**Plant Family treatments for “Photo Gallery” website** [updated 20 May 2022]**:**

**Authors:** Christopher Campbell contributed the treatments for families of Lycophytes, Monilophytes, and Extant Gymnosperms; Walter Judd contributed the treatments of the families of Angiosperms, except for Didiereaceae, Talinaceae, Frankeniaceae, and Tamaracaceae, which were contributed by Lucas Majure.

**Note**: The following 117 families of ferns, gymnosperms, and angiosperms treated in this document will eventually be included in an expanded version of the “Photo Gallery” website. They are arranged according to the same phylogenetic arrangement as those in the textbook, *Plant Systematics: A Phylogenetic Approach*. Additionally, the following fourteen families, i.e., **Ochnaceae, Linaceae, Plumbaginaceae, Grossulariaceae, Pentaphylacaceae, Cunoniaceae, Symplocaceae, Styracacee, Haloragaceae, Loganiaceae, Buxaceae, Pandanaceae, Santalaceae**, and **Monimiaceae**, will be included in the textbook, itself, in the next edition, and are therefore included at the end of the Textbook Updates document. These, when added to the 187 familial clades included in the fourth edition of the textbook, will bring the total number of vascular plant families treated in the text + website to 318.

*Tracheophytes*

*Lycophytes*

**Isoetaceae** Reichenbach

(Quillwort Family)

*Plants tufted*, perennial, evergreen aquatics to ephemeral terrestrials, **with CAM photosynthesis**; stem mostly subterranean, usually erect, **± cormose,** sometimes elongated, up to 6 cm in diameter, rarely branched, lobed, **with a vascular cambium**. Roots, usually dichotomously branched, arising between the corm lobes, **with a central air space and a singular vascular bundle**. *Leaves simple, linear, densely clustered or distichous, 2-100 cm long, dilated at base, tapering to apex, long, containing 4 transversely septate, longitudinal lacunae, with a central vascular strand, deciduous in the dry season;* the ligule inserted above a single sporangium at least initially embedded in a basal cavity of fertile leaves, the *megasporophylls and microsporophylls usually borne in alternating cycles*, occasionally protected by leaves modified into scales. Sporangia partly to completely covered by the **velum,** a membranous outgrowth of the leaf inserted above the sporangium; **megasporangium up to 20 mm long, ± indehiscent**. Spores without chlorophyll, *megaspores up to 0.8 mm in diameter*, trilete, several to hundreds in megasporangia; microspores 0.02-0.04 mm in diameter, monolete, thousands in microsporangia. Megagametophytes exposed only after megaspore opens along its ridges. Microgametophytes confined within microspore, **the sperm with many cilia**. (Jermy 1990; Taylor et al. 1993; Tryon and Tryon 1982).

***Distribution and ecology***:Nearlycosmopolitan, but poorly represented in Asia. Plants aquatic, in ponds and streams, or terrestrial on moist soil that dries out.

***Genus/species***: 1/250. ***Genus***: *Isoetes.* The genus is widespread in the continental United States and Canada.

***Economic plants and products***: None, although *Isoetes lacustris* is occasionally used as an aquarium plant.

***Discussion***: Monophyly of Isoetaceaeis supported by DNA sequences (Hoot et al. 2006; Larsén and Rydin 2016; Rydin and Wikström 2002). Among extant lycophytes, Isoetaceae are sister to the Selaginellaceae and share with that family heterospory and the presence of ligules (Fig. 6.8, 4th ed.). Isoetaceae, however, are more closely related to the large trees of *Lepidodendron* of the Carboniferous (Fig. 6.8, 4th ed.). Fossils close to extant *Isoetes* are known from the Mesozoic (Pigg 2001). The earliest divergence within *Isoetes* occurred about 147 million years ago, much earlier than would be expected given the low genetic and morphological diversity in the genus (Larsén and Rydin 2016). This divergence formed a clade whose members grow on the remains of Gondwana (except Antarctica). Later cladogenesis was associated with dispersal, sometimes over long distances, and divided the remainder of the genus into another four well-supported clades.

Species of *Isoetes* are difficult to identify due to morphological simplicity and reticulate evolution (Taylor and Hickey 1992). Habitat, texture, spore size, velum, ligule shape, pseudoligule (labium) shape, and especially patterns on the surface of megaspores have been used for identification. Megaspore surface features, however, are only accessible with microscopy; they have been differently interpreted by various authors, and the various features do not always agree with phylogenetic relationships (Larsén and Rydin 2016).

Leaves of Isoetaceae have a thick cuticle and some species lack stomata. These features limit uptake of CO2, which the roots absorb from the sediment. Quillwort spore dispersal occurs by water, ingestion by animals, and through adaptations of the megaspore surface for attachment to the feet and legs of waterfowl. Colonization and long-distance dispersal may be more difficult in heterosporous plants, like quillworts, because megaspores and microspores are not produced on the same gametophyte. *Isoetes* has a possible adaptation to promote fertilization withpockets on the megaspore surface to trap microspores (Lellinger 1979).

***Additional references***: Abeli and M. Mucciarelli2010; Blackmore et al. 2012; PPG I. 2016; Smith et al. 2006; Taylor et al. 1993.

*Monilophytes (Ferns and allies)*

*Leptosporangiate ferns*

**Gleicheniaceae** C. Presl

(Forked-fern Family)

Terrestrial, often forming thickets. Stems long, creeping, sometimes erect, with branched or stellate hairs and/or scales or glabrous. *Leaves about 30 cm to 10 m or more long, scrambling or climbing, at least once pinnate to many-times forked****,* rachis growth continuous,** pinnae branching pseudodichotomously, with **dormant buds interrupting growth and permanently arresting growth at the fork of branches,** circinate in bud.Sori round, abaxial, indusium absent. Sporangia 2-20, short-stalked, annulus oblique, not interrupted. Spores lacking chlorophyll, monolete or trilete. Gametophytes green, long-lived, more or less heart-shaped or elongate. (Kramer 1990a; Tryon and Tryon 1982; Nauman 1993a).

***Distribution and ecology***:Mostlypantropical. Usually in open, heavily disturbed habitats with mineral-poor soils.

***Genera/species***: 6/157. ***Genera***: *Sticherus* (95 spp.), *Diplopterygium* (25), *Dicranopteris* (20), *Gleichenia* (15), *Gleichenella (1)*, and *Stromatopteris (1).* Only *Dicranopteris* occurs in the United States (Alabama, Florida).

***Economic plants and products***: None.

***Discussion***: Gleicheniaceae are monophyletic (Hasebe & al. 1995; Pryer & al. 1995, 2001, 2004). The leaves of Gleicheniaceae differ strikingly from all other fern familiesin that dormant and permanently arrested buds shape leaf architecture. In most members of this family, the rachis grows continuously and bears pinnae that branch pseudodichotomously, with dormant buds providing for interrupted growth and permanently arrested growth at the fork of branches. Strongly divergent pinnae help some species hold onto other vegetation and climb over shrubs and trees. The fossil record of the family extends back to the Cretaceous and perhaps longer.

***Additional references***: PPG I. 2016; Smith et al. 2006.

**Hymenophyllaceae** Mart.

(Filmy-fern Family)

Epiphytic or terrestrial. Stems erect to decumbent, small, or usually long-creeping and slender, sometimes branched, glabrous or with reddish to dark-colored hairs. *Roots few and thin to many and stout, absent, or replaced by root-like shoots*. Leaves simple or once-pinnate to 5-pinnate, 2 mm to 40 cm at maturity, often mat-forming, short-petioled, **usually one cell thick between veins**, **cuticle absent or greatly reduced and stomata lacking,** entire or dentate, with simple and/or stellate hairs often borne on veins or leaf margins, scales usually absent, circinate in bud. *Sori marginal, indusia conical, tubular or clam-shaped*. *Sporangia borne on a mound-like receptacle or an elongate "bristle”, sessile or short-stalked*; annulus oblique, not interrupted. Spores with chlorophyll, globose, trilete. Gametophytes **filamentous to ribbonlike**, *much branched*, 0.2-1 cm, often reproducing by fragmentation or gemmae, persistent (Iwatsuki 1990; Tryon and Tryon 1982; Farrar 1993).

***Distribution and ecology***:Pantropical and south temperate. Gametophytes grow as far north as Alaska, usually in deeply sheltered, continuously moist habitats.

***Genera/species***: 9/434. ***Genera***: *Hymenophyllum* s.l. (250 spp.), *Trichomanes* s.s. (60), *Crepidomanes* (30), *Didymoglossum* (30), *Abrodictyum* s.l. (25), *Polyphlebium* (15), *Vandenboschia* (15), and *Callistopteris* (5), *Cephalomanes* (4). *Hymenophyllum*, *Trichomanes*, and *Didymoglossum* occur in the continental United States, and *Hymenophyllum* also in western Canada.

***Economic plants and products***: None.

***Discussion***: Monophyly of Hymenophyllaceae is supported by DNA sequences, morphology, and anatomy (Hasebe & al. 1995; Dubuisson 1996, 1997; Pryer & al. 2001, 2004; Ebihara & al. 2006, 2007; Dubuisson & al. 2003; Hennequin & al. 2003; Schuettpelz and Pryer 2007). The family has two subfamilies, both monophyletic based on DNA sequences (Hennequin et al. 2006; Pryer et al. 2001). Trichomanoideae (eight genera and about 184 species) have rhizomes that are covered with reddish to dark-colored hairs. Hymenophylloideae (one genus and about 250 species) has rhizomes that are nearly glabrous or sparsely covered with light-colored hairs.

The one-cell-thick leaves, absence of stomates, and lack of roots may be adaptations to the moist habitats occupied by members of the Hymenophyllaceae. The family persists largely or entirely by vegetative propagation of the sporophyte or gametophyte. The capacity for vegetative reproduction and dispersal by gametophytes of the Hymenophyllaceae allows gametophyte colonies to live indefinitely without completing a life cycle. Some species are maintained exclusively as gametophytes with sporophytes rarely or never produced.

***Additional references***: PPG I. 2016; Smith et al. 2006.

**Salviniaceae** Reichenb.

(Floating-fern Family)

Small, **free-floating aquatics,** occasionally stranded on mud. Stems creeping, thin, dichotomously branched, more or less hairy, proliferous by axillary fragmentation. Roots absent (*Salvinia*) or usually short (*Azolla*). **Leaves simple**, **2-ranked**, **floating**, 0.5-2.5 cm long, entire, not circinate in bud; in *Salvinia* 0.5-2.5 cm long, petiolate, veined, in whorls of 3, *two floating, unlobed, and with multicellular, water-repelling hairs, the third finely branched, rootlike and pendant*; in *Azolla* 0.5-1.5 mm long, sessile or short-petioled, unveined, two lobed, t*he upper aerial, photosynthetic*, and containing living colonies of the alga *Anabaena* (see Discussion), *the lower floating, mostly not photosynthetic*. Heterosporous. Sori surrounded by a membranous indusium (**forming a globose sporocarp**) borne on submerged leaves (*Salvinia*) or in pairs (with the same or different sexes) at the base of lateral branches (*Azolla*), bearing up to 10 megasporangia (*Salvinia*) or 1 megasporangium (*Azolla*). **Megasporangia covered by part of the indusium and each contains 1 megaspore**. Microsporangia contain 32 or 64 spores, aggregated into 3-10 masses (massula) covered with arrowlike barbs glochidia in *Azolla*. *Sporangia stalked, annulus absent*. *Heterosporous*. Spores globose, lacking chlorophyll, more or less perforate; megaspores 0.2-0.6 mm in diam., in *Azolla,* the apex, covered by the part of the indusium andbearing a “swimming apparatus” of three or more floats and a central columella; microspores about 3 µm in diam. Megagametophytes and microgametophytes partly protruding through sporangium wall; megagametophytes floating on water surface with archegonia directed downward; microgametophytes remaining fixed to sporangium wall (Schneller 1990a, b; Lumpkin 1993; Nauman 1993b; Tryon and Tryon 1982).

***Distribution and ecology*:** Subcospmopolitan. Members of this family grow in lakes, rivers, ponds, marshes, ditches, and rice fields. In suitable conditions growth is aggressive and can impede navigation in waterways and waterflow in ditches. It is amazing that during the very warm conditions of the Eocene, *Azolla* was abundant on the surface of the Artic Ocean, which was then largely cut off from other oceans, leading to stratification, with a layer of fresh water atop the deeper salty layers. The buildup of organic remains of these plants in sea floor sediments led to a dramatic lowering of atmospheric carbon dioxide, and initiated cooling conditons during the Tertiary (Speelman et al. 2009).

***Genera/species***: 2/21. ***Genera***: *Salvinia* (12 spp.), *Azolla* (9)*.* Both occur in North America.

***Economic plants and products***: Plants of *Azolla* have colonies of the blue-green alga, *Anabaena* in cavities of the upper leaf lobe (Van Hove and Lejeune 2002). *Anabaena* fixes atmospheric nitrogen, and *Azolla* has long been grown with rice to enhance its nitrogen levels*. Salvinia* is occasionally used as a pond-ornamental, but *S. molesta* is an invasive weed of wetland habitats.

***Discussion***: Salviniaceae are monophyletic (Nagalingum et al. 2008; Pryer 1999; Schuettpelz and Pryer 2007). The base number of *Salvinia* (*x* = 9) is the lowest base number known in ferns. Microsporangia and megaspores of *Azolla* are among the most complex of all fern reproductive structures, which may have led some authors to place *Azolla* and *Salvinia* in separate, monogeneric families. They are here considered together in Salviniaceae s.l. because their status as sister groups is strongly supported, the expanded familial clade is easily diagnosed, and their placement together reduces taxonomic redundancy.

***Additional references***: PPG I. 2016; Smith et al. 2006.

**Schizaeaceae**

(Curly-grass Family)

Terrestrial, rarely epiphytic. Roots few to many, slender, fibrous. Stems creeping to erect, with hairs. Leaves 5-50 cm long, *simple or dichotomously branched, sometimes consisting only of two wings of tissue along the midrib, in other cases expanded and fan-shaped; sterile leaves curling* (*Schizaea*). **Sporangia borne on the pinnate or subdigitate apex of the blade**, *not in discrete sori, indusium absent*, *the annulus apical or subapical*, *composed of one row of thickened cells*. **Spores monolete**, bilateral. Gametophytes filamentous, aboveground, and green (*Schizaea*) or subterranean, tuberous, and not green (*Actinostachys*) (Kramer 1990b; Tryon and Tryon 1982; Wagner1993).

***Distribution and ecology*:** Pantropical and some temperate species, especially south temperate areas. Usually plants of soils low in nutrients and/or moisture, such as open, sandy or rocky habitats or wet savannahs or boggy sites.

***Genera/species***: 2/35. ***Genera***: *Schizaea* (20 spp.), *Actinostachys* (15). Both occur in temperate North America.

***Economic plants and products***: None. However, *Lygodium*, of the related Lygodiaceae, is occasionally used medicinally, and also serves as a fiber source (basketry).

***Discussion***: Schizaeaceae are monophyletic based molecular and morphological data (Skog et al. 2002; Wikström et al. 2002). The distinctive annulus was useful for identifying fossils of the Schizaeaceae as far back as the Jurassic. Two closely related families, Anemiaceae and Lygodiaceae, have a similar annulus and share with Schizaeaceae differentiation of sterile and fertile portions of the leaves and absence of well-defined sori. These two segregate families each have a single genus. *Lygodium* has about 40 species, mostly of the tropics and south temperate regions, but one native to the southern United States), and *Anemia* includes ca. 115 species, mostly in the New World (with two species in Florida and one in Texas), and less diverse in in Africa and India. All three families are monophyletic (Skog et al. 2002; Wikström et al. 2002), and together they comprise the Schizaeales, which are monophyletic (Hasebe et al. 1995; Skog et al. 2002; Wikström et al. 2002; Pryer et al. 2001, 2004). These three families are distinguished in the following key (adapted from Kramer 1990b; Tryon and Tryon 1982).

1. Sporangia solitary, covered by an indusium-like outgrowth of the leaf blade; leaf blade branching with a dormant apex and a pair of lateral, secondary pinnae; often climbing over other vegetation by twining of the leaf rachis; medium-sized to large ferns; spores trilete. . . . . . . . . . . . . . . . . **Lygodiaceae**

1. Sporangia ± densely clustered, not covered; leaf blades simple or, if divided, not with dormant apex; not climbing; small to medium-sized ferns; spores trilete or monolete

2. Sporangia usually borne on a pair of fertile pinnae at the base of the sterile blade, the sporangia-bearing branches reduced to axes (i.e., skeletonized; spores trilete. . . . . . . . . . . . . . . . . . . . . . . . . . **Anemiaceae**

2. Sporangia borne at the apex of simple blades or of strongly modified blade segments that are not skeletonized; spores monolete. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **Schizaeaceae**

***Additional references***: PPG I 2016; Smith et al. 2006.

*Spermatophytes*

*Extant gymnosperms*

**Gnetaceae** Blume

(Gnetum Family)

Dieocious (sometimes monoecious), evergreen, lianas (rarely trees or shrubs), **with laticifers**. **Nodes multilacunar; vesseles with vestured pits**. *Leaves opposite, simple,* **petiolate***, exstipulate,* **the lamina ± elliptic, pinnately veined****(with higher order veins reticulate)***, entire, usually with drip tips*, borne on short shoots in climbing species. Compound strobili [See 4th ed. Fig. 6.13, F] are cone-like, terminal or lateral, sometimes densely clustered, and consist of a straight axis subtended by a pair of opposite, connate or free bracts. The axis bears usually 3-7 superposed **whorls** of several to many strobili subtended by and sometimes hidden by connate bracts forming a collar (also called a cupule). *Megasporangiate strobili with one ovule, an integument extending into a micropylar tube, and two enveloping, connate bracteoles (appearing as an outer integument)*. *Microsporangiate strobili have* *two connate microsporophylls, two succulent bracts, and 2 (1 in G. gemoides*) *microsporangia*. Compound microsporangiate strobili may contain some, usually sterile megasporangiate strobili above the clusters of microsporangiate strobili. **Pollen spheroidal, with minute projections**. *Seeds drupelike, 1.2-7 cm long, the fused bracteoles becoming a red, orange, or yellow, fleshy* (rarely corky) envelope, the integument developing into a hard, ribbed seed coat. Megagametophytic tissue copious, succulent. Cotyledons 2. Germination epigeal (Kubitzki 1993; Endress 1996; Hufford 1996).

***Distribution and ecology*:** Tropical and subtropical forests mostly in Asia, with fewer species in West Africa and northwestern South America.

***Genus/species***: 1/40. ***Genus***: *Gnetum.*

***Economic plants and products***: Anti-asthmatic properties for which *Gnetum parviflorum* is used in Chinese medicine have been ascribed to the presence of demethylcoclaurine hydrochloride (Schultes and Raffauf. 1990). The seeds are cooked and eaten throughout the tropics. The leaves *G. gnemonoides* of Southeast Asia are eaten. *Gnetum gnemon* contains bioactive compounds, such as saponins, tannins, flavonoids, and stilbenoids (Barua et al. 2015).

***Discussion***: *Gnetum* has been divided into two sections (Carlquist 1996a). One contains two Indomalesian tree species plus two African and nine Neotropical lianas, and the other has the remaining species of the genus, all Asian. Gnetales extend back to the Paleozoic, but macrofossils are sparse (Crane 1996). Wang (2004) discovered a cone from the Permian with unequivocal affinity with the Gnetales because its ovules have three envelopes, the innermost forming a micropyle. Rothwell and Stockey (2013) documented a micropyle in a gnetophyte cone from the Cretaceous. Current clades of *Gnetum* began diverging in the late Oligocene to mid-Miocene time, with most Asian species appearing in Miocene-Pliocene (Won and Renner 2006).

Gnetophytereproductive structures are complex, with varying degrees of connation of structures (Endress 1996; Hufford 1996). The most distinctive example of connation in *Gnetum* is the collar of the microsporangiate strobili, which is inferred to have formed by connation of bracts that makes individual bracts not discernible. The reproductive structures of all gnetophytes except a few species of *Ephedra* are pollinated by small flies, moths, beetles, an orthopter, and a hemipter (Kato et al. 1995; Endress 1996). Fertile and sterile *Gnetum* ovules produce a large pollination droplet at the tip of the tubular micropyle, which contains sugar and functions as nectar (Endress 1996, Fig. 7D). When there are no ovules in cones of microsporangiate strobili, as in *Gnetum cuspidatum*, nectar is secreted between and on the collars. Pollen is pressed out of the small opening of the microposangium to be available for pollinators. The cones emit a pleasant, stinky, or fungal-like odor. The brightly colored seeds attract and are dispersed by large birds, rodents, and monkeys (Won and Renner 2006). Amazon catfish regurgitate the seeds because of sclerenchyma needles in the seed envelope. Water dispersal is likely because of a buoyant layer in the seed coat or corkiness of the seed coat.

***Additional reference***: Liguo et al. 1999.

*Angiosperms*

*ANA Grade*

*Nymphaeales*

**Hydatellaceae** U. Hamann

(Water-tufts Family)

*Aquatic to semiaquatic*, **annual** or occasionally perennial herbs; *roots adventitious*, *numerous, and unbranched*; *stems very short and shortly branched, so plant tufted*; lower portion with irregularly scattered vascular bundles. Hairs absent except for minute, simple, multicellular hairs in leaf axils. *Leaves alternate and spiral, basal, simple*, **± linear**, *entire*, *submerged to partially emergent*, **with a single vein**, surrounded by parenchymatous bundle sheath, radiating plates of mesophyll cells alternating with wide air cavities; stipules absent. Inflorescences determinate **but reduced, forming a fasciculate head**, **with 3-8 involucral bracts**, usually axillary, **usually scapose**. **Flowers unisexual** (and plants monoecious or dioecious), **very small, bilateral** (*by reduction, and appearing radial*). **Perianth lacking**. **Stamen 1** (in each staminate flower); **filament long and slender**; **anther without an endothecium**; pollen grains monosulcate. **Carpel 1** (in each carpellate flower), distinct *and stalked*; **ovary nude** (probably superior), **with apical placentation**; **style ± absent**; **stigma consisting of 2-10, elongate hairs, each consisting of a single row of plump cells**. **Ovule 1**, with a thin-walled megasporangium; female gametophyte usually monosporic, with only 4 nuclei at maturity. Nectary lacking. **Fruit a capsule, splitting by 3 valves**, to release the single seed, *or an achene*, **with** or without **3 hygroscopic ribs**. *Seed operculate* (opening by a cap); embryo minute, **with a bilobed cotyledon-sheath** (probably 2 fused cotyledons); endosperm diploid, ± lacking at maturity, but with starchy perisperm.

***Floral formula***:

Staminate: X , T -0- , A 1 , G 0

Carpellate: X , T -0- , A 0 , G 1 ; 1-seeded capsule, achene

***Distribution and ecology***: India, Australia, and New Zealand; plants of seasonal aquatic and wetland habitats.

***Genera/species***: 1/12. ***Genus***: *Trithuria* (incl. *Hydatella*) (12 spp.). The genus does not occur in North America.

***Economic plants and products***: None.

***Discussion***: The monophyly of Hydatellaceae is strongly supported by morphology (Hamann 1976, 1998; Rudall et al. 2007, 2008; Sokoloff et al. 2011, 2013; Stevens 2001 onward; see also description, with several characters likely representing aquatic adaptations) and DNA sequences (Iles et al. 2012; Sokoloff et al. 2019). DNA characters and morphology also support a placement in Nymphaeales (Graham and Iles 2009; Moore et al. 2011; Qiu et al. 2010; Rudall et al. 2007, 2008; Saarela et al. 2007; Sokoloff et al. 2008; Soltis et al. 2011) although the family was traditionally considered to be a monocot (Cronquist 1981; Hamann 1976; see also discussion in Sokoloff et al. 2011). Phylogenetic relationships within Hydatellaceae recently have been clarified, leading to the recognition of only a single genus, *Trithuria*, including four sections distinguished by a combination of seed and fruit characters (Iles et al. 2012; Sokoloff et al. 2008, 2013). The annual habit is ancestral, with perennial species evolving within sect. *Hydatella*. The evolution of the dioecious condition is quite homoplasious. Species are often very difficult to distinguish (Marques et al. 2016; Sokoloff et al. 2008, 2019).

 The inconspicuous flowers of *Trithuria* likely are pollinated by wind and/or water, but selfing also occurs.

*Mesangiosperms*

*Magnoliids*

*Magnoliales*

**Degeneriaceae** I. W. Bailey & A. C. Smith

(Degeneria Family)

*Trees*; **nodes pentalacunar**; *pith septate* (with partitions composed of sclereids); *with spherical to ± elongate cells containing ethereal oils (aromatic terpenoids)*. *Vegetative parts lacking hairs*. *Leaves alternate*, spiral, simple, *entire*, with pinnate venation, *the blade with pellucid dots*. *Inflorescence a solitary flower, axillary* **but each flower positioned slightly above the leaf axil**. Flowers bisexual, radial, **and pendulous**. **Sepals 3**, distinct, imbricate. **Petals** *numerous*, *distinct*, imbricate. *Stamens numerous*, distinct, *with 3 veins, laminar and not differentiated into an anther and filament, and with 2 pairs of elongated microsporangia sunken into staminal tissue*; pollen grains monosulcate; and with staminodes between stamens and gynoecium. **Carpel 1**, on a short receptacle; ovary superior, with parietal (lateral) placentation; **stigma very elongated, forming a crest along one side of the carpel**, with interlocking, stigmatic papillae and incompletely closed, *and style absent*. Ovules numerous. Nectaries lacking. *Fruit a berry, with a hard rind, indehiscent or ± dehiscent*; **seed with red to orange, fleshy coat**; embryo minute, **with 3 (or 4) cotyledons**; *endosperm ruminate*.

***Floral formula***: \* K 3 , C numerous , A numerous , G 1; berry

[Replace numerous with infinity symbol]

***Distribution***: Restricted to Fiji (Viti Levu, Venua Levu, Tavenni).

***Genus/species***: 1/2. ***Genus***: *Degeneria* (2 spp.).

***Economic plants and products***: None; a botanical curiosity; an image of *Degeneria vitiensis* is on the Fijian five-dollar bill.

***Discussion***: Degeneriaceae are most closely related to Himantandraceae, Eupomatiaceae and Annonaceae (Sauquet et al. 2003). They are easily distinguished from these families by their gynoecia with a single carpel that has a very elongated stigmatic crest. The monophyly of Degeneriaceae is supported by morphology (see description, also Bailey and Smith 1942, Stevens 2001 onward, Swamy 1949, and Kubitzki 1993b), phylogenetic analyses based on DNA-sequence data (Sauquet et al. 2003; Savolainen et al. 2000; Soltis et al. 2000, 2011), and on combined analyses (Doyle and Endress 2000). The conduplicate carpel with an extremely elongated stigmatic crest was once used to support the view that *Degeneria* represented an extremely primitive genus of angiosperms. Development of the conduplicate carpel is by postgenital fusion (and not a secretion layer, as in most members of the ANA grade) as is characteristic of the families of Magnoliales, and Magnoliidae (Endress and Igersheim 2000).

 The showy flowers are pollinated by beetles. The broadly laminar stamens and staminodes were once thought to reflect the ancestral condition in angiosperms, but they are more likely indicative of adaptations to beetle pollination (Endress 1984; Thien 1980). The colorful seeds with a fleshy testa are likely bird dispersed.

*Laurales*

**Atherospermataceae**

(Southern-sassafras Family)

*Trees or shrubs; nodes unilacunar; tissues with scattered spherical cells containing ethereal oils (aromatic terpenoids)*; with tannins, benzyl-isoquinoline, **bisbenzyl-isoquinoline**, and aporphine alkaloids. Hairs simple or T-shaped. *Leaves opposite and decussate*, simple, *toothed*, *with pinnate venation*, *blade with pellucid dots*; *stipules lacking*. Inflorescences determinate, axillary or terminal, or flowers solitary. *Flowers bisexual or unisexual* (*and plants then monoecious* or andromonoecious, the latter with some plants with carpellate flowers and other plants with staminate and bisexual flowers), *radial, with a ± cup-shaped receptacle, with a floral roof*, moderate-sized to fairly large, pale green, white, or marked with pink-purple. *Tepals 4-8, distinct*, but perianth parts often differentiated, with the outer ones sepaloid and the inner petaloid, then *sepals 2-10* and *petals 5-10*, distinct, imbricate. *Stamens 4 to numerous*, distinct, often with staminodes; filaments sometimes absent, *with paired appendages*; *anthers opening by 2 flaps*; **pollen grains dicolpate or meridionally syncolpate**, with exine reduced. *Carpels 4 to numerous*, distinct; *ovary ± superior*, *with ± basal placentation*; style 1, ± terminal to gynobasic; stigmas various. Ovule 1. **Fruit a cluster of plumose achenes**, *initially surrounded by* **woody** *expanded receptacle*, *which* *irregularly opens*.

***Floral formula***: \* , T or K/C 4-many , A 4-many , G 4-many; plumose achenes

[replace “many” with the infinity symbol]

***Distribution***: New Guinea to Australia, Tasmania, New Zealand, and New Caledonia, and also South America (southern Chile). Fossils are known from Antarctica; this is a relic family and was once more widespread.

***Genera/species***: 7/20. ***Major genera***: *Daphnandra* (9 spp.) and *Dryadodaphne* (4). The familial clade is absent from North America.

***Economic plants and products***: The wood of *Doryphora* *sassafras* (southern-sassafras) is used to repel insects. Some are used as spices, e.g., *Atherosperma* (black-sassafras; bark) and *Laurelia* (Chilean laurel, Chilean-sassafras; fruits).

***Discussion***: The monophyly of Atherospermataceae is well supported by DNA sequences (Renner 1998, 1999, 2005; Renner et al. 2000) and morphology, especially the woody receptacle associated with plumose achenes (Philipson 1993; Stevens 2001 onward; see also description). *Doryphora* and *Daphnandra* form a clade that is sister to the remaining genera, i.e., *Atherosperma, Dryadodaphne*, *Laurelia, Laureliopsis*, and *Nemuaron*. All of these genera have sometimes been considered within a broadly circumscribed, but non-monophyletic Monimiaceae.

 The showy flowers of Atherospermataceae are pollinated by various insects; the plumose achenes are wind dispersed.

***Additional reference***: Stanstrup et al. 2010.

**Calycanthaceae** Lindley

(Sweetshrub Family)

*Shrubs or trees*; nodal anatomy unilacunar and usually with 2 vascular traces; *with spherical cells containing ethereal oils (aromatic triterpenoids)*; **with tryptamine alkaloids**; **stems with 4 cortical vascular bundles, these inverted** (i.e., with xylem outside the phloem). Hairs simple. *Leaves usually opposite and decussate*, simple, *entire*, with pinnate venation, *the blade with pellucid dots*, *the petiole enclosing axillary bud*; *stipules lacking*. Inflorescences determinate, *but usually reduced to a solitary flower*, terminal or axillary. *Flowers bisexual*, radial, **fairly large**, *with an expanded receptacle, forming an urn-shaped to cup-shaped hypanthium* **with a cortical vascular system**. *Tepals numerous, spiral, showy, attached to the outside and apex of hypanthium*. *Stamens 5 to numerous*, distinct, filaments short or absent; *anthers opening by longitudinal slits* (rarely valvate), with apically projecting connective; **pollen grains bisulcate**; *staminodes numerous, nectar secreting*, positioned between stamens and carpels. *Carpels 1 to numerous, distinct*, borne on the inner surface of the hypanthium; *ovaries superior*, with parietal (lateral) placentation; *styles usually slender, elongated*; stigmas decurrent. *Ovules usually 2 per carpel, but only the lower one developing*. *Nectar and food-tissue produced by staminodes, stamens and inner tepals*. *Fruit an aggregate of achenes, surrounded by persistent and fleshy to dry hypanthium*; embryo with 2-4 cotyledons, *these often spirally twisted*; **endosperm diploid, developing without paternal (pollen) contribution**, absent at seed maturity.

***Floral formula***: \* T- numerous - , A 5-numerous , G 1-numerous ; achenes

[Replace “numerous” with infinity symbol]

***Distribution***: North America, eastern Asia, and northern Australia.

***Genus/species***: 3/10. ***Major genera***: *Chimonanthus* (6 spp.; incl. *Sinocalycanthus*) and *Calycanthus* (3). Only *Calycanthus* occurs in the continental United States.

***Economic plants and products***: *Calycanthus* oil is used in perfumes, and both *Calycanthus* (sweetshrub, spicebush, strawberry-bush, Carolina allspice) and *Chimonanthus* (wintersweet) are used as ornamentals because of their showy flowers.

***Discussion***: The monophyly of Calycanthaceae is supported by morphology (see description, Kubitzki 1993, and Stevens 2001 onward), and DNA sequence data (Li et al. 2004; Massoni et al. 2016; Renner 1999; Zhou et al. 2006). The family is comprised of two major subclades: Idiospermoideae (only *Idiospermum australiense*; carpels 1-2, style absent, and cotyledons usually 3) and Calycanthoideae (*Calycanthus*, *Chimonanthus*; embryo with cotyledons spirally twisted; retaining the ancestral characters of 5 to numerous carpels, with elongated styles/stigmas, and 2 cotyledons).

 The showy flowers are pollinated by various beetles. Fruit dispersal of *Calycanthus* is by wasps (Burge and Beck 2019), which are attracted by fragrance and rewarded by food-bodies. The large fruits of *Idiospermum* merely drop to the forest floor.

***Additional references***: Nicely 1965; Staedler et al. 2009; Wood 1958.

**Hernandiaceae** Blume

(Lantern-tree Family)

*Trees, shrubs, or lianas* (climbing either by hooked branches or twining petioles); *nodes unilacunar* (with 3-7 vascular strands); *with scattered spherical cells containing ethereal oils* (aromatic terpenoids, but eventually forming mucilaginous cavities); with benzyl-isoquinoline and/or aporphine alkaloids; sometimes with cystoliths. Hairs simple, glandular or non-glandular, the latter often apically hooked. *Leaves alternate and spiral, simple, sometimes lobed, or palmately compound, entire, with palmate venation* (or the leaflets pinnately veined, if leaf palmately compound), *the blade with pellucid dots*; *stipules lacking*. Inflorescences determinate, axillary. Flowers bisexual or unisexual (and plants then polygamous, monoecious, or rarely dioecious), *usually small*, and with or without bracteoles. *Tepals 3-10,* distinct, imbricate, in 1 or 2 whorls. *Stamens 3-5; filaments usually with a pair of basal-lateral nectariferous appendages* (staminodes); *anthers opening by 2 flaps, which pull out the sticky pollen*; pollen grains without apertures, exine reduced to tiny spines. **Carpel 1; ovary inferior**, *with apical placentation*; stigma 1, ± *peltate*. Ovule 1, **with a very thick outer integument**. **Fruit a nut** *or samara*, *often associated with persistent, accrescent, distinct to fused bracteoles*; **embryo ± large**, sometimes with much folded cotyledons; **endosperm lacking**.

***Floral formula***: \* T -3-10- , A 3-5 , G 1 ; nut, samara

***Distribution***: Pantropical.

***Genus/species***: 5/60. ***Major genera***: *Hernandia* (23 spp.) and *Illigera* (20). No genera occur natively in the continental United States or Canada, although *Hernandia* *nymphaeifolia* is occasionally grown in southern Florida.

***Economic plants and products***: A few species of *Hernandia* (lantern-trees) are used as ornamentals. The common name alludes to their unusual fruits: a nut surrounded by a white to pink, fleshy, inflated cupule, which is derived from two fused bracteoles.

***Discussion***: The monophyly of Hernandiaceae is supported by morphology (see description; Kubitzki 1993c; Stevens 2001 onward) and DNA sequences (Michalak et al. 2010; Renner and Chanderbali 2000; Soltis et al. 2011). The familial clade is comprised of two subclades: Hernandioideae (*Hazomalamia*, *Hernandia*, *Illigera*; anther valves laterally hinged, pollen grains large; vascular bundles in the seed testa) and Gyrocarpoideae (*Gyrocarpus*, *Sparattanthelium*; perianth of a single whorl, cotyledons much folded). There is much variation in fruit morphology; the nuts of *Hernandia* are surrounded by fleshy, accrescent bracteoles, while the samaras of *Illigera* are laterally 4-winged and those of *Gyrocarpus* are apically 2 winged. *Illigera* and *Sparattanthelium* are lianas, the former climbing by means of tendril-like petioles and the latter by hooked lateral branches.

 The white to cream or pink, small to moderate-sized flowers are pollinated by various flies, bees and/or beetles. A unique reproductive condition has been described in *Hernandia hymphaeifolia*, in which some individuals within a population have carpellate flowers that open in the morning and staminate flowers that open in the afternoon, while other trees exhibit the reverse situation, thus encouraging outcrossing (Endress and Lorence 2004; Gottsberger 2016). Dispersal of the various fruits of Hernandiaceae is by mammals, birds, water (floating in either rivers or ocean currents), or wind.

***Additional reference***: Howard 1977,

**Siparunaceae** Schodde

(Siparuna Family)

S*mall trees, shrubs, or lianas*; *nodes unilacunar*; *tissues with scattered spherical cells containing ethereal oils* (*aromatic terpenoids*); with benzyl-isoquinoline and aporphine alkaloids. Hairs simple, *stellate, fasciculate, or peltate scales*. *Leaves opposite and decussate*, rarely whorled, simple, *toothed to entire*, *with pinnate venation*, *blade with pellucid dots*; *stipules lacking*. Inflorescences determinate, axillary or cauliflorous. **Flowers unisexual** (and plants monoecious or more commonly dioecious), radial, *with a markedly concave receptacle*, *and with a floral roof, ± small*, pale green to white or pink. *Tepals 4-6 (-7)*, *often very tiny*, distinct or connate, imbricate. *Stamens 2 to numerous*; **filaments without paired appendages**; *anther usually dehiscing by a single flap*; pollen grains without apertures, exine reduced to tiny spines. *Carpels 3 to numerous, distinct; ovaries superior, with basal placentation*; styles short; stigmas punctate to slightly elongate. *Ovule 1*, **with 1 integument**. Nectary absent. *Fruit a cluster of small drupes, enclosed in a persistent, fleshy urn-shaped to globose receptacle that opens irregularly, exposing the fruits, each often with a fleshy, persistent aril-like style*; embryo small.

***Floral formula***:

Staminate: \* , T -4-6- , A 2-many , G 0

[Put a dashed line around -4-6- tepals; replace “many” with infinity symbol]

Carpellate: \* , T -4-6- , A 0 , G 3-many ; drupes

[Put a dashed line around -4-6- tepals; replace “many” with infinity symbol]

***Distribution***: The Neotropics and a small region of West Africa.

***Genera/species***: 2/78. ***Genera***: *Siparuna* (74 spp.) and *Glossocalyx* (4). The familial clade is absent from the United States and Canada.

***Economic plants and products***: Several species of *Siparuna* are used medicinally, and their essential oils repel insects.

***Discussion***: The monophyly of Siparunaceae is well supported by DNA sequences (Renner 1999, 2005; Renner and Won 2001; Renner et al. 1997) and there is also morphological support (Renner and Hausner 2005; Stevens 2001 onward; see also description). Traditionally these two genera were placed within Monimiaceae (Philipson 1993), but they can be distinguished from that family by their ovules with only a single integument, usually stellate to lepidote hairs, anthers each opening by a single flap (rarely 2 flaps), and the cluster of drupes usually with “arillate” styles, and surrounded by an irregularly opening receptacle. Within *Siparuna*, *S. decipiens* is sister to the remaining species, and dioecy has evolved several times from monoecy.

 The flowers of Siparunaceae are pollinated by gall midges, which lay their eggs chiefly in the staminate flowers (Feil 1992; Gottsberger 2016; Renner et al. 1997). The colorful drupes, usually contrasting with the fleshy, persistent style and/or fleshy receptacle, are dispersed by birds.

***Additional reference***: Renner and Hausner 2000.

*Canellales*

**Canellaceae** Martins

(Canella Family)

*Trees or shrubs; nodes trilacunar*; with scattered spherical cells containing ethereal oils (aromatic terpenoids, and these hot, spicy, cinnamon-like); **sieve tube plastids with peripheral proteinaceous filaments**. Hairs lacking. *Leaves alternate* *and spiral* or 2-ranked, simple, *entire*, with pinnate venation, *the blade with pellucid dots*; stipules lacking. Inflorescences determinate, sometimes reduced to a single flower, terminal or axillary. Flowers bisexual, radial, with short receptacle. *Sepals 3*, distinct, imbricate. *Petals (4-)5-12*, usually distinct, imbricate. *Stamens 6 to numerous***; filaments connate**, **forming a tube that produces nectar**; **anthers connate**, *opening toward outside*, sometimes with a connective projection; pollen grains monosulcate or trichotomosulcate, released individually. *Carpels 2-6, connate*; ovary superior, **with parietal placentation**; *style short and stigma lobed*. Ovules 2 to many per carpel, campylotropous. *Fruit a berry*; seed with tiny embryo; endosperm homogeneous or ruminate.

***Floral formula***: \* K 3 , C 5-12 , A 6-numerous , G 2-6 ; berry

[Replace “numerous” with infinity symbol; circle the 2-6 carpels; circle the 6-numerous stamens]

***Distribution***: Caribbean region, South America, eastern Africa, and Madagascar.

***Genus/species***: 5/25. ***Major genera***: *Pleodendron* (7 spp.), *Cinnamodendron* (7), and *Cinnamosma* (6). Only *Canella winteriana* occurs in the continental United States (in southern Florida).

***Economic plants and products***: The inner bark and/or leaves of *Canella* (wild cinnamon, cinnamon-bark), *Pleodendron,* and *Warburgia* (pepper-bark tree) are used as a spice. *Canella* is occasionally grown as an ornamental.

***Discussion***: The monophyly of Canellaceae is supported by morphology (see description; and also Stevens 2001 onward), especially the distinctive androecium and 2-6-carpellate ovary with parietal placentation, and phylogenetic analyses of nucleotide sequences ( Müller et al. 2015; Qiu et al. 2000; Salazar and Nixon 2008; Salazar et al. 2020; Savolainen et al. 2000a; Soltis et al. 2000, 2011; Zimmer et al. 2012). The familial clade shares drimane-type sesquiterpenoids with the Winteraceae. *Canella* *winteriana* (with terminal, cymose inflorescences) is sister to a clade comprising the remaining genera (with axillary, reduced and raceme-like cymes to solitary flowers); within the axillary flowered clade, *Pleodendron* (including the Antillean species formerly of “*Cinnamodendron*”; many-seeded berries with fibrous pulp) is sister to a clade comprising *Warburgia* (large berries), *Cinnamosma* (petals connate; leaves with hypodermis), and *Cinnamodendron* (including *Capsicodendron*; stipitate berries, connective appendages). The familial clade likely originated in the Neotropics and experienced two long distance dispersal events, one to Africa (represented by *Warburgia*) and one to Madagascar (*Cinnamosma*) (Müller et al. 2015).

The flowers of Canellaceae are pollinated by a variety of insects as well as by birds; at least in *Canella* all the flowers on an individual tree are synchronized, so all have either a receptive stigma or anthers shedding pollen, and different trees are in different phases, thus enforcing outcrossing (Gottsberger 2016). The berries are taken by birds, bats or other mammals.

***Additional references***: Kubitzki 1993a; Wood 1958.

*Piperales*

**Saururaceae** Richard

(Lizard’s-tail Family)

*Herbs, usually from rhizomes*; nodes often swollen or jointed; vessel elements with numerous scalariform perforations; **vascular cambium reduced**; stem with vascular bundles usually in a single ring, but in 2 rings in *Saururus*; *with spherical cells containing ethereal oils*. Hairs simple. Leaves alternate and spiral, simple, entire, with palmate or pinnate venation, *the base ± cordate*, *with pellucid dots*; *stipules adnate to the petiole* **and intrapetiolar** (positioned between the stem and the petiole) and petiole often sheathing stem. *Inflorescences* *indeterminate*, *spikes or racemes, with numerous small flowers,* terminal, but often displaced to a position opposite the leaf due to development of axillary shoot. Flowers bisexual, radial or bilateral (but then appearing to be radial), *larger than in Piperaceae*, each flower associated with a bract, and the bracts at the inflorescence base sometimes expanded, petal-like. *Perianth lacking*. *Stamens 3-6 (-8); filaments slender*, distinct, or connate in pairs, or adnate to ovary; pollen grains usually monosulcate, **the exine punctate (with the scattered, minute holes in exine surrounded by papillae)**. *Carpels 3-5, ± connate*, but only basally fused in *Saururus*; *ovary superior to inferior* (due to adnation of stamens), *with parietal or lateral placentation*; *styles separate and as many as the carpels*; *stigmas elongate, extending along adaxial side of each style*. *Ovules 2 to numerous on each placenta*; orthotropous, with 2 integuments and with a thick- to thin-walled megasporangium. Nectaries lacking. *Fruit a capsule*, but schizocarpic in *Saururus*, with each carpel an indehiscent and 1-seeded nutlet; endosperm scanty, supplemented by perisperm.

