

Magnoliales

Magnoliales are considered monophyletic (see Donoghue and Doyle 1989; Qiu et al. 1993) on the basis of *rbcL* sequence characters, along with their septate pith, 2-ranked leaves, 3-merous perianth, boat-shaped pollen grains, seeds with a fleshy seed coat (or aril), and P-type sieve elements that contain one to several protein crystals plus starch grains (or sometimes only starch grains). The group has often been considered part of the ancestral angiosperm complex (Takhtajan 1969, 1980, 1997; Thorne 1974, 1992; Cronquist 1968, 1981, 1988; Dahlgren 1983) or as the basal clade within angiosperms (Donoghue and Doyle 1989). If this is actually the case, then it is noteworthy that the group has retained granular monosulcate pollen (Walker and Walker 1984) and primitive vessels with scalariform perforations. However, *rbcL* sequences (Qiu et al. 1993), rRNA/DNA sequences (Zimmer et al. 1989; Soltis et al. 1997), morphology, and combined evidence from rRNA and morphology (Doyle et al. 1994) suggest that Magnoliales may not be basal within angiosperms. It is therefore possible that pollen with a granular exine is an additional synapomorphy for members of the order (and that the group's common ancestor lost columellate pollen). A similar argument can be made for the presence of paracytic stomates in the Magnoliales (and also Laurales and Illiciales). These families have retained numerous apparently plesiomorphic floral characters such as distinct and often numerous, spirally arranged stamens and carpels, superior ovaries, and seeds with a minute embryo and copious endosperm. The order consists of 6 families and about 2840 species; noteworthy families include **Annonaceae**, **Magnoliaceae**, Myristicaceae, and Degeneriaceae. The *rbcL*-based analyses also place Winteraceae within the order.

References: Canright 1952, 1960; Cronquist 1981, 1988; Dahlgren 1983; Donoghue and Doyle 1989; Doyle et al. 1994; Endress 1986, 1994; Loconte and Stevenson 1991; Qiu et al. 1993; Takhtajan 1969, 1980, 1997; Taylor and Hickey 1992; Thorne 1974, 1992; Walker and Walker 1984; Weberling 1988; Wood 1958; Zimmer et al. 1989.

Magnoliaceae A. L. de Jussieu
(Magnolia Family)

Trees or shrubs; **nodes multilacunar**; *with spherical cells containing ethereal oils* (*aromatic terpenoids*); with alkaloids, usually of the benzyl-isoquinoline type. Hairs simple to stellate. *Leaves alternate*, spiral to 2-ranked, simple, sometimes lobed, *entire*, with pinnate venation, *blade with pellucid dots*; **stipules present, surrounding the terminal bud. Inflorescence a solitary, terminal flower**, but sometimes appearing axillary (on a short shoot). **Flowers** usually bisexual, radial, **with an elongate receptacle**. *Tepals 6 to numerous*, distinct, occasionally the outer 3 differentiated from the others and ± sepal-like, imbricate. *Stamens numerous*, distinct, often with 3 veins; *filaments short and thick, poorly differentiated from the anthers*; anthers with connective tissue often extending beyond the apex of the pollen sacs; pollen grains monosulcate. *Carpels* usually numerous, distinct, *on an elongate receptacle*; ovaries superior, with parietal placentation; stigma usually extending down style on adaxial surface, but sometimes reduced and terminal. Ovules usually 2 per carpel, sometimes several. Nectaries lacking. **Fruit an aggregate of follicles, which usually become closely appressed as they mature and open along the carpel midvein (i.e., abaxial surface)**, sometimes fleshy, with individual fruits becoming fused to one another as they mature, forming an indehiscent or irregularly dehiscent berrylike structure, or an aggregate of samaras; *seed with red to orange, fleshy coat* (except *Liriodendron*), usually dangling from a slender thread; embryo minute; *endosperm homogeneous* (Figure 8.36 and Figure 4.47A).

Key to Major Families of Magnoliales

1. Stamens monadelphous, their filaments connate into a tube or column; seeds arillate ...... Myristicaceae
1. Stamens distinct; seeds not arillate 2
2. Stipules present, sheathing the stem, and enveloping the apical bud; nodes multilacunar; endosperm homogeneous; perianth usually of tepals; receptacle elongate .... **Magnoliaceae**
2. Stipules lacking; nodes 3- to 5-lacunar; endosperm ruminate; perianth of sepals and petals; receptacle short to ± hemispherical 3
3. Carpel 1, the stigma running nearly its entire length; stamens laminar, with 3 veins, not packed into a tight ball; embryo with 3 or 4 cotyledons .... Degeneriaceae
3. Carpels more than 1, often numerous, the stigma ± elongate, but restricted to apical portion of each carpel; stamens short and stout, with an expanded connective, with 1 vein, and usually packed into a ball-like configuration; embryo with 2 cotyledons .... **Annonaceae**

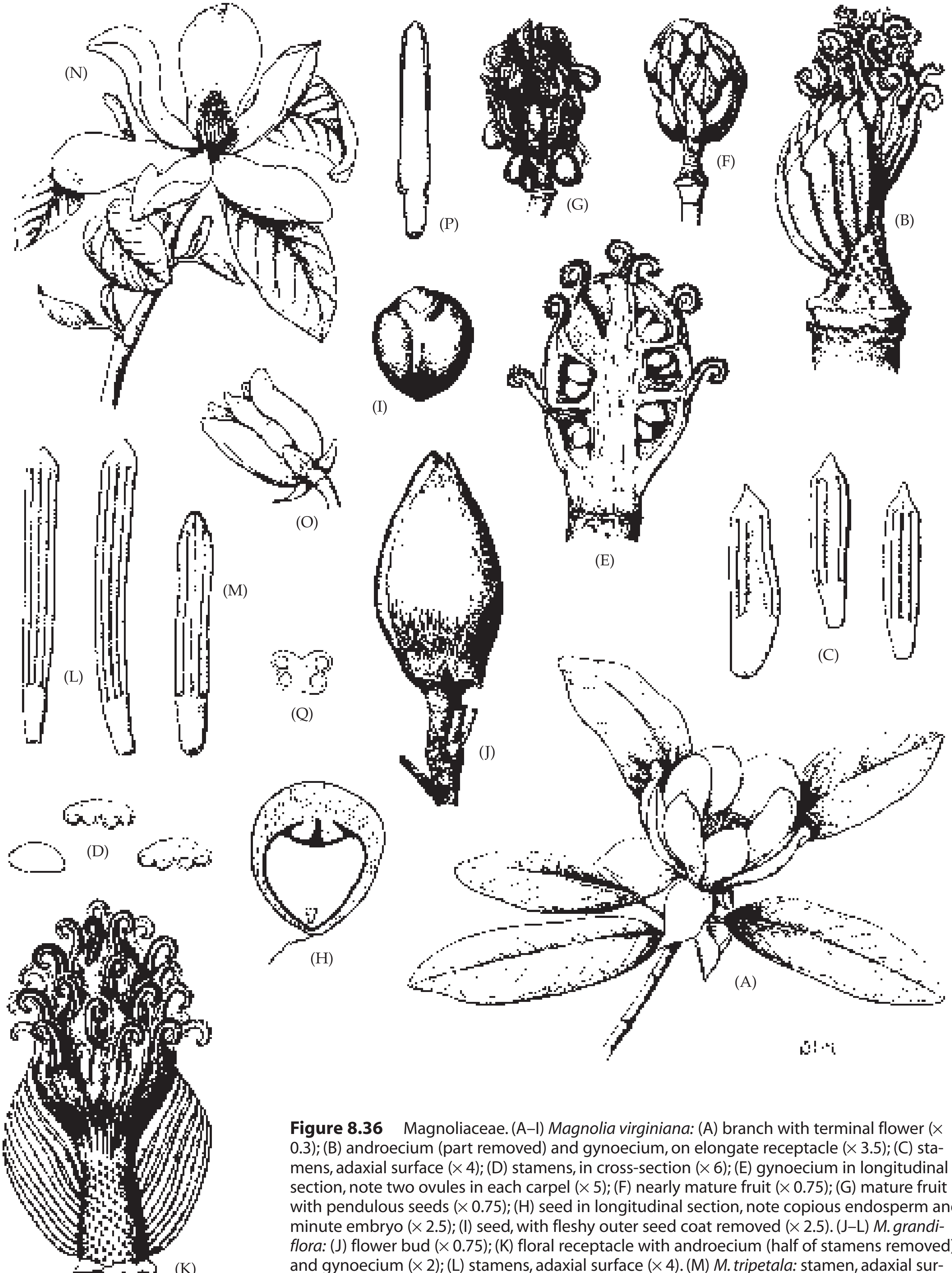


Figure 8.36 Magnoliaceae. (A–I) *Magnolia virginiana:* (A) branch with terminal flower (× 0.3); (B) androecium (part removed) and gynoecium, on elongate receptacle (× 3.5); (C) stamens, adaxial surface (× 4); (D) stamens, in cross-section (× 6); (E) gynoecium in longitudinal section, note two ovules in each carpel (× 5); (F) nearly mature fruit (× 0.75); (G) mature fruit with pendulous seeds (× 0.75); (H) seed in longitudinal section, note copious endosperm and minute embryo (× 2.5); (I) seed, with fleshy outer seed coat removed (× 2.5). (J–L) *M. grandiflora:* (J) flower bud (× 0.75); (K) floral receptacle with androecium (half of stamens removed) and gynoecium (× 2); (L) stamens, adaxial surface (× 4). (M) *M. tripetala:* stamen, adaxial surface (× 4). (N–Q) *M. acuminata:* (N) branch with terminal flower (× 0.3); (O) opening flower bud (× 0.3); (P) stamen, adaxial surface (× 4); (Q) anther in cross-section (× 6). (From Wood 1974, *A student's atlas of flowering plants*, p. 36.)

Floral formula: *, -6–∞-, ∞, $\underline{\infty}$; follicles, samaras

Distribution and ecology: Temperate to tropical regions of eastern North America and eastern Asia, and tropical South America; mainly in moist forests.

Genera/species: 2/220. ***Genera:*** *Magnolia* (218 spp.) and *Liriodendron* (2).

Economic plants and products: *Liriodendron tulipifera* (tulip tree, tulip-poplar) and several species of *Magnolia* are important ornamentals. Species of both genera are also used for timber.

Discussion: Cladistic analyses of *rbcL* sequences (Qiu et al. 1993) and morphological characters support the monophyly of Magnoliaceae. The *rbcL* gene (Qiu et al. 1993, 1995) indicates that the family is composed of a clade represented by *Liriodendron* and another represented by *Magnolia* s. l. Recognition of *Talauma*, *Michelia*, and *Manglietia* leads to a paraphyletic *Magnolia*, and therefore, we circumscribe this genus broadly. The monophyly of the *Liriodendron* clade is supported by lobed leaves, carpels with a restricted stigma, samaroid fruits, and seeds with a thin, more or less dry coat. The monophyly of the *Magnolia* clade is supported by the follicles opening along the abaxial (or outer) surface. These can be described as backward-opening follicles because in all other families with follicular fruits the opening occurs along the adaxial surface.