***Floral formula***: \* T 0 , A 3-6 , G 3-5 ; capsule, schizocarp

[Put a dashed circle around 3-6 stamens, also put a dashed line connecting 3-6 stamens to the gynoecium; put a dashed circle around the 3-5 carpels, and draw a line above the 3-5 carpels, to show that the ovary can be inferior as well as superior]

***Distribution and ecology***: North America, eastern Asia, temperate to tropical, especially of wetland habitats.

***Genus/species***: 4/6. ***Genera***: *Gymnotheca* (2 spp.), *Saururus* (2), *Anemopsis* (1), and *Houttuynia* (1). *Saururus* and *Anemopsis* occur natively in the continental United States and/or Canada, while *Houttuynia* is sparingly naturalized.

***Economic plants and products***: *Saururus* (lizard’s-tail) is used medicinally. *Houttuynia* (Chinese lizard’s-tail, fish-mint), *Anemopsis* (yerba mansa), and *Saururus* are used as ornamentals. The rhizomes of *Houttuynia* are eaten.

***Discussion***: The monophyly of Saururaceae is supported by morphology (Meng et al. 2003; Stevens et al. 2001 onward; Tucker et al. 1993; see also description) and DNA-sequences (Jaramillo et al. 2004; Massoni et al. 2014; Meng et al. 2002, 2003; Neinhuis et al. 2005; Smith and Stockey 2007). *Saururus* was supported as sister to the remaining genera in the morphology-based analysis of Tucker et al. (1993) but more recent analyses (of morphological and/or molecular characters) support the recognition of two subclades within Saururaceae: 1) a *Saururus* + *Gymnotheca* clade (synapomorphies: fibers in stem discontinuous; flower-bract stalk present) and 2) an *Anemopsis* + *Houttuynia* clade (inflorescences with showy bracts; flowers with 2 carpels). *Saururus* stands apart from the other three genera in having nearly distinct carpels, a condition considered ancestral by Tucker et al. (1993) but as a likely reversal from the clearly syncarpous gynoecium by Jaramillo et al. (2004) and Meng et al. (2003).

 The flowers of Saururaceae are pollinated by a variety of insects (especially thrips, bees, flies, beetles), but wind may also play a role. The fruits of *Saururus* are likely water dispersed, but the plants also spread vegetative (by rhizome fragments).

***Additional references***: Wood 1971; Wu and Kubitzki 1993.

*Chloranthales*

**Chloranthaceae** Sims

(Chloranthus Family)

*Trees, shrubs, or herbs*; nodes unilacunar or trilacunar; with sesquiterpene lactones, sometimes mucilaginous, often with sclereids, and *with scattered spherical cells* *containing ethereal oils*; **stems with intercalary meristem at the nodes**; wood of stems lacking vessels (in *Sarcandra*). Hairs simple or branched. **Leaves opposite and decussate***, simple, toothed* (and chloranthoid, i.e., teeth with usually a clear, persistent, swollen apex into which proceed higher order veins as well as secondary or tertiary veins), *with pinnate venation*, *blade with pellucid dots*; **petiole bases fused, forming a short to prominent sheath around the stem and the stem thus appearing swollen at the nodes**; **stipules present, interpetiolar, small and borne upon the rim of the sheath**. **Inflorescences indeterminate** (and usually **forming spikes or branched, composed of spicate units**). **Flowers** **very reduced, small**, bisexual or unisexual (and plants then dioecious or monoecious), radial or bilateral (through reduction), **sessile,** associated with 1-3 bracts. **Perianth parts in a single whorl**. *Tepals* (in carpellate flowers of *Hedyosmum*) *3, reduced*, with open aestivation, *closely associated with gynoecium, with pores (or windows) developing in center of each tepal*, *otherwise the perianth absent*. *Stamens usually 1-3*, *with filament poorly differentiated from anther*, and sometimes the stamen strongly 3-lobed (probably through connation of 3 stamens of the androecium, although alternatively through the formation of 3 lobes from a single stamen), the connective sometimes broad or with an apical extension; pollen grains monosulcate, 4-6-colpate, polyporate, or inaperturate. **Carpel 1**; ovary superior to partly inferior (and often appearing inferior, in *Hedyosmum*, due to close association with the 3 tepals) or nude, *with apical placentation*; style very short and stigma various. **Ovule 1, orthotropous**. *Fruit a drupe* (*Hedyosmum*) *or berry* (other three genera). Seeds with **inner layer of testa lignified and crystalliferous** (butlost in *Hedyosmum*, which has a thin and unspecialized testa); embryo minute.

***Floral formula***: \* T 0 or -3- , A 1-3 , G 1 ; drupe, berry

[Circle the 3 tepals, put a dashed line around the 3 stamens]

***Distribution and ecology***: Tropical North and South America, Madagascar, temperate and tropical southern and eastern Asia, south to New Guinea, New Caledonia, New Zealand, and Pacific islands. They are mainly plants of moist montane forests.

***Genus/species***: 4/77. ***Major genera***: *Hedyosmum* (45 spp.) and *Chloranthus* (18). The familial clade has no representatives in temperate North America.

***Economic plants and products***: Species of *Chloranthus* and *Hedyosmum* are sometimes used as flavorings in teas and also are used medicinally. *Sarcandra glabra* is occasionally cultivated as an ornamental.

***Discussion***: The monophyly of Chloranthaceae, a phylogenetically isolated familial clade of uncertain position, and phylogenetic relationships within the familial clade are supported by morphology (Doyle et al. 2003; Eklund et al. 2004; Endress and Doyle 2009; Stevens et al., 2001 onward; see also description) and DNA sequence data (Antonelli and Sanmartín 2011; Qiu et al. 1999, 2000; Savolainen et al. 2000a; Soltis et al. 2000, 2007, 2011; Zanis et al. 2003; Zhang and Renner 2003; Zhang et al. 2011). *Hedyosmum* is sister to the remaining genera and its carpellate flowers have retained the ancestral condition of having three tepals. Generic monophyly of *Hedyosmum* is supported by its unisexual flowers (which likely evolved independently from those of *Ascarina*), the loss of a floral bract in the staminate flowers, and the close association (and partial fusion) of the tepals to the gynoecium, along with the development of perianth windows or pores. In contrast, the *Ascarina* + *Chloranthus* + *Sarcandra* clade is supported by the synapomorphic loss of the perianth. *Ascarina* is sister to the *Chloranthus* + *Sarcandra* clade, which is supported by the adnation of the androecium to one side of the ovary. *Sarcandra* lacks vessels in the xylem of its stems, whereas in the other three genera the xylem contains vessels (elongate, with scalariform perforation plates). The cladogram topology suggests, therefore, that vessels have been lost in stems of *Sarcandra*, and in fact the roots of this genus do have primitive vessels (Carlquist 1987).

 The reduced, but unusual flowers of Chloranthaceae have attracted much botanical attention (see Crane et al. 1989; Doria et al. 2012; Doyle et al. 2003; Eklund et al. 1997, 2004; Endress 1987; Kong et al. 2002; Swamy 1953), especially given the clade’s long fossil record (Early Cretaceous). It is still uncertain whether or not the ancestral condition in the clade is bisexual or unisexual flowers, and whether or not the unusual, three lobed stamens of *Chloranthus* are the result of the fusion of three stamens or the elaboration and lobing of a single stamen. When compared with flowers of members of the ANA grade or the magnoliid clade, it seems clear that the tiny and seemingly simple flowers of Chloranthaceae are the result of reduction.

 The flowers of *Chloranthus* and *Sarcandra* are fragrant and have a showy androecium; they are pollinated by thrips (in *Chloranthus*) or bees, beetles, bugs, and flies (in *Sarcandra*). *Ascarina* and *Hedyosmum* may be wind pollinated. The berries or drupes are bird dispersed. In *Hedyosmum* the perianth becomes colorful and fleshy, assisting in attraction, and in some species the subtending floral bract is enlarged and fleshy, also assisting in dispersal.

***Additional references***: Friis et al. 2019; Todzia 1988, 1993; Todzia and Keating 1991.

*Monocots*

*Acorales*

**Acoraceae** Martinov

(Sweet-flag Family)

*Emergent aquatic, rhizomatous herbs*; *tissues with spherical cells containing ethereal oils* (phenylpropanoids, monoterpenes, sesquiterpenes, and *providing a sweet odor*) and with air-cavities, but lacking raphide crystals. *Hairs lacking* on vegetative structures. *Leaves alternate,* *2-ranked* **and equitant, and with both surfaces with the same internal anatomy (i.e., unifacial)**, but bifacial in basal sheath region, arising from apex of rhizome, simple, not differentiated into a petiole and blade, entire, with parallel venation, sheathing at base and **with small scales** (colleters) **on the inside of sheath**; stipules lacking. Inflorescences indeterminate, terminal, forming a spike of numerous, **small flowers packed together on a fleshy axis** **(a spadix)**, **associated with a longer, leaf-like bract (spathe),** **with the lower part of the inflorescence axis (scape) adnate to the lower portion of the spathe, thus scape with 2 separate vascular systems**. *Flowers bisexual*, nearly radial, **sessile**, **not individually associated with bracts**. Tepals 6, **with one slightly larger**, distinct, narrow, with open aestivation. Stamens 6; filaments distinct; pollen grains ± monosulcate. Carpels 2-3, connate; ovary superior, with apical-axile placentation, **and each lacking a dorsal carpellary bundle**; stigma punctate, sessile. Ovules several per locule, orthotropous, with a thin-walled megasporangium. Nectaries lacking, **but locules with secretory hairs**. **Fruit a berry**, with few seeds, these with elongate hairs (in *A. gramineus*) or ± glabrous (other species).

***Floral formula***: \* T - 6 - , A 6 , G 2-3 ; berry

***Distribution and ecology***: Widespread in aquatic and wetland habitats of the Northern Hemisphere.

***Genera/species***: 1/4. ***Genus***: *Acorus*. Two species occur in the continental United States and Canada, one native (*A. americanus*, diploid and fertile) and one introduced (*A. calamus,* triploid and sterile). *Acorus* *gramineus* is grown as an ornamental but is not naturalized in North America.

***Economic plants and products***: The rhizomes of *Acorus* (sweet-flag) are used medicinally (for numerous conditions), and it is also used as a pond ornamental.

***Discussion***: The monophyly of *Acorus* and their position as sister to the remaining monocots are supported by molecular data (Chase et al. 1993, 1995b, 2000, 2006; Duvall et al. 1993; Graham et al. 2006; Soltis et al. 2000, 2011), and its distinctive morphological characters are outlined by Grayum 1987, Stevens 2001 onward, Bogner and Mayo 1998, and Keating 2002; see description). Raphides are present in Araceae but absent in the tissues of Acoraceae, while the latter has ethereal oils (and thus a sweet odor) while the former lacks these molecules. The leaves of Araceae are bifacial and usually differentiated into a petiole and blade, while those of Acoraceae are mainly unifacial and lack a petiole. Finally, in *Acorus* the inflorescence axis is fused to an associated leaf (and has a double vascular supply), while in Araceae the spathe is not fused to the spadix. It is noteworthy that a spathe and spadix have evolved independently in the two familial clades.

 The “calamus” poems (referencing *Acorus calamus*) in *Leaves of Grass* by Walt Whitman express his ideas about homosexual love.

 Pollination in *Acorus* is likely by insects, especially gall-midges. Dispersal of the seeds may be by water, and the plant spreads vegetatively by fragmentation of rhizomes.

***Additional reference***: Rudall and Furness 1997.

*Alismatales*

**Butomaceae** Mirbel

(Flowering-rush Family)

*Aquatic or wetland, rhizomatous herbs*, **with rhizome apparently monopodial**; tissues aerenchymatous. Hairs lacking. Leaves alternate, arising from the rhizome, simple, entire, usually *emergent, and not differentiated into a petiole and blade*, **triangular in cross section**, with parallel venation; sheathing at base; stipules lacking; small scales present at the node inside leaf sheath. Inflorescences determinate, **umbel-like,** axillary, *and borne at the apex of a scape*. Flowers bisexual, radial, *with perianth differentiated into a calyx and corolla* (due to those of outer whorl differing in shape and to a lesser extent in color from those of inner whorl), **but all petaloid**, white or pink. *Sepals 3*, distinct, **petaloid**. *Petals 3*, distinct, imbricate. Stamens 9; filaments distinct; pollen grains monosulcate. *Carpels 6, nearly distinct* (connate only at very base); *ovaries superior*, *with parietal (lateral) placentation*; *stigmas decurrent*. Ovules numerous per carpel. Nectaries on the sides of the carpels near base. *Fruit a cluster of follicles*; *seeds with ribbed coat* (testa) and air canals; *embryo straight*; endosperm lacking.

***Floral formula***: \* K 3 , C 3 , A 9 , G 6 ; follicles

***Distribution and ecology***: Emergent wetland/aquatic herbs of more or less temperate regions, from Western Europe and northern Africa to eastern Asia, and naturalized in North America.

***Genera/species***: 1/1. ***Genus***: *Butomus* (1 sp.). *Butomus umbellatus* is naturalized in the continental U. S. and Canada.

***Economic plants and products***: The starchy rhizomes are occasionally eaten. The plant is also cultivated as an ornamental.

***Discussion***: The monophyly of Butomaceae is supported by molecular analyses (see papers cited under discussion of Alismatales) and morphology (see description; Cook 1998; Stevens 2001 onward). Butomaceae is most closely related to Hydrocharitaceae, which have connate carpels, an inferior ovary, divided styles, and fleshy fruits. Chromosome number is extremely variable in *Butomus umbellatus*.

 The flowers of *Butomus* are pollinated by various insects, especially bees and flies. Dispersal of the seeds is by water, and dispersal also occurs by vegetative fragmentation, especially by small bulbils (produced in leaf axils along the rhizome).

**Cymodoceaceae** Vines

(Manatee-grass Family)

*Marine-aquatic rhizomatous herbs*; stomata absent; roots usually branched; tissues with longitudinal air-canals. *Hairs lacking*. *Leaves alternate and 2-ranked*, *with a blade, sheathing base and ligule at their junction*; *blade simple, linear, with parallel venation, flat or terete*, entire; sheath open, with small scales present inside. Inflorescences determinate, axillary, or reduced to a solitary flower. *Flowers unisexual (and plants dioecious)*, radial, and associated with bracts. *Tepals lacking*. **Stamens** *2***, connate**, each anther often with an apical appendage; *pollen grains filamentous,* without an exine. *Carpels 2, distinct*; ovaries superior, with apical placentation, **each with an elongate unbranched, 2-branched, or 3-branched style; stigmas elongate.** Ovule 1, orthotropous. Nectaries lacking. *Fruit a nut or drupe*, sometimes with the seed germinating on the plant.

***Floral formula***:

Staminate: \* T-0- , A 2 , G 0 [circle the “2” stamens]

Carpellate: \* T -0- , A 0 , G 2 ; nut, drupe [circle the “2” carpels]

***Distribution and ecology***: Widespread submerged herbs of warm temperate to tropical, shallow marine waters (i.e., 0.5 to 40 m deep).

***Genera/species***: 5/17. ***Major genera***: *Halodule* (6 spp.) and *Cymodocea* (4). *Halodule* and *Syringodium* occur in sea-grass beds in shallow marine waters off the coast of the southeastern United States.

***Economic plants and products***: The various species of Cymodoceaceae are eaten by sea turtles, manatees, dugongs, and various species of fish. These plants are extremely important in substrate stabilization, in nutrient cycling, and in maintenance of the ecological health of nearshore environments (Kuo and McComb 1998a).

***Discussion***: The monophyly of Cymodoceaceae was initially unclear (e.g., Les et al. 1997) but has been supported by recent molecular analyses (Petersen et al. 2014, 2016; Ross et al. 2015). The monophyly of the familial clade is also supported by morphology (see description) and secondary chemistry (Stevens 2001, onward). Cymodoceaceae are probably most closely related to *Ruppia*, a group of aquatics (brackish to marine waters) with unbranched roots, one-veined leaves, long-pedunculate and densely spicate inflorescences, and long-stalked carpels (see also discussion under Potamogetonaceae, in which this genus sometimes has been placed, and Ruppiaceae family treatment on this website). Interestingly, Trias-Blasi et al. (2015) place *Ruppia* within Cymodoceaceae, although we consider the genus in Ruppiaceae (following Angiosperm Phylogeny Group 2016). Posidoniaceae, another sea-grass clade, are also related; these plants have very fibrous rhizomes, usually perfect flowers, and follicle fruits. Within the Cymodoceaceae clade, *Halodule* is supported as sister to the remaining genera by analyses of DNA sequences. *Thalassodendron* and *Amphibolis* are closely related and both have lost NADH dehydrogenase complex genes. Both also have woody, sympodial rhizomes (vs. herbaceous and monopodial rhizomes) and distinctive seeds that germinate soon after fertilization while they are still on the parental plant.

 Pollination of Cymodoceaceae is accomplished by movement of tangled masses of filamentous pollen on the water surface (at low tide) that make contact with the elongate stigmas (see Cox 1988; Cox and Knox 1989; Cox et al. 1990). The fruits or germinated seedlings are water dispersed. Vegetative spread is also accomplished by rhizome growth (forming extensive sea-grass beds).

**Posidoniaceae** Vines

(Tapeweed Family)

*Marine-aquatic, rhizomatous herbs*; *the rhizome monopodial*; **its cortex with fiber strands**; roots branched, at the nodes; tissues with longitudinal air canals. *Hairs lacking*. *Leaves alternate and 2-ranked, with blade, sheathing, base, and a ligule at their junction; blade simple, linear, with parallel venation, flat to terete*, entire, with a rounded to truncate apex, with unlignified fiber-bundles; sheath open, usually with lobe-like flanges, with small scales inside, *with numerous lignified, fiber-bundles and these persistent on rhizome*. *Inflorescences indeterminate, axillary, forming branched spikes*, with bracts. **Flowers bisexual**, radial, sessile, and not individually associated with a bract. *Tepals lacking*. *Stamens 3, distinct*, **the pollen sacs (thecae) well separated (so appearing to be 6 anthers), and anther connective broad, shield-like, with anthers deciduous;** *pollen grains filamentous*, **without an exine**. **Carpel 1;** ovary superior, with ± apical placentation; *style absent; stigma expanded, irregularly lobed*. **Ovule** 1, **campylotropous, with an outgrowth formed from the fused integuments opposite the micropyle**. Nectaries lacking. **Fruit a fleshy/spongy follicle, surrounded by persistent anther connectives**.

***Floral formula***: \* T - 0 - , A 3 , G 1 ; fleshy follicle

***Distribution and ecology***: Submerged herbs of marine waters (i.e., 0-40 m deep) of the Mediterranean Sea and off the coast of southern Australia.

***Genera/species***: 1/9. ***Genus***: *Posidonia* (9 spp.). The family does not occur in the coastal North America.

***Economic plants and products***: *Posidonia* forms ecologically important seagrass beds.

***Discussion***: The monophyly of Posidoniaceae is supported by DNA sequence data (Aires et al. 2011; Les et al. 1997) and morphology (see description, also Stevens 2001 onward), especially its distinctive floral morphology. The karyotype is unusual and consists of five larger and five smaller chromosomal pairs. *Posidonia oceanica*, of the Mediterranean, is sister to the remaining species (*P. ostenfeldii*, *P. australis*, and relatives), which are all plants of waters off the coast of southern Australia.

*Posidonia* is water pollinated, and its fruits also float in water, each eventually opening to release the seed, which sinks and quickly germinates (Kuo and McComb 1998b). Unusual ball-like masses of rhizomes and roots are often washed ashore.

***Additional reference***: Remizowa et al. 2012.

**Ruppiaceae** Horaninow

(Tasselweed Family)

*Aquatic rhizomatous herbs (of shallow, fresh water of high calcium or sulfur ion concentration, or brackish-water, to less commonly saltwater)*; tissues with longitudinal air-canals; **roots unbranched**. *Hairs lacking*. *Leaves ± alternate and 2-tanked, with a blade and sheathing base,* a ligule absent; *blade simple, linear*, **with a single vein**, *flat*, *entire below and minutely serrate above*; sheath open, its apex with slight lobes, and with 2 small scales within the sheath. Inflorescences indeterminate (**1- to few-flowered spike**), terminal, *the peduncle short to very elongate, so flowers at or very near the water’s surface*, *but sometimes very twisted in fruit*, thus pulling fruits below surface. *Flowers bisexual*, radial, sessile. *Tepals lacking*. *Stamens 2, distinct*; anthers ± sessile, each with tiny apical, connective appendage; *pollen grains elongate-arched*, **obscurely triaperturate**. *Carpels 2 to numerous, distinct*; ovaries superior, with ± apical placentation, and each with a sessile, ± peltate and funnel-like stigma; **and as each carpel matures into a fruit it usually develops a slender stalk (gynophore)**. Ovule 1, campylotropous. Nectaries lacking. *Fruit a cluster of drupelets*, **each** **usually on a long stalk**, *so gynoecium of a single flower appears to be an umbellate-cluster; the pit of each fruit with a small germination lid;* **embryo with lateral primary root.**

***Floral formula***: \* T - 0 - , A 2 , G 2-many ; drupelets

[Replace “many” with infinity symbol.]

***Distribution and ecology***: Widespread, submerged herbs of fresh or brackish waters.

***Genera/species***: 1/5-11. ***Genus***: *Ruppia* (5-11 spp.). One (or perhaps two) species of *Ruppia* (tasselweed, ditch-grass, wigeongrass) occur in the continental United States and Canada or in brackish waters along the coast.

***Economic plants and products***: Important as a food for waterfowl.

***Discussion***: The monophyly of Ruppiaceae is supported by morphology (see description; and Haynes et al. 1998; Stevens 2001 onward) and phylogenetic analyses based on DNA sequences (Ito et al. 2010, 2015). The four species *Ruppia biflora*, *R. megacarpa*, *R. tuberosa*, and *R. polycarpa* are clearly morphologically diagnosable and are successively sister to the remaining species, which comprise the widespread *R*. *maritima* complex (within which polyploidy and hybridization occur; including among other species, *R. spiralis*).

 Pollination occurs on the water’s surface, with the pollen grains forming floating chains that contact the surface-positioned stigmas. Fruit dispersal can occur by floating in water currents, although the fruits are also eaten by waterfowl and fish.

***Additional references***: Haynes 1978.

**Tofieldiaceae** Takhtajan

(False-asphodel Family)

*Rhizomatous herbs*; steroidal saponins and chelidonic acid present; **plastids of the sieve tubes in the phloem with polygonal proteinaceous crystals**. Hairs simple, glandular or not. *Leaves alternate, 2-ranked*, **unifacial (i.e., both surfaces with the same internal anatomy) and equitant**, *basal to ± along stem,* simple, linear*,* entire to serrulate, *with parallel venation*, sheathing at the base; stipules lacking. *Inflorescences determinate, terminal*, rarely reduced to a solitary flower. Flowers bisexual, radial, inconspicuous to conspicuous, and associated with a bract **and calyx-like involucre of usually 3 bracts** (calyculus). *Tepals 6, distinct*, imbricate, often petaloid. *Stamens usually 6 or 9*; filaments distinct to basally connate, sometimes adnate to tepals; **pollen grains bisulcate**. *Carpels 3, ± connate, but sometimes only slightly so,* **often on short stalks***; ovary superior*, *with axile* (when more fused) *to parietal* (when less fused) *placentation*; styles 3 or 1; stigmas truncate to capitate, sometimes 3-lobed. Ovules few to many per locule, anatropous to campylotropous, with 1 or 2 integuments; megagametophyte often developing from 2 megaspores (*Allium* type), or of normal development (*Polygonum* type). *Nectaries basal, on adjacent surfaces of ovary stalks and between carpels, similar to septal nectaries, but carpels less fused*. *Fruit septicidal capsules or follicle-like, ridged or with small bumps* (tuberculate); **seeds often appendaged**, yellow to brown or reddish.

***Floral formula***: \* T - 6 - , A 6 or 9 , G 3 ; capsule

[Circle the “3” carpels]

***Distribution***: Widespread in the Northern Hemisphere, and disjunctly in northern South America.

***Genera/species***: 5/28. ***Major genera***: *Isidrogalvia* (13 spp.) and *Tofieldia* (8). *Harperocallis*, *Pleea*, *Tofieldia*, and *Triantha* occur in the continental United States and/or Canada.

***Economic plants and products***: *Tofieldia* (False-asphodel) and *Harperocallis* (Harper’s beauty) are occasionally used as ornamentals.

***Discussion***: The monophyly of Tofieldiaceae is supported by morphology (Ambrose 1980; Cruden 1991; Remizowa et al. 2011; Zomlefer 1997b; see also description) and DNA sequences (Azuma and Tobe 2011; Iles et al. 2013; Tamura et al. 2004). *Pleea* (which retains the ancestral character of 9 stamens, and shows the derived character of having a spathe-like bract that covers the calyculus) is sister to the remaining genera (6 stamens, calyculus placed just beneath tepals). Within the latter clade, two major subclades are evident: the *Isidrogalvia* + *Harperocallis* clade (bracts of calyculus free, ovary covered with tubercles, i.e., conspicuous bumps, and carpels with separate placental vascular bundles, supplying the massive, intruding placentas; see also Remozowa et al. 2011, McDaniel 1968) and *Tofieldia* + *Triantha* clade (morphological synapomorphies unclear). The family, along with Araceae, represents a basally branching lineage in Alismatales. Traditionally these plants were placed either in a broadly circumscribed Liliaceae (Cronquist 1981) or a broadly circumscribed Melanthiaceae (Dahlgren et al. 1982; Thorne 1992).

 The flowers of Tofieldiaceae are likely pollinated by various insects; the small, often appendaged seeds are wind dispersed.

**Zosteraceae** Dumortier

(Eelgrass Family)

*Marine-aquatic, rhizomatous herbs*; **the rhizome usually monopodial**; stomata absent; roots usually unbranched, at the nodes **and in 2 groups/rows**; tissues with longitudinal air-canals; **sieve tubes with thick, pearl-like walls**. *Hairs lacking*. *Leaves alternate and 2-ranked, with blade, sheathing base, and a ligule at their junction*; *blade simple, linear, with parallel venation, flat or biconvex*, entire, but sometimes apically notched, with unlignified fiber-bundles; sheath open or closed, usually with lobe-like flanges, with small scales inside. **Inflorescences** indeterminate, **opposite leaves**, **each a flattened, spike-like axis (spadix)**, the margins of which sometimes bears lobes or appendages, **bearing 2 rows of flowers on one side**, **and the spadix closely associated with a modified leaf sheath (spathe)**. *Flowers unisexual (and plants dioecious or monoecious, and if the latter then staminate and carpellate flowers alternating in each row),* ± slightly bilateral. *Tepals and bracts lacking*. **Stamen 1**; filament absent or very *short;* **pollen grains filamentous**, without an exine; staminode sometimes present in carpellate flowers. *Carpels 2, connate*; ovary apparently superior, with apical placentation, with a single style **and 2 elongate stigmas**. Ovule 1, orthotropous. Nectaries lacking. *Fruit an achene or achene-like capsule*.

***Floral formula***:

Staminate: X T - 0 - , A 1 , G 0

Carpellate: X T – 0 - , A 0 or 1**.**, G 2 ; achene or achene-like capsule

[Circle the 2 carpels; the superscript dot by the 1 stamen in carpellate flower formula indicates a staminode]

***Distribution and ecology***: Submerged herbs of arctic to tropical marine waters (i.e., 0-12 m deep) of the Northern Atlantic and northern Pacific oceans, off the coasts of Chile, southeastern Africa, Australia, and New Zealand.

***Genera/species***: 2/20. ***Genera***: *Zostera* (14 spp.; incl. *Heterozostera*) and *Phyllospadix* (6). Only *Zostera* occurs in the waters off the continental United States and Canada.

***Economic plants and products***: *Zostera* and *Phyllospadix* form ecologically important seagrass beds, supporting a large number of economically important marine organisms (especially crabs, shrimp, and fishes).

***Discussion***: The monophyly of Zosteraceae is supported by DNA sequences (Chen et al. 2004; Coyer et al. 2013; Kato et al. 2003; Les et al. 1997, 2002) and morphology (Les et al. 2002; Stevens 2001 onward; see also description), especially the monopodial rhizome and distinctive inflorescence morphology. *Phyllospadix* (rhizome thick; roots short and thick; plants dioecious) is sister to the remaining species, which are here considered within a broadly circumscribed *Zostera* (rhizome slender; roots long, slender; plants monoecious). Genetically *Zostera* is of interest in that its genome has lost the genes relating to stomatal development, the synthesis of terpenoids, ethylene signaling, ultraviolet protection, and the production of phytochromes. Its cell walls contain sulfated galactans, facilitating water and ion retention. Osmotic equilibrium is also accomplished by organic osmolytes (sucrose, trehalose, and proline) in the tissues (Olsen et al. 2016). Some of these potential synapomorphies may be shared with other seagrasses.

Pollination is abiotic, with groups of filamentous pollen grains moving across the water surface or submerged in the water column, in either case colliding with the elongate stigmas of the carpellate flowers (Ackerman 1997a, b; Cox et al. 1992; Kuo and McComb 1998c). Seed dispersal is also by water.

*Liliales*

**Alstroemeriaceae** Dumortier

(Inca Lily Family)

*Herbs or twining vines*, rarely small shrubs, *rhizomatous, usually with swollen, storage roots*; steroidal saponins and tuliposides often present. Hairs simple. *Leaves alternate and spiral,* rarely two ranked, *borne along stem or clustered distally*, simple, entire, *with parallel or arching venation*, sometimes with clearly reticulate or percurrent venation between the primary veins, *not sheathing at the base*, usually **resupinate, i.e., the base twisted so that the abaxial surface is uppermost, so stomata on apparently upper surface**; stipules lacking. **Inflorescence determinate** (**cymose**, *often appearing umbellate*), *usually terminal*, sometimes reduced to a solitary flower. *Flowers* bisexual, bilateral or radial, *conspicuous*. *Tepals 6*, *distinct*, imbricate, *petaloid*, *usually clawed, the inner whorl often differentiated from the outer and with spots and/or lines. Stamens 6*; filaments distinct; pollen grains monosulcate. *Carpels 3, connate*; *ovary inferior* or rarely superior, *with usually axile placentation*; stigmas usually 3, ± elongated. Ovules usually numerous, with a thin megasporangium. *Nectar produced at base of tepals*. *Fruit a loculicidal capsule*, rarely a berry; seeds ± globose, brown, dry and tuberculate, or with an orange to red fleshy coat.

***Floral formula***: X or \* T - 6 - , A 6 , G 3 ; capsule

[Circle the three carpels; draw a line above the circle to indicate inferior ovary]

***Distribution***: North America (Mexico), West Indies, to Central and South America, Australia, Tasmania, and New Zealand; naturalized in the United States, Portugal, and the Canary Islands.

***Genera/species***: 4/185. ***Major genera***: *Bomarea* (100 spp.) and *Alstroemeria* (80). *Alstroemeria* is sparingly naturalized in the southeastern United States.

***Economic plants and products***: *Bomarea* and *Alstroemeria* (Inca lily) are used as ornamentals, and the starchy roots produced by plants of both genera are occasionally eaten (especially in *B. edulis,* salsilla).

***Discussion***: The monophyly of Alstroemeriaceae is supported by the resupinate leaf blades and DNA sequence data (Chacón et al. 2012a, b; Chase et al. 2006; Kim et al. 2013; Peterson et al. 2013). Their bimodal karyotype (e.g., 1 to 3 larger, metacentric chromosomes and 5 to 8 smaller, acrocentric chromosomes) is an additional possible synapomorphy. Within the family, *Alstroemeria* and *Bomarea* (Alstroemerieae) form a clade supported by DNA sequences (Aagesen and Sanso 2003; Chacón et al. 2012a, b; Chase et al. 1995; Kim et al. 2013; Peterson et al. 2013; Rudall et al. 2000) and morphology (storage roots, ovary inferior, fruit dehiscing laterally, and presence of tuliposides; Aagesen and Sanso 2003; Bayer 1998; Sanso and Xifreda 2001; Stevens 2001 onward). Alstroemerieae are sister to Luzuriageae (*Drymophila* and *Luzuriaga*; comprising 5 species), and their monophyly is supported by berry fruits (Conran and Clifford 1998; Stevens 2001 onward) and DNA sequences (Chacón et al. 2012). The tribes Alstroemerieae and Luzuriageae have often been treated at familial rank (Bayer 1998; Conran and Clifford 1998; Dahlgren et al. 1985). *Alstroemeria* and *Bomarea* were traditionally included within a broadly circumscribed Amaryllidaceae because of their inferior ovaries and umbellate inflorescences, but they are not closely related to this familial clade; note that their seeds are non-black and they lack septal nectaries (having instead perigonal nectaries).

 The showy and typically very colorful flowers of Alstroemeriaceae usually attract various insects (bees, bumblebees, beetles, butterflies, hoverflies, and perhaps also moths), but a few may be pollinated by birds. The seeds are ballistically dispersed in *Alstroemeria*, in which the capsules are explosive, shooting out the fruit valves and dry, brown seeds. The leathery to fleshy capsules open to expose the colorful, fleshy-coated seeds in *Bomarea*, which are taken by birds (Sanso and Xifreda 2001). The berries of *Drymophila* and *Luzuriaga* are probably animal dispersed.

*Asparagales:*

**Agapanthaceae** F. Voigt

(African-lily Family)

*Herbs from a tuberous, erect rhizome*; with steroidal saponins, *but without the onion- or garlic-scented sulfur compounds of Alliaceae and also without the characteristic “amaryllis” alkaloids of Amaryllidaceae*. Hairs simple. Leaves alternate, 2-ranked, ± basal, simple, flat, entire, with parallel venation, sheathing at base; stipules lacking. *Inflorescences* determinate, composed of contracted helicoid cymes and *appearing to be an umbel*, *subtended by 2 membranous to herbaceous spathelike bracts*, *terminal at the end of a long scape*. *Flowers bisexual, slightly bilateral, showy* and **blue, purple** or occasionally white; individual flowers each subtended by a threadlike bract. *Tepals 6; connate*, and perianth ± bell-shaped, the lobes imbricate, petaloid, not spotted. *Stamens 6*; filaments distinct, *adnate to* *tepals*; **anthers with middle layer of wall from outer secondary parietal cells**; pollen grains monosulcate. *Carpels 3*, connate; *ovary superior*, with axile placentation; stigma 1, small. Ovules numerous in each locule, with a thin-walled megasporangium. *Nectaries in septa of ovary*. *Fruit a loculicidal capsule; seeds flat and winged, the seed coat black, with phytomelan*, and inner layers compressed or collapsed.

***Floral formula***: X , T -6- , A 6 , G 3 ; capsule

[Draw a circle around the -6- tepals, draw a line under the formula connecting the 6 tepals and 6 stamens; circle the 3 carpels]

***Distribution***: South Africa.

***Genera/species***: 1/9. ***Genus***: *Agapanthus* (9 spp.). The genus is sparingly naturalized in the United States (California).

***Economic plants and products***: *Agapanthus* (African-lily, blue-lily, lily-of-the-Nile) is widely used as an ornamental, including many hybrids.

***Discussion***: The monophyly of Agapanthaceae is supported by analyses of DNA sequences (see citations under Asparagales and Alliaceae, in textbook) and morphology (see description; Kubitzki 1998; Snoeijer 2004; Stevens 2001 onward). *Agapanthus* was often included within Alliaceae because, like members of that family, its ovaries are superior; the similarity, however, is symplesiomorphic.

 Their flowers are pollinated by a variety of insects, especially bees. The flattened and winged seeds are likely dispersed by wing.

**Hemerocallidaceae** R. Brown

(Day-lily Family)

*Herbs* or vines, *often with rhizomes*; *naphthoquinones*, saponins often present, and typically with raphides; roots often thickened. Hairs simple. *Leaves alternate, 2-ranked* (or spirally 2-ranked), in basal rosettes or along stems, simple, *often rigid/tough*, sometimes fibrous, entire to toothed, with parallel venation, sheathing at the base (but leaves occasionally reduced, and stems then photosynthetic: *Johnsonia* and relatives); stipules lacking. Inflorescences determinate, terminal. Flowers bisexual, radial to bilateral, often showy. *Tepals 6, distinct* to ± connate, imbricate, *petaloid*, *not spotted*. *Stamens usually 6*, filaments distinct or occasionally connate, often with papillae or hairs, sometimes thickened apically, forming a globose, colorful appendage, or with apical hair-tuft; anthers opening by longitudinal slits or apical pores; pollen grains usually **trichotomosulcate** (but monosulcate in *Hemerocallis*). *Carpels 3, connate; ovary usually superior,* with usually axile placentation (or axile below and parietal above); style and stigma 1, punctate to capitate (but style apically 3-branched in *Pasithea*). Ovules few to numerous in each locule. Nectaries in septa of ovary or lacking. *Fruit a loculicidal capsule, berry*, schizocarp, or nut-like; seeds sometimes arillate, the *seed coat black (with phytomelan crust)* and inner layers ± collapsed.

***Floral formula***: \* or X, T -6-, A 6 , G 3 ; capsule, berry

[put dashed line around the 6 tepals; put dashed line around the 6 anthers; put a solid line around the 3 carpels]

***Distribution and ecology***: Widespread, and ecologically diverse but especially common in Australia; with only naturalized species in North America.

***Genera/species***: 20/100. ***Major genera***: *Dianella* (40 spp.) and *Hemerocallis* (20). Both are naturalized in the continental United States and/or Canada.

 ***Economic plants and products***: Several genera, including *Agrostocrinum*, *Dianella* (flax-lily), *Hemerocallis* (day-lily), *Phormium* (New Zealand flax), *Simethis*, *Stypandra*, and *Thelionema*, are used as ornamentals. In *Hemerocallis* a large number of hybrids and cultivars (some sterile triploids, e.g., *H. fulva* ‘Europa’) are grown. Several of the genera, especially *Dianella*, *Hemerocallis*, and *Stypandra* (blind-grass) have also been used medicinally. The flowers of some species of *Hemerocallis* are occasionally eaten. The leaves of *Phormium* (and to a lesser extent *Dianella*) provide fibers that are used in clothing, ropes, twine and nets.

***Discussion***: The monophyly of the family is supported by molecular analyses and its trichotomosulcate pollen (Chase et al. 1995, 1996, 2000, 2006; Devey et al. 2006; Fay et al. 2000; Givnish et al. 2006; Graham et al. 2006; Rudall et al. 1997; Wurdack and Dorr 2009). Neurotoxic binaphthalene-tetrol (hemerocallin) may be a chemical synapomorphy of the familial clade, however, sampling is limited (see Zomlefer 1998). The clade is sometimes treated as a subfamily within an expanded Asphodelaceae, although familial rank is adopted here (in agreement with the arguments outlined in Furness et al. 2014). Genera of Hemerocallidaceae form three major subclades: the phormioids (e.g., *Argostocrinum, Dianella, Eccremis, Phormium, Stypandra, Thelionema*), the Johnsonioids (e.g., *Johnsonia, Caesia*), and the hemerocallid clade (*Hemerocallis, Simethis*). The genus *Hemerocallis* is morphologically distinctive: note its unusual inflorescence (a double helicoid cyme), bilaterally symmetrical flowers, a karyotype having chromosomes in three intergrading size classes, based on a base number of 11, and the loss of trichotomosulcate pollen (i.e., it shows a reversal to the monosulcate condition).

 Flowers of most Hemerocallidaceae are visited by various insects (bees, butterflies, hawk-moths) although bird pollination occurs in *Phormium*; pollen and/or nectar may function as the pollinator reward. Buzz-pollination (by bees) is characteristic of *Dianella,* the Johnsonioids,and probably also several other genera; it may be the ancestral condition in the familial clade and functionally associated with the small, rounded trichotomosulcate pollen with little exine sculpturing, characteristic of the clade (Furness et al. 2014). Species with white-arillate seeds may be ant dispersed, while those with berries are probably mainly bird dispersed. Some genotypes of *Hemerocallis* spread readily by rhizome or root fragments. Polyploidy and hybridization are common in *Dianella* and some populations are apparently agamospermic.

**Laxmanniaceae** Bubani

(Ti Plant Family)

*Tufted herbs*, sometimes rhizomatous, *to shrubs or trees*, *stems sometimes with anomalous secondary growth*; tissues with raphide crystals, steroidal saponins and chelidonic acid, and mucilage sometimes present; roots often fleshy or tuberous, occasionally forming stilts. Hairs simple. *Leaves alternate, 2-ranked or spiral,* simple, linear, and flat to terete or triangular, U- or V-shaped (in cross section), sometimes differentiated into a narrow petiole-like base and broader, blade-like apical portion, entire to spinose-serrate, *with parallel venation*, sometimes with sclerenchymatous ribs extending from the vascular bundle sheath to the leaf surface, the outer bundle sheath sometimes with enlarged cells, sometimes rolled into a tube in bud, sheathing at the base; stipules lacking. Inflorescences determinate or indeterminate, terminal or axillary, sometimes scapose. *Flowers bisexual or unisexual* (and plants then dioecious), *radial*, *± showy. Tepals 6*, distinct to basally connate, imbricate, persistent, *the margins sometimes fringed* *or hairy*, *the outer whorl often differentiated from the inner*. *Stamens 6 or 3, usually distinct*, the outer 3 sometimes forming staminodes or absent; filaments free or adnate to the perianth, sometimes pubescent; anthers opening by longitudinal slits or apical pores; pollen grains monosulcate, but sometimes the sulcus encircling the grain. Carpels 3, connate; ovary superior, with axile placentation; style 1; stigma truncate or capitate to 3-lobed. Ovules 1 to numerous per locule, anatropous to campylotropous; **cells of the megasporangium wall (nucellus) enlarged, the supra-chalazal zone elongated, with central elongated cells; embryo sac with large antipodal cells**. Nectaries usually in septa of ovary. *Fruit usually a loculicidal capsule or berry*; seeds round to angular, sometimes with an aril, and seed coat black or not (with or without phytomelan); embryo sometimes curved or coiled.

***Floral formula***: \* T - 6 - , A 3-6 , G 3 ; capsule, berry

[Dashed line around the 6 tepals; dashed line connecting 3-6 stamens with 6 tepals; circle the 3 carpels]

***Distribution***: Australian region, Pacific islands, tropical Asia, Madagascar, and South America.

***Genera/species***: 14/180. ***Major genera***: *Lomandra* (50 spp.), *Thysanotus* (50), *Cordyline* (24), *Arthropodium* (16), and *Laxmannia* (14). No species are native to North America, however, *Cordyline australis* is naturalized in California.

***Economic plants and products***: Several genera, especially *Arthropodium* (renga-lily, rock-lily), *Cordyline* (*C. australis*, cabbage tree; *C. fruticosa*, ti plant; and others), *Lomandra* (mat-rush, basket-grass), and *Thysanotus* (fringe-lily), are cultivated as ornamentals. *Cordyline* is sometimes used as a fiber source.

***Discussion***: The monophyly of Laxmanniaceae is supported by DNA sequences (Chase et al. 1995, 1996; Chen et al. 2013; Davis et al. 2004; McLay and Bayly 2016; Seberg et al. 2012), but it is morphologically variable and difficult to characterize, although the familial clade exhibits several distinctive embryological characters (see description; and also Chase et al. 1996; Conran 1998, Stevens 2001 onward). The clade is often treated as a subfamily (Lomandroideae) within a very broadly circumscribed Asparagaceae. Three major subclades may be recognized within Laxmanniaceae. The genera of the *Lomandra* clade (i.e., *Acanthocarpus*, *Chamaexeros*, *Lomandra*, *Romnalda*, and *Xerolirion*) show xeromorphic leaf anatomy (e.g., leaves with sclerenchymatous ribs extending from the vascular bundle sheath to the leaf surface, the outer bundle sheath with enlarged cells), 2-ranked leaves, and seeds that lack phytomelan, and they may be the most distinctive subgroup within the familial clade. *Laxmannia* and *Sowerbaea*, both of which have leaves with a ligule, may be related to the *Lomandra* clade. The *Arthopodium* clade (i.e., *Arthropodium*, *Dichopogon*, *Eustrephus*, *Murchisonia*, *Thysanotus*, *Trichopetalum*) includes genera with spirally arranged leaves, which contain mucilage, frequently tuberous roots, flowers having fringed tepals or hairy stamens, and black seeds. The last major clade, consisting only of *Cordyline*, stands out because of its woody habit (stems with anomalous secondary growth), berry fruits, and black seeds. Some species have linear leaves while in others they are pseudopetiolate. *Cordyline* may be sister to the *Arthropodium* clade. *Chamaescilla* is sometimes placed in Laxmanniaceae, but belongs in Hemerocallidaceae (McLay and Bayly 2016).