The showy flowers of Magnoliaceae are mainly pollinated by beetles, which may be trapped in the flower for a period of time, and often eat pollen and/or various floral tissues. *Liriodendron*, however, is bee-pollinated. Protogyny and self-incompatibility lead to outcrossing. The seeds of *Magnolia*, with bright red, pink, or orange, fleshy seed coats, hang on thin threads when the follicle opens and are dispersed by birds. The fleshy syncarps of some of the tropical species are also colorful and bird-dispersed. The samaras of *Liriodendron* are dispersed by wind.

References: Agababian 1972; Canright 1952, 1953, 1960; Endress 1994b; Qiu et al. 1993, 1995; Gottsberger 1977, 1988; Nooteboom 1993; Thien 1974; Weberling 1988b; Wood 1958.

Annonaceae A. L. de Jussieu

(Pawpaw or Annona Family)

Trees, shrubs, or lianas, with conspicuously fibrous bark; *nodes trilacunar*; **vessel elements with simple perforations**, and wood with broad rays; *with scattered spherical cells containing ethereal oils* (*aromatic terpenoids*), and often with scattered sclereids; usually with alkaloids of the benzyl-isoquinoline type; often with tannins. Hairs simple, sometimes stellate, or peltate scales. *Leaves alternate, 2-ranked*, simple, entire, *often short-petioled*, with pinnate venation, blade *with pellucid dots; stipules lacking*. Inflorescences determinate, sometimes reduced to a single flower, terminal or axillary. *Flowers* usually bisexual, radial, opening and then usually **gradually increasing in size before flowering**, *with a short, flat to ± hemispherical receptacle*. *Sepals usually 3*, distinct or slightly connate, valvate or imbricate. *Petals usually 6*, distinct, *the outer 3 often larger and differentiated from the inner*, imbricate and/or valvate. *Stamens usually numerous*, **appearing peltate and packed into a ball-like or disklike configuration**, distinct, with 1 vein; *filaments short and thick, poorly differentiated from the anthers*; anthers with connective tissue extending beyond the apex of anther sacs; pollen grains various, but often monosulcate, sometimes in tetrads or polyads. *Carpels 3 to numerous*, usually distinct, usually spirally arranged; ovaries superior, with parietal placentation; stigma extending down style on adaxial surface, or ± terminal. Ovules 1 to numerous per carpel. Nectaries or food tissues sometimes on inner petals. *Fruit an aggregate of berries*, these sometimes becoming connate as they develop; seeds often arillate; embryo minute; *endosperm ruminate* (Figure 8.37).

Floral formula: *, 3, 6, ∞, $\underline{3\text{–}\infty}$; berries

Distribution and ecology: Widely distributed in tropical and subtropical regions and very characteristic of lowland wet forests.

Genera/species: 128/2300. ***Major genera:*** *Guatteria* (250 spp.), *Xylopia* (150), *Uvaria* (110), *Annona* (110), *Polyalthia* (100), *Artabotrys* (100), and *Rollinia* (65). The family is represented in the continental United States by *Asimina*, *Deeringothamnus*, and *Annona*.

Economic plants and products: Several species of *Annona* and *Rollinia* (cherimoya, guanabana, soursop, sugar apple, sweetsop) produce edible fruits. Berries of *Asimina triloba* (pawpaw) are also edible. Flowers of *Cananga odorata* (ylang-ylang) are used in perfumes, and fruits of *Monodora myristica* are used as a substitute for *Myristica fragrans* (nutmeg; Myristicaceae). *Annona*, *Cananga*, and *Polyalthia* are grown as ornamentals.

Discussion: The monophyly of the family is supported by *rbcL* sequences (Qiu et al. 1993) and several morphological features (Doyle and Lethomas 1994). Tribes and genera have been distinguished by features such as indumentum, structure of the bud, sepal and petal aestivation, shape and texture of anthers, number and shape of carpels, extent of fruit connation, and number of seeds. Fruits in which the carpels become fused as they develop, forming a fleshy syncarp, as in *Annona* or *Rollinia*, are clearly derived in relation to persistently distinct berries, as in *Asimina* or *Cananga*. Connate carpels, as in *Monodora*, are also derived. A few genera, such as *Anaxagorea*, have retained follicle fruits, but most genera are united by the apomorphy of fleshy, indehiscent fruits (berries).

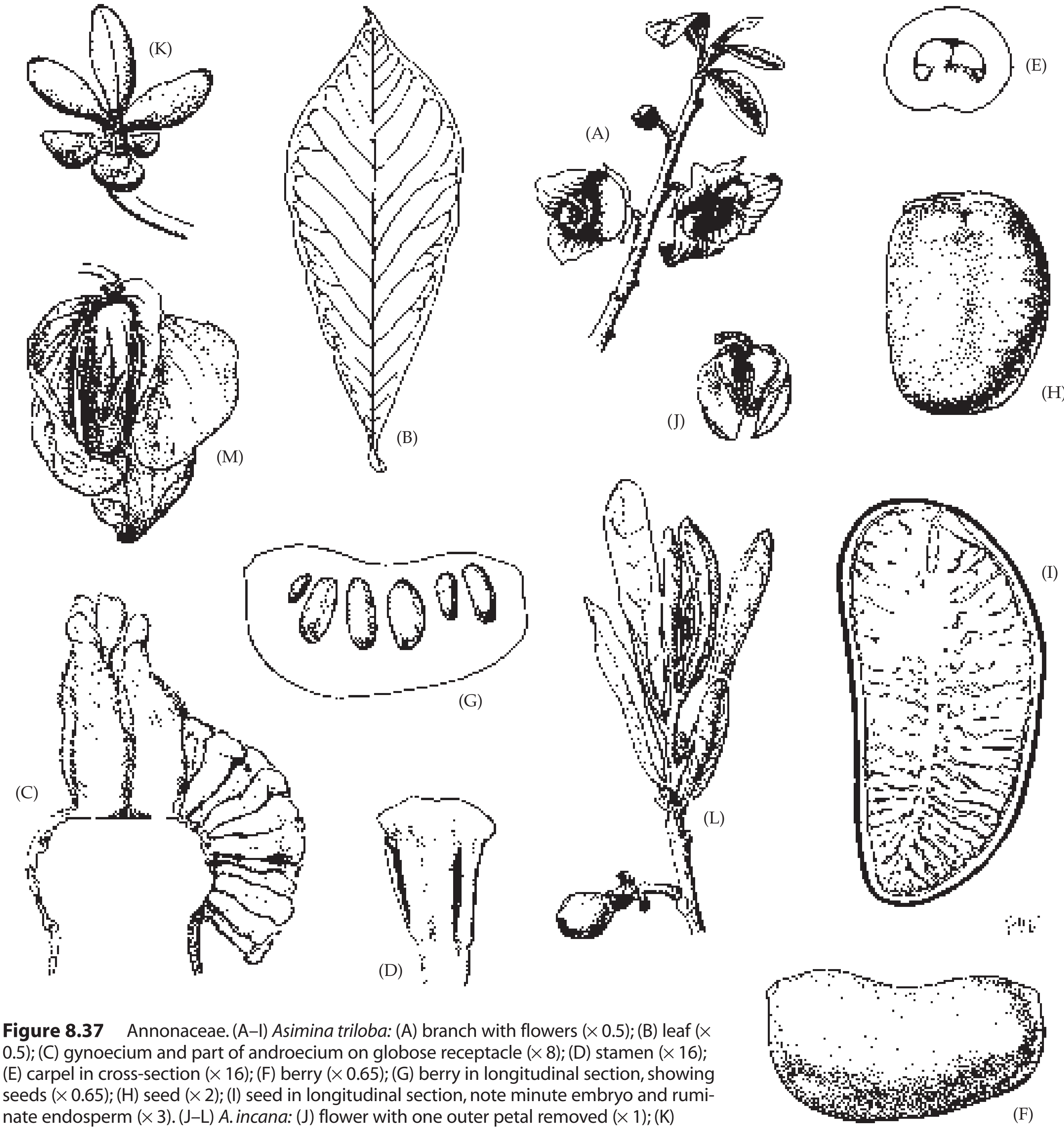


Figure 8.37 Annonaceae. (A–I) *Asimina triloba:* (A) branch with flowers (× 0.5); (B) leaf (× 0.5); (C) gynoecium and part of androecium on globose receptacle (× 8); (D) stamen (× 16); (E) carpel in cross-section (× 16); (F) berry (× 0.65); (G) berry in longitudinal section, showing seeds (× 0.65); (H) seed (× 2); (I) seed in longitudinal section, note minute embryo and ruminate endosperm (× 3). (J–L) *A. incana:* (J) flower with one outer petal removed (× 1); (K) developing fruits, note sepals (× 1.5); (L) twig with young fruit (× 1). (M) *A. obovata:* flower, one outer petal removed (× 0.5). (From Wood 1974, *A student's atlas of flowering plants*, p. 36.)

Flowers of most Annonaceae show various specializations leading to pollination by beetles, including closed flowers, fruity odors, feeding tissues, thick, fleshy petals, and structural protection of the reproductive organs. Some species of *Annona* produce heat; beetles often stay in the flowers overnight, mate there, and frequently eat floral tissues. Many species of Annonaceae produce a sticky stigmatic fluid, which protects the carpels; the often hardened and more or less peltate anther connectives reduce consumption of pollen. Outcrossing in this family is favored by protogyny. The fleshy fruits are dispersed by birds, mammals, and turtles.

References: Doyle and Lethomas 1994; Endress 1994b; Gottsberger 1988; van Heusden 1992; Kessler 1993; Norman and Clayton 1986; Qiu et al. 1993; Thorne 1974; Vander Wyk and Canright 1956; Walker 1971; Wood 1958.

Laurales

Lauraceae A. L. de Jussieu
(Laurel Family)