 Flowers of Laxmanniaceae are pollinated by various insects. The seeds of capsular species often are dispersed by wind or rain-wash. The berries of *Cordyline* are dispersed by birds, and birds also disperse the black seeds of *Eustrephus*, which contain a sweet, aril-like structure and contrast with the fleshy, orange, capsular valves. Other genera with arils are likely dispersed by ants.

**Themidaceae** Salisbury

(Cluster Lily Family)

*Herbs* from a **fibrous-** *or membranous*-**sheathed, starchy corm, the stem monopodial, forming a new stem on top of the old one each year**; **laticifers present**; with steroidal saponins, *but without onion- or garlic-scented sulfur compounds*; *roots contractile*. Hairs simple. Leaves alternate, *spiral*, ± basal, flat, angular, or terete, entire or minutely toothed, with parallel venation, sheathing at the base; stipules lacking. **Inflorescences** determinate, **appearing to be an umbel**, but actually a contracted helicoid cyme, **associated with 3 or more, scarious bracts that do not totally envelop the umbel**, *terminal at the end of a long, stout to weak scape*. Flowers bisexual, radial, often showy, *and each flower associated with a bract*. *Tepals 6, usually connate*, and perianth ± rotate or bell-shaped to ± tubular or inflated-tubular, the tube short to elongate, the lobes imbricate, *petaloid, not spotted;* a corona (outgrowth of perianth) often present. *Stamens 3 or 6*, when 3 then staminodia often present; filaments distinct to connate, adnate to tepals, sometimes appendaged; anthers basifixed or versatile; pollen grains monosulcate. *Carpels 3, connate*; *ovary ± superior*, sometimes on a gynophore, which may be adnate to the tepals by 3 flanges, with axile placentation; stigma 1, capitate to 3-lobed. Ovules 2 to several in each locule. *Nectar produced in septa of ovary*. *Fruit a loculicidal capsule*; seeds angular to ± globose, the seed coat black, with phytomelan and inner layers compressed or collapsed; embryo straight.

***Floral formula***: \* T- 6 - , A 6 or 3 + often 3**.** , G 3 ; capsule

[Circle the 6 tepals, put dashed line around 3-6 stamens, draw a line below connecting tepals and stamens, and circle the 3 carpels]

***Distribution***: Western North America, from British Columbia south to Guatemala.

***Genera/species***: 14/65. ***Major genera***: *Brodiaea* (17), *Triteleia* (15), and *Milla* (11). The family is represented in the continental United States and/or Canada by these three genera as well as *Androstephium, Bloomeria, Dichelostemma, Dipterostemon, Milla*, and *Triteleiopsis*.

***Economic plants and products***: *Brodiaea* (cluster lily)*, Dichelostemma* (firecracker flower, wild hyacinth)*, Dipterostemon* (blue dicks)*, Milla* (Mexican-star), and *Triteleia* (triplet lily) are sometimes grown as ornamentals because of their showy, colorful (white, pink, red, blue, purple) flowers.

***Discussion***: The monophyly of Themidaceae is supported by both morphological and molecular characters (Chen et al. 2013; Fay and Chase 1996; Meerow et al. 1999a; Pires and Sytsma 2002; Pires et al. 2001; Seberg et al. 2012; Stevens 2001 onward). Themidaceae are morphologically easily confused with Alliaceae, as both have umbellate inflorescences, and they often have been considered closely related to Alliaceae and placed within this family (see Dahlgren 1985), but phylogenetic analyses based on DNA sequences indicate that Themidaceae are more closely related to Hyacinthaceae (see Fig. 8.18; see also discussion under Alliaceae). They can be distinguished from Alliaceae by the lack of the onion-scented sulfur compounds, the presence of corms (vs. usually bulbs), their inflorescences with 3 or more scarious, inflorescences bracts that do not cover the floral cluster (vs. 3, enveloping, spathelike bracts), and flowers each associated with a bract (vs. individual flowers not associated with bracts). The Themidaceae are sometimes included within an expanded Asparagaceae (see Fig. 8.18) and then are named Asparagaceae subfam. Brodiaeoideae (Chase et al. 2009). Morphology-based classifications of the twentieth century divided the family into two groups, one with fibrous corms and the second with membranous corms, however, retention of fibrous corms is a shared ancestral feature and the fibrous-cormed genera do not form a clade (although the genera with membranous corms do form a clade; see below). Molecular analyses, in contrast, support a clade containing *Brodiaea, Dichelostemma*, *Dipterostemon*, and *Triteleiopsis* (anthers basifixed), a clade containing *Bessera, Dandya, Jaimehintonia, Milla*, and *Petronymphe* (membranous corm, gynophore ± adnate to perianth tube; Gándara et al. 2014; Gutierrez et al. 2017; Pires and Sytsma 2002). A third infrafamilial clade contains *Triteleia, Bloomeria*, and *Milla* (basal filament appendages forming nectar-cup, but homoplasious); within this clade *Triteleia* is supported by an extended perianth tube and loss of basal filament appendages.

 The showy flowers of Themidaceae are pollinated by various insects. Their seeds are dispersed by wind or rain-wash.

***Additional references***: Pires 2002; Preston 2017; Rahn 1998.

**Xanthorrhoeaceae** Dumortier

(Grass Tree Family)

**Trees or Shrubs with an unbranched to branched, erect trunk, to rosette subshrubs**, sometimes rhizomatous or tuberous, **stems thick, with anomalous secondary growth**; tissues with anthraquinones **and resin cavities** with styloid crystals but lacking raphides; roots contractile. Hairs simple. *Leaves alternate, spiral, in basal rosette or densely clustered at apices of stem or branches*, simple, elongate and linear, entire or serrulate, *with parallel venation*, **with a layer of sclerenchyma below the epidermis**, **not sheathing at the base**; stipules lacking. **Inflorescences** *determinate, terminal*, **massive**, **densely flowered and spikelike** (but with hidden, cymose branches), **on a thick, woody scape**. Flowers bisexual, radial, and **sessile**. *Tepals 6, distinct*, imbricate, **the outer three somewhat sepal-like and the inner three somewhat petal-like**. *Stamens 6*; **filaments** distinct, **long exerted**; pollen grains monosulcate. Carpels 3, connate; ovary superior, with axile placentation; style 1; stigma capitate, 3-lobed. Ovules few per locule. Nectaries in septa of ovary. *Fruit a loculicidal capsule*. Seeds flattened, the s*eed coat with a black crust* (phytomelan); **embryo at right angles to long axis of seed**.

***Floral formula***: \* T - 3 + 3 - , A 6 , G 3 ; capsule

[Circle the 3 carpels]

***Distribution***: Australia.

***Genera/species***: 1/30. ***Genus***: *Xanthorrhoea* (30 spp.). Not occurring in North America.

***Economic plants and products***: Several species of *Xanthorrhoea* (grass trees) have been used medicinally, and they are also used as ornamentals (although slow growing). The yellow, red, or brown resin, which is secreted from the stem and leaf bases, has been variously used, especially by aboriginal groups.

***Discussion***: The monophyly of *Xanthorrhoea* is supported by molecular analyses (McLay 2016) and the group’s distinctive morphology (see description; also Clifford 1998; Dahlgren et al. 1985; Stevens 2001 onward). Species limits are problematic because of frequent hybridization (McLay 2018). *Xanthorrhoea* can be confused with members of Dasypogonaceae (possibly in Arecales), as both show a xerophytic woody habit, but they differ in that *Xanthorrhoea* is resinous (vs. non-resinous in Dasypogonaceae), has massive, densely flowered, spikelike inflorescences (vs. solitary flower surrounded by bracts, or flowers in more or less globose heads), and differences in leaf anatomy.

 The flowers of *Xanthorrhoea* are pollinated by a wide variety of insects, as well as by birds and mammals. Dispersal of the small seeds is by wind.

*Dioscoreales*

**Nartheciaceae** Bjurzon

(Bog-asphodel Family)

*Rhizomatous herbs*; steroidal saponins present, and sometimes with chelidonic acid; **raphide crystals absent** but druses present*;* **roots with air spaces in cortex**. Hairs simple, glandular or not, sometimes moniliform. *Leaves alternate, spiral or 2-ranked,* unifacial (i.e., both surface with the same internal anatomy) or bifacial (i.e., each surface anatomically different), basal and plant forming a rosette or along the stem, simple, entire, *with parallel venation*; sheathing at the base; stipules lacking. Inflorescences indeterminate or mixed (i.e., partly determinate and partly indeterminate), terminal. Flowers bisexual, radial. *Tepals 6, distinct to strongly connate*, imbricate, *petaloid*, and glabrous to variously pubescent. *Stamens 6*; filaments distinct, strongly to only very slightly adnate to tepals, glabrous to densely pubescent; pollen grains monosulcate. *Carpels 3, connate; ovary superior to half-inferior, with axile placentation* (when 3-locular) *or axile below and parietal above* (when ovary 1-locular above, and 3-locular below); **style 1**; stigma capitate, ± 3-lobed. Ovules numerous per carpel, anatropous to campylotropous. Nectaries in the septa of the ovary, or lacking. *Fruit a loculicidal capsule*, *associated with persistent perianth*; seeds occasionally appendaged.

***Floral formula***: \* T - 6 - , A 6 , G 3 ; capsule

[Put a dashed line round the 6 tepals, draw a line below formula connecting the 6 stamens to the tepals; circle the 3 carpels]

***Distribution***: Widespread in the Northern Hemisphere, mainly temperate, but with a few tropical extensions (northern South America, western Malesia).

***Genera/species***: 4-5/41. ***Major genera***: *Aletris* (30 spp.) and *Narthecium* (7). Both, along with *Lophiola*, occur in the continental United States and/or Canada.

***Economic plants and products***: *Aletris* (colic-root, star-grass) is occasionally used medicinally, and both *Aletris* and *Narthecium* (bog-asphodel) are occasionally grown as ornamentals.

***Discussion***: The monophyly of Nartheciaceae is well supported by DNA sequences (Caddick et al. 2000, 2002; Fuse et al. 2012; Merckx et al. 2008; Tamura et al. 2004; Tobe et al. 2018; Zhao et al. 2008) although morphological support is weak (Ambrose 1980; Zomlefer 1997a; see also description). The presence of orbicules (i.e., minute globose bumps) with a circular perforation on the inner walls of the anther locules may be an additional synapomorphy of the family (Merckx et al. 2008). *Metanarthecium* and *Aletris* (both with alternate and spirally arranged leaves and syntepalous flowers) represent basal branches to the *Lophiola* + *Narthecium* + *Nietneria* clade, which is supported by the following putative synapomorphies: loss of a perianth tube, carpels congenitally fused, the loss of septal nectaries, style with a single central longitudinal cavity, and 2-ranked, equitant leaves. Additionally, *Narthecium* has filaments covered with moniliform hairs. *Lophiola* is distinctive in having the inflorescences and flowers densely pubescent and the adaxial tepal surface covered with moniliform hairs (and for these reasons has often been placed in the Haemodoraceae; see Cronquist 1981, Robertson 1976). Traditionally, the remaining genera of the familial clade were either placed in a broadly circumscribed Liliaceae (Cronquist 1981) or Melanthiaceae (Dahlgren et al. 1985; see also discussion in Zomlefer 1997). In the analysis of Merckx et al. (2008), *Metanarthecium* is nested within the phylogenetic structure of *Aletris*, supporting its inclusion within *Aletris* (see also Caddick et al. 2000, 2002), whereas in the analyses of Fuse et al. (2012) and Tamura et al. (2004) the two genera do not form a clade, suggesting that they should be maintained. And if *Aletris* and *Metanarthecium* comprise a clade then flowers with connate tepals may be synapomorphic, with distinct tepals being a retained plesiomorphic condition in the other genera (Zomlefer 1997).

 The flowers of Nartheciaceae are pollinated by various insects, especially bees and flies. Seed dispersal may be by wind or rain-wash.

***Additional reference***: Remizowa et al. 2008.

*Pandanales*

**Cyclanthaceae** A. Richard

(Panama Hat Family)

*Palm-like herbs* or vines, rhizomatous or with erect stems, unbranched or branched, usually with mucilage canals, rarely with laticifers, and silica bodies absent. Hairs often absent, but when present, simple or branched. *Leaves alternate and spiral or 2-ranked, or with the 2-ranks spiraled, with an open sheath*, **petiole**, *and expanded blade*, simple, *but usually split into 2 parts, or sometimes palmately divided, usually 2- or 3-costate*, **±** **plicate**, entire-margined, with parallel or pinnate-parallel venation; stipules lacking. **Inflorescences spadixlike**, *with 2 to several spathelike bracts*, these sometimes petaloid, axillary or terminal. *Flowers unisexual* (*plants monoecious*), usually ± radial, *sessile*, *densely packed together, usually in spirally arranged groups, each with a carpellate flower surrounded by 4 staminate flowers*, but in whorls around the spadix, with the carpellate and staminate whorls alternating (in *Cyclanthus*), and adjacent flowers sometimes partially to strongly fused/confluent. *Tepals 4 to many, or absent*, distinct to connate *in staminate flowers*; *4*, distinct to connate, *in carpellate flowers*. *Stamens usually numerous; filaments basally connate*; pollen grains monosulcate to uniporate. *Staminodes of carpellate* *flowers usually 4*, opposite the tepals and ± adnate to them, *usually much elongated*. *Carpels 4, connate*; ovary ± superior to inferior, with parietal to ± apical placentation; adjacent flowers in *Cyclanthus* fused into rings (around spadix); stigmas ± flattened. **Ovules numerous per carpel**. Nectary absent. *Fruit a berry, and individual fruits often connate, forming a multiple fruit (fleshy syncarp), irregularly opening to expose colorful flesh*.

***Floral formula***:

Staminate: \* , T -4-many- , A many , G 0

[Put a dashed line around the 4-many tepals, put a dashed line around the many stamens; replace “many” with infinity symbol]

Carpellate: \* , T -4- , A 4**. ,** G 4 ; berry, fleshy syncarp

[Put dashed line around the 4 tepals; connect the 4 staminodes to the 4 tepals with a dashed line below formula; circle the 4 carpels, and put a line above and below the 4 carpels]

***Distribution***: Mexico and the Caribbean south to South America.

***Genera/species***: 12/230. ***Major genera***: *Asplundia* (100 spp.), *Dicranopygium* (54), and *Sphaeradenia* (52). The family does not occur in the United States or Canada.

***Economic plants and products***: *Carludovica palmata* (Panama hat plant) is the source of fibers used to make hats or baskets; it is also used for roof thatching. Several genera, e.g., *Asplundia*, *Carludovica*, *Cyclanthus*, and *Dicranopygium* are occasionally grown as ornamentals.

***Discussion***: The monophyly of Cyclanthaceae is supported by both morphology and DNA sequences (da Silva Leal 2018; Eriksson 1994a; Harling 1958; Harling et al. 1998; Rudall and Bateman 2006; Stevens 2001 onward; see also description). Cyclanthoideae (only *Cyclanthus bipartitus*) is sister to a clade comprised of the remaining genera (i.e., the Carludovicoideae). The monophyly of *Cyclanthus* is supported by its deeply bifid leaves, presence of laticifers, poorly developed plications, and inflorescences with staminate and carpellate flowers in whorls/rings. The monophyly of Carludovicoideae is supported by its carpellate flowers with 4, elongate, filiform staminodes. The two subfamilies are also well differentiated anatomically (Tomlinson and Wilder 1984). The habit and plicate leaves are reminiscent of those of Arecaceae, but the families are not closely related. It is noteworthy that the plications are developmentally distinct in the two familial clades (Wilder 1976).

 The flowers of Cyclanthaceae are pollinated by various beetles (Beach 1982; Eriksson 1994b; Gottsberger 1991). The fleshy fruits are dispersed by mammals and birds.

*Commelinales*

**Philydraceae** Link

(Frogsmouth Family)

*Herbs*, from rhizomes or corms; tissues sometimes with styloid crystals, but raphides absent. Hairs simple, *wooly*. *Leaves alternate, 2-ranked, usually equitant* (at least basally), *unifacial* and flattened to terete, ± basal or along stem, simple, entire, *with parallel venation*, with air canals, sheathing at the base; stipules lacking. *Inflorescences indeterminate*, terminal. **Flowers** *bisexual*, **bilateral**, **sessile**, *opening for only a single day*, *and in the axils of spathe-like bracts*. *Tepals 6*, **highly modified**, *petaloid, imbricate, and persistent,* **the 2 adaxial outer tepals along with the adaxial inner tepal all connate, forming a seemingly single adaxial tepal, which opposes the large outer abaxial tepal, and also with 2, much small, inner lateral tepals, and thus appearing as a perianth of 4 parts;** all of the tepals sometimes slightly fused basally. **Stamen 1;** anther straight to curved or coiled;*filament adnate to base of outer abaxial tepal**and sometimes also the 2 small, lateral tepals*; pollen grains monosulcate, sometimes in tetrads. *Carpels 3, connate; ovary superior*, with axile placentation or intruded-parietal placentation above and axile below; style 1; stigma capitate, slightly 3-lobed. Ovules many per carpel. *Nectaries absent*. *Fruit a loculicidal capsule*, sometimes fleshy and only tardily dehiscent; *seeds with a germination cap* (operculum).

***Floral formula***: X T - 3 + 2 + 1 - , A 1 , G 3 ; capsule

[Circle the 3 tepals, draw a line between the single stamen and the 2 + 1 stamens; circle the 3 carpels]

***Distribution***: Australia to Southeast Asia.

***Genera/species***: 4/6. ***Genera***: *Helmholtzia* (2 spp.), *Philydrella* (2), *Orthothylax* (1), and *Philydrum* (1). *Philydrum* rarely has naturalized in North and South Carolina.

***Economic plants and products***: *Philydrum* is occasionally cultivated as a wetland ornamental.

***Discussion***: The monophyly of Philydraceae is supported by the distinctive flowers (see description; Hamann 1998; Stevens 2001 onward) and DNA sequences (Saarela et al. 2008; Zuntini et al. 2021). *Philydrella* may be sister to the remaining genera. *Helmholtzia* and *Orthothylax* form a clade and both have much branched inflorescences.

 The pollinators of the showy flowers are unknown, but cultivated material of *Philydrum* appears to reproduce by selfing. The small seeds are likely dispersed by water and/or wind.

*Poales*

**Flagellariaceae** Dumortier

(Whip Vine Family)

Rhizomatous **vines**; tissues with cyanogenic glycosides and saponins, and cells with silica bodies are associated with the vascular bundles. Hairs absent. *Stem terete, solid,* **without axillary buds**, **but sometimes dichotomously branching**. *Leaves alternate, 2-ranked, differentiated into a sheath and blade, borne along the stem*, simple, entire, *with parallel venation*; sheath closed, **the blade** basally constricted and **terminating in a tendril**; stipules lacking. *Inflorescences indeterminate, terminal.* Flowers bisexual, radial, individually ± inconspicuous. *Tepals 6, ± distinct*, imbricate, *± petaloid*, persistent, **each with only a single vascular bundle**. *Stamens 6*; filaments distinct; *anthers slightly sagittate*; pollen grains uniporate. *Carpels 3, connate; ovary superior, with axile placentation*; style 1, short, **solid**, with 3 branches; stigmas elongated, along adaxial side of each style branch. *Ovules 1 per locule,* ± orthotropous; **megagametophyte developing from 2 megaspores** (*Allium* type). Nectaries lacking. *Fruit a drupe*; seed usually only one.

***Floral formula***: \* T - 6 - , A 6 , G 3 ; drupe

[Circle the 3 carpels]

***Distribution***: Tropical Africa, southern Asia to northern Australia, and Pacific islands.

***Genera/species***: 1/5. ***Genus***: *Flagellaria* (5 spp.). The genus does not occur in North America.

***Economic plants and products:*** Its uses are very minor; species of *Flagellaria* are used for thatch and making baskets.

***Discussion***: The monophyly of Flagellariaceae is supported by molecular data (Wepfer and Linder 2014) and by their distinctive morphological characters (see description; Sajo and Rudall 2012, and Tomlinson and Posluszny 1977).

 The pollination biology of *Flagellaria* is unknown; the showiness of the inflorescences and their fragrance would suggest that they are visited by insects, but wind pollination has been suggested. The colorful (white to red) drupes likely are dispersed by birds.

**Joinvilleaceae** Tomlinson & A. C. Smith

(Ohe Family)

*Rhizomatous, herb, with erect, grass-like stems*. *Hairs simple or branched, often ± sharp-pointed*; *adaxial leaf surface with multicellular microhairs*. Stem terete, hollow, unbranched, with cells containing silica bodies adjacent to fibers surrounding vascular bundles. *Leaves alternate, 2-ranked, borne along the stem, differenced into a sheath and blade, with a ligule borne at their junction*, simple, entire, *with parallel venation*, *the sheath open*, usually apically auriculate, the **blade plicate**, narrowed toward base, with apex acute to acuminate, *lacking a tendril*, the foliar epidermis with alternating long and short cells and the latter with silica bodies; stomata with dumbbell-shaped guard cells; stipules lacking. *Inflorescences indeterminate, terminal*. Flowers bisexual, radial, inconspicuous, ± sessile. *Tepals 6, ± distinct*, imbricate, *bract-like and with thickened bases*, persistent, **each with 3 vascular bundles**. *Stamens 6*; filaments distinct, free or slightly adnate to base of perianth; *anthers* *sagittate*; pollen grains uniporate. *Carpels 3, connate,* with supernumerary vascular bundles*; ovary superior, with axile placentation*, style 1, very short, *hollow*, with 3 branches; stigmas elongated, along adaxial side of each style branch. *Ovules 1 per locule*, orthotropous. Nectaries lacking. *Fruit a berry*, *with 1-3 seeds*. Outer seed coat (testa) fleshy, inner part (tegmen) hard.

***Floral formula***: \* T - 6 - , A 6 , G 3 ; berry

[Circle the 3 carpels]

***Distribution***: Malay Peninsula west into the Pacific islands.

***Genera/species***: 1/4. ***Genus***: *Joinvillea* (4 spp.). Not occurring in North America.

***Economic plants and products***: None.

***Discussion***: The monophyly of the Joinvilleaceae is supported by DNA sequences (Givnish et al. 2010) and its leaves that are plicate in bud (see also description; Bayer and Appel 1998; Newell 1969; Tomlinson and Smith 1970). *Joinvillea* is grass-like in appearance, and it is sister to the Ecdeiocoleaceae + Poaceae clade. Like grasses, it has 2-ranked leaves with an open sheath and ligule, and *Joinvillea* shares a remarkable number of putative apomorphies with grasses, such as hollow stems, the leaf blade with alternating long and short epidermal cells, epidermal microhairs, and dumbbell-shaped, stomatal guard cells. It is easily distinguished from grasses, however, in having plicate leaves, flowers with six tepals, carpels with supernumerary vascular bundles, three locules, each with a single ovule, and berry fruits; additionally, it lacks the characteristic grass floret.

 The flowers of *Joinvillea* are wind pollinated; their berries are dispersed by birds.

***Additional reference***: Sajo and Rudall 2012.

**Mayacaceae** Kunth

(Bog-moss Family)

*Wetland or aquatic, clubmoss-like herbs* with adventitious roots; *roots, stems, and leaves with longitudinal air canals with transverse diaphragms of stellate cells*. *Hairs only in the leaf axils, filamentous and composed of a single row of cells*. Leaves alternate and spiral, **scattered along stem**, *simple, ± linear to filiform*, entire **except for 2 apical teeth**, **with a single vein** *and elongate, air canals with transverse diaphragms, one canal on each side of midvein,* **sessile and not sheathing**; stipule lacking. *Inflorescences of solitary, axillary flowers*, these on short to elongate pedicels, held above the surface of the water. Flowers bisexual, radial, *with perianth differentiated into a calyx and corolla*. Sepals 3, distinct. *Petals 3, distinct*, imbricate, white to pink or rose, **and each with a single vascular strand**. **Stamens 3**, alternate with the petals; filaments slender, distinct; **anthers opening by terminal ± pores** (and sometimes anther with apical tubule); pollen grains monosulcate. Carpels 3, connate; *ovary superior, with parietal placentation*; style 1; stigma capitate to slightly 3-lobed. Ovules 2 to numerous on each placenta, **associated with an obturator** (outgrowth of the placenta), orthotropous, with a thin megasporangium. Nectaries lacking. *Fruit a loculicidal capsule*; seeds ridged, *with an operculum* (cap),

***Floral formula***: \* K 3 , C 3 , A 3 , G 3 ; capsule

[Put a circle around the 3 carpels]

***Distribution and ecology***: North and South America, and a restricted portion of Africa; plants of wetland and aquatic habitats. Naturalized populations also occur in southern Asia and Australia.

***Genera/species***: 1/4-10. ***Genus***: *Mayaca* (4-10 spp.). The family is represented in North America (southeastern United States) by *Mayaca*.

***Economic plants and products***: *Mayaca* is occasionally used as an aquarium plant.

***Discussion***: The monophyly of Mayacaceae is supported by its distinctive morphological characters (see description, also Stevens 2001 onward; Stevenson 1998; Thieret 1975). There has been little phylogenetic study of the group and species limits within *Mayaca* are especially problematic. The submerged and terrestrial forms of the same species are often quite different in appearance.

 Pollinators are likely various bees, but selfing also occurs; seed dispersal is by water. Dispersal by fragmentation of the plant body also occurs.

***Additional references***: de Carvalho et al. 2009; Lourteig 1952; Oriani and Scatena 2012.

*Zingiberales*

**Costaceae** Nakai

(Spiral-ginger Family)

*Rhizomatous herbs*, the stems unbranched, or occasionally branched (in *Tapeinochilus*); *tissues without ethereal oils*, but with steroidal saponins. Hairs simple. Leaves alternate, **spirally arranged and 1-ranked, so like a spiral staircase** (**spiromonostichous**), simple, entire, shortly petiolate, with a well-developed blade, *with pinnate venation*, a sheathing base, **which is closed, i.e., forming a tube around stem**, *and a ligule*; the leaf sheath with air canals, but these usually lacking in petiole, and canals separated into segments by diaphragms composed of stellate-shaped cells; stipules lacking. **Inflorescences indeterminate, cone-like spikes, unbranched, lacking axillary cymose units**, *terminal on leafy stem or on a separate leafless stem*, or reduced to solitary axillary flower (in *Monocostus*), *with conspicuous, green to colorful bracts*, **these subtending 1-2 flowers** *and with an extrafloral nectar gland*. Flowers bisexual, bilateral. *Sepals 3, connate, and calyx tube 2- or 3-lobed*. *Petals 3, connate, with one lobe larger than the others*, imbricate. *Stamen 1, usually petaloid, grasping the style*; **staminodes 5**, *large, connate, petaloid* (*forming a labellum*), *often with a crisped margin*; basal part of staminal filament and labellum connate, forming a short tube; *anther with pollen sacs* (thecae) *usually well separated*, *and usually attached in ± middle of the filament*; **pollen grains with apertures** (pantoporate, spiraperturate, disulcate, or mixed sulcate-porate), **with a well-developed exine**. *Carpels usually 3*, but 2 in *Dimerocostus*, connate; *ovary inferior*, with axile placentation; *style enveloped in groove between pollen sacs of the anther*; stigma cup-shaped with a ciliate margin **or consisting of 2 ciliate, half-moon-shaped structures with a dorsal, bilobed appendage**. Ovules ± numerous. Nectaries 2, *in the apical part of the ovary,* **above ovary locules**. *Fruit usually a loculicidal or irregularly opening capsule*; seeds arillate; **embryo with cotyledonary sheath that is divided into a basal portion and a bladelike distal part that bears a conelike outgrowth**; endosperm poorly developed but perisperm present, with **benzoquinones** and fatty oils.

***Floral formula***: X , K 3 , C 2 + 1 , A 5**.** + 1 , G 3 ; capsule

[Circle the 3 sepals, circle the 2+1 petals, circle the 5 staminodes, above the formula draw a line connecting the single stamen to the 3 carpels, draw a circle around the 3 carpels, and draw a line above the carpels indicating an inferior ovary]

***Distribution and ecology***: Pantropical; mainly in lowland, tropical rainforests.

***Genera/species***: 7/137. ***Major genera***: *Costus* (106 spp.), *Tapeinochilos* (16). *Costus pulverulentus* is sparingly naturalized in the United States (Florida).

***Economic plants and products***: Representatives of all genera are used as ornamentals, but species of *Costus* (spiral-ginger), *Tapeinochilus* (wax-ginger), *Chamaecostus* (firey costus), and *Monocostus* (lemon-ginger) are the most important. *Hellenia speciosa* (crepe-ginger) is used as a starch source and in the production of steroids.

***Discussion***: The monophyly of Costaceae is supported by morphology (Kirchoff 1988; Kirchoff and Rutishauser 1990; Kress 1990, 1995; Specht and Stevenson 2006; Stevens 2001 onward; see also description) and DNA sequences (Kress 1990, 1995; Kress et al. 2001, 2005; Sass et al. 2016; Specht 2006; Specht and Stevenson 2006; Specht et al. 2001). A clade comprised of *Monocostus*, *Dimerocostus*, and *Chamaecostus* is sister to a clade containing the remaining genera, within which the large genus *Costus* s.s. is sister to the *Paracostus* + *Hellenia* + *Tapeinochilus* clade. *Costus*, as traditionally circumscribed, is not monophyletic, and thus *Helleria* (= *Cheilocostus*), *Paracostus*, and *Chamaecostus* recently have been recognized as generic clades.

 Bee pollination is ancestral (and still common) in Costaceae, but bird pollination has evolved several times (Kay et al. 2005; Salzman et al. 2015). The seed-arils often contrast in color with the inflorescence bracts, and bird dispersal is common. The extrafloral nectaries (on inflorescence bracts) attract ants, which provide protection (Schemske 1981).

***Additional reference***: Andre et al. 2015.

**Heliconiaceae** Vines

(Lobster-claw Family)

*Large herbs from a cormlike rhizome, forming a pseudostem* (by the imbrication of elongate leaf sheaths that surround the scape) *or erect stems elongate with distinct internodes, and then tightly enclosed by leaf sheaths*; tissues with raphide crystals. Hairs branching or absent. *Leaves alternate, 2-ranked, large, simple, but often tearing between the veins*, entire, *with a well-developed blade, pinnate venation*, and sheathing base; petiole with air canals composed of stellate-shaped cells; stipules lacking. *Inflorescences* arising from a long scape, *terminal, erect or pendulous*, *indeterminate, but composed of determinate (cymose) units in the axils of spathaceous, boat-shaped, keeled, variously colored bracts*. *Flowers* bisexual, *bilateral*, **resupinate** or not; the individual flowers subtended by crested bracts. *Tepals 6*, in 2 whorls, petaloid, all at least basally connate, **and 5 connate most of their length, forming a 5-toothed boat-shaped structure, but 1 member of the outer whorl ± distinct from the others**; the tepals (or their lobes) imbricate. *Stamens 6, with 5 fertile* **and one represented by a scalelike staminode**, positioned opposite the distinct tepal; *filaments adnate to the tubular part of the perianth*; *anthers* *elongate*; pollen grains lacking apertures, **asymmetric, the 2 hemispheres differing in form** (i.e., heteropolar), the exine very reduced. Carpels 3, connate; *ovary inferior*, with basal-axile placentation; style slender; stigma capitate. *Ovule 1 per locule*. Nectaries in septa of ovary. **Fruit a ± drupaceous schizocarp**, *sometimes not breaking apart* (then a drupe with 3 pits); **the pits operculate**. **Seeds with thin, undifferentiated coat**, without an aril; endosperm and perisperm present.

***Floral formula***: X , T -5 + 1- , A 5 + 1**.** , G 3 ; drupaceous schizocarp

[Circle the 5 strongly fused tepals, draw a line below formula connecting the stamens to the 5 fused tepals; circle the 3 carpels; draw a line above the carpels indicating an inferior ovary]

***Distribution***: Tropical Americas, and Sulawesi and New Guinea to Pacific Islands.

***Genera/species***: 1/200. ***Genus***: *Heliconia* (200 spp.). *Heliconia latispatha* is sparingly naturalized in the United States (southern Florida).

***Economic plants and products***: Several species of *Heliconia* are popular ornamentals, grown for their diverse and colorful inflorescence bracts (Berry and Kress 1991).

***Discussion***: Thee monophyly of Heliconiaceae is supported by several striking morphological characters (see description; Andersson 1998; Kress 1990, 1995; Stevens 2001 onward) and DNA sequences (Iles et al. 2017; Kress and Specht 2006; Marouelli et al. 2010). *Heliconia* subg. *Heliconiopsis*, along with a few Ecuadorian species (e.g., *H. brenneri, H. virginalis, H. wilisiana*) are sister to a clade comprising the remaining species (all Neotropical). Erect inflorescences with resupinate flowers (i.e., with the distinct tepal on upper side of flower) are ancestral in *Heliconia*, although both pendulous inflorescences and non-resupinate flowers have evolved within the clade.

 Hummingbirds pollinate the Neotropical species of *Heliconia*, which have amazingly colorful bracts and flowers (opening during the day) while bats pollinate the Paleotropical species, which have green bracts and green to white flowers (opening in the evening) (Kress 1985a, b). The metallic blue or red drupes or drupaceous mericarps are dispersed by birds.

**Strelitziaceae** Hutchinson

(Bird-of-paradise Flower Family)

*Large herbs from a cormlike rhizome,* **or shrubs to banana-like trees with erect and woody stems** (but lacking secondary growth), often suckering; **tissues with phenylphenalenones**, raphide crystals. **Roots with medulla with scattered wide vessels and strands of phloem**. Hairs ± absent. *Leaves alternate, 2-ranked, often large, simple, but often tearing between the veins, entire, with a well-developed blade, pinnate venation, sheathing base*; petiole (and often also leaf midrib) with air canals, these separated into segments by diaphragms composed of stellate-shaped cells; ligule absent; stipules lacking. *Inflorescences terminal or axillary, erect, indeterminate, but composed of determinate* *(cymose)* *units in the axils of conspicuous, ± boat-shaped bracts*. *Flowers bisexual, bilateral*; individual flowers subtended by ribbed bracts. *Sepals 3, distinct, petaloid and often contrasting in color with the petals*. *Petals 3, basally connate, the 2 anterior ones larger than the posterior one; in Strelitzia the 2 anterior petals ± connate, forming a sagittate structure*, which centrally forms a groove enclosing filaments and style. *Stamens 5 or 6 and staminodes lacking*; filaments distinct, elongate; *anthers elongate*; pollen grains lacking apertures, exine very reduced. Carpels 3, connate; *ovary inferior*, with axile placentation; style 1, slender; *stigmas 3, sometimes divided, elongate*. Ovules numerous. Nectaries in septa of ovary. *Fruit a woody, loculicidal capsule; seeds ± spherical, with colorful hairy arils*, **and with a rudimentary operculum, or operculum lacking; inner seed coat (tegmen) reduced to a cuticle**; endosperm and perisperm present.

***Floral formula***: X , K 3 , C 2 + 1 , A 5-6 , G 3 ; capsule

[Circle the 2 + 1 petals; circle the 3 carpels; draw a line above the carpels to indicate an inferior ovary]

***Distribution***: South America, South Africa, and Madagascar.

***Genera/species***: 3/7. ***Major genus***: *Strelitzia* (5 spp.). The familial clade does not occur natively in the United States or Canada.

***Economic plants and products***: *Ravenala madagascariensis*, *Strelitzia nicolai*, and *S. reginae* are popular ornamentals in tropical and subtropical regions.

***Discussion***: The monophyly of Strelitziaceae is supported by morphology (see description; Andersson 1998; Kress 1990, 1995; Stevens 2001 onward) and DNA sequences (Cron et al. 2012; Kress and Specht 2006; Kress et al. 2001, 2005; Sass et al. 2016). Strelitziaceae are sister to Lowiaceae, and both clades have flowers with the perianth whorls differentiated and the two lateral petals differentiated from the median petal. Relationships among the three genera of Strelitziaceae are uncertain; in some analyses *Ravenala* (with six stamens) is sister to the *Strelitzia* + *Phenakospermum* clade (showing a reduction to five stamens) (e.g., Kress and Specht 2006; Kress et al. 2005), while in others *Phenakospermum* (with terminal inflorescences) is sister to a *Ravenala* + *Strelitzia* clade (with axillary inflorescences; e.g., some analyses of Cron et al. 2012). *Strelitzia nicolai*, which shows the ancestral condition of an erect stem, is sister to the remaining species of that genus, all of which have short, cormlike and dichotomously ranching stems (Cron et al. 2012).

 The flowers of *Ravenala* are pollinated by the ruffed lemur; those of *Strelitzia* are pollinated by sunbirds; and those of *Phenakospermum* are pollinated by nectar-feeding bats (Andersson 1998; Frost and Frost 1981; Kress and Stone 1993; Kress et al. 1994). The black seeds contrast with colorful arils, i.e., orange in *Strelitzia*, blue in *Ravenala*, and red in *Phenakospermum*, and they are dispersed by birds.

*Eudicots*

*Ranunculales*

**Eupteleaceae** K. Wilhelm

(Asian-elm Family)

*Deciduous trees* with vessel elements with scalariform-reticulate perforation plates. Hairs simple. *Leaves alternate and spiral, simple, compound serrate to irregularly dentate, with pinnate venation*; stipules lacking. **Inflorescences of solitary**, pedicellate **flowers**, *each in the axil of a bract*, *with the bracts separated by very short internodes*, *and borne on the proximal portion of the new vegetative shoots*, *thus appearing fasciculate.* Flowers bisexual, radial (but with only 2 planes of symmetry, **but bilateral early in development**), *pendulous*. **Perianth absent**. *Stamens 6 to numerous*; **filaments shorter than the anthers**; **anthers opening by inconspicuous valves**, **with apical extension of the connective**; **pollen grains hexacolpate** to tricolpate. *Carpels 6 to numerous*, *distinct,* **each borne on a stalk, growing asymmetrically as developing into the fruit**; *ovaries superior*, with parietal (lateral) placentation; *style**absent*; **stigma brush-like**, *elongated, decurrent along one side of ovary*. Ovules1-3 per carpel; **megagametophyte with antipodal cells not persisting**. Nectary lacking. **Fruit a cluster of samaras** (if 1-seeded) **or samara-like fruits** (if 2- or 3-seeded).

***Floral formula***: \* T - 0 - , A 6-many , G 6-many ; samaras

[Replace “many” with the infinity symbol]

***Distribution***: Temperate eastern Asia.

***Genera/species***: 1/2. ***Genus***: *Euptelea* (2 spp.). Not occurring in North America.

***Economic plants and products***: *Euptelea* (Asian-elm) is occasionally used as an ornamental tree.

***Discussion***: The monophyly of Eupteleaceae is well supported by morphological characters (see description; Endress 1993b; Nast and Bailey 1946; Ren et al. 2007; Smith 1946; Stevens 2001 onward) and molecular evidence (Cao et al. 2016; Wang et al. 2009). *Euptelea* was earlier considered to be related to Trochodendraceae (of the Trochodendrales), Cercidiphyllaceae and Hamamelidaceae (of the Saxifragales), or families of the Magnoliidae (Cronquist 1981; Endress 1993; Nast and Bailey 1946). Although limited to just two species of eastern Asia today, fossils indicate that *Euptelea* was once widespread in the Northern Hemisphere.

 The flowers are likely mainly wind pollinated, although pollen-gathering bees may assist in moving pollen. The winged fruits are wind and/or water dispersed.

***Additional reference***: Rix and Endress 2016.

**Lardizabalaceae** R. Brown

(Zabala-fruit Family)

**Twining lianas** or erect shrubs; stems with a ring of vascular bundles separated by wide intervascular rays; some with short-shoots; often with triterpenoid saponins; *buds scaly*. Hairs, when present, simple. *Leaves alternate and spiral, palmately* or occasionally pinnately *compound*, *or trifoliolate*, the **leaflets** **entire**, sometimes shallowly lobed, *usually pinnately veined*, stipules usually lacking. Inflorescences indeterminate, axillary, often pendulous. *Flowers usually unisexual* (and the plants monoecious or dioecious), *radial;* receptacle small, but becoming expanded in *Sargentodoxa*. *Sepals usually 6*, sometimes reduced to 3, *distinct*, *petaloid*, imbricate, or inner ones imbricate and outer ones valvate. *Petals usually 6, distinct*, not overlapping, *producing nectar*, *smaller than the showy sepals*, sometimes lacking. *Stamens usually 6*; filaments distinct to *connate*; *anther connective often forming apical appendage*; pollen grains tricolpate; staminodia sometimes present in carpellate flowers (and petaloid in *Sargentodoxa*). *Carpels 3 to numerous*, *distinct*, sessile to stalked; *ovaries superior*, each with parietal (lateral) to ± laminar (ovules scattered over inner surface) placentation; *style very short or absent* (except in *Sargentodoxa*); stigma usually flattened-peltate. Ovules usually numerous in each carpel (but reduced to 1 in *Sargentodoxa*). *Fruit a cluster* *of* *globose to* *elongated* **berries** *or fleshy follicles,* andthe individual berries of *Sargentodoxa* clearly stalked.

***Floral formula***:

Staminate: \* K 3-6 , C 6 or 0, A 6 , G 0-many**.**

[put a dashed line around the 6 stamens; replace “many” with infinity symbol, and note superscript dot]

Carpellate: \* K 3-6 , C 6 or 0 , A 0 or 6**.** , G 3-many ; berries, fleshy follicles

[Replace many with infinity symbol; note superscript dot indicating staminodes]

***Distribution***: Temperate to subtropical, South America (Chile) and eastern Asia.

***Genera/species***: 7/52. ***Major genera***: *Stauntonia* (40 spp.) and *Akebia* (6). *Akebia quinata* is naturalized in the eastern United States.

***Economic plants and products***: Fruits of *Akebia* (akebi, akebia), *Lardizabala* (zabala-fruit), and *Stauntonia* are occasionally eaten. *Akebia quinata* is commonly grown as an ornamental. Several genera are used medicinally in China.

***Discussion***: The monophyly of Lardizabalaceae is supported by molecular data (Hoot et al. 1995a, b, 2015; Kofuji et al. 1994; Wang et al. 2002) and morphology (see description; Christenhusz 2012; Stevens 2001 onward; Wu and Kubitzki 1993). *Sargentodoxa* (Sargentodoxoideae: reddish sap; petaloid staminodia, receptacle expanded and fleshy in fruit) is sister to the remaining genera (Lardizabaloideae: ovules ± numerous per carpel, filaments connate, but reversals to distinct occur). Within the Lardizabaloideae, *Decaisnea* and *Sinofranchetia* probably represent basal lineages, while the remaining genera (i.e., *Bouquila, Lardizabala, Akebia*, and *Stauntonia*) form the core clade of the family (and have laminar placentation). Within this clade, the Chilean *Bouquila* and *Lardizabala* are sister to the eastern Asian *Akebia* and *Stauntonia*.

 The showy flowers of Lardizabalaceae are pollinated by various insects. The berries or fleshy follicles probably attract birds or mammals (monkeys, rodents).

***Additional references***: Ernst 1964; Spongberg and Burch 1979; Zhang and Ren 2008, 2011.

*Proteales*

**Nelumbonaceae** A. Richard

(Sacred-lotus Family)

**Aquatic, rhizomatous herbs**; **stems with vascular bundles scattered but inside endodermis**, **lacking a vascular cambium**, **and with conspicuous air canals**; **roots adventitious**, produced at the nodes of rhizome; tissues with aporphine and benzyl-isoquinoline alkaloids; **laticifers present**. **Hairs lacking**. **Leaves vertically 2-ranked, in groups of 3 along rhizome, within the group with a cataphyll on the lower side and a cataphyll subtending an expanded leaf on the upper side**, *simple*, **peltate**, **with a central disk**, **entire, long-petiolate, with blade submerged, floating, or emergent**, *with palmate venation*, the midrib unbranched, **but other main veins each with a dichotomous branch**, **the margins upward-rolled when young (involute)**; **epicuticular waxes of clustered tubules** (water repelling); **the petiole with air canals**. **Inflorescences of solitary, axillary flowers**. *Flowers bisexual, radial*, **large**, **with complex cortical vascular system**, **with an expanded, obconic receptacle**, **and** **borne on long peduncles,** *raised above water surface*. **Sepals 2,** *distinct*. *Petals numerous*, *distinct*, imbricate, forming a spiral, the outer 2-5 smaller and greenish, thus sepal-like. **Stamens numerous**; filaments distinct; **anther connective with terminal appendage**; pollen grains tricolpate. **Carpels 10 to numerous**, *distinct*; *ovary superior*, **but immersed in receptacle**, with a single locule and ± apical placentation; **style short to absent**; stigma expanded, truncate. Ovules 1 per carpel, **the outer integument very thick**. Nectary lacking. **Fruit a cluster of nuts**, **sunken into the expanded, spongy, obconic receptacle that has emergent/exposed druse crystals**; each nut with an apical pore. Seed with large, green embryo; with the 2 **cotyledons forming a sheath around the plumule**; **radicle aborting**.