Trees or shrubs, or twining, parasitic vine (*Cassytha*); *nodes unilacunar*; *with scattered spherical cells containing ethereal oils* (*aromatic terpenoids*); usually with tannins; usually with benzyl-isoquinoline and/or aporphine alkaloids. **Leaves alternate and spiral**, occasionally opposite, *but never 2-ranked,* simple, rarely lobed, **entire**, with usually pinnate venation, or sometimes the lowermost pair of secondary veins more prominent and arching toward apex and venation ± palmate, and all veins clearly visible, connected to adaxial and abaxial leaf surfaces by lignified tissue, blade *with pellucid dots; stipules lacking*. Inflorescences determinate to seemingly indeterminate, axillary. *Flowers* bisexual or unisexual (plants then ± dioecious), radial, *with distinctly concave receptacle*, usually small, pale green, white, or yellow. *Tepals usually 6*, distinct or slightly connate, imbricate. *Stamens usually 3–12; filaments often with pairs of basal-lateral nectar- or odor-producing appendages* (staminodes), the 3 innermost stamens often also reduced to nectar- or odor-producing staminodes; *anthers opening by 2 or 4 flaps that curl from the base upward and pull out the sticky pollen*, often dimorphic; pollen grains without apertures, exine reduced to tiny spines. **Carpel 1**; *ovary superior, with ± apical placentation*; stigma 1, capitate, truncate, lobed, or elongate. *Ovule 1*. **Fruit a drupe or occasionally a 1-seeded berry**, *often associated with the persistent fleshy to woody receptacle* (*and sometimes also tepals*) *that often contrast in color with the fruit* (*i.e., fruit with a cupule*); **embryo large, with fleshy cotyledons; endosperm lacking** (Figure 8.38)**.**

Floral formula: *, 6, 3–12 + paired glands , $\underline{1}$; drupe

Distribution and ecology: Widespread in tropical and subtropical regions and especially diverse in Southeast Asia and northern South America; characteristic of tropical wet forests.

Genera/species: 50/2500. ***Major genera:*** *Litsea* (400 spp.), *Ocotea* (350), *Cinnamomum* (350), *Cryptocarya* (250), *Persea* (200), *Beilschmiedia* (150), *Nectandra* (120), *Phoebe* (100), and *Lindera* (100). The following occur in the continental United States and/or Canada: *Cassytha*, *Cinnamomum*, *Licaria*, *Lindera*, *Litsea*, *Persea*, *Sassafras*, and *Umbellularia*.

Economic plants and products: The family contains spice plants such as *Laurus nobilis* (bay leaves), *Cinnamomum verum* (cinnamon), *C. camphora* (camphor), and *Sassafras albidum* (sassafras). *Persea americana* (avocado) is an important tropical fruit tree. *Beilschmiedia*, *Ocotea*, *Litsea*, and a few other genera contain species used for timber.

Discussion: Lauraceae belong to the large order Laurales, which consists of 9 families and about 3000 species; major families include Calycanthaceae, **Lauraceae**, Monimiaceae, and possibly Chloranthaceae. The order usually has been considered part of the magnolid complex (also including Magnoliales and Illiciales) and represents an early divergent lineage within the angiosperms (see introduction to this chapter).

Laurales are clearly monophyletic; synapomorphies include their unilacunar nodes, opposite, 2-ranked leaves, cup-shaped receptacle, and pollen with sculptured apertures; some of these have been lost in many species. The monophyly of the order also is supported by DNA sequences (Qiu et al. 1993; Renner, personal communication), although the inclusion of Chloranthaceae is not supported by molecular data. Calycanthaceae are probably basal within Laurales. The more derived families, including Monimiaceae, Lauraceae, and relatives, are united by the additional apomorphies of a single ovule per carpel and pollen grains with spinules. Monimiaceae and Lauraceae form a clade diagnosed by pollen grains lacking apertures and with a reduced exine, stamens with paired appendages, and anthers opening by flaps (Donoghue and Doyle 1989). Monimiaceae and Lauraceae may be sister taxa. Lauraceae clearly are monophyletic (see description).

Lauraceae differ from Monimiaceae in their usually alternate and spiral, entire leaves (vs. opposite, toothed to entire leaves) and single carpel (vs. numerous carpels). Chloranthaceae are distinct because they have reduced flowers with stamens opening by longitudinal slits (not flaps), opposite and often toothed leaves, wood lacking vessels, and swollen nodes with sheathing stipules.

Lauraceae traditionally have been divided into two subfamilies. *Cassytha* is placed in the monotypic subfamily Cassythoideae on the basis of numerous specializations relating to its parasitic and viny habit, while all remaining genera are placed in the heterogeneous, and probably paraphyletic "Lauroideae."

Characters such as wood anatomy, stamen number, arrangement and number of anther locules, tepal persistence and form, fruit and cupule morphology, and inflorescence structure have been stressed in taxonomic groupings within "Lauroideae" (Burger 1988; Rohwer et al. 1991; van der Werff 1991; Rohwer 1993a, 1994; van der Werff and Richter 1996). Three tribes currently are recognized (see van der Werff and Richter 1996). Laureae have apparently racemose to umbellate inflorescences with involucral bracts and introrse anthers of the third whorl, and include *Litsea*, *Lindera*, *Laurus*, *Sassafras*, and *Umbellularia*. Perseeae, such as *Ocotea*, *Nectandra*, *Licaria*, *Persea*, *Phoebe*, and *Cinnamomum*, have cymose inflorescences lacking involucral bracts, and extrorse anthers of the third whorl. Finally, Cryptocaryeae, such as *Beilschmiedia* and *Cryptocarya*, include plants similar to Perseeae, but their inflorescences have the lateral flowers of the three-flowered cymose units are not quite opposite. Identification of genera and species is extremely difficult without flowering and fruiting material. Generic

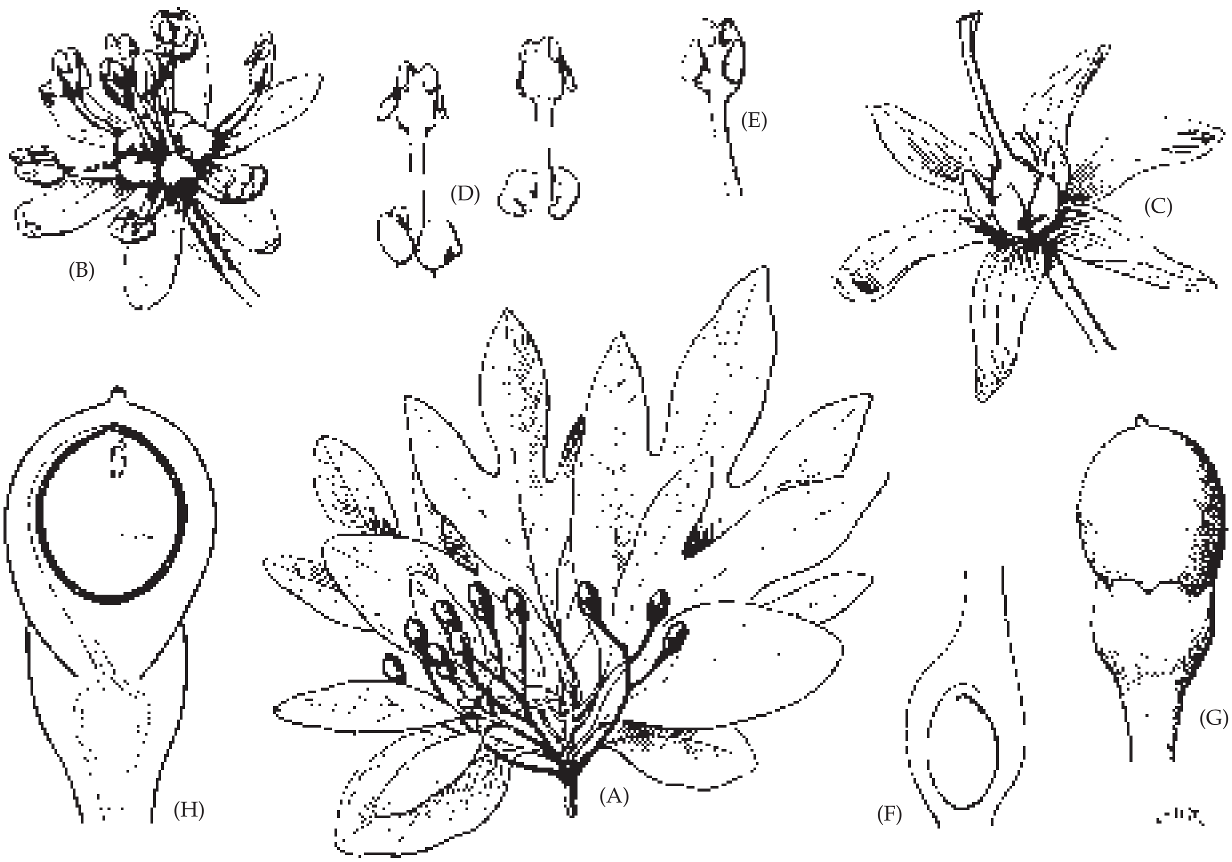


Figure 8.38 Lauraceae. *Sassafras albidum:* (A) fruiting branch (× 0.5); (B) staminate flower, androecium with nine stamens in three whorls of three (× 5); (C) carpellate flower, note staminodes (× 5); (D) two stamens of third whorl, each with two glands, note anthers opening by introrsely and laterally opening valves (× 6); (E) stamen of first whorl, note introrsely opening valves (two removed) (× 6); (F) ovary in longitudinal section, with single apical ovule (× 10); (G) mature drupe and cupule (× 3); (H) fruit and cupule in longitudinal section, note embryo with large, fleshy cotyledons (one cotyledon removed to show plumule and radicle) (× 4). (From Wood 1974, *A student's atlas of flowering plants*, p. 37.)

delimitation, which is often problematic, is discussed by van der Werff (1991) and Rohwer et al. (1991).

Flowers of Lauraceae are insect-pollinated, with flies and bees being the most common visitors. Modified staminodes that are paired at the base of some of the stamens produce odor and/or separate the stamens of the inner whorl and outer whorls; they sometimes also secrete nectar. In *Persea americana* outcrossing is enforced by a complicated system that involves two floral types, A and B flowers. The flowers have two periods of opening on successive days. In A flowers stigmas are receptive in the morning of the first day, while anthers open in the afternoon of the second day. In B flowers stigmas are receptive in the afternoon of the first day, and anthers shed their pollen during the morning of the second day. All the flowers open on any particular tree will be in the same stage. Thus, trees of both A and B types are necessary for cross-pollination. Many other species of *Persea* (and some other genera) have similar systems. The drupes are dispersed mainly by birds, but dispersal by mammals also occurs. The color of the drupes often contrasts with that of the cupule, increasing the attractiveness of the fruits.

References: Boyle 1980; Burger 1988; Cronquist 1981, 1988; Dahlgren 1983; Donoghue and Doyle 1989; Doyle et al. 1994; Kubitzki and Kurz 1984; Qiu et al. 1993; Rohwer 1993a, 1994; Rohwer et al. 1991; Takhtajan 1969, 1980; Thorne 1974, 1992; van der Werff 1991; Weberling 1988b; Wood 1958.