***Floral formula***: \* K 2 , C many , A many , G 10-many ; nuts

[replace “many” with infinity symbol]

***Distribution and ecology***: Eastern North America and eastern Asia south to northern Australia; plants of wetland and aquatic habitats.

***Genera/species***: 1/2. ***Genus***: *Nelumbo* (2 spp.). *Nelumbo lutea* is native in the continental United States and Canada (eastern region) and *N. nucifera* is naturalized in the southeastern United States.

***Economic plants and products***: The two species of *Nelumbo* have edible rhizomes and seeds; both are also used as ornamentals (in ponds and wetland habitats). *Nelumbo nucifera* is the sacred flower in Buddhism and Hinduism.

***Discussion***: The monophyly of Nelumbonaceae is supported by DNA nucleotide sequences (Xue et al. 2012) and numerous distinctive morphological synapomorphies (see description; Hayes and Carlquist 2000; Stevens 2001 onward; Williamson and Schneider 1993). Molecular data clearly place Nelumbonaceae in the Proteales, although it shows some convergent similarities to Nymphaeaceae relating to the aquatic habit (e.g., tissues with air canals, floating, long-petioled leaves, solitary flowers with long peduncles) and was once placed in that family (Lawrence 1951; Wood 1959).

 The large, showy flowers are pollinated by various insects (bees, beetles, flies, and thrips); dispersal of the nuts occurs as a result of the mature receptacles floating in the water, and slowly releasing the nuts. The seeds are extremely long-lived (up to ca. 1300 years!) (Shen-Miller et al. 1995, 2002).

***Additional reference***: Kubo et al. 2009.

**Sabiaceae** Blume

(Pao-hua Family)

*Trees, shrubs, or lianas*; with tannins and pentacyclic triterpenoids; secondary phloem with broad or flaring rays. Hairs simple. *Leaves alternate and spiral or 2-ranked, simple to pinnately compound*, with a terminal leaflet, entire to variously toothed, *with pinnate venation*; stipules lacking. Inflorescences determinate, terminal or axillary, sometimes reduced to a solitary flower. *Flowers usually bisexual*, radial or bilateral, *tiny*, **with sepals, petals and stamens ± opposite each other**. **Sepals usually 5**, distinct to basally connate, imbricate (quincuncial), *and equal in size or the inner 2 much smaller*. **Petals usually 5**, *distinct*, imbricate (quincuncial), and equal in size *or more commonly the inner 2 much smaller, and lobed*. **Stamens and staminodes together 5**, all fertile (*Sabia*) *or the 2 opposite the inner petals with pollen and the 3 others staminodes* (remaining genera); filaments ± basally adnate to petals, *usually* *apically swollen*; **anthers with only 2 pollen sacs** (thecae), *and connective often thickened, cup-shaped*; **pollen tricolporate**. *Carpels usually 2*, **connate**; ovary superior, with axile placentation; style terminal (when flower is at anthesis), 1 or rarely 2; stigma(s) capitate to punctate. Ovules usually 2 per locule, campylotropous to orthotropous, with usually 1 integument, **the sporangium apex exposed**. **Nectar disk often ± lobed, surrounding base of gynoecium**. *Fruit a drupelet or nutlet*, with 1 seed per pit/nutlet, if developed from 2 carpels then schizocarpic, *and fruit developing asymmetrically so that styles become ± gynobasic*. **Seeds with curved embryo, and the cotyledons folded or coiled**; endosperm scanty or lacking.

***Floral formula***: \* or X , K 3 + 2 , C 3 + 2 , A 5 or 2 + 3**.** , G 2 ; drupelet, nutlet

[Put a dashed line around the 3+2 sepals, circle the 2 carpels]

***Distribution***: Neotropics and Sri Lanka and Southeastern Asia to Malesia.

***Genera/species***: 4/108. ***Major genera***: *Meliosma* (80 spp.) and *Sabia* (20). The group does not occur in the United States or Canada.

***Economic plants and products***: A few species of *Meliosma* are grown as ornamentals.

***Discussion***: The monophyly of Sabiaceae is supported by DNA sequences (Qiu et al. 2000; Soltis et al. 2011; Yang et al. 2018; Zúñiga 2015) and morphology (see description; Kubitzki 2007; Ronse de Craene and Wanntorp 2008; Ronse de Craene et al. 2015a, b; Stevens 2001 onward; Wanntorp and Ronse de Craene 2007). The family is striking, and until recently was of problematic placement, because its phylogenetic position (i.e., sister to the rest of Proteales, an early-divergent lineage within the eudicot clade) is more basal than would be expected given its 5-merous flowers, syncarpous gynoecium, and tricolporate pollen, suggesting that homoplasy has occurred in these distinctive floral features. The family, of course, is not a member of the Pentapetalae. Within Sabiaceae, *Sabia* (lianas; retention of radial flowers with 5 functional stamens) is sister to the *Ophiocaryon* + *Kingsboroughia* + *Meliosma* clade (bilateral flowers with only 2 fertile stamens; retention of arborescent habit).

 Most species of *Meliosma* have explosively dehiscent anthers that are held under tension by the staminodes; in addition, pollen collects on the broad anther connective. Their flowers are likely visited by insects, especially bees. The small drupes may be dispersed by birds.

***Additional reference***: Van Beusekom 1971.

*Trochodendrales*

**Trochodendraceae** Eichler

(Wheel-tree Family)

*Evergreen or deciduous trees with* tracheid-like vessel-elements with scalariform to scalariform-reticulate perforation plates; nodes unilacunar to multilacunar; flavonoids, tannins, unbranched to branched sclereids or secretory cells present. *Hairs absent* (plants glabrous) or nearly so (then hairs simple). Stems uniform and all long, or with long and short shoots (and these bearing only a single leaf at a time). *Leaves alternate* and spiral or 2-ranked, sometimes distally clustered, *simple*, with pinnate or palmate venation, *± toothed, each tooth with a glandular apex* (chloranthoid); petiole base sometimes sheathing (and enclosing axillary bud); *stipules absent*. *Inflorescences terminal*, but sometimes seemingly axillary (deflexed to lateral position by axillary shoot), determinate (raceme-like with terminal flower, sometimes with basal cymose branching) or indeterminate (racemes or spikes). *Flowers bisexual, radial*, conspicuous or inconspicuous, **with a cortical vascular system**, sometimes sessile. Perianth nearly absent (of 0-5 very inconspicuous, bract-like tepals) or present and easily visible (of 4 tepals, and in fossil representatives also of 5 or even more numerous tepals). *Tepals distinct*, open to imbricate in bud. *Stamens numerous* (and spiral) *to only 4* (and then positioned opposite tepals); filaments slender; *anthers* ± apiculate, *opening by 2 valves*; pollen grains tricolpate, the **exine striato-reticulate**. *Carpels numerous to 4*, **laterally connate, each with 5 vascular bundles (3 dorsal and 2 lateral)**; *ovary superior to slightly inferior* (due to expanded receptacle), with ± axile placentation; *each carpel with single recurved* (extant) or incurved (many fossil taxa) *style*, and decurrent stigma. Ovules few to numerous per carpel. N**ectary on abaxial surface of each carpel, positioned below each style,** with nectar released through modified stomata. **Fruit a capsule, composed or a whorl of follicle-like units, each of which opens ventricidally, with the ventral side of each carpel becoming much extended during fruit development, so that the styles spread laterally/horizontally (***Trochodendron***) or even become more or less basal (***Tetracentron*, and several fossil genera**)**. **Seeds** *flattened, ± winged*, **with a chalazal**, **hair-pin vascular bundle**.

***Floral formula***: \* T -0-5- , A 4-many , G 4-many ; follicle-like capsule

[circle the 4-many carpels; replace word many with infinity symbol]

***Distribution***: Eastern Asia. Neither genus occurs natively in North America.

***Genera/species***: 2/2. ***Genera***: *Trochodendron* (1 sp.), *Tetracentron* (1).

***Economic plants and products***: *Trochodendron aralioides* (wheel-tree) is occasionally used as an ornamental.

***Discussion***: The monophyly of Trochodendraceae is supported by both morphological (Doyle and Endress 2000; Manchester et al. 2020; Stevens et al. 2001 onward; see also description) and molecular (Hilu et al. 2003; Hoot et al. 1999; Qiu et al. 2005; Savolainen et al. 2000a, b; Soltis et al. 2000, 2011; Sun et al. 2013) characters. In addition to nucleotide sequence synapomorphies, the Trochodendraceae show a 4 kb expansion of the inverted repeat region in their chloroplast genome (including five genes usually in the single-copy region). Trochodendraceae are the sole family of Trochodendrales, a relic clade that was once much more widely dispersed than it is now (i.e., with fossil occurrences also in North America, northeastern Asia, and Europe). Although traditionally considered transitional between the families of the Magnoliidae and various clades with reduced, wind-pollinated flowers (e.g., some Proteales, some Saxifragales, Fagales, some Rosales; Cronquist 1981; Endress 1986), Trochodendrales are phylogenetically adjacent to Proteales and Buxales, and comprise one of the basally branching lineages of eudicots (Fig. 8.3). Although once thought to have vesselless wood (Bailey and Nast 1945), primitive vessel-elements actually are present (Li et al. 2011; Ren et al. 2007).

 *Tetracentron* *sinense* is considered to be quite distinct morphologically from *Trochodendron aralioides*, as it differs in having long + short shoots (vs. shoots uniform and all long), deciduous and cordate-veined (vs. evergreen and pinnate-veined) leaves, spicate (vs. cymose) inflorescences, sessile (vs. pedicellate) flowers, with only four tepals and stamens (vs. with numerous stamens and ca. 6-17 carpels), and small (vs. larger) fruits with basal (vs. ± lateral) styles. The flowers of *Tetracentron* have an obvious perianth, while that of *Trochodendron* is extremely inconspicuous (i.e., represented by only 0-5 small bract-like structures; Endress 1986). However, both genetic evidence (Leu et al. 2007) and phylogenetic reconstruction (Manchester et al. 2020) suggest that the perianth of *Trochodendron* is reduced. Trochodendraceae are much more diverse (and geographically widespread) when fossil genera are considered, e.g., having species with racemes, flowers with more numerous tepals, fruits with incurved (instead of recurved) styles, and also differently shaped fruits; these fossils not only bridge the morphological gap separating extant *Trochodendron* and *Tetracentron*, but also expand the known variability of the familial clade (Manchester et al. 2018a, b, 2020).

 The flowers of Trochodendraceae produce nectar and attract a variety of insect pollinators (flies, bees, butterflies). The follicle-like fruits open to release small, ± winged seeds that are dispersed by wind.

***Additional references***: Endress 1993c; Erbar 2014; Nast and Bailey 1945.

*Gunnerales*

**Gunneraceae** Meisner

(Giant-rhubarb Family)

**Small to gigantic herbs**, often rhizomatous; stems with several vascular cylinders**, producing modified adventitious roots (“glands”) that produce mucilage and provide entry point for *Nostoc* (a cyanobacterium), which form N-fixing colonies inside stem tissues**; tannins present. Hairs simple, sometimes glandular, *and prickles often also present*. **Nodes multilacunar**. *Leaves alternate and spiral, simple*, sometimes lobed, *toothed*, *usually with palmate venation*, crowded at the stem tips; stipules lacking, *but stems usually with stipule-like scale-leaves (cataphylls)*. Inflorescences determinate but appearing indeterminate, axillary. Flowers bisexual or more commonly unisexual (plants then ± monoecious or dioecious), *biradial*, *small*, with or without an associated bract. *Sepals 2*, distinct or connate, *valvate*, occasionally lacking, the margins sometimes hair-fringed, the base sometimes inflated. *Petals 2 or 0, sepal-like*, distinct, open in bud. *Stamens usually 2*; filaments short; pollen grains tricolpate. **Carpels 2**, *connate*; **ovary inferior**, **with apical placentation**; *styles 2*, *each with an elongated, strongly papillose stigma*. **Ovule solitary in the single locule**; **megagametophyte tetrasporic, 16-celled** (*Peperomia*-type). Nectary lacking. **Fruit usually a drupe**.

***Floral formula***:

Bisexual: \* K 2 , C 2 or 0 , A 2 , G 2 ; drupe

[Circle the 2 carpels, and put a line above indicating inferior ovary]

Staminate: \* K 2 (0) , C 2 or 0 , A 2 , G 0 or 2**.**

[pistillode; circle the 2 sterile carpels, and put a line above]

Carpellate: \* K 2 , C 2 or 0 , A 0 , G 2 ; drupe

[Circle the 2 carpels, and put a line above indicating inferior ovary]

***Distribution***: Widely distributed in the Southern Hemisphere: Mexico south through South America, central and southern Africa, tropical Asia to the Pacific Islands, and Australasia.

***Genera/species***: 1/60. ***Genus***: *Gunnera* (60 spp.). Not native to the continental United States, but a single species (*G. tinctoria*) is very sparingly naturalized in California.

***Economic plants and products***: *Gunnera* (giant-rhubarb, Chilean-rhubarb, dinosaur food) is often planted as an ornamental in moist to wet environments. *Gunnera tinctoria* is naturalized in Europe (especially Ireland and the Great Britain), the Azores, New Zealand, and California.

***Discussion***: The monophyly of Gunneraceae is supported by morphology (description; see also Ronse de Craene and Wanntorp 2006; Stevens 2001 onward; Wanntorp and Ronse de Craene 2005; Wilkinson and Wanntorp 2007) and molecular characters (Wanntorp and Wanntorp 2003; Wanntorp et al. 2001, 2002). *Gunnera herteri* (subg. *Ostenigunnera*; annual herb) is sister to a large clade comprising the perennial species having stems with several vascular cylinders; within this clade, *G. perpensa* (subg. *Gunnera*; flowers bisexual) is sister to the remaining species, all of which show the putative apomorphy of cataphylls (= modified prophylls) on the stem. Within this cataphyll clade, four subgenera are recognized, the largest of which is subg. *Panke* (stems covered by cataphylls, lacking elongated rhizomes). Gunneraceae are most closely related to Myrothamnaceae, and they are the only two families in the Gunnerales. Both are wind pollinated, with small, unisexual, 2-merous flowers. They are, however, quite different morphologically (Wilkinson 2000).

 The tiny flowers of Gunneraceae are probably wind pollinated, and the small fruits are dispersed by birds or mammals (and probably also abiotically).

***Additional reference***: Wanntorp et al. 2003.

*Dilleniales*

**Dilleniaceae** Salisbury

(Dillenia Family)

*Trees, shrubs*, *lianas*, or rarely herbs; triterpenoids, tannins, and **raphide crystals present**; **cork cambium deep-seated** (but superficial in *Dillenia* and relatives), some with successive cambia. Hairs simple, fasciculate, or stellate, *usually sclerified* **and/or silicified**, rarely gland-headed. *Leaves usually alternate and spiral*, *usually simple*, entire to serrate, **the teeth** (when present) **with clear, glandular expanded apices**, *with* *pinnate venation*, **the secondary veins ± straight and parallel**, *terminating in the teeth* (when present), and **connected by percurrent tertiary veins** (except in *Hibbertia*, where ± reticulate), **with epidermis silicified**; stipules absent, *but petiole often with wings that ± surround stem*. Inflorescences determinate, terminal or axillary, sometimes reduced to a solitary flower. Flowers usually bisexual, radial or occasionally bilateral (mainly due to androecial form). *Sepals usually 4 or 5, distinct*, *imbricate*, *persistent, and slightly to dramatically accrescent in fruit*. *Petals usually 3-5, distinct*, imbricate, **usually ± wrinkled**. *Stamens usually 5 to numerous*, sometimes with staminodes, centrifugal in development (when numerous); filaments distinct to connate (and then usually in fascicles); anthers opening by longitudinal slits or apical pores; pollen grains tricolporate or tricolpate. *Carpels 1 to numerous*, *usually distinct*; *ovaries superior*, *with parietal (lateral) placentation*; styles as many as carpels; stigmas ± punctate or peltate. Ovules 1 to numerous per carpel. **Nectary absent**. *Fruit usually a follicle, aggregate of follicles, or berries, often enclosed by fleshy, accrescent sepals*. **Seeds usually arillate** (but arils very reduced in many species of *Dillenia*).

***Floral formula***: \* K 4-5 , C 3-5 , A 1-numerous , G 1-numerous ; follicles, berries

[Put dashed line around the stamens; replace “numerous” with infinity symbol.]

***Distribution***: Pantropical, with extension into temperate zone in Australia and Tasmania.

***Genera/species***: 11/420. ***Major genera***: *Hibbertia* (225 spp.), *Dillenia* (65), *Tetracera* (50), and *Doliocarpus* (45). The family does not occur natively in North America.

***Economic plants and products***: A few species of *Hibbertia* and *Dillenia* are grown as ornamentals because of their large, striking, yellow or white flowers. Some species of *Dillenia* are used medicinally.

***Discussion***: The monophyly of Dilleniaceae is supported by morphology (Stevens 2001 onward; Horn 2007) and DNA nucleotide sequences (Horn 2009). *Tetracera* (Delimoideae; lianas, seeds with fimbriate arils) is sister to the remaining genera (which have ± non-fimbriate arils). Among these, the Doliocarpoideae (*Doliocarpus*, *Davilla*, and relatives; mainly lianas, inflorescences lacking prophylls, without cymose branching, ovules 2 per carpel, stigmas peltate) are sister to the Hibbertioideae + Dillenioideae clade. The Hibbertioideae (only *Hibbertia*) have non-sheathing leaves and their secondary veins are not connected by percurrent tertiary veins, while the Dillenioideae (*Schumacheria*, *Didesmandra*, *Acrotrema*, *Dillenia*) have petiole wings that clasp the stem and secondary veins connected by well developed, percurrent tertiaries. The cork cambium initiation in Dillenioideae is superficial, not deep seated as in the rest of the family.

 Pollination is mainly by bees, which gather the pollen by vibrating the often porose anthers (see also Endress 1997). Seeds are often bird dispersed, as in *Tetracera* and many species of *Dillenia* with the follicles opening to expose shiny, black seeds and bright red arils; in *Curatella* and *Doliocarpus* the white arils contrast with the black seeds and red fruit wall. Many *Hibbertia* with inconspicuous arils are dispersed by ants. Finally, the species of *Dillenia* with large, indehiscent fruits, containing non-arillate seeds, and surrounded by fleshy, accrescent sepals are mammal dispersed, e.g., fruits of *D. indica* are dispersed by elephants, although water dispersal is also possible (Horn 2007).

***Additional reference***: Tucker and Bernhardt 2000.

*Saxifragales*

**Cercidiphyllaceae** Engler

(Katsura Tree Family)

*Deciduous trees* **with branches forming long- and short-shoots**. Hairs ± absent. **Leaves usually opposite and decussate** (but often appearing 2-ranked on long-shoots, and arrangement of short-shoot leaves difficult to discern), **the margins rolled adaxially in bud, i.e., vernation involute**, *simple*, *with palmate venation*, entire to obscurely or clearly toothed, *each tooth with a glandular apex* (chloranthoid), **the leaves dimorphic**, *those of the short-shoots ovate, cordate at base, and obviously crenate, those of the long-shoots ovate to elliptic, non-cordate, and entire to obscurely serrate/crenate*, **and only one leaf at a time borne on each short-shoot**; *stipules present*, adnate to adaxial surface of petiole base. Inflorescences indeterminate, **± head-like** **fasciculate** (but longer and racemose in some fossils), terminal on sympodial short-shoots. *Flowers unisexual* (*and the plants* *dioecious*), *± bilateral*, reduced and inconspicuous, bracteate or not, *and the individual flowers of the fascicle difficult to differentiate*. **Perianth absent**. *Stamens of the floral cluster/fascicle numerous* (and it is impossible to determine the number belonging to each staminate flower); *anthers elongate*; pollen grains tricolpate. **Carpel only 1 per flower** (but some fossils with 2, distinct carpels per flower), *but individual flowers closely clustered* and thus carpellate fascicle appearing as a single, 2- to several-carpellate “flower,” **each carpel oriented so that its suture is abaxial** (in relation to the inflorescence axis; but the suture is adaxial in relation to the vestigial floral axis); *ovary nude* (likely superior), with parietal (lateral) placentation; style elongate, with stigma decurrent along its entire length. Ovules numerous per carpel, **each with a long, chalazal appendage** (eventually forming a wing). Nectary absent. *Fruit a follicle*. **Seeds winged, with a chalazal, hair-pin vascular bundle**.

***Floral formula***:

Staminate: X T - 0 - , A several, G 0

Carpellate: X T - 0 - , A 0 , G 1 ; follicle

***Distribution***: Eastern Asia.

***Genera/species***: 1/2. ***Genus***: *Cercidiphyllum* (2 spp.). The genus is rarely naturalized in temperate regions of eastern North America.

***Economic plants and products***: *Cercidiphyllum* (katsura tree) is grown as an ornamental, shade tree.

***Discussion***: The monophyly of Cercidiphyllaceae is supported by molecular analyses (Feng et al. 1998; Li et al. 2002; Qi et al. 2012; Zhu et al. 2019) and by the numerous putative morphological synapomorphies (Endress 1993a; Krassilov 2010; Stevens 2001 onward; Swamy and Bailey 1949; see description). Fossils indicate that the familial clade was once widespread across the Northern Hemisphere (Crano and DuVal 2013; Krassilov 2010); although now fairly restricted in distribution, the populations of *Cercidiphyllum* are genetically variable, and this variation correlates with both ecology and geography (Qi et al. 2012). An assessment of fossil representatives significantly expands our knowledge of the morphological variation exhibited by Cercidiphyllaceae (see Crane and Stockey 1986), and fossil taxa also assist in the interpretation of the morphology of extant species. Cercidiphyllaceae are probably sister to Daphniphyllaceae and putative synapomorphies include the dioecious condition and inconspicuous flowers; together, these two form the sister clade to Hamamelidaceae. Before the advent of molecular data, the family often has been considered to be related to Trochodendraceae (Cronquist 1981; Endress 1986).

 The reduced flowers are wind pollinated, and the winged seeds are also dispersed by wind.

***Additional reference***: Remizowa et al. 2009.

**Iteaceae** J. Agardh

(Sweetspire Family)

*Shrubs to trees*; vessel elements usually scalariform perforation plates, but occasionally also simple; **with C-glycosylflavones**; *stems often with chambered pith, the axillary buds sometimes superposed*. Hairs simple, eglandular or glandular (and secreting resin). *Leaves alternate and spiral*, sometimes distally clustered, *simple*, *usually ± serrate*, and the teeth often glandular, occasionally spiny, *with ± pinnate venation*; *stipules usually present*. Inflorescences indeterminate or determinate, terminal or axillary. *Flowers usually bisexual, radial, with short hypanthium*. *Sepals 5*, ± distinct, **valvate** *or open*, ± erect. *Petals 5, distinct*, valvate or imbricate, sometimes clawed and then limb spreading to reflexed, persistent. *Stamens 5,* and occasionally also with 5 staminodes; filaments sometimes flattened and with toothed wings; *anther connective often forming a globular apical appendage*; *pollen grains usually bilaterally symmetric, biporate* (*Itea*) but tricolporate (in *Pterostemon*). *Carpels 2* (in *Itea*) or 5 (in *Pterostemon*), connate; ovary superior to inferior, *with axile placentation*; *styles 2, connate* (postgenitally fused) *at least at the ± capitate stigma*, or with a single elongate style with 5-lobed stigma. Ovules few to numerous per carpel, with 2 integuments. Nectar disk on inner surface of hypanthium, occasionally absent. *Fruit usually a septicidal capsule*, *with the fruiting stigmas separating from each other*, occasionally indehiscent and 1 seeded. Seeds often with a curved embryo.

***Floral formula***: \* K 5 , C 5 , A 5 , G 2 ; capsule

[Connect the K C and A with a line below, representing the hypanthium; circle the 2 carpels, and put a line both below and above the 2]

***Distribution***: Eastern North America, Mexico, southern Africa, and southern and southeastern Asia.

***Genera/species***: 2/21. ***Genera***: *Itea* (18 spp.) and *Pterostemon* (3). Only *Itea virginica* occurs natively in the continental United States; the familial clade most diverse in Asia.

***Economic plants and products***: A few species of *Itea* (sweetspire) are cultivated as ornamentals because of their showy inflorescences and colorful fall foliage.

***Discussion***: The monophyly of Iteaceae is supported by DNA sequence data (Fay et al. 2000; Fishbein and Soltis 2004; Fishbein et al. 2001; Jian et al. 2008; Savolainen et al. 2000b; Soltis et al. 2007, 2011) and the presence of C-glcosylflavones (Bohm et al. 1988). Iteaceae possess few obvious morphological synapomorphies, although its two genera are easily diagnosed, each having several morphological synapomorphies: *Itea* (pith chambered, petals valvate, anthers with globular connective appendage, pollen grains bilaterally symmetrical, and styles postgenitally fused at least at the stigma, with globose stigma separating in fruit) and *Pterostemon* (gland-headed hairs producing resins, flattened/winged filaments, 5 staminodes, and the loss of a nectary) (Carlsward et al. 2011; Kubitzki 2007a, c; Stevens 2001 onward). Because the two genera are so distinct, *Pterostemon* is sometimes placed in its own family, and recognized as the sole genus of Pterostemonaceae (Kubitzki 2007c). Within *Itea*, the single North American species, *I. virginica*, and the single African species, *I. rhamnoides*, may be closely related, and they likely are also related to extinct European species (Hermsen 2013), although *I. virginica* also has been considered closely allied to the eastern Asian, *I. japonica* (Spongberg 1972). Iteaceae are most closely related to the Grossulariaceae and Saxifragaceae; they are easily distinguished from the former by their pinnately veined leaves, short hypanthium, ovaries with axile placentation, and capsular fruits, and from the latter by the woody habit.

 The rather showy flowers of Iteaceae are pollinated by various insects (especially butterflies, bees, and wasps); their small seeds are dispersed by wind and water.

**Paeoniaceae** Rafinesque

(Peony Family)

**Herbs**, shortly rhizomatous, to ± shrubs; **stems with cortical vascular bundles**; vessel elements usually with scalariform perforation plates; tissues with phenolics, but tannins absent. Hairs lacking, or present and simple. *Leaves alternate and spiral*, **ternately** (i.e., once or twice divided into groups of 3 leaflets) *or pinnately compound*, *the leaflets often deeply 3- to 5-lobed or dissected*, entire, *with pinnate venation*; *stipules lacking*. Inflorescences usually of solitary flowers. Flowers bisexual, *radial*, with receptacle expanded, slightly concave, with perianth spiral, **the calyx and corolla not well differentiated**, and associated with 2-6 bracts, these sometimes intergrading with the sepals. *Sepals* (3-) *5* (-7), distinct, imbricate. *Petals 5-10* (*to numerous*), distinct, imbricate. **Stamens numerous**, arising from 5 vascular bundles and **developing centrifugally** (i.e., from center of flower toward periphery); pollen grains tricolporate. *Carpels 3-8* (*to numerous*), **distinct**; *ovaries superior*; **styles very short or lacking**, *each with an expanded stigma*. Ovules many per carpel, **with the outer integument extremely thick**; **megaspore mother cells several in each ovule**, **megagametophytes often more than one**. Nectary usually a lobed disk surrounding gynoecium, but sometimes apparently non-functional. **Fruit a cluster of thick-walled follicles**. **Seed with coat (testa) fleshy, vascularized, and funicle also fleshy (aril-like)**, the seed sometimes contrasting in color with the fruit; **zygote initially undergoes nuclear division without formation of cell walls, resulting in a proembryo with numerous free nuclei**; **several embryos initially developing in each seed**, but only one matures.

***Floral formula***: \* K 5 , C 5-10 (-many) , A many , G 3-8 ; follicles

[Replace “many” with the infinity symbol]

***Distribution***: Widespread in temperate regions of the Northern Hemisphere.

***Genera/species***: 1/35. ***Genus***: *Paeonia* (35 spp.). The genus is native in the western United States; additionally, *Paeonia* *officinalis* and *P. lactiflora* are rarely naturalized in temperate regions of the continental United States and Canada.

***Economic plants and products***: *Paeonia officinalis* (common peony), *P. lactiflora* (Chinese peony), and *P*. x *suffruticosa* (tree peony) are popular ornamentals, grown for their large, beautiful flowers. Several species are used medicinally in China.

***Discussion***: The monophyly of Paeoniaceae is supported by morphology (see description; Stevens 2001 onward; Tamura 2007) and DNA nucleotide sequences (Ferguson and Sang 2001; Sang et al. 1997, 2004). Species of *Paeonia* sect. *Moutan* (the tree peonies, e.g., *P. delavayi, P. lutea, P. rockii, P*. *szechuanica, P*. x *suffruticosa*) form a clade that is sister to the remaining species. Phylogenetic hypotheses of *Paeonia* are more network-like than tree-like, due to very frequent speciation via hybridization, with the hybrid-derived species either having the same chromosome number as the parents or being polyploid (Ferguson and Sang 2001; Pan et al. 2007; Sang et al. 1997, 2004; Zhou et al. 2014). The popular ornamental *P*. x *suffruticosa* (with numerous, florally diverse cultivars) is the result of hybridization between several wild Chinese species (Sang et al. 2004). Although *Paeonia* frequently has been considered within the Ranunculaceae (note the separate carpels, follicles) or to be related to Dilleniaceae (both have centrifugally developing stamens) (Cronquist 1981), molecular evidence supports a placement within Saxifragales, as sister to the woody clade (Altingiaceae, Hamamelidaceae, and relatives).

 The showy flowers of *Paeonia* are pollinated by bees, wasps, beetles, flies, and butterflies; seed dispersal is by birds or mammals (rodents). Some species attract ants to their flower buds, but these insects are not pollinators, and instead they likely provide protection against herbivory.

**Penthoraceae** Britton

(Ditch-stonecrop family)

*Herbs*, **with rhizomes**, often producing dimorphic (submerged and emergent) shoots, the cortex with aerenchymatous tissue, the vessel elements with scalariform perforations, with various phenolic compounds. **Hairs** simple, **glandular**. Leaves alternate and spiral, simple, **the blade with stomata on both surfaces**, *serrate* (*and the teeth glandular*), with venation pinnate; stipules absent. Inflorescences determinate, **with scorpioid branches**, terminal and axillary. Flowers bisexual, radial, *with a short, ± bowl-shaped hypanthium*. *Sepals 5-8*, ± distinct, *unequal and valvate*. *Petals usually absent*, but occasionally present, inconspicuous and 1-8. *Stamens 10*; filaments distinct; pollen grains tricolporate and **slightly flattened at the poles**. **Carpels** **5-8**, connate in their basal portions; *ovary half inferior* (but becoming ± superior in fruit), **with intruded-parietal placentation** (in upper, free portion of each carpel); styles as many as the carpels, **submarginal**; stigmas separate, capitate. Ovules numerous on each placenta. Nectary absent. **Fruit a capsule, with the free portion of each of the matured carpels basally circumscissilely dehiscent,** *becoming reddish when nearly mature*. *Seed coat with minute projections*.

***Floral formula***:

\* K 5-8 , C 0-8 , A 10 , G 5-8 ; capsule

[Connect K-C-A with a line below, indicating a hypanthium; circle the 5-8 carpels, and draw a short line right before and after the numbers to indicate half-inferior ovary]

***Distribution***: Eastern North America and Eastern Asia; predominantly in sunny, wetland habitats.

***Genera/species***: 1/2. ***Genus***: *Penthorum* (2 spp.). *Penthorum sedoides* native in the eastern United States and Canada, and introduced in southern British Columbia south to Oregon.

***Economic plants and products***: *Penthorum* is used medicinally and as an aquarium-plant.

***Discussion***: Monophyly of Penthoraceae is supported by several morphological characters (see description; Carlsward et al. 2011, Haskins and Hayden 1987, Stevens 2001 onward, and Thiede 2007), especially the unusual circumscissile capsules. Molecular analyses (Chen et al. 2016; Fishbein et al. 2001; Morgan and Soltis 1993; Savolainen et al. 2000a, b; Soltis et al. 2000, 2011) support a phylogenetic placement as sister to Haloragaceae. In contrast, *Penthorum* traditionally has been placed either in Saxifragaceae s.l. (Cronquist 1981) or in Crassulaceae (Hutchinson 1973).

 The greenish to white flowers are presumably insect pollinated. The tiny seeds are mainly water dispersed, although wind dispersal also is possible.

***Additional reference***: Spongberg 1972.

*Zygophyllales*

**Krameriaceae** Dumortier

(Ratany Family)

*Rhizomatous*, **hemiparasitic**, *shrubs to herbs*, sometimes with thorns, **connected to the host plant by numerous haustoria**, with tannins and scattered sclereids. Hairs simple. **Nodes unilacunar**. *Leaves alternate and spiral, usually simple* (rarely trifoliolate), *entire*, with obscurely palmate-reticulate venation; *stipules absent*. Inflorescences indeterminate, terminal, or flowers solitary and axillary. **Flowers** bisexual, **bilateral (due primarily to form of calyx and corolla)**. *Sepals* (4-) *5, distinct*, **petaloid, the 3 outer ones larger than the 2 inner**, imbricate, reflexed or not. *Petals* (4-) *5*, **the adaxial (upper) 3 clawed**, *distinct or connate* (by the lower, clawed portion), **the abaxial (lower) 2 thick/glandular, smaller, with epidermal cells secreting β-acetate substituted free fatty acids**. **Stamens** (3-) **4**; filaments distinct to basally connate, ± thick, often adnate to the clawed petals; **anthers opening by apical ± pores**; pollen grains tricolporate to triporate, **with minute, longitudinal ridges** (**striae**, i.e., pollen striate). **Carpels 2, but appearing to be 1 (i.e., pseudomonomerous, with one carpel aborting early in development)**; ovary superior, with apical placentation; *style single,* **curved**, with small, recessed stigma. **Ovules 2 per gynoecium**. Nectary absent. **Fruit nut-like,** *usually globose,* **with retrorsely barbed spines**, with a single seed. **Embryo with cordate cotyledons**; endosperm absent.

***Floral formula***: X K 2 + 3 , C 3 + 2 , A 4 , G 2 ; spiny nut

[Circle the 3 upper petals; circle the 2 carpels; put a dashed line below the 4 stamens connecting them to the 3 petaloid petals; also put a dashed line around the 4 petals]

***Distribution and ecology***: In arid regions of southern North America and the West Indies, south into South America.

***Genera/species***: 1/18. ***Genus***: *Krameria* (18 spp.). The genus occurs in the continental United States.

***Economic plants and products***: *Krameria* (ratany, rhatany) is occasionally used as a dye plant (phlobaphenes, reddish phenolic substances) or in products connected to oral or dental hygiene.

***Discussion***: The monophyly of Krameriaceae is well supported by numerous distinctive morphological characters (Robertson 1973; Simpson 1982, 1989, 2007; Simpson et al. 2004; Stevens 2001 onward; see description) and molecular characters (Simpson et al. 2004). The familial clade is comprised of two major clades (both of which contain South American as well as North American species). The first (including *K. bicolor, K. cistoidea, K. paucifolia*, and relatives) is characterized by species with rugose secretory petals and fruit-spines with 1 or 2 terminal whorls of retrorse barbs) and the second (including *K. erecta, K. lanceolata, K. ramosissima*, *K. ixine*, *K. tomentosa* and relatives) includes species with striations on their secretory petals (either over the entire surface or restricted to the tip), connivant sepals, and triporate pollen. Although DNA evidence supports a relationship with Zygophyllaceae, *Krameria* was once considered to be related to either the Leguminosae or Polygalaceae (Fabales).

 The showy flowers of *Krameria* attract both lipid-gathering and pollen gathering bees (Carneiro et al. 2015; Simpson et al. 1977). The spiny fruits become are externally transported on the feathers/hair of birds or mammals. Frequently the fruits seem to mature without development of the included seed.

*Oxalidales*

**Brunelliaceae** Engler

(Brunellia Family)

*Trees*. *Hairs simple,* **brownish**. **Leaves opposite and decussate**, *odd-pinnately compound*, but sometimes reduced to trifoliolate or unifoliolate, *usually ± serrate*, the leaflets with pinnate venation, and *secondary veins ending in the teeth*; *stipules present, sometimes divided,* usuallyborne on the stem, *and leaflets also associated with stipule-like structures (stipels)*. Inflorescences determinate, axillary. Flowers bisexual or unisexual (and plants then ± dioecious or polygamous), radial. *Sepals 4-6* (-8), *usually* *distinct, valvate*. *Petals usually absent* (but 1 or 2 initially present in flowers of *B. ephemeropetala*, and then distinct, pubescent). *Stamens 8-12* (-16); filaments distinct; anther connective with small apical protrusion; pollen grains tricolporate; staminodes usually present in carpellate flowers. *Carpels 2-8, distinct; ovaries superior*, with apical-parietal (lateral) placentation; styles recurved, *each with an elongate, decurrent stigma*; carpellodes usually present in staminate flowers. Ovules 2 per carpel. *Nectar disk* (a short androgynophore, see Matthews and Endress 2002) *present*. *Fruit a cluster of hairy, spreading follicles*, **the ventral side of each carpel growing more than the dorsal, thus pushing styles into a horizontal position**, **and when mature the hard endocarp separating from the rest of the fruit,** and exposing the seeds. **Seed coat hard, shiny, the testa with subepidermal sclerenchymatous layer and palisade innermost layer; raphe raised**. Embryo large.

***Floral formula***: \* K 4-6 , C 0 , A 8-12 , G 2-8 ; follicles

***Distribution and ecology***: Central and South America and the Antilles, in moist montane/cloud forests.

***Genera/species***: 1/65. ***Genus***: *Brunellia* (65 spp.). Not in the continental United States or Canada.

***Economic plants and products***: *Brunellia* (palo bobo, among others) occasionally used medicinally (to reduce fever).

***Discussion***: The monophyly of Brunelliaceae is supported by morphology (Orozco 2001; Stevens 2001 onward; see also description) and DNA sequences (Pillon et al. 2021; Valencia et al. 2020). Relationships within the family are still poorly known, but *B. ovalifolia, B. stuebelii*, and *B. pauciflora* may represent early divergent lineages. *Brunellia* was once included within Cunoniaceae (Hufford and Dickson 1992) but molecular data supports familial recognition (see discussion under Cunoniaceae) within Oxalidales, where it is sister to Cephalotaceae or Elaeocarpaceae. It is of interest that petals are lacking (presumably lost) in Cephalotaceae and usually also lost in Brunelliaceae (but present in a single species, *B. ephemeropetala*; Orozco et al. 2017).

 The small flowers likely are pollinated by a variety of insects. The seeds are probably dispersed by birds.

***Additional references***: Cuatrecasas 1970 and 1985; Kubitzki 2004a.

**Cephalotaceae** Dumortier

(Australian Pitcher-plant Family)

**Carnivorous herbs**, from rhizomes with scale leaves. Hairs simple, both eglandular and glandular. **Leaves** *alternate and spiral*, *in rosettes*, **simple**, **dimorphic**, *some flat and photosynthetic* **and others pitcher-like and carnivorous**; photosynthetic leaves entire, with ± pinnate venation, and with sessile glands; **carnivorous leaves with a colorful lid and pitcher, the former (i.e., lid) at the apex of the petiole, and the latter (the pitcher) with 2 prominent anterior ribs, opening toward the base of leaf, with a conspicuous ribbed-toothed rim around the mouth-opening, with downward-pointing epidermal cells below the rim, and with sessile, glandular hairs inside pitcher (enzyme producing) and also glandular hairs on outer pitcher surface and mouth (nectar producing)**; **stipules lacking**. Inflorescences determinate, *the branches forming scorpioid cymes*, *terminal*, **± scapose**. Flowers bisexual, radial, **with a hypanthium**. *Sepals 6, ± distinct*, *petaloid*, **apically incurved**, valvate and imbricate. *Petals absent*. *Stamens 12*; filaments distinct; **anther connective abaxially swollen**; pollen grains tricolpate. *Carpels 6, distinct*; *ovaries superior*, with basal-parietal (lateral) placentation; *stigmas decurrent along styles*. Ovules 1 or 2 per carpel. *Nectar produced by glandular-pubescent inner surface of hypanthium*. **Fruit a cluster of hairy achenes**; **seed coat mostly collapsed**.

***Floral formula***: \* K 6 , C 0 , A 12 , G 6 ; achenes

[Draw a line connecting K-C-A to indicate presence of a hypanthium]

***Distribution and ecology***: Southwestern Australia, in moist acidic habitats (e.g., bogs, with *Sphagnum*).

***Genera/species***: 1/1. Genus: *Cephalotus* (1 sp.). Not native or naturalized in North America.

***Economic plants and products***: *Cephalotus follicularis* (Australian or Albion pitcher-plant) is a strange and beautiful species and is widely cultivated by carnivorous plant enthusiasts.

***Discussion***: The monophyly of Cephalotaceae is well supported by its numerous putative morphological synapomorphies (see description; Conran 2004; Matthews and Endress 2002; Parkes and Hallam 1984; Stevens 2001 onward) and by several gene modifications (involving co-option of stress-responsive protein lineages) connected to the evolution of a digestive physiology (Fukushima et al. 2017). The amazing carnivorous leaf represents a modified axis of an ancestrally pinnately compound leaf (Franck 1976). The carnivorous leaves of *Cephalotus* are morphologically and developmentally quite different from the pitcher-leaves of both Sarraceniaceae and Nepenthaceae. Cephalotaceae are most closely related to Brunelliaceae, and their flowers are remarkably similar, sharing the apomorphic characters of the loss (or near loss) of petals and distinct carpels with decurrent stigmas.

 Pollination of the rather small flowers is by various insects, while the fruits are wind dispersed.

**Elaeocarpaceae** de Jussieu

(Fairy-petticoats Family)

*Trees to shrubs,* occasionally only subshrubs; trunks sometimes with buttress-roots; often with tannins, ellagic acid, triterpenes, saponins, and pyrrolizidine and tropane alkaloids. Hairs simple, eglandular or gland-headed, occasionally stellate. Leaves alternate and spiral or 2-ranked, or opposite and decussate, **simple**, *toothed* or occasionally entire, with pinnate or palmate venation, *often turning orange, red, or yellow before dropping*; *stipules present*. Inflorescences determinate or indeterminate, axillary or terminal, sometimes reduced to a solitary flower. *Flowers usually bisexual*, *radial*, *± pendent*. *Sepals 4 or 5*, distinct to basally connate, usually valvate. *Petals 4 or 5,* but often absent in *Sloanea*, *usually distinct*, *their margins usually toothed to fringed, usually valvate*. *Stamens usually numerous*, centrifugal in development; *filaments distinct*, **usually shorter than anthers**, borne on a nectar disk or enlarged receptacle or androgynophore; **anthers opening by transverse slit or apical pores or very short slits, distally often tubular-porose**, *and connective often apically elongated*; pollen grains usually tricolporate. Carpels 2-8, connate; the ovary superior, with axile placentation; **style single**, sometimes distally branched; stigma punctate. Ovules 1 to many per locule. *Fruit usually a loculicidal capsule,* *sometimes spiny or bristly*, *a* *drupe* with often sculptured endocarp, or a berry. Seeds sometimes with a fleshy seed coat or aril; **inner layer of seed coat (tegmen) with vascular bundles**.

***Floral formula***: \* K 4-5 , C 4-5 , A many , G 2-8 , capsule, drupe

[Circle the 2-8 carpels]

***Distribution***: Tropical Mesoamerica and the Caribbean south through South America, Madagascar, temperate to tropical southern and eastern Asia, south to Australia, Tasmania, New Zealand, and Pacific islands.

***Genera/species***: 12/635. ***Major genera***: *Elaeocarpus* (350 spp.), *Sloanea* (150), *Tetratheca* (50), and *Aceratium* (20). No genera occur natively in temperate North America, but *Aristotelia chilensis* is rarely naturalized in California.

***Economic plants and products***: The larger species of *Elaeocarpus* and *Sloanea* provide timber. Various species of *Elaeocarpus* (fairy-petticoat tree, fringe-bells, blue-marble tree, blueberry tree, bead tree), *Tetratheca* (black-eyed susan), *Aristotelia*, and *Crinodendron* *hookerianum* (Chilean lantern-tree) are grown as ornamentals because of their beautiful flowers and/or fruits. The fruits of *Aristotelia* *chilensis* (maqui berry, Chilean wineberry) and several species of *Elaeocarpus* are edible.

***Discussion***: The monophyly of Elaeocarpaceae is supported by DNA sequences (Crayn et al. 2006; Savolainen et al. 2000b; Sun et al. 2016; Pillon et al. 2021); the plants are morphologically diverse, but the flowers with numerous anthers opening apically and with fairly short filaments are characteristic. A clade comprising *Sloanea*, *Vallea* and *Aristotelia* (tribe Sloaneae: characterized by stamens opening by 2 apical pores) is sister to the remaining genera (tribe Elaeocarpeae: which have stamens opening by a single apical pore or slit). Within the latter clade, *Crinodendron*, *Peripentadenia* and *Dubouzetia* (with capsular fruits) represent early diverging lineages, related to a clade containing the large and non-monophyletic *Elaeocarpus* along with close relatives (with drupes or berries), and including the tremand clade (*Tremandra*, *Tetratheca*, *Platytheca;* withstellate hairs, stipules absent, and dehiscent fruits).