Illiciales

Illiciales, containing 3 families and about 175 species, are considered monophyletic because of their branched sclereids, the coarsely reticulate and semitectate exine of the pollen, and elongated outer layer of cells (as seen in cross-section) of the seed coat (Donoghue and Doyle 1989; Doyle et al. 1994). Members of this group are similar to Magnoliales and Laurales in their woodiness, simple, coriaceous leaves with pellucid dots, and flowers with usually numerous parts. Placement of Winteraceae here is problematic (Qiu et al. 1993); the family may actually be a member of the Magnoliales. Illiciaceae and Schizandraceae (a small family of vines) are additionally united by the apomorphic characters of pollen grains with three (or six) furrows (colpi), a feature that is otherwise limited to the tricolpate clade, and unilacunar nodes. Illiciales may be among the most basal lineages of angiosperms (see introduction to this chapter) and may be more closely related to Nymphaeales than usually admitted (Chase, personal communication; D. and P. Soltis, personal communication).

References: Cronquist 1981, 1988; Donoghue and Doyle 1989; Doyle et al. 1994; Qiu et al. 1993; Takhtajan 1969; Thorne 1974; Zimmer et al. 1989.

Illiciaceae A. C. Smith
(Star Anise Family)

Trees or shrubs; nodes unilacunar; with scattered spherical cells containing ethereal oils (*aromatic terpenoids*) *and branched sclereids*; often with tannins. Hairs simple. *Leaves alternate*, often clustered at the tips of the shoots, simple, *entire*, with pinnate venation, *blade with pellucid dots; stipules lacking*. *Inflorescences* determinate, but reduced to 1–3 flowers, *axillary*. Flowers bisexual, radial, with convex to shortly conical receptacle. *Tepals usually numerous*, distinct, the outer usually sepal-like, and the innermost sometimes minute, imbricate. *Stamens usually numerous*, distinct; *filaments short and thick, poorly differentiated from the anthers;* anthers with connective tissue extending between and beyond the apex of the pollen sacs; pollen grains tricolporate, but colpus morphology different from that of the eudocots. *Carpels usually 7 to numerous*, distinct, in a single whorl; ovaries superior, with ± basal placentation; stigma extending down style on adaxial surface. **Ovules 1 per carpel**. Nectar produced at base of stamens. **Fruit a starlike aggregate of 1-seeded follicles; seeds with smooth, hard coat**; embryo minute; *endosperm homogeneous* (Figure 8.39).

Floral formula: *, -7–∞- , 7–∞ , $\underline{7–∞}$; follicles

Distribution: Southeastern Asia, southeastern United States, Cuba, Hispaniola, and Mexico; mainly in moist forests.

Genus/species: 1/37. ***Genus:*** *Illicium*.

Economic plants and products: Anise oil is extracted from *Illicium verum* (star anise). Some species are used medicinally, and a few are used as ornamentals.

Discussion: The genus *Illicium* is divided into two subgroups: section *Illicium*, which has laxly held, elongate inner tepals, and section *Cymbostemon*, which has ± erectly held, ovate to suborbicular inner tepals. The former probably is paraphyletic.

Flowers of *Illicium* are pollinated by a wide variety of small insects, particularly flies. The plants are self-incompatible. The follicles dehisce elastically, shooting out the smooth seeds. Both pollination and seed dispersal appear to be quite local. Most species also form extensive clones due to the production of rhizomes.

References: Doyle et al. 1990, 1994; Keng 1993; Roberts and Haynes 1983; Smith 1947; Thien et al. 1983; Thorne 1974; White and Thien 1985; Wood 1958.

Winteraceae Lindley
(Winter's Bark Family)

Trees or shrubs; nodes trilacunar; **vessels lacking**, with elongate, slender tracheids only; *with scattered spherical cells containing ethereal oils* (*aromatic terpenoids*). Hairs usually lacking. *Leaves alternate*, simple, *entire*, with pinnate venation, blade *with pellucid dots*, **abaxial surface of stomates usually plugged by wax deposits**; stipules lacking. Inflorescences determinate, sometimes reduced to a single flower, terminal or axillary. Flowers usually bisexual, radial, with short receptacle. **Sepals usually 2–4**, distinct to connate, valvate, sometimes falling as a cap. *Petals usually 5 to many*, distinct, imbricate. *Stamens numerous*, distinct; *filaments ± flattened to laminar, usually poorly differentiated from the anthers*; anthers with connective tissue sometimes extending beyond the apex of the pollen sacs; **pollen grains uniporate, usually released**

Key to Major Families of Illiciales

1. Flowers with perianth clearly differentiated into sepals and petals; nodes trilacunar; vessels lacking; pollen with single germination pore (uniporate), released in tetrads; fruits follicles or berries. . . . . **Winteraceae**
1. Flowers with perianth of tepals, the outermost sometimes sepal-like; nodes unilacunar; vessels present; pollen with 3 germination furrows (tricolpate) and released in monads; fruits follicles, forming a starlike structure . . . . **Illiciaceae**