 The often rather showy flowers are pollinated by various insects, but those of *Crinodendron* may be hummingbird pollinated. The species with fleshy, often colorful (blue, but also red) fruits are probably mainly bird dispersed. The iridescent blue coloration of *Elaeocarpus* fruits is structural, due to layers of cellulose that cause interference coloration (Lee 1991, 2007). Even the capsular-fruited taxa, e.g., *Sloanea*, likely are bird or mammal dispersed as their seeds have a colorful sarcotesta or aril contrasting with the capsular valves.

***Additional references***: Coode 2004; Smith 1954.

*Malpighiales*

**Achariaceae** Harms

(Chaulmoogra Family)

*Trees, shrubs*, or rarely lianas or herbs; with cyclopentenoid cyanogenic glucosides and/or cyclopentenyl fatty acids, often also sulphones, flavonolignans, chaulmoogric oils. Hairs usually simple. *Leaves alternate and spiral or 2-ranked, simple*, but sometimes lobed or dissected, *entire to variously toothed, but never salicoid,* with pinnate venation, *with petiole often with upper pulvinus; stipules usually present*. Inflorescences determinate or indeterminate, axillary or cauliflorus, sometimes reduced to a solitary flower. *Flowers bisexual or more commonly unisexual* (*plants then usually monoecious*), radial, **with many more petals than sepals and these not in a simple alternating relationship**, whorled or spirally arranged. Sepals 2-5, distinct to basally connate. *Petals 4-15, distinct to basally connate, imbricate, each often with a basal, adaxial scalelike appendage*. *Stamens usually numerous*, sometimes with staminodes; filaments distinct and sometimes basally adnate to petals; *anthers elongate*; pollen grains tricolporate. *Carpels 2-10, connate; ovary superior, with parietal placentation*; style elongate to short, unbranched to branched; stigma capitate to punctate, often lobed. Ovules few to numerous; **female gametophyte penetrating the chalazal region**. **Nectar disk absent**. *Fruit a berry or loculicidal capsule, often with warts, bristles, spines, or wings*; *seeds arillate or not*; **cells of outer part of tegmin elongated, large and sclereidlike**; embryo green.

***Floral formula***:

Staminate: \* , K 2-5 , C 4-15 , A many , G 0 or 2-10**.**

[Put dashed line around 2-5 sepals; put dashed line around 4-15 petals; below the formula connect petals and stamens with a dashed line; replace “many” with infinity symbol; circle the 2-10 sterile carpels]

Carpellate: \* , K 2-5 , C 4-15 , A 0-many**.** , G 2-10 ; berry, capsule

Put dashed line around 3-5 sepals; put dashed line around 4-15 petals; replace “many” with infinity symbol; circle the 2-10 carpels]

***Distribution***: Pantropical.

***Genera/species***: 31/154. ***Major genera***: *Hydnocarpus* (40 spp.), *Ryparosa* (18), *Lindackeria* (13), *Carpotroche* (11), and *Caloncoba* (10). The family does not occur in the United States or Canada.

***Economic plants and products***: Several genera, e.g., *Gynocardia* (petarcurrah) and *Carpotroche* (pan de lepra) are used medicinally or as insecticides. Several species of *Hydnocarpus* are the source of chaulmoogra oil, used in treatment of eczema, leprosy, and other skin conditions. The fruits of *Pangium* *edule* (pangi fruit, football fruit) are poisonous, but eaten after processing.

***Discussion***: The monophyly of Achariaceae is supported by DNA sequences (Chase et al. 2002; Groppo et al. 2010, 2013; Pagart 2017; Savolainen et al. 2000b; Sosa et al. 2003) and morphology (see description; Stevens 2001 onward). Phylogenetic relationships within Achariaceae are still rather unclear; one major subclade includes *Acharia*, *Gynocardia*, *Kiggelaria*, *Pangium*, *Ryparosa*, and relatives (usually with scales on petals) and another includes *Caloncoba*, *Camptostylus*, *Carpotroche*, *Lindackeria*, *Xylotheca*, and relatives (petal-scales absent). The position of *Hydnocarpus* is unclear. Most of these genera, along with many of the Salicaceae, were included traditionally within a paraphyletic and non-diagnosable Flacourtiaceae (see Cronquist 1981; Lemke 1988).

 Pollination probably is mainly by various insets, but lizard pollination has been recorded in *Guthriea*. The seeds or fruits are dispersed by birds or mammals.

**Caryocaraceae** Voigt

(Souari-tree family)

*Trees or shrubs*; with tannins, often various triterpenes and terpenoid saponins; **nodes penta- to multi-lacunar**. Hairs simple. Leaves alternate and spiral (*Anthodiscus*) or opposite and decussate (*Caryocar*), **compound (and trifoliolate)**, *the leaflets variously toothed*, with pinnate venation, **with branched sclereids in mesophyll and petiole**; *stipules present*, intrapetiolar or interpetiolar, colleters present, and the leaflets often associated with stipule-like structures. Inflorescences indeterminate, terminal. **Flowers** bisexual, radial, **large**. *Sepals usually 5*, slightly to strongly connate, imbricate. *Petals usually 5*, imbricate, and usually distinct (*Caryocar*) or connate and forming a calyptra (*Anthodiscus*), **and protective in bud**. *Stamens numerous*, connate basally; **filaments** free or basally adnate to petals, **elongated and showy**, **and the innermost staminodial,** **both with specialized bulging, perforated, odor-producing cells**; pollen grains tricolporate. *Carpels 4-20, connate; ovary superior, with basal placentation*; *styles equaling number or carpels,* and each style with a single vascular bundle (*Caryocar*) or 2 vascular bundles from adjacent carpels (*Anthodiscus*); stigmas impressed-punctate. **Ovules 1 in the locule of each carpel, erect, sessile**, anatropous to campylotropous, with 2 integuments (*Caryocar*) or a single integument (*Anthodiscus*). Nectary at base of staminodes (*Caryocar*), perhaps absent (in *Anthodiscus*). *Fruit a drupe*, with the pit often with radiating, spine-like fibers, splitting into 1-seeded units; seeds usually kidney-shaped; embryo with hypocotyl/radicle straight (*Caryocar*) or spirally twisted (*Anthodiscus*).

***Floral formula***: \* K 5 , C 5 , A many , G 4-20 ; drupe

[Circle the 5 sepals; put a dashed circle around the 5 petals; circle the many stamens, and put a dashed line below and connecting A and C; circle the 4-20 carpels.]

[Put a circle around the five sepals, put a dashed line around the five petals; circle the numerous stamens, and replace “many” with infinity symbol; circle the 4-20 carpels]

***Distribution***: Central and South America, especially Amazonia.

***Genera/species***: 2/28. ***Genera***: *Caryocar* (18 spp.), *Anthodiscus* (10).

***Economic plants and products***: Some species of *Caryocar*, especially *C. brasilense, C. coriaceum,* and *C. nuciferum* (pequi, souari) produce nutritious and edible fruits, and useful oils are extracted from the pit/seeds. However the fruits of other species are poisonous, e.g., *C. glabrum*, which is used as a fish poison. Several are used medicinally. A few are timber trees, e.g. *C*. *villosum*.

***Discussion***: The monophyly of Caryocaraceae is well supported by morphology (see description; Prance 2014; Sousa Paiva et al. 2019; Stevens 2001 onward) and DNA sequences (Korotkova et al. 2009; Nunez et al. 2020a; Xi et al. 2012). The bulging and perforated, odor-producing cells on the filaments of the stamens and staminodes are especially distinctive. *Caryocar* and *Anthodiscus* can be distinguished by numerous morphological characters (see description; and also Dickinson 1990; Nunez et al. 2020; Prance and Freitas da Silva 1973; Prance 2014; Stevens 2001 onward). The family is of uncertain position within Malpighiales, but may be related to Chrysobalanaceae, Dichapetalaceae, and Malpighiaceae. Caryocaraceae were traditionally placed in the Theales (Cronquist 1981), a “group” now known to be non-monophyletic, with some families, e.g., Ochnaceae and Clusiaceae, now in Malpighiales, and others, e.g., Theaceae, Actinidiaceae, in Ericales, or Dipterocarpaceae, in Malvales. This placement was mainly based on their showy flowers with five petals and numerous stamens.

 The flowers of *Caryocar* are primarily bat pollinated although hawkmoths and arboreal marsupials also visit the flowers (Gribel and Hay 1993; Nunez et al. 2020b) while those of *Anthodiscus* may be insect (bee) pollinated (Prance 2014). Extrafloral nectaries on the buds of *Caryocar brasiliense* attract ants, which provide protection from herbivory (Olivera 1997). The fruits of *Caryocar* are dispersed by agoutis and rheas (see Nunez et al. 2020b; Prance 2014), but previously may have been dispersed by now extinct megafauna (Collevatti et al. 2003).

***Additional references***: Daytas de Araujo 1995; Mathews and Endress 2011; Prance 1990.

**Dichapetalaceae** Baillon

(Ratbane Family)

*Trees, shrubs, or lianas* with hook-like branches; often with fluoracetic acid, fluoro-fatty acids, and pyridine alkaloids (*very poisonous*), often with mucilage cells. *Hairs simple, with minute bumps*. *Leaves alternate*, spiral, *simple*, *entire*, *with pinnate venation, the blade often with nectar glands on the abaxial (and sometimes also adaxial) surface*; stipules present, sometimes fimbriate. **Inflorescences** determinate, **epiphyllous** **(i.e., arising from the petiole or base of the blade)** or occasionally axillary. *Flowers usually bisexual*, radial to bilateral. *Sepals 5*, distinct to slightly connate, imbricate. *Petals 5*, distinct or connate, often ± clawed, **apically 2-lobed or notched**, occasionally some lobed and some unlobed, often inflexed, imbricate to ± valvate, **turning black when dried**. **Stamens 5**, sometimes only 2-3 fertile and with remaining ones nonfunctional (staminodes); filaments free or adnate to corolla; pollen grains tricolporate. *Carpels 2-4*, *connate*; ovary superior to inferior, with axile placentation; style 1 or as many as the carpels; stigma(s) punctate or lobed. Ovules 2 per locule, with a thin sporangium wall. Nectary a disk or a ring of lobes (perhaps modified staminodes). *Fruit usually a hairy, flattened or lobed drupe*, with a 1- to 4-seeded pit (with 1 seed per locule), but sometimes dehiscent. Seeds sometimes arillate, **with vascular bundles in the seed coat (testa)**; endosperm scanty or lacking.

***Floral formula***: \* or X K 5 , C 5 , A 5 , G 2-4 ; drupe

[Put a dashed line around the 5 petals; connect the 5 petals to the 5 stamens by a dashed line; circle the 2-4 carpels, also draw a line above the carpels as ovary is sometimes inferior.]

***Distribution***: Pantropical.

***Genera/species***: 3/170. ***Major genera***: *Dichapetalum* (135 spp.) and *Tapura* (20). Not occurring in the continental United States and Canada.

***Economic plants and products***: A few species of *Dichapetalum* (ratbane, gifblaar) are used as poisons, to kill rats and mice. They also cause accidental livestock deaths.

***Discussion***: The monophyly of Dichapetalaceae is supported by DNA sequences (Savolainen et al. 2000b; Soltis et al. 2011; Wurdack and Davis 2009; Yakandawala et al. 2010), although there is also some support from morphology (see description; Matthews and Endress 2008; Prance 1972, 2014; Stevens 2001 onward). Of these putative synapomorphies, the epiphyllous inflorescences are especially striking, although epiphyllous inflorescences have evolved in other angiosperms, and characterize, for example, the Helwingiaceae + Phyllonomaceae clade (Aquifoliales) and *Turnera* (of the Passifloraceae, Malpighiales).

 The flowers of Dichapetalaceae are probably mainly bee pollinated. Birds or mammals disperse the fleshy fruits.

***Additional references***: Dickinson 1978; Prance 1984.

**Erythroxylaceae** Kunth

(Coca Family)

*Trees or shrubs; with tropane and pseudotropane alkaloids* (including cocaine and cinnamylcocain), also hygroline ecgonine alkaloids and often tannins; **nodes** trilacunar, **with lateral bundles originating well below the central one, and stems thus with cortical bundles**. *Hairs absent*. *Leaves alternate*, spiral or 2-ranked (but opposite in *Aneulophus*), *simple*, **entire**, *with pinnate venation, and usually with 2, obscure to pronounced, longitudinal fold-lines, one on each side of midvein*; stipules usually intrapetiolar, often connate (but one stipule on stem at each side of petiole base, and thus interpetiolar, in *Aneulophus*), and associated with colleters. Inflorescences determinate (and reduced, *fasciculate*), axillary. *Flowers usually bisexual* occasionally unisexual (and plants then ± dioecious)*, radial,* and often ± distylous in *Erythroxylum*. *Sepals 5*, slightly connate, valvate or imbricate. *Petals 5, distinct, ± clawed and usually with an adaxial, ± bilobed appendage* (forming a corona), **and petals longer than calyx lobes**, *postgenitally connected*, **and protective of the inner floral parts in bud**. *Stamens 10; filaments basally connate*; pollen grains tricolporate. *Carpels 2-3* (-4), *connate*; *ovary* *superior*, with apical-axile placentation; styles as many as the carpels, or ± fused and forming a single style; stigmas various, but often ± capitate. Ovules 1 or 2 per locule, often only 1 locule fertile. Nectary associated with androecial tube. *Fruit usually a drupe* (but a 2- or 3-seeded capsule in *Aneulophus*). Seeds rarely arillate (*Aneulophus*).

***Floral formula***: \* K 5 , C 5 , A 10 , G 2-3 , drupe

[Circle the 5 sepals, circle the 10 stamens, circle the 2-3 carpels]

**Distribution**: Pantropical.

***Genera/species***: 4/240. ***Major genus***: *Erythroxylum* (230 spp.). A single species of *Erythroxylum* is naturalized in southern Florida.

***Economic plants and products***: *Erythroxylum* *coca* and *E. novogranatense* are the source of cocaine, a dangerous narcotic drug. Chewing coca leaves is a common practice among Andean peoples (Plowman 1979), and in the 1800s coca extracts were added to wine and soft drinks. Cocaine was removed from Coca-Cola in 1906 but coca-leaf extract is still used as a flavoring in several soft drinks (Davis 1997).

***Discussion***: The monophyly of Erythroxylaceae is supported by morphology (Stevens 2001 onward; see description) and DNA-sequences (Savolainen et al. 2000b; Schwarzbach and Ricklefs 2000; Sun et al. 2016; Wurdack and Davis 2009). The small genus *Aneulophus* is sister to the clade comprising the remaining three genera, and this genus is unusual in having opposite leaves, flowers lacking petal-appendages, and capsular fruits with arillate seeds. The species of the *Erythroxylum* + *Nectaropetalum* + *Pinacopodium* clade have alternate leaves, petals with indistinct to conspicuous appendages, and drupaceous fruits. The Neotropical species of *Erythroxylum* form a clade nested within the various Paleotropical species (White et al. 2019).

 Flowers of Erythroxylaceae are fragrant and nectar-producing and pollinated by various insects (bees, wasps, flies, butterflies). The bright red drupes are probably mainly bird dispersed.

***Additional references***: Bittrich 2014; Bohm et al. 1982.

**Elatinaceae** Dumortier

(Waterwort Family)

*Herbs or subshrubs of aquatic to wetland habitats*, often creeping and rooting adventitiously at nodes; stems often with longitudinal air-canals, often resinous; ellagic acid sometimes present; **nodes unilacunar**. Hairs absent (*Elatine*) or simple, eglandular and gland-headed (*Bergia*). *Leaves usually opposite and decussate*, simple, entire, crenate to serrate, *with marginal water-secreting glands or glandular hairs*, with obscure, ± pinnate venation; *stipules present, scarious*. Inflorescences determinate or reduced to a solitary flower, axillary. *Flowers bisexual, radial, small and inconspicuous*, sometimes cleistogamous. *Sepals 2-5*, distinct to basally connate. *Petals usually 2-5*, distinct, imbricate. *Stamens 2-10*, distinct; filaments free; pollen grains tricolpate to ± tricolporate. *Carpels 2-5, connate; ovary superior*, with usually axile placentation; styles as many as the carpels; stigmas capitate. **Ovules many per carpel**. Nectaries ± absent. *Fruit a septicidal capsule*; seeds tiny, *straight to strongly curved*; **the cells of the testa in vertical lines**; endosperm lacking.

***Floral formula***: \* , K 2-5 , C 2-5 , A 2-10 , G 2-5 ; capsule

[Put a dashed line around the 2-5 sepals; circle the 2-5 carpels]

***Distribution and ecology***: Widely distributed, temperate to tropical; plants of often ephemeral, wetland to aquatic habitats.

***Genera/species***: 2/35. ***Genera***: *Bergia* (25 spp.) and *Elatine* (10). Both genera occur in the United States and Canada.

***Economic plants and products***: *Elatine* (waterwort) is occasionally used as an aquarium plant.

***Discussion***: The monophyly of Elatinaceae is strongly supported by DNA sequences (Cai et al. 2016; Davis and Chase 2004; Razifard et al. 2017a; Soltis et al. 2011; Wurdack and Davis 2009), although morphological support is somewhat weaker (Kubitzki 2014a; Popiela et al. 2017; Stevens 2001 onward; Tucker 1986; see also description). *Elatine* is derived compared with *Bergia*, having solitary, 2-4-merous flowers, longitudinal air-spaces in its stems, and the loss of hairs. Within *Elatine*, *E. alsinastrium* is sister to the remaining species, which are comprised of two major subclades: the first with 4-merous species, and the second with 3-merous (or 2-merous) species. Elatinaceae are sister to Malpighiaceae (Davis and Chase 2004; Wurdack and Davis 2009), and both have opposite leaves with glands, lack nectaries, and have the odd petal adaxial (Stevens 2001 onward).

 Although the flowers of *Elatine* are inconspicuous and often selfing, some speciation by allopolyploidy has occurred, e.g., both *E. hexandra* and *E. americana* are allopolyploids, and arose through hybridization, so some outcrossing must occur (Razifard et al. 2017b). The flowers of *Elatine* and *Bergia* probably attract generalized insect pollinators. The small seeds may be dispersed by waterfowl (stuck on with mud).

**Humiriaceae** Jussieu

(Umiri or umiry-balsam Family)

*Trees or shrubs*; *stems often sharply angled, with long pointed buds*; with ellagic acid, tannins, various terpenes, coumarins, and phytosteroids, **with secretory cavities or ducts, usually with aromatic** (umiry-balsam) **sap**; **vessel elements with vestured pits**; **sieve tube plastids with both protein crystaloids and starch**; **nodes pentalacunar**. Hairs simple. *Leaves alternate, often 2-ranked*, *simple*, *glandular-toothed* or entire, with pinnate venation, *involute in bud and when unrolled at maturity often with longitudinal lines*; stipules present or absent. Inflorescences determinate, terminal or axillary. Flowers bisexual, radial. *Sepals 5*, variously connate, imbricate, sometimes 2 smaller than the other 3. *Petals 5*, distinct, *usually quite narrow*, imbricate, sometimes convolute. Stamens 10 (but sometimes 5 of these staminodes) to very numerous; **filaments variably connate, and with interdigitated hairs distally, forming a tube**; anthers with 2 thecae, each bilocular, or 4 or 2, and each unilocular, **the connective usually prolonged beyond thecae**; pollen grains usually tricolporate. *Carpels usually 5,* connate; ovary superior, with axile placentation; style single; stigma capitate to lobed. **Ovules 1 or 2 per locule**. Nectar disk present around ovary, sometimes lobate. **Fruit a drupe with an operculate (i.e., with germination valves)**, **thick-walled**, *usually 1-3 seeded* **pit** (endocarp); the surface of the pit smooth **or more commonly variously sculpted** (ridged, bullate, corrugated), *often with resinous cavities;* the fleshy outer portion (mesocarp) juicy or fibrous. Seed with green, straight to ± curved embryo; sometimes with high oil content.

***Floral formula***: \* K 5 , C 5 , A 10-many , G 5 ; drupe

[Circle the 5 sepals; circle the 10-many stamens; circle the 5 carpels]

***Distribution and ecology***: Mesoamerica to South America, with a single species (of *Sacoglottis*) in coastal West Africa. Mainly are species of Neotropical rainforests.

***Genera/species***: 8/60. ***Major genera***: *Vantanea* (16 spp.), *Humirastrum* (16), *Schistostemon* (9), and *Sacoglottis* (8). No genera occur in the continental United States and Canada.

***Economic plants and products***: A few provide locally used aromatic balsam and/or seed-oil. Several are used medicinally (for a wide range of conditions).

***Discussion***: The monophyly of the family is supported by both morphological (see description; also Herrera et al. 2010, Cuatrecasas 1961, Kubitzki 2014b, and Stevens 2001 onward) and DNA sequence data (Xi et al. 2012). *Vantanea* and *Humiria* are supported as successive sisters to the clade containing the remaining genera in analysis of Herrera et al. (2010). *Humiria* + remaining genera form a clade supported by a reduction in the number of stamens (i.e., 30 or less, vs. 50 or more in *Vantanea*), and anthers with unilocular thecae (vs. bilocular in *Vantanea*). *Humiria* differs from the remaining genera in the retention of two ovules per locule (vs. a reduction to only one ovule per locule in the *Duckesia + Hylocarpa + Endopleura + Humirastrum + Sacoglottis + Schistostemon* clade). Additionally, *Vantanea* has paracytic stomata, while the remaining genera have anomocytic stomata; its petals each have three vascular traces, while petals are single-traced in the other genera. In contrast, in the analysis of Xi et al. (2012) *Schistostemon* is sister to the remaining genera; however, this result is poorly supported and only a few taxa are included. Humiriaceae are placed within Malpighiales, possibly sister to the parietal placentation clade (Xi et al. 2012), or unplaced within the order (Soltis et al. 2011). Traditionally (see Cronquist 1981) the family was considered to be related to Linaceae (also of Malpighiales).

 Flowers of Humiriaceae are insect (mainly bee) pollinated; their fruits are dispersed by mammals and birds, or in water (by floating).

**Picrodendraceae** Small

(Black-Ironwood Family)

*Trees to shrubs*, with pentacyclic triterpenoids (a group of sesquiterpenes), mucilage cells present or absent, *laticifers lacking*; plants usually poisonous. Hairs simple. *Leaves usually alternate and spiral*, but sometimes opposite and decussate or whorled, *simple, palmately compound, or trifoliolate*, entire to variously toothed, with pinnate venation or only midrib evident; **with stomates having subsidiary cells on top of guard cells**; stipules absent or present, on petiole or stem, with colleters, rarely also with small stipule-like structures at petiole apex. Inflorescences determinate, but sometimes appearing indeterminate, usually axillary, sometimes reduced to a solitary flower. *Flowers unisexual* (*plants dioecious or monoecious*), *radial, ± inconspicuous*. *Sepals usually 4-8*, distinct to basally connate, usually imbricate. *Petals lacking*. *Stamens 2 to numerous*; *filaments distinct to connate*; **pollen grains with 4 to numerous pores; exine usually echinate (spiny)**, or occasionally verrucose (wrinkled). *Carpels usually 3; ovary superior, usually 3-lobed*, with axile placentation; styles usually 3, or 1 with 3 well-developed branches, *and each branch usually undivided*; stigmas various, often expanded or elongated. *Ovules 2 in each locule*. Nectar disk present or absent. *Fruit a schizocarp with segments elastically dehiscent from a persistent central column*, or a drupe; seeds with or without an aril.

***Floral formula***:

Staminate: \* , K 4-8 , C 0 , A 2-many , G 0

[Put a dashed line around the 2-many stamens; replace “many” with infinity symbol]

Carpellate: \* , K 4-8 , C 0 , A 0 , G 3 ; schizocarp

[Circle the 3 carpels]

***Distribution***: Pantropical.

***Genera/species***: 25/96. ***Major genera***: *Austrobuxus* (22 spp.), *Pseudanthus* (9), and *Aristogeitonia* (7). Three species of *Tetracoccus* occur in the United States (southern California). In addition, *Picrodendron* is native just to the south of the United States, in the Bahamas and Greater Antilles.

***Economic plants and products***: *Androstachys johnsonii* (Lebombo-ironwood) produces valuable, hard and durable timber, and *Picrodendron baccatum* (black-ironwood) is used as an ornamental (in windbreak hedges). A few genera, including *Tetracoccus*, are medicinal.

***Discussion***: The monophyly of Picrodendraceae is supported by DNA sequences and pollen morphology (Grimsson et al. 2019; Hayden et al. 1984; Soltis et al. 2011; Wurdack and Davis 2009; Wurdack et al. 2004; Xi et al. 2012). The familial clade is comprised of three major subclades: tribe Podocalyceae (only *Podocalyx* *loranthoides*; stomata anomocytic, vs. paracytic in the other subclades), Caletieae (e.g., *Austrobuxus*, *Dissiliaria*, *Petalostigma*, and *Pseudanthus*), and Picrodendreae (e.g., *Aristogeitonia*, *Oldfieldia*, *Picrodendron*, and *Tetracoccus*). The family was traditionally considered within Euphorbiaceae, as the subfamily Oldfieldioideae (Webster 2014).

 The small flowers of many Picrodendraceae are pollinated by generalized insect visitors. Those with schizocarpic fruits are ballistically dispersed, while those with drupes are probably bird dispersed.

***Additional references***: Sutter et al. 2006.

**Podostemaceae** Kunth

(Riverweed Family)

**Herbs of fast-flowing water** (*as in rapids or waterfall*), *of bizarre form and often resembling lichens, mosses, or seaweeds*; **plant body ± thalloid, with roots, stems, and leaves often not obvious**; sometimes with xanthones, often with laticifers; **silica bodies abundant in epidermis and associated tissues**; **vascular system very reduced**; **cuticular waxes absent**. **Roots photosynthetic**, *creeping to ± floating, thread-like, ribbon-like, or flattened and crustose or foliose*, **attached to substrate by adhesive hairs** (which secrete a polysaccharide super-glue associated with cyanobacteria); the root apical meristem radial and with a root cap, or highly modified and bilateral with a dorsiventral root cap, or root cap lacking, and sometimes meristem linear-elongate and appearing like fasciation. **Stems** (*and often also flowers*) **arising endogenously within the roots**, reduced or elongate, simple or branched (and then not from leaf axils), prostrate or erect, **attached to substrate by hapters** (**disklike holdfasts**), and with or without an apical meristem. Hairs simple, and prickles occasionally present. *Leaves present or absent*, *extremely variable in size and form*, sometimes heterophyllous, alternate and spiral or 2-ranked, opposite or whorled, simple or compound, often repeatedly forked, entire, toothed, lobed, or dissected, with venation obscure or lacking, with or without stomata, the leaf base ± sheathing and sometimes with stipule-like appendages. Inflorescences ± determinate, sometimes reduced to a solitary flower, terminal, or in sheath pockets, or arising from endogenous buds. *Flowers bisexual, radial or bilateral*, conspicuous or inconspicuous, sessile or pedicellate; *the flower or group of flowers often surrounded by a cup or enclosed in a tubular covering*. **Perianth not differentiated, of tepals**, *these 2-numerous*, but sometimes vestigial or absent, *distinct to connate*, usually imbricate, *and sepal-like or petal-like*. *Stamens 1 to numerous*; filaments distinct or basally connate; pollen grains tricolporate, tricolpate to pentacolpate, or pantoporate, sometimes in dyads. *Carpels 2 or 3, connate; ovary superior*, with axile or free-central placentation; styles usually 2 or 3, or these fused with long branches; stigmas 1-3, variable, often elongate. Ovules 2 to numerous per locule, with thin-walled megasporangium; **female gametophyte tetranucleate** (*Apinagia* type) **and protruding through the micropyle**; **double fertilization absent, the polar nucleus degenerating without being fertilized**; **endosperm absent**. Nectary absent. *Fruit a septicidal capsule*, **ribbed** or not. *Seeds tiny, often with a mucilaginous testa*; *germinating embryo often without a radicle* (primary root), *then all roots adventitious*; the embryonic shoot (plumule) also sometimes reduced or absent.

***Floral formula***: \* or X , T -2-many- , A 1-many , G 2-3 ; capsule

[Put a dashed line around 2-many tepals; put a dashed line around 1-many stamens; replace word many with infinity symbol; circle the 2-3 carpels]

***Distribution and ecology***: Pantropical, with temperate extensions in eastern North America and eastern Asia. Plants of rapidly flowing water of rapids or waterfall, usually in sunny places and oligotrophic waters. Flowering occurs when the water level drops.

***Genera/species***: 54/300. ***Major genera***: *Apinagia* (50 spp.), *Ledermanniella* (26), *Hydrobryum* (23), and *Rhyncholacis* (23). Only *Podostemum ceratophyllum* is native to the eastern United States and Canada.

***Economic plants and products***: Species of *Dicraeanthus*, *Macropodiella*, *Marathrum*, and *Thelethylax* are eaten. The leaves of *Rhyncholais* are used as a pepper-like spice (Cook and Rutishauser 2007). Several genera are used medicinally. These plants are ecologically significant, maintaining fish populations.

***Discussion***: The monophyly of Podostemaceae is strongly supported by both DNA sequences (along with a 49,000 BP inversion in the large single copy region of the chloroplast genome) (Kita and Kato 2001; Koi et al. 2012, 2015; Sun et al. 2016) and their strange morphology (Cook and Rutishauser 2007; Rutishauser 1997; Stevens 2001 onward; see also description). Subfamily Tristichoideae are sister to the Weddellinoideae + Podostemoideae clade (supported by the 2-carpellate gynoecium and the loss of a primary root). Morphologically, Tristichoideae (7 genera, with *Terniopsis* + *Cussetia* sister to rest) are quite plesiomorphic, e.g., having radial root apical meristems and root caps, having shoot apical meristems, scale-like leaves, and primary roots producing shoots. Their monophyly is supported by the putative synapomorphies of pantoporate pollen and flowers with a perianth of three connate tepals. Weddellinoideae (only the genus *Weddellina*) are supported by their solitary terminal flowers, and gynoecium with a single globose stigma. Finally, the largest subfamily, Podostemoideae (48 genera, with *Diamantina* sister to the rest) are the most specialized; their putative synapomorphies include root apical meristems bilateral and root cap highly modified or absent, the loss of a stem apical meristem, the loss of stomata, an embryo with the plumule reduced or lacking, epidermal cells with dimorphic chloroplasts, flowers enveloped by a tubular structure, bilaterally symmetrical flowers, and pollen 3- or 5-colpate (see Cook and Rutishauser 2007; Stevens 2001 onward; Tippery et al. 2011). The unusual morphology of these plants has led to many problems of specific and generic delimitation. Many species are local endemics, and thus are endangered.

Most species of Podostemaceae have inconspicuous flowers what are wind pollinated or selfing (when submerged), but some, e.g., *Apinagia*, *Mourera*, and *Weddellina*, have showy, insect pollinated flowers. The minute seeds are probably water and/or wind dispersed.

***Additional reference***: Jäger-Zürn and Grubert 2000; Koi et al., 2022.

**Putranjivaceae** Meisner

(Childlife-tree Family)

*Trees or shrubs*, **with glucosinolates** (**mustard oil glucosides**), sesquiterpene lactones, and curcurbitacins (triterpenes). Hairs simple or stellate. *Leaves usually alternate and 2-ranked or spiral*, simple, entire to variously toothed, with pinnate venation; *stipules present*. Inflorescences determinate (*usually fasciculate*), axillary or cauliflorous, sometimes reduced to a solitary flower. *Flowers usually unisexual* (*and plants usually dioecious*), radial. *Sepals* (appearing as tepals) *usually 4-5*, *distinct*, usually imbricate. **Petals lacking**. *Stamens* (2-) *3 to numerous*; filaments distinct; pollen grains tricolporate. *Carpels 1-3* (-9), connate, occasionally on a short gynophore; ovary superior, with axile placentation; styles as many as the carpels; **stigmas large***, ± peltate, kidney-shaped, disk-like, bilobed or petal-like*. *Ovules 2 per locule*; **megaspore mother cells 2 or 3**. Nectar disk present or absent. **Fruit a drupe**; **seeds with testa vascularized**.

***Floral formula***:

Staminate: \* , K 4-5 , C 0 , A 2-many , G 0

[Replace many with infinity symbol]

Carpellate: \* , K 4-5 . C 0 , A 0 , G 1-3 ; drupe

[Circle the 1-3 carpels]

***Distribution***: Pantropical, with warm temperate extensions in Florida and Japan.

***Genera/species***: 2/216. ***Genera***: *Drypetes* (incl. *Sibangea*) (213 spp.) and *Putranjiva* (4). Two species of *Drypetes* occur in the United States (Florida).

***Economic plants and products***: The fruits of a few species of *Drypetes* are eaten, and the seeds of *Putranjiva roxburghii* (childlife-tree) provide oil (for burning). Both genera are occasionally used medicinally. *Putranjiva roxburghii* is often used as an ornamental tree; *Drypetes lateriflora* (Guiana-plum) is occasionally grown as an ornamental in Florida.

***Discussion***: The monophyly of Putranjivaceae is supported by DNA sequences (Chase et al. 2002; Kathriarachchi et al. 2005; Soltis et al. 2011; Sun et al. 2016; Wurdack and Davis 2009; Wurdack et al. 2004) and phenotypic characters, especially the presence of glucosinolates (Levin 2014; Matthews and Endress 2013; Rodman et al. 1998; Stevens 2001 onward; Tokuoka and Tobe 1999; see also description). It is noteworthy that glucosinolates have evolved twice within angiosperms – in the stem lineage of Brassicales and in the stem lineage of Putranjivaceae (Rodman et al. 1998). *Putranjiva* (disk absent, stamens 2 or 3) is sister to *Drypetes* (disk present, stamens usually 4 to many). Phylogenetic relationships within *Drypetes* require more study; the species of sect. *Drypetes* have single-carpelled gynoecia, while those of sects. *Oligandrae* and *Sphragidia* have syncarpous gynoecia (of 2 or 3 carpels). Traditionally *Drypetes* and *Putranjiva* were placed in Euphorbiaceae subfam. Phyllanthoideae, as tribe Drypeteae (Webster 1967, 1994a, b).

 The inconspicuous flowers are pollinated by insects. The red, orange, yellow, white, or brown drupes are usually bird dispersed. The leaves of *Drypetes diversifolia* are entire-margined as adults, but strongly spinose-serrate in seedlings and juvenile shoots.

**Rafflesiaceae** Dumortier

(Corpse-flower Family)

**Stem or root parasites on *Tetrastigma* (Vitaceae), with the vegetative body living inside the host** (i.e., endophytic) **and consisting of undifferentiated, uniseriate to multiseriate, filament-like clusters of cells; chlorophyll absent and chloroplasts perhaps lost. Roots, stems, and leaves lacking**. Inflorescences initiated as an obovoid cluster of cells, **eventually erupting from the surface of the host, and producing several scale-like bracts and a single flower**. *Flowers usually unisexual* (and plants monoecious) but occasionally with bisexual flowers along with unicellular ones in *Rhizanthes*, radial, **medium-sized to gigantic, producing an odor of rotting flesh**. Tepals in 2 whorls, **both petaloid**, imbricate or valvate, *the outer whorl of 5 or 8 parts*, these ± distinct in *Rhizanthes* and *Sapria* but basally connate in *Rafflesia*, and also adnate to the inner whorl, *the inner whorl of 5 or 8 parts*, these ± distinct in *Rhizanthes* and *Sapria*, but completely connate in *Rafflesia*, *distally forming a diaphragm* (with a central opening, into the floral chamber) *and proximally fused to outer perianth whorl*; **novel ring structure present**, *this short in* *Rafflesia*, *but elongated and forming a hypanthium-like structure*, internally ribbed or not, *to which the perianth parts are attached in* *Rhizanthes* and *Sapria*, and in *Sapria* *also forming a diaphragm*, while in *Rhizanthes* *also forming worm-like appendages*. *Perianth and/or ring structure often with branched or club-shaped hairs* (ramenta; possibly odor producing). **Androecium and gynoecium adnate, forming a gynostemium**. **Stamens numerous, adnate to a central column** (*pistillode, ridged or not*); **anthers sessile, opening by 1 or 2 pores, and borne on the lower side of a disk-shaped structure** (part of the pistillode); **pollen grains without apertures**. *Carpels 4-8* (possibly more), difficult to distinguish, connate, **lacking distinct carpel primordia**, **and ovary locules initiating by splitting of tissue** (i.e., schizogenous); **ovary ± inferior**, **the locules irregular**, **placentation parietal, with ovules scattered on the locules**; style 1, **distally forming an expanded, disk-like structure**; *stigmas in a ring around the underside rim of the disk-like structure*; apical portion of disk-like structure with conical structures. **Ovules numerous per carpel**. **Fruit berry-like but splitting irregularly**, *with slimy pulp*; **seeds with testa not fully surrounding embryo; the embryo undifferentiated**.

***Floral formula***:

Staminate: \* , T -5 or 8 + 5 or 8- , A many , G 4-8**.**

[Among perianth parts put a dashed line around the second 5; above the formula draw a line connecting the many stamens and 4-8 sterile carpels; replace “many” with infinity symbol; draw a line above the 4-8 sterile carpels, and circle the 4-8 sterile carpels; also connect the outer and inner perianth parts by a line below the formula]

Carpellate: \* , T -5 or 8 + 5 or 8- , A many**.** , G 4-8 ; berry-like

Among perianth parts put a dash dashed line around the second 5; replace “many” with infinity symbol; draw a line above the formula connecting the many staminodes and the 4-8 carpels; draw a line above the 4-8 carpels; and circle the 4-8 carpels; also connect the outer and inner perianth parts by a line below the formula]

***Distribution and ecology***: Southern China, Assam, Bhutan, Thailand, and western Malesia. Currently only parasites on *Tetrastigma* (Vitaceae).

***Genus/species***: 3/26. ***Genera***: *Rafflesia* (22 spp.), *Sapria* (3), and *Rhizanthes* (2). Absent from North America.

***Economic plants and products***: In a few regions *Rafflesia* (corpse-flower) is economically important as a tourist attraction, due to its beautiful, fetid, and gigantic flowers (in *R. arnoldii* up to a meter in diameter, and the largest among the flowering plants!).

***Discussion***: The monophyly of the Rafflesiaceae is supported by both its extremely divergent morphology (Nikolov and Davis 2017; Nikolov et al. 2014; Stevens 2001 onward) and its equally strange DNA sequences (Bendiksby et al. 2010; Davis et al. 2007; Xi et al. 2013). All species of Rafflesiaceae parasitize only *Tetrastigma* (Vitaceae) and interestingly there has been extensive horizontal gene transfer (of both mitochondrial and nuclear genes) from this host into the parasite. The horizontally transferred genes even include some “ghost” sequences that entered the stem lineage of Rafflesiaceae from long-extinct, non-Vitaceae hosts (Xi et al. 2013). The outgroups (Euphorbiaceae) have very small flowers, and the floral gigantism of Rafflesiaceae may relate to selection pressure relating to carrion fly pollination or the parasitic habit. Morphological characters appear to be quite homoplasious, e.g., the distinctive floral chamber and diaphragm have evolved independently in *Rafflesia* and *Sapria*, which have flowers that are developmentally quite different (although morphologically convergent).

The phylogenetic position of Rafflesiaceae may make Euphorbiaceae slightly non-monophyletic, since Euphorbiaceae subfam. Peroideae probably are sister to a Rafflesiaceae + rest of Euphorbiaceae clade. Peroideae have distinctive fruits with membranous, fragile, and non-vascularized septa, and they are often recognized as a distinct family (Periaceae; see APG IV 2016). Traditionally Rafflesiaceae included six additional genera (Meijer 1993; see also discussion in Nickrent 2020), all parasitic, but these have been segregated on the basis of molecular analyses and are actually related to diverse eudicot clades; these are *Bdallophyton* and *Cytinus* (of the Cytinaceae, in the Malvales), *Mitrastemma* (of the Mitrastemonaceae, in the Ericales), and *Apodanthes*, *Berlinianache*, and *Pilostyles* (of the Apodanthaceae in the Cucurbitales). Their traditional placement resulted from convergent morphological similarities related to the parasitic habit.

The unusual flowers of Rafflesiaceae look and smell like a rotting carcass and attract carrion flies (Beaman et al. 1988; Nikolov and Davis 2017). The fleshy fruits (with their seeds in a slimy pulp) are eaten and dispersed by mammals.

***Additional references***: Kuijt 1969; Meijer 1993.

*Fabales*

**Quillajaceae** D. Don

(Soapbark-tree or Quillay Family)

*Shrubs to trees*, **with triterpenoid saponins**; **styloid crystals in the phloem** (of bark, twigs, leaf veins), but druse crystals also present (in cortex and pith of young stems, spongy mesophyll of leaves). Hairs simple, with minute bumps. *Leaves alternate and spiral*, simple, usually toothed, with pinnate venation; stipules present, on petiole. Inflorescences determinate, terminal. Flowers bisexual and unisexual (staminate) on the same plant, radial, **with a strongly lobed hypanthium** (**and lobe extending to ± midpoint of each sepal**). *Sepals 5, distinct, ± triangular, valvate*. *Petals 5, distinct, imbricate* (*and contorted*), *clawed*. *Stamens 10*, distinct, **with 5 opposite the sepals and borne at apex of nectiferous hypanthium lobe, and 5 opposite the petals and borne near base of ovary in the v-shaped, hypanthial sinus, so appearing below nectary**; filaments slender; pollen grains tricolporate and with 3 pseudocolpi, the **exine striate**. *Carpels 5*, basally connate **and deeply longitudinally grooved/separated**; ovary superior, **with parietal placentation**; *styles as many as the carpels; stigmas decurrent*. Ovules several in each carpel, in 2 marginal rows; carpellodes in staminate flower. **Inner surface of strongly lobate hypanthium producing nectar**. **Fruit a strongly lobed capsule** (but appearing as a whorl of follicles), **dehiscent along the entirety of each lobe** (i.e., ventrally and dorsally). **Seeds winged**.

***Floral formula***: \* K 5 , C 5 , A 5 + 5 , G 5 , lobate capsule

[Draw a line connecting K+C+A below numbers, indicating a hypanthium]

***Distribution***: Temperate South America.

***Genera/species***: 1/2. ***Genus***: *Quillaja* (2 spp.).

***Economic plants and products***: Saponins (extracted from the inner bark) are used in soaps, shampoos, cosmetics, and as an emulsifier in fire extinguishers. The triterpenoid saponins are immunoadjuvant and used in the manufacture of vaccines. The wood is a timber source. Finally, *Quillaja saponaria* (soapbark tree, quillay) is sometimes cultivated, especially in California, and makes a beautiful, drought tolerant street tree.

***Discussion***: The monophyly of Quillajaceae is strongly supported by morphology (see description; Kubitzki 2007e; Lersten and Horner 2005; Stevens 2001 onward). Traditionally, *Quillaja* has been placed in Rosaceae (Robertson 1974) and considered to be related to *Kageneckia*, which has follicle fruits and winged seeds. Molecular data, however, clearly place *Quillaja* in Fabales (APG IV 2016), and its carpels are actually connate (but deeply lobed), not distinct as in *Kageneckia*.

Interestingly, *Dakotanthus*, a Cretaceous fossil from western North America, may be related (Manchester et al. 2018c). Its flowers are similar, also showing the unusual, lobed nectar-disk and dimorphic positioning of the two staminal whorls. The carpels are connate, however, the fruit is an unlobed capsule with axile placentation. Thus, Quillajaceae may once have had a much broader geographical distribution.

Flowers of *Quillaja* attract a wide variety of insect pollinators (Díaz-Forestier et al. 2009); their seeds are wind dispersed.

***Additional references***: Bello et al. 2007; Luebert 2013.

**Surianaceae** Arnott

(Bay-cedar Family)

*Shrubs or trees*; with tannins, triterpenoid diol (surianol), and sclereids. Hairs simple, non-glandular or gland-headed. *Leaves alternate, spiral or 2-ranked*, *simple or occasionally pinnately compound, entire*, with pinnate venation, with stomata on both surfaces or only on abaxial surface, rarely with nectaries on midrib or petiole; stipules present or absent, occasionally with colleters. Inflorescences determinate, terminal or axillary, sometimes reduced to a solitary flower. *Flowers usually bisexual, radial*. *Sepals* *usually 5*, distinct or basally connate. *Petals 5*, but absent in *Stylobasium*, *distinct*, imbricate, sometimes shortly clawed*. Stamens 10, or only 5 and then with 5 or fewer staminodes*; filaments distinct; pollen grains tricolporate. *Carpels 1-5*, **distinct**; *ovary superior*, **with basal placentation**, borne on receptacle, or (in *Recchia*) on a gynophore; **each carpel with a gynobasic style**; stigmas capitate or club-shaped. **Ovules 1-5 per carpel, surrounded by mucilage**, anatropous to campylotropous, **with 1 integument**. **Nectary usually absent**, but with a nectariferous gynophore in *Recchia*. **Fruit indehiscent**, *a nut, drupe, or berry, solitary or clustered* (then an aggregate fruit); seeds with embryo curved or folded; endosperm ± lacking.

***Floral formula***: \* , K 5 , C 5 , A 5-10 , G 1-5 ; drupes, nuts ,berries

***Distribution and ecology***: Pantropical, but most diverse in Australia and Mexico; *Suriana* is characteristic of coastal habitats.

***Genera/species***: 5/8. ***Major genera***: *Recchia* (3 spp.) and *Stylobasium* (2). *Suriana maritima* is native to the United States (Florida).

***Economic plants and products***: *Suriana maritima* (bay-cedar) is used medicinally and as an ornamental, especially in coastal regions where salt-tolerance is desirable.

***Discussion***: The monophyly of Surianaceae is supported by morphology (see description; Bello et al. 2007; Schneider 2007; Stevens 2001 onward) and DNA sequences (Bello et al. 2009; Crayn et al. 1995; Forest et al. 2007). The *Recchia* + *Cadellia* clade is sister to a clade comprised of *Suriana*, *Guilfoylia*, and *Stylobasium*. The gynobasic styles have led some botanists (see Brizicky 1962) to place the family in the Simaroubaceae, although in that family the style is a united structure (i.e., the gynoecium is syncarpous, although the ovaries are distinct) while in Surianaceae the carpels are distinct and each has its own style.

 The showy flowers with white, yellow, or orange petals are insect pollinated, except for *Stylobasium*, which lacks petals, has inconspicuous flowers, and may be wind pollinated. The nuts of *Suriana* float, and are dispersed by ocean currents. Species with drupes probably are bird dispersed.

*Rosales*

**Elaeagnaceae** A. L. de Jussieu

(Oleaster Family)

*Trees, shrubs*, or occasionally lianas, *often with thorns*; **with nitrogen-fixing bacteria** *(Frankia)* **in root nodules***;* with tannins; wood with **phloem stratified into hard and soft layers, vessels with vestured** or non-vestured **pits**; **nodes unilacunar**. **Stems, leaves and hypanthium/calyx covered with silver, gold, and/or copper-colored, stellate hairs and/or peltate scales.** Leaves alternate and spiral or opposite and decussate, *simple*, **entire**, *with pinnate venation*; stipules absent. Inflorescences indeterminate, sometimes reduced to a single flower; axillary. Flowers bisexual or unisexual (and plants then usually monoecious or dioecious), *radial, with a* **petaloid***, ± tubular and distally flaring hypanthium, constricted above the ovary.* Sepals usually 4, distinct (but appearing connate due to their attachment to petaloid hypanthium), valvate, **usually ± petaloid. Petals absent**. *Stamens 4 or 8*, distinct, alternating with the sepals(when 4) or alternating and opposing the sepals (when 8), inserted on hypanthium; pollen grains usually tricolporate. **Carpel 1, but probably pseudomonomerous;** ovary superior, with basal placentation; stigmas decurrent or capitate; style 1, elongate. Nectar produced by a disk or lobes on inner surface of hypanthium, or absent. **Fruit an achene, surrounded by ± fleshy, persistent lower portion of hypanthium** (i.e., portion below constriction) *and fruit thus appearing drupe-like*; endosperm reduced or absent.

***Floral formula***: \* K 4 , C 0 , A 4-8 , G 1 , achene (surrounded by fleshy hypanthium)

[Draw a line connecting K, C, and A to indicate the hypanthium.]

***Distribution and ecology***: Widely distributed in temperate North America, Europe and Asia, and extending south into tropical Southeast Asia and Australia. Many grow in prairie habitats, but others are plants of temperate to tropical forests. These plants are able to fix atmospheric nitrogen through the action of *Frankia* (an actinomycete bacterium).

***Genera/species***: 3/55. ***Major genus***: *Elaeagnus* (45 spp.). *Shepherdia* and *Elaeagnus* occur in the continental United States and Canada, the latter genus with both native and naturalized species.

***Economic plants and products***: Fruits of the sea-buckthorn (*Hippophae rhamnoides*), Russian olive or oleaster (*Elaeagnus angustifolia*), and buffaloberry (*Shepherdia argentea*) are eaten (used in jams, in drinks). Several species are used as ornamentals because of their golden or silvery foliage.

***Discussion***: The monophyly of Elaeagnaceae is supported by both morphology (see description; Bartish and Swenson 2004; Gardner 1958; Stevens 2001 and ongoing) and DNA sequences (Richardson et al., 2000b; Soltis et al. 2000; Sun et al. 2016; Zhang et al. 2011). *Elaeagnus* (polygamous to monoecious) is supported as the sister group to the *Shepherdia* + *Hippophae* clade (dioecious).

The fragrant flowers of *Elaeagnus* and *Shepherdia* are pollinated by various insects, but those of *Hippophae* are wind pollinated. The achenes, with their colorful, fleshy accrescent hypanthium, are taken and dispersed by birds. The fruits of *Hippophae* dry out during the winter and also can be carried by spring floods.

***Additional reference***: Graham 1964.

*Cucurbitales*

**Coriariaceae** de Candolle

(Tanner-bush Family)

*Shrubs, sometimes scandent, to suffrutescent herbs*; stems sharply quadrangular; **roots** **with nitrogen-fixing bacteria** (*Frankia*) **in nodules**; with ellagic and gallic acids, tannins, sesquiterpenes, and **with coriolic fatty acid** (in seeds). Hairs scale-like (trichomoids) at nodes, otherwise simple. *Leaves opposite and decussate*, sometimes appearing 2-ranked, or 3-whorled, *simple, entire, with palmate venation*; *petioles very short*; stipules present, minute; *with the leaves and stem together often appearing like an elongated compound leaf*. Inflorescences indeterminate (*racemes*), axillary or terminal. Flowers bisexual or bisexual and staminate on the same plant, *radial*. *Sepals 5, distinct*, imbricate (quincuncial). *Petals 5, distinct*, **with open aestivation or valvate**, *smaller than sepals at anthesis*, **but enlarging and becoming fleshy in fruit**, *often keeled adaxially*. *Stamens 10, distinct*; filaments free or those opposite a petal adnate to its keel; **anther with septum between sporangia of theca not developed**; pollen grains tricolporate, with the furrows short. *Carpels usually 5,* connate, *but appearing ± distinct* (**due to ovary bulging**); *ovary superior* with ± apical placentation, *with 1 ovule per locule*, *with each carpel having its own somewhat gynobasic style*; **stigma extending all around style and for most of its length**. Nectary absent. **Fruit a cluster of achenes or nutlets, surrounded by fleshy, red, orange, or purple-black, accrescent corolla**. **Seeds with outer layer of testa with cuboidal, thick-walled, tannin-filled cells**.

***Floral formula***: \* K 5 , C 5 , A 10 , G 5 ; achenes

[Circle the 5 carpels; draw a dashed line connecting stamens to petals]

***Distribution and ecology***: Highly disjunct, occurring in Mexico to southern South America, the Mediterranean, eastern and southern Asia, to New Guinea, New Zealand, and Pacific islands. Many species occur on disturbed or early successional habitats.

***Genera/species***: 1/ ca. 17. ***Genus***: *Coriaria* (17). None are native to the continental United States or Canada.

***Economic plants and products***: *Coriaria myrtifolia* (tanner-bush) his used for tanning leather. The species are highly poisonous.

***Discussion***: Coriariaceae are sister to Corynocarpaceae (within Cucurbitales), and the two represent an early divergent branch within the order, sharing the putative synapomorphies of entire margined leaves, flowers with a superior ovary, and one ovule per locule (Stevens 2001 onward). They differ from the core Cucurbitales (i.e., Begoniaceae, Cucurbitaceae, Datiscaceae), which have stems with separate vascular bundles (vs. a ring of xylem and phloem in Coriariaceae and Corynocarpaceae), leaf margin with cucurbitoid teeth (vs. margin entire), an inferior ovary (vs. superior ovary) with parietal placentation and numerous ovules per carpel (vs. apical placentation and only one ovule per carpel), and unisexual flowers (vs. often bisexual flowers). All these families share the putative apomorphy of palmately veined leaves.

 The monophyly of Coriariaceae is supported by both morphology (see description; Kubitzki 2011; Stevens 2001 onward) and DNA nucleotide sequences (Yokoyama et al. 2000; Renner et al. 2020). Phylogenetic analyses support the recognition of two major subclades within *Coriaria*: a Southern Hemisphere clade (leaves deciduous, plants andromonoecious, i.e., staminate and perfect flowers on same plant) with species such as *C. ruscifolia*, *C. microphylla* (from the Americas), *C. arborea, C. pteridoides*, and *C. sarmentosa* (and others, native to New Zealand), and *C. papuana* (New Guinea), and a Northern Hemisphere clade (evergreen leaves, perfect flowers), with species such as *C. japonica* (Japan), *C. terminalis*, *C. nepalensis,* and *C. sinica* (eastern Asia), and *C. myrtifolia* (Mediterranean region).

 The family often has been considered to be evolutionarily isolated and of problematic taxonomic position, with traditional placements near Ochnaceae, Malpighiaceae, or Sapindales (Good 1930), placements like reflecting the strongly lobed ovary of Coriariaceae. Cronquist (1981) placed the family in his Ranunculales.

 The flowers of *Coriaria* are wind pollinated, and the colorful (red, orange, purple-black) fruits with an accrescent, fleshy corolla, are mainly bird dispersed.

**Datiscaceae** Dumortier

(Durango-root Family)

*Herbs*; stems with medullary vascular bundles; **roots with N-fixing bacteria (*Frankia*) in nodules**. Hairs simple, often gland-headed. *Leaves alternate and spiral, pinnately compound to deeply divided*, but becoming simple and lobed to unlobed distally on shoots, dentate to serrate, *with pinnate venation*; stipules lacking. Inflorescences determinate, terminal or terminal and axillary. *Flowers unisexual* (*and* *plants dioecious*), or occasionally unisexual and bisexual (and plants androdioecious, i.e., with some plants with staminate flowers and others with staminate and bisexual flowers), radial. **Tepals** (actually sepals, **with petals absent**), *3-10, distinct or basally connate*, *inconspicuous*, valvate. *Stamens 6 to numerous in staminate flowers*, but (2-) 3-5 in bisexual flowers; **filaments** *distinct*, **very short**; *anthers ± elongate*; pollen grains tricolporate. *Carpels 3-5, connate; ovary inferior*, *ribbed*, *with parietal placentation*; *styles equaling number of carpels, each deeply bifid*; *stigmas elongate*, with multicellular papillae. Ovules numerous on each placenta; **female gametophyte bisporic, 8-nucleate** (*Allium* type). Nectaries absent. *Fruit a capsule, opening apically*. Seeds with a cap (operculate); endosperm scanty or lacking.

***Floral formula***:

Staminate: \* , T -3-10- , A 6-many , G 0

[replace “many” with infinity symbol]

Carpellate: \* , T -3-8- , A 0 , G 3-5 ; capsule

[Circle the 3-5 carpels, and draw a line above the circle]

Bisexual: \* , T -3-8- , A 3-5 , G 3-5 ; capsule

[Circle the 3-5 carpels, and draw a line above the circle]

***Distribution***: Western North America, and Crete to India.

***Genera/species***: 1/2. ***Genus***: *Datisca* (2 spp.). *Datisca* is native in the western United States.

***Economic plants and products***: *Datisca cannabina* (bastard-hemp) has been used as a dye plant; *D*. *glomerata* (Durango-root) is toxic and causes livestock poisoning.

***Discussion***: The monophyly of Datiscaceae is supported by morphology (see description; Stevens 2001 onward; Swensen and Kubitzki 2010) and DNA sequences (Liston et al. 1992; Schaefer and Renner 2011; Swensen et al. 1998). The large trees *Octomeles* and *Tetrameles* were once included in Datiscaceae, but DNA sequence data has shown that they belong in their own (although related) family: Tetramelaceae (Savolainen et al. 2000b; Schaefer and Renner 2011; Swensen et al. 1994, 1998).

The inconspicuous flowers are wind pollinated, and the small seeds likely are dispersed by wind or rain-wash.

*Fagales*

**Nothofagaceae** Kuprianova

(Southern Beech Family)

*Trees or shrubs*; tannins present; bark sometimes with horizontal lenticels; **the buds protected by stipules**. Hairs simple, eglandular, **and peltate gland-headed**. *Leaves alternate and 2-ranked or spiral, simple, variously toothed, doubly toothed*, or entire, *with pinnate venation*; stipules present and attached at their base *or peltate,* and associated with colleters. Inflorescences determinate, *in small, often 3-flowered cymes*, but these sometimes reduced to 1 or 2 flowers (or rarely with more numerous flowers), axillary, *the staminate and carpellate flowers in different inflorescences*. *Flowers unisexual (plants monoecious)*, radial, inconspicuous. Staminate flowers with perianth of usually 3-5 and most commonly 4 tepals, these inconspicuous, connate and forming a narrowly campanulate to tubular structure (and the tepal number sometimes obscure at maturity), and 4-20 stamens, with their filaments distinct to connate, but in subg. *Lephozonia* the 3 flowers of the cyme closely associated and forming a false-flower (i.e., appearing to be a single flower) with a 6-14-lobed, broadly campanulate perianth, and 15-90 stamens; pollen grains 3-10-colpate, with short colpi and these usually with raised margins. Carpellate flowers usually (1-) 3-7 per reduced cyme **and associated with a 1- to 4-valved cupule**, *each valve variously ornamented,* i.e., with stalked, glandular appendages, or horizontal flaps/ridges (lamellae), and with simple, non-glandular hairs or glabrous, **and possibly derived from stipules or bracts**, with perianth reduced to a mere rim (derived from 4 or fewer tepals), often with staminodes, *and with 2-3 carpels*, these connate, *the ovary inferior*, with axile placentation, the stigmas separate, decurrent along upper side of each style. Ovules 2 per locule, but all except 1 aborting, with a single integument. Nectaries lacking. *Fruit* **a triangular or ± flattened** *nut*, **usually ± winged, usually associated with a 2- or 4-valved cupule** (but lost in *N. resinosa*); endosperm lacking.

***Floral formula***:

Staminate: \* T -3-14- , A 4-90 , G 0

Carpellate: \* T -4- , A 0 , G 2-3 , nut (with cupule)

[Put a circle around the 3-14 tepals of staminate flower, also put a dashed line around the 4-90 stamens; put a circle around the 4 tepals of carpellate flower, and circle the 2-3 carpels, and draw a line above this circle, indicating that the ovary is inferior.]

***Distribution***: Temperate to tropical; southern South America, New Guinea to eastern and southern Australia, Tasmania, New Zealand, and New Caledonia; once much more widespread in Australia, and also in Antarctica (based on fossils). *Nothofagus* *antarctica* is the southernmost tree species in the world, growing as far south as Hoste Island, Chile. The biogeographical history of the extant clades within *Nothofagus* reveals a mixture of vicariance to explain trans-Antarctic disjunctions in subgenera *Lophozonia* and *Fuscospora*, and dispersal from Australia to New Zealand to explain secondary disjunctions.

***Genera/species***: 1/43. ***Genus***: *Nothofagus* (43 spp.). The genus does not occur in North America.

***Economic plants and products***: Some species of *Nothofagus* (southern beech, roble) provide valuable timber. A few are used as ornamental trees.

***Discussion***: The monophyly of Nothofagaceae is well supported by morphology (Heenan and Smissen 2013; Manos 1997) and DNA nucleotide sequences (Cook and Crisp 2005; Manos 1997; Martin and Dowd 1993; Sauquet et al. 2012; Setoguchi et al. 1997; Xiang et al. 2014; Yang et al. 2021). These analyses also indicate that *Nothofagus* is comprised of four subclades, usually recognized as subgenera (but occasionally as genera). Subgenus *Lophozonia* is sister to the remaining groups and shows the putative apomorphies of cupule valves unicellular-pubescent and the staminate flowers actually being false-flowers, resulting from the developmental fusion of the three flowers of the cyme, and having a broadly campanulate perianth of 6-14 lobes and usually more than 20 stamens (Rozefelds and Drinnan 1998). This section also has stalked, glandular appendages on the cupular valves, and lacks the horizontal flaps/ridges found on the valves in the remaining subgenera (i.e., subg. *Fuscospora*, *Brassospora*, *Nothofagus*). Subgenus *Fuscospora* likely diverged next, and its monophyly is supported by details of hair morphology and pollen form (pollen apertures with heavy thickening). Subgenus *Brassospora* and *Nothofagus* form a clade (stipule attachment peltate); the former is supported by conduplicate leaf vernation, a tubular perianth in the staminate flowers, connate filaments, and cupule valves glabrous, only 2 valves per cupule, and associated with usually three, 2-carpellate flowers, and the latter by stomata parallel to the leaf midrib. Additionally, pollen characters are quite useful in distinguishing the four subgenera (Fernández et al. 2016; Heenan and Smissen 2013; Manos 1997). The phenetic analysis of Hill and Read (1991), based on leaf morphology and anatomy and cupule characteristics, recovered a similar taxonomic pattern. *Nothofagus* has often been considered to be closely related to *Fagus* (beech) and placed in Fagaceae (Cronquist 1981; Kubitzki 1993), however phylogenetic analyses (see those cited in Fagales introduction) support its placement in Nothofagaceae, as sister to the other families within Fagales. The family also differs from Fagaceae in its wood anatomy (e.g., wood with radial multiples of vessels, narrow heterocellular rays) (Wheeler et al. 2022).

 The reduced flowers are wind pollinated, and the small nuts are wind dispersed. Hybridization often occurs among closely related species.

 ***Additional references***: Hill et al. 2015; Knapp et al. 2005; Philipson and Philipson 1979; Ramirez 1987; Veblen 1996.

**Ticodendraceae** Gómez-Laurito & P. Gómez

(Tico-tree Family)

*Trees*, probably with tannins; bark smooth to roughened, not exfoliating in thin layers. **Hairs T-shaped, not glandular**. *Leaves alternate, 2-ranked, simple, serrate, with pinnate venation, the secondary veins each running into a tooth*; **the blade with hypodermal idioblasts** (these sometimes with druses); *stipules present*, *large*, **enclosing stem**. Inflorescences determinate, axillary, *the staminate flowers in compact cymes, in trimerous whorls, along a spike-like inflorescence* (and rarely this terminated by a carpellate flower), and **the carpellate flowers solitary** (*in leaf axils*) *and associated with 3 bracts*, basally fused or not, with evidence of reduction from a 3-flowered cyme. *Flowers unisexual* (*the plants usually dioecious*), *radial*, *inconspicuous*. *Tepals very reduced, forming an inconspicuous rim* and presumably connate. *Stamens usually 8-10*; filaments distinct; pollen grains triporate; a few staminodes sometimes present in carpellate flowers. *Carpels 2, connate; ovary inferior*, with axile placentation, **and with 4 locules, due to secondary division of the locule of each carpel**; *stigmas 2, running the entire length of the styles*. Ovule 1 per locule, all except 1 aborting in each gynoecium, **hemitropous**, with 1 **very thick integument**. Nectary lacking. *Fruit a slightly asymmetric/flattened drupe*, **with longitudinally ridged pit**.

***Floral formula***:

Staminate: \* , T -0- , A 8-10 , G 0

Carpellate: \* , T -rim- , A 0 , G 2 ; drupe

[Circle the 2 carpels; draw a line above the 2]

***Distribution and ecology***: Central America (from southern Mexico to Panama) in moist montane forests or cloud forests.

***Genera/species***: 1/1. ***Genus***: *Ticodendron* (1 sp.). The genus does not occur in the United States or Canada.

***Economic plants and products***: None.

***Discussion***: The monophyly of Ticodendronaceae is supported by DNA-based phylogenetic analyses (see references cited under Fagales) and their distinctive morphological characters (Hammel and Burger 1991; Hickey and Taylor 1991; Kubitzki 1993d; Stevens 2001 onward; Tobe 1991), which also indicate a placement in Fagales. The family now consists only of the single, recently discovered species *Ticodendron incognitum*, but the familial clade was widespread and more diverse early in the Tertiary (Chambers and Poinar 2014; Gómez-Laurito and Gómez 1989, 1991; Manchester 2011). It represents a relic and distinctive lineage of the *Normapolles* complex.

 The flowers of *Ticodendron* are wind pollinated. The drupes may be mammal dispersed.

***Additional reference***: Carlquist 1991.

*Myrtales*

**Vochysiaceae** A. Saint-Hilaire

(Quaruba Family)

*Trees, shrubs or occasionally lianas*, often accumulating aluminum, with tannins, mucilage cells, and sclereids. *Hairs often brown*, simple, T-shaped, or stellate. *Leaves usually opposite and decussate* *or ± 2-ranked*, or whorled, *simple, entire, with pinnate venation*; *stipules usually present, small, often modified and forming colleters-like glands*. Inflorescences determinate, terminal or axillary. **Flowers** *bisexual*, **bilateral or without plane of symmetry**, **hypanthium lost**. *Sepals 5*, basally connate, **usually unequal in size, the largest one with a nectariferous spur**, *borne free on the sepal or adnate to one side of inferior ovary* (rarely lost), the lobes imbricate. *Petals usually 1-5*, distinct, *clawed*, imbricate. **Stamen 1**, in the plane of symmetry, or outside plane of symmetry; **filament straight in bud**; *anther as long as filament*; pollen grains tricolporate; staminodes present or absent. *Carpels usually 3, connate*; ovary superior or inferior, with axile placentation, or when gynoecium pseudomonomerous, lateral or apical placentation; *style 1*; stigma punctate to capitate. Ovules 2 to several per locule (when ovary 3-locular) or 1 or 2 ovules per gynoecium (when ovary pseudomonomerous and unilocular), sometimes with several megagametophytes per ovule. *Fruit a loculicidal capsule, or nutlet associated with accrescent and persistent, wing-like calyx lobes* (a pseudosamara). Seeds often winged and/or hairy; endosperm present or absent.

***Floral formula***: X , K 5 , C 1-5 , A 1 , G 3 ; capsule, nutlet

[Circle the 5 sepals; circle the 3 carpels, draw a line both above and below the 3 carpels]

***Distribution***: Mainly in the Neotropics, but a few in West Africa.

***Genera/species***: 8/220. ***Major genera***: *Vochysia* (140 spp.), *Qualea* (40), *Erisma* (20), and *Ruizterania* (20). The familial clade does not occur in the United States or Canada.

***Economic plants and products***: The seeds of *Erisma calcaratum* (cambará) are a source of oil, and they are also used in making soap, detergent, and candles.

***Discussion***: The monophyly of Vochysiaceae is supported by morphology, especially their unusual flowers (see description; Kawasalo 2007; Litt and Stevenson 2003a, b; Stevens 2001 onward) and DNA sequences (Sytsma et al. 2004). Traditionally, two tribes were recognized within the family Vochysieae (*Callisthene*, *Qualea*, *Ruizterania*, *Salavertia*, and *Vochysia*) and Erismeae (*Erisma*, *Erismadelphus*, and *Karupodendron*). The monophyly of Erismeae is well supported by molecular data, and the clade is also supported by the putative synapomorphies of a unilocular ovary with only one or two ovules, and the nutlet fruits associated with wing-like calyx lobes. In contrast, the monophyly of Vochysieae is problematic, and its genera retain several putative plesiomorphic characters, e.g., a trilocular gynoecium with axile placentation, two to several ovules per locule, and a loculicidal capsule. It is interesting that the ovary is initiated in an inferior position, but in Vochysieae it is superior at maturity (Litt and Stevenson 2003 a); the mature ovary is inferior in Erismeae.

 Traditionally Vochysiaceae were placed close to Polygalaceae (of the Fabales) or Malpighiaceae (of the Malpighiales) (see Cronquist 1981, 1988; Takhtajan 1980, 1997); Its position within Myrtales was not accepted until the advent of molecular data, although placement within this order is also supported by the stems with internal phloem, vessel elements with vestured pits, and carpels completely connate. Surprisingly, the Vochysiaceae has lost the hypanthium and inflexed stamens so characteristic of most other Myrtales.

 The flowers are visited by bees and moths. Their often-winged seeds or pseudosamara fruits are wind dispersed, but a few are water dispersed.

*Crossosomatales*

**Staphyleaceae** Martynov

(Blatternut family)

*Trees or shrubs*, often rhizomatous or producing root-suckers, the trunk sometimes buttressed; with tannins and mucilage cells. Hairs simple. **Leaves opposite and decussate, odd pinnately compound to trifoliolate** (rarely unifoliolate), *leaflets serrate, with pinnate venation*, **the axis usually with bract-like to glandular stipule-like structures near attachment of leaflets**; *stipules present, borne on stem, small and scale-like to expanded and/or elongate and membranous*, *often interpetiolar* and the adjacent pair adnate, sometimes with colleters. Inflorescences determinate, usually terminal, erect to pendulous. *Flowers bisexual, radial*, *with a ± short hypanthium*. *Sepals 5*, distinct to connate, *often petaloid*. *Petals 5*, *distinct*, imbricate (quincuncial). *Stamens 5*; *filaments distinct, ± flattened; anthers sagittate*; pollen grains tricolporate. **Carpels** *usually 2-3*, **connate** or rarely nearly free (*Euscaphis*); *ovary usually superior, with axile placentation*; *styles at least partially free proximally, connate distally, with a single, capitate, often slightly lobed stigma*. Ovules few to several per locule. *Lobed nectar disk on adaxial surface of hypanthium*, intrastaminal or stamens between the lobes. *Fruit ± stalked*, *a globose to 3-lobed berry, inflated and papery, dehiscent or indehiscent, apically 2- or 3-lobed capsule*, and with the fruiting carpels ± apically separating from each other developmentally (and thus lobed), or an aggregate of fleshy, ± red follicles. Seeds round to angular, **with coat many layered (multiplicative)**, hard or rarely with a fleshy outer layer (in *Euscaphis*), and *with a large, distinctive hilum showing the scars of multiple vascular strands*; embryo green, with large cotyledons.

***Floral formula***: \* K 5 , C 5 , A 5 , G 2-3 , berry, papery capsule, cluster of follicles

[Put dashed circles around 5 sepals, and 5 petals, and 2-3 carpels; draw a line below connecting K-C-A to indicate hypanthium]

***Distribution***: Temperate North America to Andean South America, Europe and western Asia, and temperate to tropical Asia, from southern India to eastern Asia and through Malaysia and Indonesia to New Guinea.

***Genera/species***: 4-5/50. ***Major genera***: *Dalrympelea* (25), *Turpinia* (13), and *Staphylea* (10). Only *Staphylea* occurs in continental United States and Canada.

***Economic plants and products***: Several species of *Staphylea* (bladdernut) and *Euscaphis japonica* (Korean sweetheart-tree) are grown as ornamentals because of their showy flowers and interesting fruits. The seeds of *Staphylea* are occasionally used as beads. The seeds of *S. pinnata* are sometimes cracked and the contents eaten.

***Discussion***: Staphyleaceae are a clade within Crossosomatales, an ordinal clade that is recognized largely on the basis of molecular data. Possible morphological synapomorphies of the order include flowers with a hypanthium (which bears a nectary adaxially), a stalked gynoecium, and postgenital connation of the carpels (Matthews and Endress 2005). Staphyleaceae are related to the Stachyuraceae (leaves simple, alternate, and the 4-merous flowers in pendulous racemes, lacking a hypanthium) and Crossosomataceae (leaves simple, alternate or opposite, the flowers with a well-developed hypanthium and separate carpels, and with arillate seeds).

The monophyly of Staphyleaceae is supported by morphology (see description; Stevens 2001 onward) and DNA sequences (Harris et al. 2017; Savolainen et al. 2000b; Simmons 2007; Sosa and Chase 2003). Generic circumscriptions are problematic; traditionally three genera, i.e., *Turpinia*, *Staphylea*, and *Euscaphis*, were recognized, based on fruit type, i.e., berries, inflated capsules, and fleshy follicles respectively, but unfortunately both *Turpinia* and *Staphylea,* when defined by fruit type, are not monophyletic. Christenhusz (2018) placed all species of Staphyleaceae in an expanded *Staphylea*, Simmons (2007) recognized only two genera, placing the Old World species of *Turpinia* in *Dalrympelea* and all other species of the familial clade in an expanded and morphologically heterogeneous *Staphylea*, and Harris et al. (2017) provided molecular evidence supporting the monophyly of five major species-groups (although the phylogenetic relationships among these groups are still far from clear). *Dalrympelea* (Paleotropical, in distribution, formerly misplaced in *Turpinia*) and *Turpinia* (Neotropical) both have berries and small, bract-like stipules, but they can be distinguished, because the former has the stipules completely or partially fused, while the latter has distinct stipules. *Euscaphis* (a single species, in eastern Asia) has membranous stipules, flowers with separate carpels, and striking fruits: red, fleshy follicles opening to expose blue-black seeds. Finally, *Staphylea*, (distributed in temperate regions of North America, Europe, and Asia) can be distinguished by its papery and inflated, 2- or 3-lobed capsules, membranaceous, expanded and/or elongated stipules, and flowers in more or less drooping inflorescences (vs. ± erect in the other genera). DNA sequence data (Harris et al. 2017) strongly suggest that *Staphylea* is not monophyletic – and instead is composed to two clades, not each other’s closest relatives, i.e., the Asian-North American *Staphylea* clade (including *S. bolanderi, S. forrestii, S. holocarpa, S. trifolia*, and relatives), and a smaller, Old World *Staphylea* clade (i.e., *S. bumalda, S. colchica,* and *S. pinnata*). These two clades are here retained within *Staphylea*, pending more detailed morphological and molecular investigations. Some analyses suggest that *Euscaphis* is sister to the remaining genera, while others place *Dalrympelea* in this position. The taxonomic uncertainty, in part, may relate to reticulate evolution; perhaps *Turpinia* originated from a hybridization event between species of *Euscaphis* and *Dalrympelea* (Harris et al. 2017).

 The genera *Tapiscia* and *Huertea* were traditionally placed in Staphyleaceae (Cronquist 1981; Pax 1893) but these differ in many morphological and anatomical characters (e.g., alternate and spiral leaves, paracytic stomata, mainly multicellular hairs, cylindrical filaments, and an unvascularized nectar disk; see also Dickison 1986, 1987), and DNA sequence data indicate that they are not closely related to *Dalrympelea, Euscaphis, Staphylea*, and *Turpinia*. They are now placed in Tapisciaceae (of the Huerteales).

 The showy, usually white flowers of Staphyleaceae are pollinated by a variety of insects, especially bees and flies. The papery capsules of *Staphylea* probably are wind and/or water dispersed. The berries of *Dalrympelea* and *Turpinia* are dispersed by birds, while the red follicles, which contrast with globose, black seeds, of *Euscaphis* likely are also bird dispersed.

***Additional references***: Howard 1977; Spongberg 1971; Weaver 1980.

**Crossosomataceae** Engler

(Rockflower family)

*Shrubs* or rarely trees, often densely branched; with tannins, including gallic and ellagic acids, inulin also present. Hairs simple or branched, glandular or non-glandular. *Leaves usually alternate and spiral* (and sometimes fascicled), or (in *Apacheria*) opposite and decussate, *simple*, **usually small**, *entire* to apically 2 or 3 toothed, with pinnate venation or only midvein evident; *stipules present or absent*, fused to petiole or not. **Inflorescences of solitary flowers**, these terminal or axillary. *Flowers bisexual, radial, with a short, cup-shaped to elongate and tubular hypanthium*. Sepals usually 4-5 (occasionally more), distinct, imbricate. *Petals 4-5* (occasionally more)*, distinct*, imbricate, often clawed. Stamens 4 to numerous; filaments distinct; anthers non-sagittate; **tapetum cells polyploid and multinucleate**; pollen grains tricolporate. *Carpels 1-5* (-9), *distinct*, stalked to sessile; *ovaries superior, each with parietal placentation*; stigmas capitate to slightly decurrent. Ovules 1 to many per carpel, **amphitropous or campylotropous**. *Lobed nectar disk at apex of hypanthium* (but lacking in *Velascoa*). *Fruit a follicle or aggregate of follicles*. Seeds disk-shaped, **with a fimbriate to irregular aril, the seed coat with fibrous endotegmen**; embryo curved.

***Floral formula***: \* K 4-5 , C 4-5 , A 4 - many , G 1-5 , follicle or cluster of follicles

[Connect the K + C + A with a line underneath the formula, to indicate hypanthium]

***Distribution and ecology***: Western North America (United States and Mexico), in arid habitats.

***Genera/species***: 4/7. ***Genera***: *Crossosoma* (3 spp.), *Glossopetalon* (2, but *G. spinescens* with 8 subspecies), *Apacheria* (1), and *Velascoa* (1). All except *Velascoa* occur in the continental United States.

***Economic plants and products***: The species of *Crossosoma* are occasionally grown as ornamental shrubs.

***Discussion***: Crossosomataceae are supported as monophyletic based on both molecular (Alan & Ayers 2021; Oh 2010; Sosa & Chase 2003) and morphological (Sosa 2007; Stevens 2001 onward) data. The familial clade is related to Staphyleaceae and Stachyuraceae (see discussion under Staphyleaceae), although prior to the advent of molecular data it often was considered to be related to Rosaceae (based on floral morphology; see Cronquist 1981). The family likely is comprised of two clades: a *Velascoa* + *Crossosoma* clade (lacking stipules, with non-striate follicles), and a *Glossopetalon* + *Apacheria* clade (stipulate, with striate follicles) (Allen & Ayers 2021; Oh 2010), although an analysis based only on *rbcL* sequences supported *Crossosoma* as sister to the remaining genera (Sosa & Chase 2003). The four genera are quite distinctive: *Apacheria* because of its opposite leaves, often with a few distal teeth; *Crossosoma* because if its more or less numerous stamens (a secondary increase); *Glossopetalon* because of its expanded petiole bases and usually only single carpel, and *Velascoa* because of its elongated hypanthium, lack of a nectar disk, and glandular-hairy stems. *Glossopetalon* was traditionally included in the Celastraceae; its transfer to Crossosomataceae (Thorne & Scogin 1978) has since been confirmed by DNA-sequence data.

 The flowers of species of Crossosomataceae are visited by various insects (bees, flies, beetles) and hummingbirds.

***Additional references***: Kapil & Vani 1963; Matthews & Endress 2005; Scogin & Tatsuno 1982.

*Brassicales*

**Bataceae** Perleb

(Saltwort Family)

*Low shrubs* with stems erect, arching, and/or prostrate, 4-angled to ± terete; tissues with glucosinolates but without myrosin cells, and **with (hydroxy) proline betaines** (protective from drought, high salinity, and high temperatures), also with crystals of calcium oxalate and sodium chloride, and lacking both anthocyanins and betalains. Hairs simple, *but plants nearly glabrous*. *Leaves opposite and decussate, simple*, entire, **succulent/fleshy and terete**, *with 2 obscure vascular traces, and each leaf bearing a basal-abaxial appendage*; stipules present by minute, glandular (perhaps representing colleters). Inflorescences indeterminate (**cone-like or spike-like**), **with ± densely packed, small flowers**, usually axillary. *Flowers unisexual* (and plants dioecious or monoecious), *radial*, but cryptically bilateral in staminate flowers due to form of the calyx; each flower subtended by a bract, **but bracteoles lacking**; *pedicel absent or very short*. **Sepals** *of staminate flowers 4*, **connate, modified and forming a sheath with 3 lobes much reduced and 1 lobe well developed, initially surrounding the rest of the flower, then splitting**; **lacking in carpellate flowers***. Petals of staminate flowers 4*, *distinct, long-clawed*, imbricate; **lacking in carpellate flowers**. *Stamens 4*; filaments slender, distinct; pollen grains usually tricolporate, **the exine (in cross section) homogeneous and spongy**, **without columellae**. *Carpels 2*, connate; **ovary nude**, *with parietal placentation*, **and each carpel divided so ovary 4-loculate**; lacking a gynophore; **style absent**; stigmas 2, ± capitate. Ovules 2 per carpel (so 1 per locule). **Nectary lacking**. *Fruit a drupe with 4 pits*, *often each fruit of the infructescence fused with adjacent fruits to form a drupaceous syncarp* (multiple fruit). Seeds with straight to slightly curved embryo.

***Floral formula***:

Staminate: \* , K 1 + 3 , C 4 , A 4 , G 0

[Circle the 1+3 sepals]

Carpellate: \* , K 0 , C 0 , A 0 , G 2 ; drupe

[Circle the 2 carpels]

***Distribution and ecology***: Northern Australia and southern New Guinea, warm temperate to tropical North and South America. Halophytic shrubs of littoral zones, tidal marshes, and in and among mangroves.

***Genera/species***: 1/2. ***Genus***: *Batis* (2 spp.). The genus (represented by *Batis maritima*) grows in the United States (coastal regions in southern California, and from coastal Texas east to Florida and north to North Carolina).

***Economic plants and products***: The leaves of *Batis* (saltwort) are eaten in salads and pickled. The plant is also ecologically valuable, aiding in soil stabilization in coastal regions.

***Discussion***: The monophyly of Bataceae is well supported by its array of distinctive morphological characters (Bayer and Appel 2003a; Rogers 1982; Ronse de Craene 2005; Stevens 2001 onward; see also description). *Batis* is comprised of two species: *B. maritima* (adjacent fruits of infructescence fused together, plants dioecious; Neotropical) and *B. argillicola* (fruits not fused, plants monoecious; northern Australia and New Guinea). Bataceae are related to Koeberliniaceae (see Figure 8.86) and are either sister to the small Old-World clade Salvadoraceae or nested within this familial clade (and sister to *Azima*). Both Salvadoraceae and Bataceae have opposite leaves, paracytic stomata, and only two ovules per carpel.

 The inconspicuous flowers of *Batis* are wind pollinated. The fruits float in sea water and are distributed by currents.

***Additional reference***: Swanepoel et al. 2020; Uphof 1930.

**Caricaceae** Dumortier

(Papaya Family)

*Usually soft-stemmed shrubs to trees*, *the stems stout*, often with prickles, underground parts often forming tubers; **plants with laticifers** *and ± milky to yellow sap*; *producing glucosinolates (mustard oil glucosides) and myrosin*, **but idioblastic myrosin cells absent**, and with the proteolytic enzyme papain. Hairs simple, glandular or not, rarely stinging. *Leaves alternate and spiral*, *simple and usually palmately lobed to palmately compound*, entire to serrate, *usually palmately veined*; stipules usually absent, rarely present and spine-like, *but very young leaves associated with colleters* (on branches of major veins, between developing leaves, paired at petiole base, etc.). *Inflorescences determinate* or reduced to a solitary flower, *axillary*. *Flowers usually unisexual* (and plants usually dioecious, but the staminate plants occasionally with some bisexual flowers, or rarely monoecious, and sometimes varying in sexual expression), radial, with short and inconspicuous hypanthium. *Sepals 5*, connate. *Petals 5*, **strongly connate in staminate flowers**, but distinct or only slightly fused in carpellate flowers, *imbricate and contorted*. Stamens 5 or 10; filaments distinct or slightly connate, **adnate to corolla tube**; pollen grains tricolporate. *Carpels 5*, connate; ovary superior, *with parietal or intruded-parietal placentation*, or sometimes with ± axile placentation. *Ovules numerous* on each placenta; **style apically branched**; **stigmas expanded, each usually lobed/divided**. **Nectary on pistillode of staminate flowers**, but carpellate flowers with stigmatic secretion. **Fruit a berry**, sometimes 5-lobed or -winged; **seeds with a fleshy outer part of the coat (sarcotesta)** *that surrounds the hard portion of the testa* (**with** **lignified ribs**); *embryo straight* with 2 flat cotyledons; endosperm present.

***Floral formula***:

Staminate: \* K 5 , C 5 , A 5-10 , G 5**.**

[Put a circle around the 5 sepals, circle also the 5 petals, draw a line below the formula connecting the 5-10 stamens to the 5 petals; circle the 5 sterile carpels]

Carpellate: \* K 5 , C 5 , A 0 , G 5 ; berry

[Circle the 5 sepals, put a dashed line around the 5 petals; circle the 5 carpels]

***Distribution***: Mainly Neotropical, i.e., southern North America (Mexico, southern Florida, Caribbean) south through South America, but also central Africa.

***Genera/species***: 6/35. ***Major genera***: *Vasconcella* (21 spp.) and *Jacaratia* (8). Only *Carica papaya* occurs in the continental U.S. (in Florida, where at least some populations may result from very early, pre-Western contact introductions, as they have small, golf ball-sized berries and can occur in remote hammocks in the Everglades).

***Economic plants and products***: *Carica papaya* (papaya) is the source of an economically important, melon-like fruit eaten worldwide, and fruits of *Vasconcella pubescens* (mountain papaya) are eaten in the Andes. In addition, *C. papaya* is the source of papain (extracted from the latex), which is widely used as a meat tenderizer.

***Discussion***: The monophyly of Caricaceae is supported by both morphology (see description; Kubitzki 2003a; Stevens 2001 onward) and DNA sequences (Carvalho 2015; Carvalho and Renner 2012; Kyndt et al. 2005). The African *Cylicomorpha* is sister to the remaining species, which are all Neotropical. The *Carica* + *Horovitzia* + *Jerilla* clade has ovaries with a single locule and parietal placentation, while the remaining genera, i.e., *Cylicomorpha, Jacaratia*, and *Vasconcella*, have more or less 5-loculate ovaries and axile placentation.

The presence of the proteolytic enzymes papain and chymopapain are deterrents to insect herbivory. The showy flowers of Caricaceae attract a variety of floral visitors, i.e., moths, bees, flies, and mosquitoes. The berry fruits are animal dispersed.

***Additional references***: Miller 1982; Ronse de Craene & Smets 1999.

**Koeberliniaeae** Engler

(Allthorn Family)

*Trees or shrubs* **with all branches forming photosynthetic thorns**; *with myrosin cells* **but glucosinolates absent (lost)**; **secondary phloem with intercellular spaces**. Hairs simple, unicellular. *Leaves alternate and spiral, simple, entire*, **with midvein only**, **reduced to minute** (i.e., to 3 mm long), **scale-like, quickly deciduous structures**; stipules present, but obscure and quickly deciduous. *Inflorescences indeterminate*, axillary, with floral bracts. Flowers bisexual, radial, *with a short gynophore*. *Sepals usually 4, distinct*. *Petals usually 4, distinct*, imbricate, slightly clawed. *Stamens* *usually 8*, all ± the same length; filaments distinct; pollen grains tricolpate. *Carpels 2* (-3), connate; ovary superior, **with axile placentation, the locules obliquely oriented**; stigma slightly expanded, lobed or not. Ovules few to numerous per locule, campylotropous, with a thin-walled megasporangium. Nectar gland at base of each stamen. *Fruit a 1- or 2-seeded berry*; **seeds with outer portion of testa with massive cuticle**; the embryo curved; endosperm scanty.

***Floral formula***: \* , K 4 , C 4 , A 8 , G 2 ; berry

[Circle the 2 carpels]

***Distribution and ecology***: North America (southwestern United States and northern Mexico) and disjunctly in South America (Bolivia); plants of desert habitats.

***Genera/species***: 1/2. ***Genus***: *Koeberlinia* (2 spp.). *Koeberlinia* *spinosa* occurs in the United States (southern California and Arizona to southern Texas).

***Economic plants and products***: *Koeberlinia spinosa* (althorn, junco, crown-of-thorns) is occasionally used as an unusual ornamental (usually as a barrier plant); it is also used medicinally. The wood is sometimes used for tool handles or wood carving.

***Discussion***: The monophyly of Koeberliniaceae is supported by several analyses of taxa of Brassicales (see citations under discussion of the order) and by morphology (see description; and Gibson 1979; Holms et al. 2008; Kubitzki 2002; Stevens 2001 onward; Swanepoel et al. 2020). It is curious that the clade lacks glucosinolates but has retained the now functionless enzyme myrosinase! Koeberliniaceae are most closely related to Bataceae, Salvadoraceae, and Tiganophytaceae (Swanepoel et al. 2020). *Koeberlinia* has been variably placed by taxonomists, but often has been included within a broadly circumscribed Capparaceae (see Cronquist 1981; Thorne 1992).

 The usually foul-smelling flowers of *Koeberlinia* are pollinated by flies, moths, and bees. The small berries are dispersed by birds.