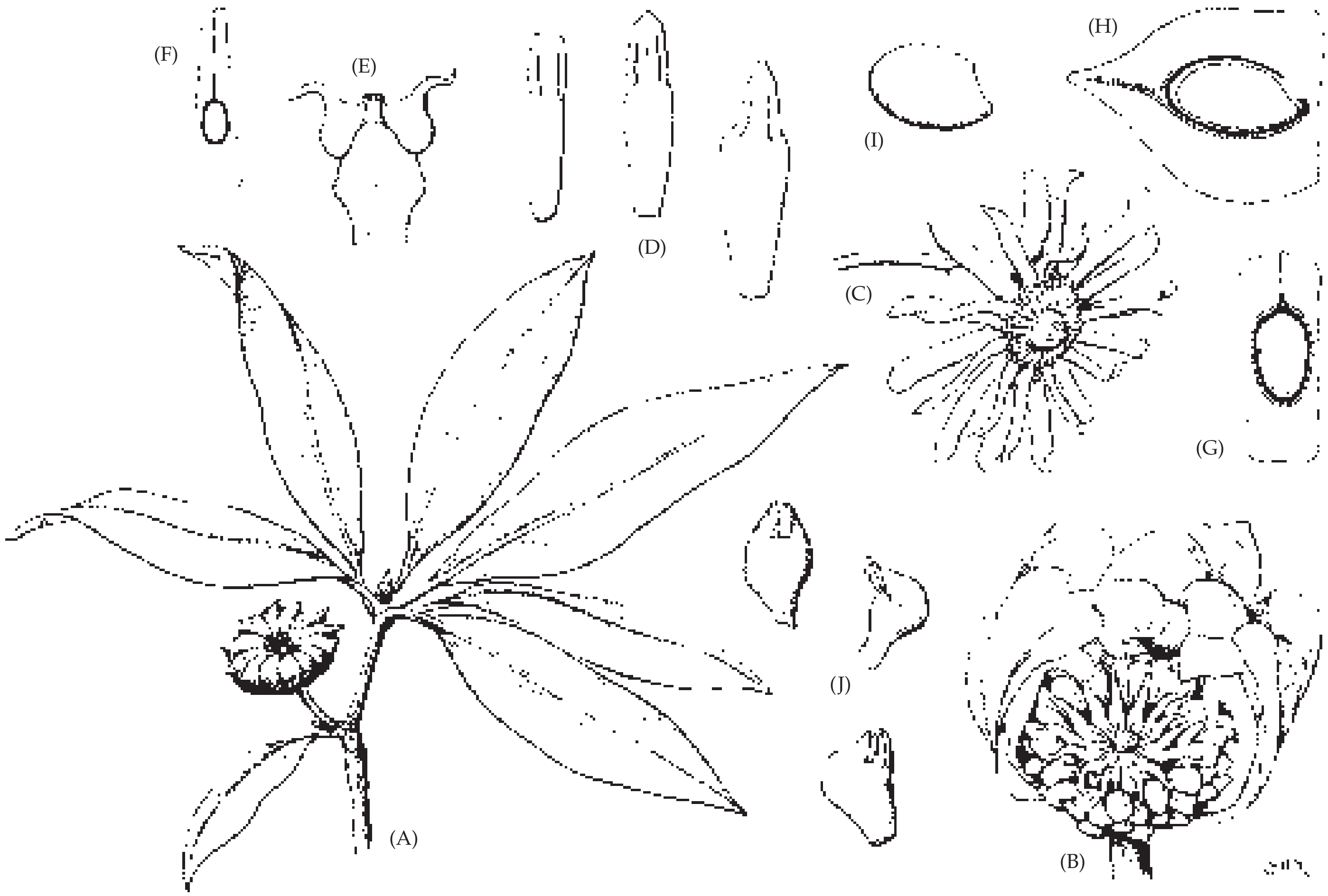


Figure 8.39 Illiciaceae. (A–I) *Illicium floridanum:* (A) fruiting branch (× 0.5); (B) opening flower bud with receptive carpels (× 4); (C) flower, later stage at shedding of pollen (× 1.5); (D) stamens, inner, outer, and an unusual subtepaloid form (× 7); (E) two carpels on receptacle (× 4); (F) carpel in longitudinal section, note single ovule (× 15); (G) mature fruit, with single seed, endosperm stippled (× 3); (H) mature fruit in cross-section (× 3); (I) seed (× 3). (J) *I. parviflorum:* stamens (× 3). (From Wood 1958, *J. Arnold Arb.* 39: p. 317.)

in tetrads. *Carpels 1 to numerous*, usually distinct, in a single whorl; ovaries superior, with parietal placentation; stigma extending down adaxial surface of style or ± capitate. Ovules 1 to several. Nectaries usually lacking. *Fruit a cluster of follicles or berries*, sometimes becoming connate as they mature; embryo minute; *endosperm homogeneous*.

Floral formula: *, 2–4, 5–∞ , ∞, 1–∞; berries, follicles

Distribution and ecology: New Guinea, Australia, New Caledonia (and other islands of the southwestern Pacific), Madagascar, South America, and Mexico.

Genera/species: 5/90. ***Major genera:*** *Tasmannia* (40 spp.) and *Bubbia* (30). The family is not represented in the continental United States or Canada, but *Drimys* occurs in Mexico. Most are understory species of moist forests, cool montane forests, or restricted to swampy habitats.

Economic plants and products: The bark of *Drimys winteri* (Winter's bark) has been used medicinally.

Discussion: Phylogenetic relationships within Winteraceae have been assessed through cladistic analyses of morphology (Vink 1988) and rDNA sequences (Suh et al. 1993). Morphological and DNA characters agree on the close association of *Zygogynum*, *Exospermum*, *Belliolum*, and *Bubbia*. Vink (1988) treats this group as *Zygogynum* s. l. Suh et al. (1993), however, maintain *Bubbia*, which they consider to be sister to the *Zygogynum-Exospermum-Belliolum* clade. *Drimys* possesses the unusual autapomorphy of a reduced, more or less capitate stigma. *Tasmannia* may be sister to the abovementioned genera, a hypothesis supported by ribosomal DNA sequences and by its low chromosome number.

The lack of vessels in Winteraceae has often been considered a retained ancestral condition (see discussion in Bailey and Nast 1945; Thorne 1974; Cronquist 1981, 1988), a conclusion that is quite unparsimonious (Young 1981).