***Additional reference***: Tobe and Raven 2008.

**Limnanthaceae**R. Brown

(Meadowfoam Family)

*Annual herbs*; *producing glucosinolates* (*mustard oil glucosides) and with myrosin cells*; with tannins, erucic and **ellagic acids**, **and fructan sugars accumulated as isokestose oligosaccharides**; vascular bundles in a ring, **without a cambium**. Hairs simple, if present. *Leaves alternate and spiral*, *simple and pinnately lobed or dissected or pinnately compound*, and leaflets sometimes lobed, entire, with obscure pinnate venation; *stipules lacking*. Inflorescences indeterminate (racemes) and terminal, but usually leafy-bracted, so flowers solitary and arising from leaf axils. Flowers bisexual, radial, **lacking bracteoles**. *Sepals usually 5 or 3*, rarely 4, slightly connate basally, *valvate*. *Petals usually 5 or 3*, rarely 4, *distinct*, **usually convolute** (**contorted**), but rarely open, *usually conspicuous*, occasionally inconspicuous. *Stamens usually 10 or 6*; filaments distinct, with nectar gland at the base of each filament; **pollen grains oblong to kidney-shaped, heteropolar, with a ring-aperture parallel to equator** (**zonosulcate**). *Carpels 2-5, connate* (**but ovary region deeply lobed so carpels appearing distinct**), **the carpel wall without vascular bundles**; ovary superior, *with basal-parietal placentation*; **style** 1, **gynobasic**, **hollow**, usually ± distally branched; stigmas punctate to capitate. **Ovules 1 per carpel**, **with 1 integument** and a thin-walled megasporangium; **female gametophyte tetrasporic**, with only 6 or 7 cells, i.e., 1 or 2 antipodals absent. **Fruit a schizocarp of globose, spiny to tuberculate nutlets**; **seeds with testa with vascular bundles**; *embryo straight*, the cell walls **with xyloglucans**; endosperm lacking.

***Floral formula***: \* , K 3-5 , C 3-5 . A 6-10 , G 2-5 ; schizocarp

[Put a dashed line around the 3-5 sepals; put a circle around the 2-5 carpels]

***Distribution and ecology***: Temperate North America; mainly plants of vernal pools and moist to wet meadows.

***Genera/species***: 2/8. ***Genera***: *Limnanthes* (7 spp.) and *Floerkea* (1). Both genera occur in the United States and Canada.

***Economic plants and products***: The seeds of *Limnanthes alba* (meadowfoam) are high in oil, which is rich in stable fatty acids and glucosinolate derivatives; the oil is used as an emollient and softening agent in skin and hair care products. *L. douglasii* (poached-egg plant) is grown as an ornamental.

***Discussion***: The monophyly of Limnanthaceae is supported by DNA sequences (Cardinal-McTeague et al. 2016; Edger et al. 2018; Meyers et al. 2010), morphology (Bayer and Appel 2003c; Stevens 2001 onward; see also description), and secondary chemistry (Pollard and Amuti 1981). *Floerkea* *proserpinacoidea* is sister to the genus *Limnanthes*. *Floerkea* is derived in having 3-merous flowers and inconspicuous petals, while *Limnanthes* has retained showy, 5-merous flowers. The Limnanthaceae are one of the basally branching lineages of Brassicales (see Figure 8.86) but often have been placed in Geraniales because of their 5-petaled flowers, lobed ovary, and schizocarpic fruits (Cronquist 1981). Dahlgren (1975) first placed the family in Brassicales, based on the presence of mustard oils, and this has been confirmed by DNA-based phylogenetic analyses (see citations in introduction to Brassicales).

 The showy flowers of *Limnanthes* are pollinated by various solitary bees and honey bees. Most species of *Limnanthes* are outcrossing, but a few species, and also *Floerkea*, are selfing (and have inconspicuous flowers). The fruit segments are water dispersed.

***Additional references***: Jain 1976; Ornduff 1971.

**Moringaceae** Martynov

(Horseradish-tree Family)

*Trees, sometimes with swollen trunks, shrubs, or small woody subshrubs with tuberous roots; producing glucosinolates* (*mustard oil glucosides*) *and with myrosin cells*, sometimes cyanogenic, **usually with gum/mucilage ducts in pith of twigs and in bark**. Hairs simple. *Leaves alternate and spiral*, **once to 3-times pinnately compound**, entire, with pinnate venation; stipules present, usually glandular, and glands also at base of leaf axes. *Inflorescences determinate, axillary*. **Flowers** *bisexual*, **nearly radial to strongly bilateral, but always bilateral in early development**, **with a short** (*cup-shaped*) **to elongate** (*tubular*) **hypanthium**. *Sepals 5, distinct*, imbricate, equal or unequal in size, **and petaloid**. *Petals 5, distinct*, **one only slightly to much larger than the others**, *often forming a banner*, imbricate. **Stamens 5, opposite the petals**, *alternating with 3-5 staminodes*; filaments distinct or slightly connate, upcurved to straight; **anthers with only one locule (theca), opening by a single slit**; pollen grains tricolporate. *Carpels usually 3*, connate; ovary superior, *with parietal placentation* **and borne on a gynophore**; style 1, *hollow*; *stigma truncate and porate*. Ovules numerous on each placenta, **with outer integument vascularized**. **Nectary on inner surface of hypanthium**. **Fruit an elongated, loculicidal, and explosively-dehiscent capsule**. *Seeds 3-angled, winged or unwinged*, **with the middle part of the testa thick, and outer and inner parts with helical thickenings**; *embryo straight*; endosperm ± lacking.

***Floral formula***: \* or X , K 5 , C 5 , A 5 + 5**.** , G 3 ; capsule

[Draw a line under the formula connecting K, C, and A; circle the 3 carpels]

***Distribution and ecology***: Africa and Madagascar to India; plants of more or less arid habitats.

***Genera/species***: 1/13. ***Genus***: *Moringa* (13 spp.). *Moringa oleifera* is naturalized in the United States (Florida).

***Economic plants and products***: *Moringa oleifera* (horseradish-tree, drumstick-tree) is widely grown in the tropics because of its nutritious and flavorful leaves, flowers, and young fruits, which are high in protein, iron, vitamin A and C, and calcium. In addition, a horseradish-like condiment is made from the roots. The seeds of *M. oleifera* and a few other species are the source of oil (used in soaps and cosmetics) (see also Olsen 1999 onward).

***Discussion***: The monophyly of Moringaceae is strongly supported by morphology (Kubitzki 2003b; Olson 2002b, 2003; Stevens 2001 onward; see also description) and DNA sequences (Olson 2002a, b). *Moringa* *drouhardii*, *M. hildebrandtii*, *M. stenopetala*, and *M. ovalifolia* form a basal paraphyletic group, and all are trees with bottle-like trunks, having more or less radially symmetrical flowers. This grade gave rise to a clade of nine species, supported by the synapomorphy of strongly bilateral flowers. Two subclades are evident within the bilateral-flowered clade: the slender-tree clade (i.e., *M. concanensis*, M. *oleifera*, and *M. peregrina*) and the tuberous-shrub clade (i.e., *M. arborea*, *M. borziana*, *M. longituba*, *M. pygmaea*, *M*. *rivae*, and *M. ruspoliana*). Moringaceae are most closely related to Caricaceae (see Fig. 8.86), and represent one of the basally branching lineages of Brassicales.

 The showy, fragrant, white, yellow to reddish flowers of *Moringa* are pollinated by bees. The seeds are dispersed by wind or water.

***Additional references***: Olsen 2010; Ronse de Craene et al. 1998.

**Resedaceae** Martinov

(Mignonette Family)

*Trees, shrubs, lianas, or herbs*; *producing glucosinolates* (*mustard oil glucosides*) *but myrosin cells* *absent or restricted to particular tissues*; stems occasionally with sclereids in cortex, occasionally with successive cambia. Hairs simple, occasionally clustered. *Leaves usually alternate and spiral* (but opposite and decussate in *Borthwickia*), *simple to deeply dissected*, or sometimes compound, and then trifoliolate, entire to toothed, with pinnate venation; stipules present and minute, sometimes glandular or forming spines, or absent. *Inflorescences indeterminate*, terminal to axillary, rarely reduced to a solitary flower (in *Tirania*). *Flowers usually bilateral*, with a short hypanthium or this lacking; *receptacle usually forming a short to elongate gynophore or androgynophore*. *Sepals (2-) 4-8*, distinct or slightly connate (but strongly connate in *Borthwickia*). *Petals (2-) 4-8*, occasionally lacking, *distinct*, valvate or occasionally imbricate, *usually unequal in size, each often differentiated into a claw and limb, the latter usually dissected or lobed, and appendaged at the junction of claw and limb*, or petals with distal and proximal parts only slightly differentiated and unlobed, or petals undifferentiated. *Stamens 3 to numerous*, *all ± the same length and short to very elongated*; filaments distinct to basally connate; pollen grains tricolpate to ± tricolporate. *Carpels 2-8, connate to partly so* (but distinct in *Secamoides*, and nearly distinct in *Caylusea*); *ovary superior, with axile or more commonly parietal placentation* (but rarely ± basal or lateral); styles/stigmas usually as many as the carpels, *these ± short, or style absent*, *and often with ovary open apically-adaxially* (in *Reseda* and close relatives); stigmas lobed or unlobed, punctate, capitate-expanded, or elongate. Ovules 1 to several per carpel, anatropous to campylotropous, with thick- to thin-walled megasporangium. Nectar disk usually present, ± asymmetric, usually on androgynophore. *Fruit an ovoid to elongate capsule, often ± apically open*, rarely a berry, drupe, or schizocarp of dry, follicle-like mericarps. *Seeds ± kidney-shaped, often arillate*; embryo curved or folded; endosperm scanty or absent.

***Floral formula***: X , K 4-8 , C 4-8 , A 3-many , G 2-8 ; capsule

[Put a dashed line around 4-8 sepals, circle the 2-8 carpels]

***Distribution and ecology***: Widespread in the Northern Hemisphere and also in southern Africa; plants often of arid, calcareous, and/or saline habitats, and many species are weedy.

***Genera/species***: 8/95. ***Major genera***: *Reseda* (68 spp.) and *Forchhammeria* (10). One native and several introduced species of *Reseda* occur in the United States and/or Canada.

***Economic plants and products***: *Reseda luteola* (dyer’s weed) is a source of the flavonoid luteolin, a bright yellow dye. *Reseda odorata* (mignonette) is an ornamental, and it is also used in the perfume industry.

***Discussion***: The monophyly of the Resedaceae is supported by DNA sequences (Cardinal-McTeague 2016; Chen et al. 2016; Hall et al. 2004; Su et al. 2018) but morphological support is lacking. *Borthwickia* (only *B. trifoliata*; putative synapomorphies: opposite, trifoliolate leaves, strongly connate calyx, an undivided stigma) is sister to the Stixideae + Resedeae clade. The monophyly of Stixideae (4 genera, 20 spp., including *Forchhammeria* and *Stixis*) is supported by vestured pits and drupaceous fruits. Stixideae also have axile placentation (as also does *Borthwickia*). Both *Borthwickia* and the genera of Stixideae have flowers reminiscent of those of *Capparis* (which has parietal placentation), and all were traditionally placed in Capparaceae (see Kers 2003). In contrast, the flowers of Resedeae (Resedaceae s.s.; 3 genera, ca. 75 spp.) are quite different from those of *Capparis* (Kubitzki 2003d), and this tribe is strongly supported by DNA sequences (Martín-Bravo et al. 2017) and morphology (putative synapomorphies: petals clawed, with limb more or less fringed, and with a ligule at their junction, gynoecium usually open apically, with parietal placentation, and details of glucosinolate biosynthesis; see also Kubitzki 2003d; Stevens 2001 onward). Within Resedeae, *Caylusea* and *Sesamoides* are successively sister to *Reseda* s.l. (including *Ochradenus*, *Oligomeris*, and *Randonia*) (Martín-Bravo et al. 2017). Note that although the family has no morphological synapomorphies, and cannot be easily diagnosed, members of Resedaceae can be identified using the diagnostic features of *Borthwickia*, Stixideae, or Resedeae, the family’s three major subclades.

 The showy flowers of Resedaceae are pollinated by various insects. Ant dispersal is characteristic of Reseda, with the arillate seeds providing the reward, although rain-wash or wind may also play a role.

***Additional reference***: Arber 1942.

**Tropaeolaceae** Jussieu ex de Candolle

(Indian-cress or Nasturtian Family)

*Herbs or vines*, *producing glucosinolates (mustard oil glucosides)* and with myrosin cells; often with rhizomes, tubers, or tuber-like roots. Hairs simple. *Leaves alternate* and spiral*, simple, often variously palmately lobed or palmately dissected, occasionally palmately compound*, *otherwise entire*, **usually** **peltate**, *with palmate venation* (but pinnate within leaflets when compound**), the petioles often elongate, sometimes twining**; stipules usually present. *Inflorescences usually of solitary, axillary flowers*, but entire shoot can be considered a raceme with leafy bracts. **Flowers** bisexual, **strongly** **bilateral**, **with a short hypanthium**, **usually forming a well-developed, nectar spur**, *often with elongate*, sometimes twining *pedicel*. Sepals 5, distinct. *Petals 5, distinct, imbricate*, **the 3 lower ones usually different from the 2 upper ones** (and 3 lower ones rarely lacking), *usually clawed, often toothed, ciliate, or dissected*, and the apex emarginate or not. *Stamens 8*; filaments distinct; pollen grains usually tricolporate. *Carpels 3, connate*; ovary superior, *with axile placentation*; **style impressed in ovary apex**; stigma 3-lobed. **Ovules** 2 in each locule but **only 1 maturing**, with a thin-walled megasporangium. **Fruit a schizocarp**, *separating into 3 drupe-like or nut-like mericarps*, rarely a 3-winged samara; *seed with straight embryo*, the cotyledons thick, **with xyloglucans**; endosperm absent.

***Floral formula***: X K 5 , C 2 + 3 , A 8 , G 3 , schizocarp

[Note: Draw a line connecting K + C + A indicating the hypanthium; circle the 3 carpels]

***Distribution***: Southern North America (Mexico) to southern South America, and naturalized widely elsewhere.

***Genera/species***: 1/105. ***Genus***: *Tropaeolum* (incl. *Magallana*, *Trophaeastrum*). *Tropaeolum majus* has naturalized in temperate North America.

***Economic plants and products***: Several species, especially *Tropaeolium majus* (Indian-cress, naturtian, nasturtium), are grown as ornamentals because of their showy, colorful flowers. Additionally, all plant parts can be eaten, having a hot-spicy flavor similar to water cress (*Nasturtium officinale*). The tubers of *T. tuberosum* (isaña, mashua) are eaten in the Andes, and this plant (as well as other species) also are used medicinally.

***Discussion***: The monophyly of Tropaeolaceae is supported by morphology (see description; Stevens 2001 onward; Bayer and Appel 2003b) and DNA sequences (Andersson and Andersson 2000). The familial clade consists of a single genus, *Tropaeolum*, and its species belong to one of two major subclades: sect. *Tropaeolum* (tropical species; leaves simple to deeply lobed, but lobes less than 4/5 of the distance from petiole to leaf apex, petals usually ± ciliate to serrate, with non-emarginate apices) and sect. *Chilensia* (southern temperate species; leaves palmately divided to, or almost to, the petiole or palmately compound, petals not ciliate, with emarginate apices). Tropaeolaceae are most closely related to Akaniaceae, sharing the putative apomorphies of flowers with a hypanthium and only 8 stamens (see Ronse de Craene and Smets 2001).

 The colorful flowers of *Tropaeolum* are pollinated by various insects as well as birds. Dispersal of those species with fleshy fruit segments is often by birds.

***Additional reference***: Hershkovitz et al. 2006.

*Malvales*

**Bixaceae** Kunth

(Annatto Family)

*Trees, shrubs, or perennial herbs*, often with tannins, ellagic acid, sometimes with flavonoid sulphates; **with secretory canals or cells, producing yellow to red, resinous substances**, sometimes also with mucilage cells or canals. Hairs simple, **gland-headed**, *and head sometimes peltate*, sometimes also with eglandular hairs, and these never stellate or tufted*. Leaves alternate and spiral* or 2-ranked, simple, unlobed to occasionally palmately lobed, or palmately compound, entire to toothed, *with usually palmate* *venation*, but pinnate in *Diegodendron*; *stipules present*, *often sheathing terminal bud*, ± encircling stem in *Diegodendron*. Inflorescences determinate, usually terminal. *Flowers bisexual, radial to bilateral*, **large**. *Sepals 5*, distinct, sometimes associated with glands. *Petals 5*, *distinct*, imbricate or convolute, white, pink, or yellow. *Stamens numerous*; *filaments distinct*, sometimes slightly 2- to 5-clustered; anthers straight to curved, *opening by longitudinal slits or pores*; pollen grains tricolporate. *Carpels 2-5*, connate; ovary superior, usually unlobed, but lobed in *Diegodendron*, *with parietal, partly axile and partly parietal, or completely axile placentation*; style 1, usually gynoterminal, but gynobasic in *Diegodendron*; stigma ± lobed. Ovules usually numerous per carpel, but only 2 per carpel in *Diegodendron*, anatropous to campylotropous. Nectar disk present. *Fruit usually a loculicidal capsule*, but indehiscent in *Diegodendron*, *warty* (*Diegodendron*), *covered with elongated spine-like outgrowths* (*Bixa*) *or ± smooth* (*Cochlospermum*, *Amoreuxia*). *Seeds with conspicuous, elongated hairs* (*Cochlospermum, Amoreuxia*), *with pulpy, red testa* (*Bixa*), *or with very thin testa* (*Diegodendron*); embryo with curved or folded cotyledons.

 ***Floral formula***: \* or X, K 5 , C 5 , A many , G 2-5 ; capsule

[Replace “many” with infinity symbol; circle the 2-5 carpels]

***Distribution***: Pantropical.

***Genera/species***: 4/23. ***Genera***: *Cochlospermum* (13 spp.), *Bixa* (5), *Amoreuxia* (4), and *Diegodendron* (1). Only *Amoreuxia* occurs natively in the United States (Arizona, New Mexico, and Texas).

***Economic plants and products***: *Bixa orellana* (annatto, achiote, lipstick-tree) produces an orange-red dye (annatto) used in coloring foods. Both *Bixa* and *Cochlospermum* are used medicinally, and both are grown as ornamentals because of their showy flowers.

***Discussion***: The monophyly of Bixaceae is supported by DNA sequences (Fay et al. 1998; Johnson-Fulton and Watson 2017; Savolainen et al. 2000a) although morphological support is rather weak (see description; Stevens 2001 onward). *Cochlospermum* and *Amoreuxia* together form a clade (putative synapomorphies: anthers opening by pores, capsule differentiated into woody exocarp and membranous endocarp, which separate, seeds hairy and more or less curved), which is sister to the *Bixa* + *Diegodendron* clade (putative synapomorphies: glandular hairs peltate, fruit covered with projections). The monophyly of *Bixa* is supported by its inverted, U-shaped anthers, completely parietal placentation, and seeds with a red, pulpy testa. *Diegodendron* is morphologically distinctive, i.e., having the apomorphies of 2-ranked leaves, a gynobasic style, deeply lobed ovary, only 2 ovules per carpel, and an indehiscent fruit). *Cochlospermum* is non-monophyletic, with *Amoreuxia* nested within its phylogenetic structure; bilateral flowers and the herbaceous habit are derived (Johnson-Fulton and Watson 2017). Although the family has few morphological synapomorphies, its members are easily recognized because the subclades, i.e., *Cochlospermum* + *Amoreuxia*, *Bixa*, and *Diegodendron*, are each easily diagnosed. Bixaceae is most closely related to Cistaceae and Dipterocarpaceae (see references under Malvales).

 The showy flowers of Bixaceae are pollinated mainly by bees, although bat pollination has also been reported. The hairy seeds of *Cochlospermum* and *Amoreuxia* are wind dispersed, while the fleshy, red seeds of Bixa are dispersed by birds.

***Additional reference***: Ronse de Craene 1989.

*Picramniales*

**Picramniaceae** Fernando and Quinn

(Bitterbush Family)

*Trees or shrubs*; leaves, twigs, and bark with betulinic acid and similar triterpenes, **anthraquinones, and very bitter C5-sugar linked anthracenone derivatives**. Hairs simple. *Leaves alternate and spiral*, *pinnately compound*, occasionally trifoliolate, but unifoliate in *Aenigmanu*, the leaflets entire, with pinnate venation; stipules lacking (but present in *Aenigmanu*). Inflorescences determinate, terminal or axillary. Flowers unisexual (**plants dioecious**), *radial*, *very small*. *Sepals 3-5* (-6), distinct to connate, imbricate or valvate. *Petals 3-5* (-6), occasionally absent, *distinct*, imbricate. *Stamens 3-5* (-6), **opposite the petals**, represented by staminodes, or absent, in carpellate flowers; *filaments distinct*, but in *Nothotalisia* and *Aenigmanu* connate, and adnate to a central column, forming an androgynophore (with a distal pistillode); pollen grains tricolporate. *Carpels 2-4*, *connate*; ovary superior, sessile on a small disk or with a gynophore, with axile placentation, but sometimes only 1 carpel fertile; *styles short, recurved, and as many as the carpels*; stigmas small, ± ellipsoid; a minute pistillode in staminate flowers. *Ovules 2 per locule*. *Nectar disk present*, intrastaminal or around base of ovary, or absent. *Fruit a few-seeded berry*, *samaroid capsule*; **seed oils with C18 acetylenic tariric acid and petroselenic acid**; endosperm lacking.

***Floral formula***:

Staminate: \* , K 3-5 , C 3-5 , A 5 , G 3-4**.**

[Put a dashed line around 3-5 sepals; circle the 2-4 sterile carpels]

Carpellate: \* , K 3-5 , C 3-5 , A 0-5**.** , G 2-4 ; berry, samaroid capsule

[Put a dashed line around 3-5 sepals; circle the 2-4 carpels]

***Distribution***: Neotropical.

***Genera/species***: 4/50. ***Genera***: *Picramnia* (41 spp.), *Alvaradoa* (5), *Nothotalisia* (3), and *Aenigmanu* (1). *Picramnia* and *Alvaradoa* occur natively in the United States (southern Florida).

***Economic plants and products***: *Picramnia* *pentandra* (bitterbush) is grown as an ornamental; *Picramnia* is also used medicinally.

***Discussion***: The monophyly of Picramniaceae is supported by DNA sequences (Fernando et al. 1995; Logacheva and Shipunov 2017; Savolainen et al. 2000a, b; Shipunov et al. 2020; Thomas et al. 2021), secondary chemistry (Jacobs 2003), and morphology (Fernando and Quinn 1995; Kubitzki 2007b; Stevens 2001 onward; Thomas 2011). *Picramnia* may be sister to the *Nothotalisia* + *Alvaradoa* + *Aenigmanu* clade, and each of the four genera is supported as monophyletic (by both molecular and morphological characters). *Picramnia* has the putative synapomorphic character of a vascularized seed coat, and *Alvaradoa* has the likely synapomorphies of gynoecia with only a single fertile carpel, which develops into a samaroid capsule. *Aenigmanu* has unifoliate leaves and lobed berries. *Nothotalisia* and *Aenigmanu* both have an androgynophore in their staminate flowers.

 Traditionally *Alvaradoa* and *Picramnia* were placed within Simaroubaceae (Cronquist 1981; Takhtajan 1997; see also discussion in Kubitzki 2007); the genera *Nothotalisia* and *Aenigmanu* were only recently described (Thomas 2011; Thomas et al. 2021). Both Picramniaceae and Simaroubaceae have intensely bitter bark, but the chemicals involved are different in the two familial clades – anthracenone derivatives vs. triterpenoids of the quassinoid type (Jacobs 2003; Simão et al. 1991). They also both have pinnately compound leaves. Of course, Simaroubaceae differ in having carpels distinct in the ovary region and only fused by their styles (vs. connate in the ovary region but with separate styles, in Picramniaceae) with only a single ovule per locule (vs. 2 ovules per locule), and fruits usually an aggregate of drupes or samaras (vs. simple fruits, either a berry or samaroid capsule). Analysis of DNA sequences place Picramniaceae as an isolated family (in its own order) within the Malvoid clade, and well separate from the Sapindales.

 The inconspicuous flowers of Picramniaceae may be visited by various generalized insect pollinators; but *Alvaradoa* is usually considered to be wind pollinated. The berries of *Nothotalisia, Aenigmanu,* and *Picramnia* probably are dispersed mainly by birds; *Alvaradoa* is wind dispersed.

***Additional references***: Brizicky 1962; Pirani 1993.

*Caryophyllales [core clade]*

**Didiereaceae** (Majure)

**Petiveriaceae** Meissner

(Pigeonberry Family)

Herbs, shrubs, trees, lianas, or vines; stem usually with concentric rings of vascular bundles or alternating concentric rings of xylem and phloem; betalains present; rhomboid crystals and styloid crystals present; sometimes with garlic smell (due to cysteine sulfoxide derivatives). Hairs usually simple. *Leaves alternate and spiral, simple, with pinnate venation;* stipules lacking. **Inflorescences indeterminate (racemes or spikes),** axillary or terminal. Flowers usually bisexual, radial or weakly bilateral. *Tepals 4* (5 in *Seguieria*), *usually distinct*, imbricate. *Stamens 4 to numerous*; filaments distinct; pollen grains tricolpate to polycolpate or pantoporate. *Carpel 1; ovary superior, with ± basal placentation*; *styles distinct*, **very short or absent**; *stigmas capitate, linear, or represented by a tuft of hairs*. *Ovule 1 per carpel*, ± campylotropous. Nectaries lacking. *Fruit a single-seeded berry, samara, utricle, or barbed achene*; embryo curved; endosperm lacking, replaced by perisperm.

***Floral formula***: \* T -4- , A 4-numerous , G 1 ; berry, samara, utricle, achene

[replace word “numerous” with infinity symbol]

***Distribution and ecology:*** Most diverse in warm temperate to tropical regions of the Americas, but also occurring natively in tropical Africa, eastern Australia, New Caledonia and the New Hebrides. In addition, *Rivina* is widely naturalized in the Old World (warm regions of Asia, Africa, Madagascar, Australia, Pacific islands). Plants growing in a variety of habitats but frequently of open, disturbed areas.

***Genera/species***: 9/20. ***Major genera***: *Seguieria* (6 spp.), *Hilleria* (3) and *Trichostigma* (3). *Petiveria*, *Rivina*, and *Trichostigma* occur in the continental United States.

***Economic plants and products***: Both *Petiveria* (guinea hen-weed) and *Rivina* (pigeonberry, rouge plant) are used medicinally, and *Rivina* is also an ornamental (showy, bright red berries). *Trichostigma* (hoopvine) has been used for basketry and barrel hoops.

***Discussion***: Petiveriaceae share with Nyctaginaceae a gynoecium consisting of a single carpel (Ronse de Craene 2013) and the two are sister clades; the monophyly of Petiveriaceae is supported by both morphology (see description) and DNA sequences (Brockington et al. 2009; Yang et al. 2015, 2017; Thulin et al. 2018). *Seguieria*, a genus with 5-merous flowers, may be sister to the remaining taxa. *Rivina* is closely related to *Trichostigma* and both have berry fruits. The Petiveriaceae have frequently been treated within an expanded Phytolaccaceae, as the subfamily Petiverioideae or Rivinoideae (see discussion under Phytolaccaceae).

 The flowers of Petiveriaceae probably attract a variety of insect pollinators. The bright red berries of *Rivina* and the purple-black ones of *Trichostigma* (contrasting with persistent red tepals) are dispersed by birds. The fruits of *Petiveria*, with their four to numerous stout barbs, are externally transported (sticking into clothing, hair, etc.). The species with samaras are dispersed by wind.

***Additional references***: Carlquist 1998; Rogers 1985.

**Talinaceae** (Majure)

*Caryophyllales (Polygoninieae)*

**Frankeniaceae** (Majure)

**Nepenthaceae** Dumortier

(Asian Pitcher Plant Family)

Usually *carnivorous* **lianas**, **climbing by twining portion of leaves**, occasionally shrubs to subshrubs, sometimes epiphytic; **stems with cortical** and medullary **vascular bundles**. Hairs simple to variouslybranched*, also with gland-headed hairs* (on leaves and stems, secreting nectar or water). **Leaves** alternate, spiral, **± sessile**, **with proximal portion forming a photosynthetic lamina (phyllodium), the middle portion narrowed, forming a twining tendril (cirrhus), and the distal portion highly modified, forming an urn-shaped to cylindrical, pitcherlike trap (ascidium) with an expanded, ± flat lid (operculum)** *usually with nectar glands on its underside and between its teeth***, and** **the pitcher, itself, with a slippery, ridged-rim or lip (peristome)** *and 2 longitudinal wings*; inner surface of the pitcher smooth and waxy above and *with digestive glands in lower portion*; stipules absent. Inflorescences indeterminate (usually a raceme or raceme-like), terminal (but sometimes appearing lateral). **Flowers unisexual** (and **plants dioecious**), radial, **and not associated with bracts or bracteoles**. **Tepals** *usually 4,* usually distinct, imbricate. Stamens 8 to numerous; **filaments connate and forming a column**; *anthers crowded together in a head-like structure*; pollen grains in tetrads, **± without apertures**. *Carpels usually 4, connate*; ovary superior, **with axile placentation;** **style short; stigma flattened, expanded and discoid**. **Ovules numerous in each locule, each with an elongated outer integument**. Nectar producing glandular-hairs on adaxial surface of tepals. *Fruit a loculicidal capsule*. **Seeds minute, filiform-spindle-shaped**.

***Floral formula***:

Staminate: \* T - 4 - , A 8-numerous , G 0

Carpellate: \* T - 4 - , A 0 , G 4 ; capsule

[Circle the 8-numerous stamens, use infinity symbol for “numerous” and circle the 4 carpels]

***Distribution and ecology***: Madagascar, Sri Lanka, southern Asia to New Guinea, northern Australia, and New Caledonia; carnivorous plants characteristic of open, nutrient-poor, moist montane habitats.

***Genera/species***: 1/180. ***Genus***: *Nepenthes* (180 spp.). The genus does not occur in North America.

***Economic plants and products***: *Nepenthes* is widely cultivated (in greenhouses) as a curiosity because of its unusual and beautiful, prey-catching and digesting leaves.

***Discussion***: The monophyly of Nepenthaceae is well supported by both morphological (Cheek and Jebb 2001; Kubitzki 2003c; Stevens 2001 onward; see description) and molecular (Alamsyah and Ito 2013; Meimberg and Heubl 2006; Meimberg et al. 2001) characters. *Nepenthes pervillei* (Seychelles), *N*. *madagascariensis*, *N. masoalensis* (both Madagascar), and *N. distillatoria* (Sri Lanka) represent basally branching lineages. The acidic, pitcher fluid contains viscoelastic biopolymers (which increase the surface tension, keeping insects trapped in fluid, and eventually drowning), digestive enzymes (including proteases and chitinases), pathogen-suppressing proteins and naphthoquinones (deterring growth of fungi, bacteria). Various arthropods (or even small vertebrates) are attracted by the colorful, nectar-producing pitcher-leaves; they slip and fall into the pitcher-fluid, and eventually are digested. The same plant often produces pitchers of various forms. The leaf is developmentally complex, with the phyllodium representing the leaf base, the cirrhus the petiole, and the pitcher the involute-vernate lamina (Troll 1932). The longitudinal pitcher-wings may represent the true leaf margins.

 The long-functioning flowers are pollinated by various flies (especially blowflies, midges, mosquitos), bees, beetles, moths, and butterflies; the flowers produce various odors (fetid, musty, fungus-like or sweet). The tiny, tailed seeds are possibly wind dispersed.

***Additional references***: Ravee et al. 2018; Rottloff et al. 2011.

**Tamaracaceae** (Majure)

*Santalales*

**Balanophoraceae** Richard

(Snake-mushroom Family)

*Fleshy, root parasitic herbs*, **without chlorophyll**, *and yellow, red, or brown*; **roots lacking**, and above-ground to ± below-ground inflorescences developing **from a ± spherical, irregularly lobed, or branched tuber**, sometimes with rhizome-like outgrowths, **and derived from tissues of the parasite or the parasite and host mixed**, containing tannins, starch, or less often a waxy substance, balanophorin. **Vegetative stems lacking, and inflorescences developing endogenously (within tubers), erupting at maturity and leaving a collar-like structure**. Hairs simple. *Leaves/inflorescence bracts alternate and spiral* or 2-ranked, opposite and decussate, or whorled, *scale-like*, triangular, peltate, or distally expanded and club-shaped, **without stomates**, sometimes lacking, entire, with obscure, ± parallel venation; stipules lacking. **Inflorescences indeterminate, terminal, spadix-like, with numerous, densely packed, minute flowers**, branched or unbranched, *and fungus-like*. *Flowers unisexual* (*and plants monoecious or dioecious*), usually radial. *Tepals 0-14*, distinct to basally connate, valvate or imbricate, in staminate flowers*; tepals usually absent or very reduced, 0-4*, distinct to connate in carpellate flowers. *Stamens 1-4* (-6) or rarely more numerous, *often opposite the tepals*; *filaments distinct to more commonly connate*, free from perianth; *anthers dithecal, monothecal, or multithecal*, (i.e., with 2 to several pollen sacs), *distinct to connate into a multiloculate synandrium*, opening by slits or pores; pollen grains tricolpate, tricolporate, triporate or polyporate. *Carpels usually 2-3*, but sometimes apparently only 1 (and pseudomonomerous), connate; *ovary inferior or nude*, **solid** (i.e., **without locules**) and with 1 or 2 female gametophytes, and these conditions perhaps derived (by reduction) from free-central placentation; style(s) 1, as many as carpels, or absent; stigma(s) punctate to capitate. *Ovules extremely reduced*, 1 or 2 per gynoecium, without recognizable sporangium wall or integuments. Nectar production often occurring, possibly extrafloral. **Fruit an achene**; seed with or without a testa; **the embryo undifferentiated, without a suspensor**; endosperm present.

***Floral formula***:

Staminate: \* , T -0-14- , A 1-6 , G 0

[Put a dashed line around the 0-14 tepals]

Carpellate: \* , T -0-4- , A 0 , G 1-3 ; achene

[Put a dashed line around the 0-4 tepals; circle the 1-3 carpels; put a line above the 1-3 carpels]

***Distribution***: Pantropical, with temperate extension in eastern Asia.

***Genera/species***: 14/40. ***Major genera***: *Balanophora* (15 spp.), *Ombrophytum* (4), and *Scybalium* (4). No member of the familial clade occurs in the United States or Canada, although *Scybalium* occurs nearby (in the Caribbean).

***Economic plants and products***: Essentially none, although a few species are eaten locally.

***Discussion***: The genera *Mystropetalon*, *Dactylanthus*, and *Hachettia* traditionally have been included in Balanophoraceae (as subfamilies Mystropetaloideae and Dactylanthoideae), but their inclusion renders the family biphyletic. Therefore, they here are excluded (following Su et al. 2015; see also Nickrent 1997 onward, 2020) and are recognized as Mystropetalaceae (and characterized by their flowers being less reduced than in Balanophoraceae s.s.). Although the family has long been of uncertain position, it is now clear that both Mystropetalaceae and Balanophoraceae s.s. belong within Santalales. The monophyly of Balanophoraceae, as restrictively circumscribed, is supported by DNA sequences (Nickrent 1997 onward; Su et al. 2015) and the clade’s distinctive morphology (Kuijt 1969; Kuijt and Dong 1990; Kuijt and Hansen 2015d; Stevens 2001 onward; see also description), although there is morphological convergence between Balanophoraceae and Mystropetalaceae, and to a lesser extent Cynomoriaceae (only *Cynomorium*). *Cynomorium* is only distantly related, belonging most likely in Saxifragales (Bellot et al. 2016; Nickrent 2020; Nickrent et al. 2005) although it has sometimes been placed in Rosales (Zhang et al. 2009). Balanophoraceae have undergone rapid evolutionary changes in their DNA nucleotide sequences, and host genes have become incorporated into their mitochondrial genome.

 The flowers of Balanophoraceae are pollinated by various insects (especially flies, beetles, and bees), mammals, and birds. Dispersal of the small achenes is poorly understood.

***Additional reference***: Gonzalez and Mauseth 2010.

**Cervantesiaceae** Nickrent and Der

(Buffalo-nut Family)

*Root parasitic trees or shrubs*, sometimes with thorns, with or without rhizomes; often with acetylenic acids and/or thionins (antimicrobial and cytotoxic peptides); **wood lacking vasicentric tracheids**. *Roots modified to form haustoria*. Hairs simple. *Leaves green, with chlorophyll, alternate and spiral,* simple, entire, with pinnate venation, the apex sometimes spinose, the mesophyll with groups of silicified cells; stipules lacking. Inflorescences determinate or indeterminate, sometimes reduced to a solitary flower, terminal or axillary. *Flowers bisexual or unisexual* (*and then usually dioecious*) but carpellate flowers often with well-developed staminodes, radial, pedicellate or sessile, *± small to medium-sized*. *Calyx absent*. *Petals 4-5, distinct to slightly connate, valvate*, usually green or yellow-green, sometimes orange tinged, *with hair-tufts opposite stamens*, and these sometimes sticky, then ± adhering to stamens. *Stamens 4-5, opposite the petals*, distinct; filaments free or adnate to base of petals; anthers opening by slits; pollen grains with 3 apertures. **Carpel apparently 1** (possibly pseudomonomerous); *ovary nearly superior to inferior* (and position changing during floral/fruit maturation), with free-central placentation; style 1, long to short or absent; stigma ± capitate to lobed; pistillode present in staminate flowers. Ovules 2-3 per gynoecium, pendulous atop straight to twisted column, with 1 integument or without an integument. *Nectar disk present*, **with variously developed lobes between the petals**. *Fruit a non-viscus drupe, often with accrescent petal bases, and unusual because exocarp and associated petal bases sometimes dehiscing, mesocarp hard, and endocarp absent*, with a single seed.

***Floral formula***: \* , K 0 , C 4-5 , A 4-5 , G 1 ; drupe

[Circle the 1 carpel; add a line above and below the 1 carpel]

***Distribution and ecology***: Tropical and warm temperate, eastern North America to South America, western and central Africa, Madagascar, eastern to southern Asia, to Malesia. Root parasites.

***Genera/species***: 8/21. ***Major genera***: *Acanthosyris* (6 spp.) and *Scleropyrum* (4). *Pyrularia* is native in the eastern United States.

***Economic plants and products***: The fruits of *Acanthosyris* are occasionally eaten. *Pyrularia* (buffalo-nut) is extremely poisonous because it contains thionins (snake-oil poisons), which have a physiological effect similar to that of cobra venom.

***Discussion***: The monophyly of Cervantesiaceae is well supported by DNA sequences (Der and Nickrent 2008; Nickrent et al. 2010; Rogers et al. 2008; Su et al. 2015; Zhou et al. 2019), however morphological support is weak (see Nickrent 1997 onward, 2016a; Nickrent et al. 2010; Norverto 2011; and description). *Acanthosyris*, *Cervantesia*, and *Jodina* form a clade that is sister to the five remaining genera. Cervantesiaceae is probably most closely related to Thesiaceae, which in North America includes *Buckleya* (native; shrub with 2-ranked leaves; drupes) and *Thesium* (introduced; herb with spiral leaves; achenes). The genera of Cervantesiaceae can also be confused with Comandraceae, but Cervantesiaceae differ from Comandraceae in their woody habit (vs. herbs) and flowers that have well-developed, almost perianth-like lobes on the nectar disk (vs. disk not as strongly lobed). The Cervantesiaceae, Thesiaceae, and Comandraceae were traditionally included in a broadly circumscribed and non-monophyletic Santalaceae (Cronquist 1981; Kuijt 1969; Kuijt and Hansen 2015).

 The usually greenish flowers of Cervantesiaceae are likely insect pollinated. Their drupes are dispersed by birds, mammals, or water (floating).

**Comandraceae** Nickrent and Der

(Bastard Toadflax Family)

*Rhizomatous, root-parasitic* **herbs**; lacking cystoliths. *Roots modified to form haustoria*. Hairs simple. *Leaves green, with chlorophyll, alternate and spiral*, simple, entire, with pinnate venation, the mesophyll with groups of silicified cells; stipules lacking. Inflorescences determinate, axillary or terminal. *Flowers all bisexual, or bisexual and staminate together* (andromonoecious), radial, pedicellate, *showy*, often with hypanthium (also interpreted as a corolla tube). *Calyx absent*. *Petals usually 5, distinct or connate* (and connate portion often interpreted as a hypanthium), greenish to white (rarely pinkish), *with a tuft of hairs opposite each stamen*, **these hairs sticky and becoming attached to connective of each anther**. *Stamens usually 5, opposite the petals*, distinct; filaments free, on ovary or hypanthium (could also be interpreted as adnate to corolla tube); anthers opening by slits; pollen grains tricolpate. **Carpel apparently 1** (perhaps pseudomonomerous); *ovary inferior*, with free-central placentation; style 1, with stylar canal; stigma capitate to punctate. Ovules usually 3 per gynoecium, pendulous on elongate, twisted column, with 1 integument. Nectar disk slightly lobed, atop ovary. *Fruit a non-viscid drupe, unusual because exocarp leathery to fleshy, mesocarp hard, and endocarp thin*, with a single seed; **zygote with first division vertical**.

***Floral formula***: \* , K 0 , C 5 , A 5 , G 1 ; drupe

[Draw a dashed line below formula connecting 5 petals and 5 stamens; circle the 1 carpel and draw a line above it]

***Distribution and ecology***: Temperate North America, southwestern Europe (Balkans), and Asia Minor. Root parasitic herbs.

***Genera/species***: 2/2. ***Genera***: *Comandra* (1 sp.) and *Geocaulon* (1). Both *Comandra umbellata* and *Geocaulon lividum* occur in the United States and Canada.

***Economic plants and products***: Both genera were used medicinally by native Americans.

***Discussion***: The monophyly of Comandraceae is supported by DNA sequences (Der and Nickrent 2008; Nickrent et al. 2010; Su et al. 2015; Zhou et al. 2019). The herbaceous habit, apparent single carpel, details of embryology, and perhaps also the anthers sticking to the petal-hairs area constitute putative morphological synapomorphies (Fernald 1928; Nickrent 1997 onward, 2016b; Nickrent et al. 2010, 2019; Stevens 2001 onward). *Comandra* (terminal inflorescences, bisexual flowers, fruits with leathery exocarp) is sister to *Geocaulon* (axillary inflorescences, unisexual and bisexual flowers, fruits with fleshy exocarp). The familial clade is related to families such as Cervantesiaceae, Santalaceae, Thesiaceae, and Viscaceae. Both genera of Comandraceae traditionally were included within an expanded Santalaceae (e.g., Cronquist 1981; Kuijt 1969; Kuijt and Hansen 2015). Comandraceae can be confused with herbaceous members of Schoepfiaceae, but Comandraceae lack an epicalyx and are unicarpellate. They are distinguished from Cervantesiaceae by their herbaceous habit.

 The showy flowers of Comandraceae are pollinated by bees, flies, beetles, and butterflies. The fruits are dispersed by birds and mammals.

***Additional reference***: Smith and Smith 1943.

**Misodendraceae** J. Agardh

(Feather-mistletoe Family)

**Stem- or epiphytic, parasitic shrubs**, on branches of *Nothofagus*; plants green, with chlorophyll; stems warty or not, ± thick, often with successive cambia, **stem apices aborting and growth sympodial**; **sieve tube plastids lacking both starch and protein inclusions**. *Roots modified to form haustoria*. Hairs absent or simple. *Leaves alternate and spiral*, simple, entire, *with palmate to ± parallel venation*, *or veins reduced*, the blade expanded or reduced and scale-like, sometimes heterophyllous; **mesophyll** **undifferentiated**, often with scattered groups of silicified cells; stipules lacking. Inflorescences determinate, but appearing indeterminate (*catkin-like spikes or racemes*), axillary. *Flowers usually unisexual* (**and plants dioecious**), radial, the carpellate flowers sessile. *Calyx absent*. **Petals absent in staminate flowers**, *3 in carpellate flowers*, ± *distinct* (but connate at extreme base) **and adnate to gynoecium, except near petal margins**, valvate, greenish. *Stamens 2-3*; filaments distinct; **anthers with 1 pollen sac (theca), opening by an apical slit**; **pollen grains 4-19-porate or polycolporate**, **the exine surface minutely spiny**. *Staminodes of carpellate flowers 3*, **alternating with the petals and basally adnate to gynoecium, emerging from near base of slits** (between petals). *Carpels 3, connate*; *ovary ± inferior, but staminodes attached near ovary base,* *with free-central placentation*; style very short; stigmas 3-lobed; inconspicuous pistillode in staminate flowers. Ovules 3 per gynoecium, pendulous from the top of the column, not internally differentiated. Nectar disk lobed, intrastaminal in staminate flowers, and ± epigynous disk between petals and style in carpellate flowers. **Fruit an achene**, **attached to 3 accrescent, long-plumose staminodes** (*growing from slits on the fruit*); seed lacking a testa; embryo with cotyledons ± connate, **the radicle replaced by a sticky sheath**; endosperm green.

***Floral formula***:

Staminate: \* , K 0 , C 0 , A 2-3 , G 3**.**

[Circle the 3 sterile carpels]

Carpellate: \* , K 0 , C 3 , A 3**.** , G 3 ; achene

[Draw a line above the 3 carpels, circle the 3 carpels]

***Distribution and ecology***: Cool temperate, southern South America. Plants are stem-parasites, restricted to *Nothofagus* (Nothofagaceae).

***Genera/species***: 1/8. ***Genus***: *Misodendron* (8 spp.). The clade does not occur in North America.

***Economic plants and products***: None.

***Discussion***: The monophyly of Misodendraceae is supported by DNA sequences (Vidal-Russell and Nickrent 2007) and the familial clade is related to Schoepfiaceae and Loranthaceae (Der and Nickrent 2008; Malécot and Nickrent 2008; Nickrent et al. 2010; Su et al. 2015; Vidal-Russell and Nickrent 2008). The monophyly of the family is also supported by several distinctive morphological synapomorphies (Kuijt 1969; Kuijt and Hansen 2015a; Nickrent 1997 onward; Stevens 2001 onward; Zavaro and Crisci 1997; see also description). *Misodendron* *quadriflorum* is sister to the remaining species in the analysis of Vidal-Russell and Nickrent (2007; based on molecular data), but not in the morphology-based analysis of Zavaro and Crisci (1997). The stem-parasitic habit has evolved several times within Santalales. The condition is a synapomorphy of Misodendraceae, but is also synapomorphic for Viscaceae, and has evolved within Loranthaceae, Santalaceae, and Amphorogynaceae.

 The pollination biology of *Misodendron* is unknown, although the inconspicuous flowers likely are insect pollinated. The achenes, with their elongate, feathery staminodes, are dispersed by wind.

***Additional references***: Carlquist 1985; Skottsberg 1913; Smith and Smith 1943.

**Opiliaceae** Valeton

(Bally-coma Family)

*Root-parasitic trees, shrubs*, or occasionally lianas; **tissues with siliceous cystoliths**. *Roots modified to form haustoria*. Hairs usually absent, but simple when present. *Leaves green, with chlorophyll, alternate, 2-ranked or spiral*, simple, entire, with pinnate venation, **the lamina with tubercles when dried because of numerous mesophyll cystoliths**, **and mesophyll cells not silicified**; stipules absent. Inflorescences determinate, but often appearing indeterminate, axillary or cauliflorous. *Flowers bisexual or less commonly unisexual* (plants then ± dioecious), radial, *small*, usually pedicellate, and without bracteoles. *Calyx inconspicuous*, reduced to a cup-like rim, or with 4-5 small teeth, or entirely lacking. *Petals 4-5, but lacking in carpellate flowers*, *distinct or basally connate* (rarely more strongly connate), *valvate*. *Stamens 4-5, opposite the petals*, distinct; filaments free or adnate to petals; anthers opening by slits; pollen grains tricolporate. *Carpels 2-5*, connate; *ovary superior to half-inferior*, with free-central to basal placentation; style 1, hollow, or absent; stigma ± capitate. **Ovule 1**, *pendulous from free-central axis*, or basal and erect (in *Agonandra*), in unilocular ovary, with 1 integument or not differentiated. Nectar glands alternating with stamens or forming a disk or cup. *Fruit a non-viscus drupe*; embryo with usually 3 or 4 cotyledons; endosperm abundant.

***Floral formula***: \* , K 4-5 or 0 , C 4-5 or 0 , A 4-5 , G 2-5 ; drupe

[Put a dashed line around the 4-5 petals; connect the stamens with the petals by a dashed line, drawn under the formula; circle the 2-5 carpels; put a line half-way through the carpels (to indicate half-inferior ovary)]

***Distribution and ecology***: Pantropical, with temperate extension in Australia; root parasites, in various habitats.

***Genera/species***: 12/36. ***Major genera***: *Agonandra* (10 spp.) and *Urobotrya* (7). The familial clade does not occur in the United States and Canada.

***Economic plants and products***: A few genera (i.e., *Cansjera*, *Champereia*, *Melientha*, and *Opilia*) have edible fruits.

***Discussion***: The monophyly of Opiliaceae is supported by DNA sequences (Der and Nickrent 2008; Le et al. 2017; Nickrent et al. 2019; Su et al. 2015) and morphology, especially the presence of siliceous cystoliths (but these probably lost in *Anthobolus*) (Koek-Noorman and van Rijekevorsel 1983; Kuijt and Hansen 2015b; Le et al. 2017; Nickrent 1997 onward; Nickrent et al. 2010; Stevens 2001 onward; see description). Relationships within Opiliaceae are only weakly supported, but the genera *Lepionurus*, *Agonandra*, and *Anthobolus* may represent more or less basal branches. The last is morphologically divergent and often has been placed in the Santalaceae s.l. Kuijt and Hansen (2015b) divide the family into four subgroups based on characters of inflorescence structure and pollen morphology, but these correspond poorly with the four tribes recognized by Le et al. (2017) based on DNA sequences. Opiliaceae are sister to the families of the Santalales s.l. complex, e.g., Comandraceae, Cervantesiaceae, Thesiaceae, Santalaceae s.s., and Viscaceae (Nickrent et al. 2010), from which they can be distinguished by the presence of silicified cystoliths and gynoecia with a single ovule.

 The inconspicuous flowers of Opiliaceae are pollinated by insects or wind. The fleshy fruits are probably bird dispersed.

**Schoepfiaceae** Blume

(Whitewood Family)

*Root-parasitic trees, shrubs, or perennial herbs, often rhizomatous*, sometimes with tubers. *Roots modified to form haustoria*. Hairs simple. *Leaves green, with chlorophyll, alternate and spiral*, simple, usually entire, with pinnate venation, the apex sometimes spinose, with silicified walls of epidermal cells. Inflorescences determinate to indeterminate, axillary or terminal, sometimes reduced to a solitary flower. *Flowers bisexual*, radial, sometimes sessile, *showy*, often **heterostylous**, **and usually with a cup-shaped epicalyx derived from fused bracts and bracteoles**, but absent in *Arjona*. *Calyx reduced to a short rim* (calyculus) *or absent*. *Petals usually 4-5, connate*, *with corolla urn-shaped* (*Schoepfia*) *or trumpet-shaped* (*Arjona* and *Quinchamalium*), *valvate*, greenish white to colorful*, often with a tuft of hairs on each corolla lobe opposite each anther. Stamens usually 4-5, opposite the petals*, distinct; filaments adnate to petals, elongate to nearly absent; anthers opening by slits**; pollen grains heteropolar, apertures ± confluent**, very diverse in number and form. *Carpels 2-3, connate*; *ovary half-inferior to inferior*, with free-central placentation; style long; stigma capitate to 3-lobed. Ovules 2 or 3 per gynoecium, pendulous, with 1 integument or often without differentiated integuments, the female gametophyte growing into the style in *Quinchamalium*. ± Epigynous nectar disk present. Fruit an achene (*Arjona*), *a non-viscid drupe* (*Schoepfia*), *or ± non-developed and accessory pseudofruit*, lacking a pericarp and with embryo and endosperm surrounded by accrescent bracts (*Quinchamalium*); seed lacking a testa.

***Floral formula***: \* , K rim or 0 , C 4-5 , A 4-5 , G 2-3 ; achene, drupe, accessory fruit

[Circle the 4-5 petals; draw a line below formula connecting the petals to the stamens; circle the 2-3 carpels; draw a line above the 2-3 carpels, and another line partly through the 2-3 carpels, to show ovary inferior to half-inferior]

***Distribution***: Neotropics and southeastern Asia to western Malesia.

Genera/species: 3/58. Genera: *Schoepfia* (25 spp.), *Quinchamalium* (25), and *Arjona* (8). Only *Schoepfia* occurs in the United States (southern Florida).

***Economic plants and products***: Edible tubers are produced by *Arjona*.

***Discussion***: The monophyly of Schoepfiaceae is supported by DNA sequences (Der and Nickrent 2008; Liu et al. 2018; Nickrent et al. 2010, 2019; Su et al. 2015) and although morphological support is rather weak (see description), the group’s morphological characters clearly distinguish it from other members of the basal “Olacaceae s.l. complex (Malécot et al. 2004; Nickrent 1997 onward; Nickrent et al. 2010). *Schoepfia* is sister to the *Arjona* + *Quinchamalium* clade, which is supported by their flowers with showy, trumpet-shaped corollas, and terminal spike-like inflorescences. *Schoepfia* traditionally was included in the broadly circumscribed, non-monophyletic “Olacaceae,” while *Arjona* and *Quinchamalium* were placed within Santalaceae s.l. Molecular data (see references cited above and under Santalales) support their placement in Schoepfiaceae, in a clade along with Misodendraceae and Loranthaceae.

 The usually showy flowers of Schoepfiaceae are pollinated by various insects, especially bees, butterflies, and flies. The drupes of *Schoepfia* are probably dispersed by birds.

***Additional references***: Kuijt 1969; Kuijt and Hansen 2015c; Robertson 1982; Werth and Baird 1979; Vidal-Russell 2019.

**Ximeniaceae** Horaninow

(Hogplum Family)

*Root-parasitic trees or shrubs*; with sclereids; often with tannins, saponins, quinones, triterpenoids, sesquiterpenes, steroids, and/or oleic, acetylenic, nervonic, ximenynic, and related acids; branches with axillary thorns in *Ximenia*. *Roots modified to produce haustoria* (connecting to other plants). Hairs simple, sometimes glandular. *Leaves green, with chlorophyll*, *alternate and spiral*, simple, entire, with pinnate or palmate venation, often with silicified walls of mesophyll and epidermal cells; stipules lacking. Inflorescences determinate and **± umbellate**, axillary. *Flowers bisexual*, radial, ± showy. *Sepals usually 4 or 5*, slightly connate, *lobes small*. *Petals usually 4 or 5, distinct*, valvate or imbricate, *often with hairs*, and these conspicuous in *Ximenia*. *Stamens 4-12*, distinct, **usually in 2 whorls**; filaments free or adnate to petals, short to elongate; anthers opening by slits or an elongated pore; pollen grains 3 or 4 zonoaperturate (and apertures elongate to round). *Carpels 2-4, connate; ovary superior*, with axile/free-central placentation, *with 2-4 locules*, at least in the lower portion of ovary; style 1, short to long; stigma ± capitate. *Ovules 1 per locule*, elongate, pendulous, with 1 or 2 integuments or without differentiated integuments. Nectar disk present or absent. *Fruit a non-viscid drupe*, **high in lipids**; embryo with cotyledons connate or not; endosperm present.

***Floral formula***: \* , K 4-5 , C 4-5 , A 4-12 , G 2-4 ; drupe

[Put a dashed line around the 4-5 sepals; below the formula connect the petals and stamens by a dashed line; circle the 2-4 carpels]

***Distribution and ecology***: Pantropical, with warm temperate extensions in North and South America. Root parasites, growing in a variety of plant communities.

***Genera/species***: 4/13. ***Major genus***: *Ximenia* (10 spp.). Only *Ximenia* is native in the United States (Florida).

***Economic plants and products***: *Malania olifera* (garlic-fruit tree) and *Ximenia americana* (hogplum, tallowwood, yellow-plum) provide seed oils, and both are used medicinally. The yellow drupes of *X*. *americana* are eaten.

***Discussion***: The monophyly of Ximeniaceae is supported by DNA sequences (Malécot and Nickrent 2008; Nickrent et al. 2010, 2019; Su et al. 2015) and morphology (Malécot et al. 2004; Nickrent 1997 onward; see also description). Ximeniaceae traditionally were included within a broadly circumscribed, and non-monophyletic “Olacaceae,” which represented the complex of basal branching clades within Santalales (see Nickrent 2020; Nickrent et al. 2010). Other segregates of “Olacaceae” include Erythropalaceae, Strombosiaceae, Coulaceae (all non-parasitic), and Olacaceae s.s. (which, like Ximeniaceae, are root parasites). Although *Ximenia* will produce haustorial attachments to the roots of many different host species, it is a facultative root parasite, and can be grown in a pot without a host, seemingly with no negative effects (Robertson 1982).

 The flowers are pollinated mainly by bees and wasps. The colorful drupes are dispersed by birds and/or mammals, but they can also float in water, and thus can be dispersed abiotically.

***Additional reference***: DeFillips 1969.

*Berberidopsidales*

**Berberidopsidaceae** Takhtajan

(Coral-vine Family)

**Vines or scandent shrubs**; *axillary buds in pairs*, with cyanogenic glycosides. Hairs (when present) simple. *Leaves alternate and spiral, simple, entire or spinose-serrate, with palmate venation*; stipules lacking. Inflorescences determinate (but raceme-like), terminal, or flowers solitary (sometimes 2 or 3) and axillary. Flowers bisexual, radial, *and pendulous*. **Perianth of tepals***, all except the outermost petaloid, these spiral, (9-) 12 (-15), distinct*, imbricate (*Berberidopsis*) or of sepals and petals, these whorled, 5 sepals and 5 petals, distinct, imbricate (*Streptothamnus*). *Stamens 6 to numerous*; *filaments usually short* (but long in *Streptothamnus*), distinct; pollen grains tricolpate or tricolporate. Carpels 3-5, connate; ovary superior, **with parietal placentation**; **style thick, hollow**; stigma capitate to punctate or slightly lobed. Ovules numerous per carpel. Nectar disk usually present. *Fruit a berry*. Seeds with tiny embryo.

***Floral formula***: \* T - 9-15 - , A 6-many , G 3-5 ; berry

[Replace “many” with infinity symbol; put a circle around the 3-5 fused carpels]

***Distribution***: Highly disjunct, in southern Chile and eastern Australia. The closely related Aextoxicaceae is restricted to southern Chile.

***Genera/species***: 2/3. ***Genera***: *Berberidopsis* (2 species), *Streptothamnus* (1).

***Economic plants and products***: *Berberidopsis corallina* (coral-vine) is sometimes grown as an ornamental due to its beautiful, pendent clusters of red flowers. Its stems are used in basket making by indingenous people in southern Chile.

***Discussion***: Berberidopsidaceae are related to Aextoxicaceae and both are placed in the Berberidopsidales, a grouping not evident until the advent of molecular data and likely related to the asterid clade (APG IV 2016; Hilu et al. 2003; Moore et al. 2010, 2011; Soltis et al. 2011, 2018; Zhang et al. 2020). Both families show leaves with cyclocytic stomata; their staminal filaments are usually short and the floral phyllotaxy is spiral (all very unusual conditions within the core eudicots). They are easily distinguished because Berberidopsidaceae has alternate leaves (vs. opposite in Aextoxicaceae), simple hairs (vs. peltate scales), bisexual (vs. unisexual) flowers, with a syncarpous ovary (vs. only a single carpel), and berries (vs. dry drupes). The monophyly of Berberidopsidaceae is supported by their parietal placentation and seed anatomy (see Stevens 2001 onward). *Streptothamnus* has not been included in a phylogenetic analysis and its placement within Berberidopsidaceae was doubted by Ronse de Craene (2017). If excluded than a perianth of tepals may be an additional family synapomorphy. Traditionally *Berberidopsis* and *Streptothamnus* were placed in Flacourtiaceae (Cronquist 1981; Warburg 1893), most genera of which are now placed in either Salicaceae or Achariaceae (of the parietal placentation clade of Malpighiales).

 The flowers are insect or bird pollinated and the berries likely bird dispersed.

***Additional references***: Baas 1984; Kubitzki 2007; Ronse de Craene 2004.

*Ericales*

**Actinidiaceae** Engler and Gilg

(Kiwifruit Family)

*Trees, shrubs, or twining lianas*; with tannins and iridoids, and sometimes with mucilage. Hairs simple to variously branched, multiseriate, often flattened, eglandular or glandular. *Leaves usually alternate and spiral*, *simple*, *toothed*, *with ± pinnate venation*; stipules absent or present and minute. Inflorescences determinate, axillary, sometimes reduced to a solitary flower. **Flowers unisexual** (*plants monoecious or dioecious*), *but often appearing bisexual*, radial. *Sepals usually 5*, distinct to basally connate, imbricate (usually quincuncial). *Petals usually 5*, distinct to basally connate, imbricate (usually quincuncial). *Stamens usually numerous*, developing centrifugally, occasionally as few as 10; filaments distinct, and free or adnate to base of petals; *anthers ± sagittate, inverting just before anthesis*, *opening by 2 apical (morphologically basal) pores or pore-like slits*; pollen grains tricolporate. *Carpels 3 to numerous*, connate; *ovary superior*, with axile placentation, often with an apical depression; **styles as many as the carpels or style 1 and distally branched***, but sometimes with a single, unbranched style,* hollow or not; stigmas ± elongate, when a single style, capitate or peltate. Ovules 10 to numerous per locule, with 1 integument and a thin-walled megasporangium. Nectar secreting tissue at base of petals. *Fruit usually a berry, with seeds in placental pulp, occasionally a leathery, loculicidal capsule*.

***Floral formula***:

Staminate: \* , K 5 , C 5 , A 10-many , G 3-many**.**

[Put a dashed line around 5 sepals; put a dashed line around 5 petals; under the formula connect the petals and stamens with a dashed line; circle the 3-many sterile carpels; replace many with an infinity symbol]

Carpellate: \* , K 5, C 5 , A 10-many**.** , G 3-many ; berry

[Put a dashed line around 5 sepals; put a dashed line around 5 petals; under the formula connect the petals and staminodes with a dashed line; circle the 3-many carpels; replace many with an infinity symbol]

***Distribution***: Neotropics and tropical to temperate eastern to southern Asia to northern Australia.

***Genera/species***: 3/415. ***Genera***: *Saurauia* (350 spp.), *Actinidia* (40), and *Clematoclethra* (25). *Actinidia* is occasionally naturalized in the eastern United States.

***Economic plants and products***: Several species of *Actinidia* have edible fruits, the most important of which is *A. deliciosa* (kiwifruit; hexaploid), which is closely related to and hybridizes with *A. chinensis* (wild kiwi; a diploid). *Actinidia polygama* (silver-vine) contains actinidine and dihydroactinidiolide, and is an amazing cat attractant, having an effect similar to catnip, but much more powerful. Finally, several species of *Actinidia*, especially *A. kolomikta* (variegated kiwi vine), are used as ornamentals. A few species of *Saurauia* and *Clematoclethra* are also occasionally grown as ornamentals.

***Discussion***: The monophyly of Actinidiaceae is supported by DNA sequences (Rose et al. 2018), but morphological synapomorphies are unclear (see Dressler and Bayer 2004). *Saurauia* (trees or shrubs, a retained ancestral character) is sister to the *Actinidia* + *Clematoclethra* clade, diagnosed (in part) by its lianous habit. *Actinidia* and *Saurauia* have styles entirely or distally distinct, while *Clematoclethra* has a simple, unbranched style. Having an androecium with numerous stamens is the derived condition in the family (a secondary increase based upon having only ten stamens). Hybridization (including introgressive hybridization), polyploidy, and reticulate evolution are common in *Actinidia*, leading to difficulties in both the recognition of species and phylogeny reconstruction (Atkinson et al. 1997; Chat et al. 2004; Li et al. 2002; Liu et al. 2010, 2017; Yao et al. 2015). It is also noteworthy that within *Actinidia* chloroplasts are paternally inherited, while mitochondria are maternally inherited. Species of *Actinidia* sect. *Leiocarpae* constitute a paraphyletic assemblage, which gave rise to a clade containing the remaining species (sharing the apomorphy of lenticels on the fruit exocarp).

 The showy flowers of Actinidiaceae are insect pollinated (mainly bees); the berries are dispersed by birds and mammals.

***Additional references***: Dickinson 1972; Löfstrand and Schönenberger 2015.

**Clethraceae** Klotzsch

(Sweet Pepperbush Family)

*Trees and shrubs*; with tannins and triterpenes. *Hairs simple, fasciculate, and/or stellate*. *Leaves alternate and spiral, often distally clustered on branches*, *simple, entire to toothed*, with pinnate venation (*Clethra*) or palmate venation (*Purdiaea*), occasionally with hair-tuft domatia on abaxial surface; stipules lacking. Inflorescences indeterminate, branched or not, terminal or axillary. *Flowers usually bisexual*, radial (*Clethra*) or slightly bilateral (*Purdiaea*), *with ± spreading perianth*; **the pedicel without a pair of bracteoles**, the floral bracts inconspicuous to occasionally expanded and conspicuous. *Sepals usually 5*, distinct to ± connate, imbricate (quincuncial), equal in size (*Clethra*), or the outer conspicuously larger than the inner (*Purdiaea*). *Petals usually 5, distinct to basally connate*, imbricate (quincuncial). *Stamens usually 10*; filaments distinct and free or adnate to petals at their very base; *anthers ± sagittate, inverting just before anthesis, opening by 2 apical* (morphologically basal) *pores or pore-like slits*; pollen grains tricolporate. *Carpels usually 3* (*Clethra*) *or 5* (*Purdiaea*), connate; *ovary superior*, with axile or apical-axile placentation; *style 1, hollow, internally fluted, often apically branched*; stigmas 3- or 5-lobed, or unlobed. *Ovules numerous per locule* (*Clethra*) *or only 1 per locule* (*Purdiaea*), with 1 integument and a thin-walled megasporangium. Nectar disk usually present, around base of ovary. *Fruit a loculicidal capsule* (*Clethra*) *or an indehiscent pod* (*Purdiaea*). Seeds with a very thin coat (testa) (*Clethra*) or the testa absent at maturity (*Purdiaea*), unwinged or winged.

***Floral formula***: \* or X , K 5 , C 5 , A 10 , G 3-5 ; capsule, indehiscent pod

[Put dashed circle around 5 sepals and 5 petals; below the formula, connect the petals and stamens with a dashed line; circle the 3-5 carpels]

***Distribution and ecology:*** Eastern Asia to Malesia, and in the Southeastern United States and Mexico, extending south through the Greater Antilles to South America, and also one species on Madeira; plants of usually moist habitats of acidic soils.

***Genera/species***: 2/95. ***Genera***: *Clethra* (83 spp.) and *Purdiaea* (12). Only *Clethra* occurs in the eastern United States and Canada.

***Economic plants and products***: Several species of *Clethra* (sweet pepperbush, sweetbush, summersweet) are used as ornamentals.

***Discussion***: The monophyly of Clethraceae is well supported by DNA sequences (Anderberg and Zhang 2002) although putative morphological synapomorphies are still rather unclear. *Purdiaea* traditionally was included in Cyrillaceae (Uphof 1942), based on its indehiscent fruits and seeds lacking a testa at maturity, but DNA-based phylogenetic analyses support it as the sister group of *Clethra*, and the two are quite similar in floral morphology (when compared with *Cyrilla* and *Cliftonia*), e.g., both have sagittate anthers that invert just before the flower opens, and the anthers open by two apical pores or pore-like slits (Anderberg and Zhang 2002; Fior et al. 2003; Schneider and Bayer 2004). The monophyly of *Clethra* is strongly supported and this species-rich clade is comprised of two major subclades (Fior et al. 2003; Sleumer 1967): *Clethra* sect. *Clethra* (seeds unwinged or in *C. arborea* with small wings at each end formed by irregular and fused cells, also including *C. alnifolia*, *C. acuminata*, *C. barbinervis*, *C. canescens*, and relatives), and *Clethra* sect. *Cuellaria* (seeds surrounded by a wing formed by free, elongated, flattened, and regular cells, including *C. alexandri*, *C. cubensis*, *C. mexicana*, *C. occidentalis*, *C. ovalifolia*, *C*. *scabra*, and relatives). *Clethra* once occurred in Europe (based on the fossil record) and *C. arborea*, growing only on Madeira, may be a relic related to these European fossils. There is much variation in chromosome number within *Clethra*, with species ranging from diploids to decaploids. *Purdiaea* is also monophyletic, with *P. belizensis* and *P. nutans* positioned as successive sisters to a clade comprising the Cuban endemic species.

 The white to pink, fragrant, and showy flowers of *Clethra* and *Purdiaea* attract a diverse array of insects (bees, wasps, beetles, butterflies) and also hummingbirds. The tiny, often winged, seeds of *Clethra* are wind dispersed, as are the small, indehiscent fruits of *Purdiaea*, with their associated, expanded calyx.

***Additional references***: Berazaín and Rodríguez 1992; Judd 2008; Thomas 1961; Wilbur and Hespenheide 1967.

**Cyrillaceae** Lindley

(Titi Family)

*Trees or shrubs*, often spreading by root sprouts; with tannins and ellagic acid; **sieve tube plastids with protein crystalloids and fibers**. Hairs simple (when present). *Leaves alternate and spiral*, *simple*, *entire*, with pinnate venation; stipules lacking, but colleters present in *Cyrilla*. Inflorescences indeterminate (racemes), terminal or axillary. *Flowers bisexual, radial, not pendulous and with spreading perianth*, with a pair of bracteoles on the pedicel. *Sepals usually 5*, distinct or basally connate. *Petals usually 5, basally connate*, **but appearing to be distinct**, imbricate, sometimes thickened and glandular in middle portion adaxially, *the corolla ± rotate*. *Stamens 5-10*; filaments distinct, ± terete or expanded basally; **anthers not inverting and opening by longitudinal slits, facing towards the center of the flower**; pollen grains usually tricolporate, greater than 11µm and exine usually without ornamentation (psilate). *Carpels 2-5*; *ovary superior*, with apical-axile placentation; **style 1 and short or absent**, *apically branched*, **and solid**; stigmas (or stigma-lobes) as many as the carpels, truncate to punctate. **Ovules 1-3 per locule**, with 1 integument and a thin-walled megasporangium. Nectar disk around base of ovary. **Fruit indehiscent**, *grooved or winged*, **with 1-5 seeds**, *thus an achene or samara, or a small, sometimes winged, indehiscent pod*. **Seeds with testa absent at maturity**.

***Floral formula***: \* , K 5 , C 5 , A 5-10 , G 2-5 ; achene-like, samara-like, indehiscent pod

[Put a dashed line around the 5 sepals; circle the 2-5 carpels]

***Distribution and ecology***: Southeastern United States, southern Mexico, Central America and the West Indies, south to northern South America; plants of moist to wet and acidic habitats, and occurring in cloud forests, pine forests, swamps, bogs, or along streams.

***Genera/species***: 2/10. ***Genera***: *Cyrilla* (9 spp.) and *Cliftonia* (1). Both genera occur in the United States.

***Economic plants and products***: *Cyrilla* (titi, leatherwood) is occasionally grown as an ornamental. It is also an important nectar source for honey.

***Discussion***: The monophyly of Cyrillaceae is supported both by morphology (see description; Copeland 1953; Kubitzki 2004b; Stevens 2001 onward; Thomas 1960, 1961; Vijayaraghaven and Dhar 1978) and DNA sequences (Anderberg and Zhang 2002). *Cyrilla* has flowers with five stamens and its fruits are unwinged; while *Cliftonia* has ten stamens and three- to five-winged fruits. Although *Cyrilla* is often considered to consist of only a single species, *C. racemiflora* (see Thomas 1960, 1961), it is extremely variable, and may include as many as nine species; more study is needed (see Matick 1935; Berazaín 2009). Although the familial clade is now restricted to the Americas, fossils suggest that in the Tertiary it also grew in western Europe.

 The showy, white to pink or violet flowers of Cyrillaceae are pollinated by various insects (especially bees). The small, indehiscent fruits are wind and/or water dispersed.

**Diapensiaceae** Lindley

(Pincushion-plant Family)

*Evergreen, often mat-forming, tiny shrubs, or herbs*; **the secondary wood without rays**; with ellagic acid and accumulating aluminum. Hairs simple. *Leaves alternate and spiral*, sometimes crowded on stems, simple, variously toothed or entire; **nodes usually trilacunar**. Inflorescences indeterminate, *often scapose*, or reduced to a solitary flower, terminal or axillary. *Flowers bisexual*, radial. *Sepals 5*, distinct or connate basally, imbricate. *Petals 5*, nearly distinct (*Galax*) *to connate*, the lobes imbricate, *shallowly to deeply toothed or entire*. **Stamens 5**, *often alternating with 5 staminodes*; **filaments flattened**, distinct or connate (monadelphous), *adnate to corolla tube*; anthers with usually 2 pollen sacs (thecae), but only 1 pollen sac in Galax, opening by longitudinal or transverse slits, **± incurved**, sometimes with appendages; pollen grains tricolporate. *Carpels 3, connate; ovary superior*, with axile placentation, but often becoming parietal above, style single, hollow, sometimes distally branched; stigma usually 3 lobed. Ovules few to numerous per carpel, anatropous to campylotropous, with 1 integument and a thin-walled megasporangium; **female gametophyte with persistent antipodal cells**, these occasionally numerous. Nectariferous tissue sometimes around ovary base. *Fruit a loculicidal capsule;* seeds small.

***Floral formula***: \* , K 5 , C 5 , A 5 + 5. , G 3 ; capsule

[Put a dashed line around the 5 carpels; circle the 5 petals; put a dashed line around the 5+5 stamens and staminodes; draw a line connecting stamens and petals under the formula; circle the 3 carpels]

***Distribution and ecology***: Arctic to north-temperate regions of North America, Europe, and Asia. Plants usually of arctic or alpine, open and rocky habitats.

***Genera/species***: 6/17. ***Major genera***: *Diapensia* (7 spp.) and *Shortia* (4). These two, along with *Galax* and *Pyxidanthera,* occur natively in the United States and/or Canada.

***Economic plants and products***: The leaves of *Galax urceolata* (beetleweed) are used in the florist trade.

***Discussion***: The monophyly and phylogenetic structure of Diapensiaceae is supported by DNA sequences (Higashi et al. 2015; Hou et al. 2015; Rönbloom and Anderberg 2002; Rose et al. 2018; Ye et al. 2020), and their monophyly is also supported by morphological characters (Palser 1963; Rönbloom and Anderberg 2002; Scott 2004; Stevens 2001 onward; Wood and Channell 1959; Xi and Tang 1990; see also description). *Galax* (Galaceae; petals nearly distinct, anthers with 1 pollen sac) is sister to the remaining genera (Diapensieae; petals clearly connate, anthers with 2 pollen sacs). Within the Diapensieae, *Pyxidanthera* is sister to the *Berneuxia* + *Schizocodon* + *Diapensia* + *Shortia* clade. The two arctic species of *Diapensia* (*D. lapponica, D. obovata*) are sister to the five species of the Himalayan-Hengduan Mountain clade (Hou et al. 2015; Ye et al. 2020). Tetraploids have repeatedly arisen from diploid ancestors in *Galax urceolata* (Servick et al. 2015).

 The showy flowers of Diapensiaceae are pollinated mainly by bees and flies. The small seeds likely are dispersed by wind and rain-wash.

**Marcgraviaceae** Berchtold & J. Presl

(Shingle-vine Family)

*Lianas* or rarely shrubs, *sometimes ± epiphytic*, *with adventitious roots and/or weakly twining*; tannins, various terpenes, and calcium oxalate raphides present; often with globular to dendritic sclereids. *Hairs absent*. *Leaves alternate, spiral or 2-ranked*, *monomorphic or heterophyllous, then with small, cordate-based leaves on sterile, root-climbing branches, and much larger leaves on fertile, rootless, pendulous branches*, with developing leaves enclosing shoot apex, the blade **entire** (but occasionally appearing crenate due to presence of marginal glands), *with pinnate venation*, **with marginal to abaxial, flat to cavity-forming, nectar glands** (often turning black); *stipules lacking*. *Inflorescences indeterminate* (and racemes, spikes, or umbels), terminal, erect or pendulous. *Flowers bisexual, radial,* **the subtending or pedicel-associated bracts cup-, pitcher-, boat- or spur-shaped and nectar-producing**, these associated with all the flowers, or in *Marcgravia*, only with specialized, aborted flower buds. *Sepals 4-5, ± distinct*, imbricate. *Petals 3-5, distinct to partly connate, or completely connate and then forming a cap* (deciduous upon floral opening). *Stamens* 5 to *numerous*; filaments ± flattened, distinct or basally connate; pollen grains usually tricolporate. *Carpels 2 to numerous,* connate*; ovary superior*, with **intruded-parietal** to axile **placentation**; *stigma 1, ± sessile*, or on short style, often lobed. Ovules numerous per carpel, with a thin-walled megasporangium. **Fruit a fleshy**, *variously opening capsule*; **seeds embedded in fleshy placental tissue**; endosperm ± absent.

***Floral formula***: \* K 4-5 , C 3-5 , A 5-many, G 2-many ; fleshy capsule

[Dashed-circle around the 3-5 petals; dashed circle around the 5-many carpels; replace “many” with infinity symbol; circle around the 2-many carpels]

***Distribution***: Neotropical.

***Genera/species***: 7/130. ***Major genera***: *Marcgravia* (60 spp.), *Souroubea* (20), and *Schwartzia* (18). No species are native or naturalized in the continental United States.

***Economic plants and products***: Species of *Marcgravia* are occasionally grown as ornamentals. Species of *Souroubea* are used medicinally (as a sedative) because of physiologically active pentacyclic triterpenes.

***Discussion***: The monophyly of Marcgraviaceae is supported by both morphology (see description, especially the nectar-producing floral bracts; see also Dressler 2004; Stevens 2001 onward) and DNA-sequence data (Anderberg et al. 2002; Morton et al. 1996; Savolainen et al. 2000b; Schönenberger et al. 2005; Ward & Price 2002). The familial clade is comprised of two large subclades: 1) Marcgravioideae (only *Marcgravia*), the monophyly of which is supported by the strongly heterophyllous shoots, 2-ranked leaves, nectariferous bracts borne on sterile pedicels, and 4-merous flowers with the petals connate and forming a deciduous cap; and 2) Noranteoideae (all other genera), without obvious morphological synapomorphies, and the plants with spiral, monomorphic leaves, nectariferous bracts associated with fertile flowers, and 5-merous flowers with petals distinct to only basally connate (and not forming a cap). The large genome size of Noranteoideae, however, may be synapomorphic (Schneider et al. 2015). Generic delimitation is based upon inflorescence form and the position and form of the nectar-producing bracts (Dressler 2004, 2017), but the umbellate inflorescences of *Marcgravia* and *Marcgraviastrum* evolved independently.

 The unusual and showy inflorescences of Marcgraviaceae probably are pollinated mainly by moths, birds, and bats, although selfing may also be common (Bailey 1922; Dressler 2004; Sazima et al. 1993, 1980; Tschapka et al. 2006). The fleshy fruits and seeds are often reddish and attract birds and mammals.

***Additional references***: Schönenberger et al. 2010; Von Balthazar and Schönenberger 2013.

*Garryales*

**Eucommiaceae** Engler

(Chinese-rubbertree Family)

**Deciduous** *trees*; tissues with iridoids (e.g., acucubin, eucommioside, eucommiol), alkaloids, saponins and sapogenins, tannins, inulin, and with sclereids, *and laticifers with elastic latex* (*gutta*); **nodes unilacunar**. Hairs simple. *Leaves alternate and spiral*, simple, *± serrate*, the teeth glandular, with pinnate venation; stipules absent. *Inflorescences axillary, fasciculate or reduced to a solitary flower, in axil of bracts on proximal portion of new shoots*. *Flowers unisexual* (*plants dioecious*), radial, and lacking bracteoles. **Perianth absent**. *Stamens 4-12*; **filaments** *distinct*, **very short***; anthers elongate*, **with apically prolonged connective**; pollen grains tricolporate. *Carpels 2*, connate; **ovary nude**, **flattened**, *with a single locule* (due to 1 carpel aborting) and with apical placentation; style 1, very short; stigmas 2, elongated, reflexed. Ovules 2, but only 1 developing, with 1 integument, **and micropyle long**. Nectary absent. **Fruit a samara**. Seed ± flattened, with seed coat membranous.

***Floral formula***:

Staminate: \* , T -0- , A 4-12 , G 0

Carpellate: \* , T -0- , A 0 , G 2 ; samara

[Circle the 2 carpels]

***Distribution***: China; but the fossil record indicates that the clade was once widespread in the Northern Hemisphere (Call and Dilcher 1997; Manchester et al. 2009).

***Genera/species***: 1/1. ***Genus***: *Eucommia* (1 sp.). *Eucommia ulmoides* is rarely naturalized in the eastern United States (Vincent 2002).

***Economic plants and products***: *Eucommia ulmoides* (Chinese-rubbertree) is used as a shade tree, is a medicinal plant (high blood pressure), and is the source of gutta-percha, which is used to insulate wire-ropes and cables, and also for dental supplies. The seed-oil is used industrially.

***Discussion***: The monophyly of Eucommiaceae, i.e., *Eucommia ulmoides,* is well supported by morphology (see description; Stevens 2001 onward; Zhang 2016) and its isolated phylogenetic position (Soltis et al. 2011). The tree can easily be recognized by the presence of gutta-percha; when the leaves and elm-like fruits are carefully torn apart, the torn halves remain attached by elastic strands. The Eucommiaceae are sister to Garryaceae (in Garryales, an order of the Asterid clade), a relationship supported by the presence of elastic latex (gutta, or gutta-percha), the dioecious condition, unilocular ovaries, and apical placentation, as well as DNA nucleotide sequences. However, *Eucommia* has often been placed in the Hamamelidae because of its reduced/inconspicuous flowers (Cronquist 1981; Zhang et al. 1990). The fruits of *Eucommia* are superficially similar to those of *Ulmus* (Ulmaceae) and the families sometimes have been considered to be related (Varossieau 1942).

 The flowers of Eucommiaceae are wind pollinated; the samaras are also wind dispersed.

*Icacinales*

**Icacinaceae** Miers

(Monkey-chair Family)

*Trees, shrubs, often scandent shrubs or lianas*, these twining, with nodal to internodal tendrils, or merely with scandent branches, the lower part of stem rarely enlarged, with monoterpenoids, diterpenoids, and/or sesquiterpenoids, iridoids, and various alkaloids; **vessel elements with simple perforations**; secondary growth normal or occasionally anomalous, e.g., alternating wedges of xylem and phloem (*Pyrenacantha*), successive cambia (some *Icacina*). Hairs unicellular, simple or T-shaped, eglandular, but sometimes apically ± swollen, sometimes distally hooked (uncinate), occasionally clustered and then appearing stellate. *Leaves usually alternate and spiral*, but occasionally opposite and decussate, *simple* but sometimes palmately lobed, entire or less commonly variously toothed, with pinnate to palmate venation; stipules absent. Inflorescences determinate or indeterminate, terminal, axillary, or cauliflorous. *Flowers small*, bisexual or less commonly unisexual (and plants then dioecious or monoecious), usually *radial*. *Sepals usually 4-5* (but absent in *Pyrenacantha*), *connate*, usually imbricate or valvate. *Petals usually 4-5*, free or more commonly slightly connate, often pubescent adaxially, *usually valvate*. *Stamens usually 4-5*; filaments distinct and free for adnate to corolla tube; anthers with connective sometimes extended into an appendage; pollen grains usually tricolpate, tricolporate, to triporate. *Carpels usually 3* (**but usually uniloculate**), connate; *ovary superior*, **with apical placentation in the single locule**; stigma usually capitate, punctate or peltate. *Ovules 2 per locule,* with 1 integument. Nectar disk present or absent. *Fruit a drupe; endocarp thin to thick, laterally ± compressed, smooth to longitudinally veined or ribbed, or pitted,* sometimes with tubercles protruding into locule. Seed 1; embryo straight to curved; endosperm sometimes ruminate.

***Floral formula***: \* K 4-5 , C 4-5 , A 4-5 , G 3 ; drupe

[Put a circle around the 4-5 sepals; put a dashed line around the 4-5 petals; draw a dashed line between the corolla and androecium; circle the 3 fused carpels.]

***Distribution***: Pantropical.

***Genera species***: 23/150. ***Major genera***: *Iodes* (30), *Pyrenacantha* (30), *Rhyticaryum* (12), and *Phytocrene* (11). None native to the continental United States, although *Mappia* reaches the Greater Antilles.

***Economic plants and products***: The tubers and seeds of *Icacina oliviformis* (false-yam) provide starch. *Pyrenacantha malvifolia* (monkey-chair) is grown as an ornamental because of its unusual dramatically expanded, above aground, basal stem. *Pyrenacantha* and a few other genera are used medicinally (see also Potgieter and Dumo 2016).

***Discussion***: Icacinaceae, as broadly circumscribed, have been shown to be extremely polyphyletic (Byng et al. 2014; Kårehed 2001; Lens et al. 2008; Savolainen et al. 2000b; Soltis et al. 2000, 2001; Stull et al. 2015, 2020; Zhang et al. 2020), and numerous genera, as a result, have been excluded – and placed in Metteniusaceae (of the Metteniusales, a basal lineage of either the campanulid or lamiid clades), in Cardiopteridaceae and Stemonuraceae (and placed in either the Cardiopteridales or Aquifoliales), in Oncothecaceae (Oncothecales; a basal lineage in the core asterids), and in Pennanthaceae (a basal lineage of Apiales). The monophyly of Icacinaceae s.s., the only family of Icacinales (a basal lamiid lineage), is supported by DNA sequence data, although only recently has the separation of Icacinaceae from Metteniusaceae become clearer (Byng et al. 2014; Lens et al. 2008; Stull et al. 2015, 2020; Zhang et al. 2020). The morphological characters of Icacinaceae (and the phenetically similar Metteniusaceae) may exhibit the features of ancestral members of the core asterid clade. Icacinaceae have unilacunar nodes, while the nodes of Metteniusaceae are usually trilacunar or pentalacunar (Bailey and Howard 1941). Cronquist (1981) considered the family to be related to Celastraceae and Aquifoliaceae, among others, and placed it in his Celastrales.

 The molecular analyses of Stull et al. (2015) support the *Mappia* + *Nothapodytes* clade as sister to the remaining genera of Icacinaceae, while other analyses place this clade in a more nested position (Stull et al. 2020). These two genera have retained the shrub to tree habit, while the derived condition of scandent shrubs to lianas is characteristic of most of the remaining genera (Potgieter and Duno 2016). Angulo et al. (2013) analyzed the phylogeny of *Mappia* and relatives using both morphological and molecular characters. Variation in wood anatomy in Icacinaceae has been assessed by Lens et al. (2008). The morphology of the endocarp is taxonomically informative at the generic level (del Rio et al. 2020). Hair morphology is also taxonomically significant in the group (Heintzelman and Howard 1948).

 The small flowers of Icacinaceae appear to be insect pollinated. The usually red to black drupes are dispersed by birds or mammals, although those of *Merrilliodendron* float and may, in part, be water dispersed.

*Solanales*

**Hydroleaceae** Edwards

(False Fiddleleaf Family)

*Herbs* to shrubs; internal phloem absent, and cortex often with air-canals; *1 or 2 axillary thorns per node often present*; with terpenoids, tannins, and alkaloids. Hairs simple, gland-headed or non-glandular. *Leaves alternate and spiral, simple*, entire to minutely serrate, with pinnate venation; stipules lacking. Inflorescences usually determinate, terminal or axillary. *Flowers bisexual, radial* to slightly bilateral. *Sepals usually 5, only slightly connate*, persistent*. Petals usually 5, connate*, and forming wheel-shaped to bell-shaped corolla, *not plicate*, *blue or white*, the lobes imbricate (quincuncial). *Stamens usually 5*, distinct; *filaments adnate to the corolla*, **usually conspicuously and abruptly broadened/lobed at base**; pollen grains tricolporate. *Carpels 2* (-5), connate, oriented obliquely to the median plane of the flower; *ovary superior, with axile placentation* and usually 2 locules**; styles usually 2, spreading**; stigmas slightly funnel-shaped to capitate. *Ovules numerous in each locule*, with 1 integument and a thin-walled megasporangium. Lobed nectar disk present or absent. *Fruit a loculicidal, septicidal, or irregularly dehiscent capsule*; seeds ovoid to cylindrical, **with longitudinal ridges**.

***Floral formula***: \* , K 5 , C 5 , A 5 , G 2 ; capsule

[Circle the 5 sepals; circle the 5 petals; draw a line under the formula connecting the petals and stamens; circle the 2 carpels]

***Distribution and ecology***: Tropical and warm temperate North and South American, Africa, Asia, and Australia; plants of aquatic and wetland habitats.

***Genera/species***: 1/11. ***Genus***: *Hydrolea* (11 spp.). Both native and naturalized species of *Hydrolea* occur in the eastern United States.

***Economic plants and products***: Species of *Hydrolea* (false fiddlehead, skyflower) are occasionally used medicinally or as ornamentals.

***Discussion***: The monophyly of Hydroleaceae is supported by morphology (see description; Bittrich and Amaral 2016; Stevens 2001 onward) and DNA sequences (Cosner et al. 1994; Ferguson 1998; Refulio-Rodriguez and Olmstead 2014; Soltis et al. 2011). Traditionally, *Hydrolea* was included in the Hydrophyllaceae (now placed within an expanded Boraginaceae, a group with scorpioid cymes), but its endosperm development is quite different from that of genera formerly placed in Hydrophyllaceae (Di Pulvio de Basso 1990). Molecular data place *Hydrolea* in the Solanales, as the sister group of Sphenocleaceae, a family with spicate inflorescences, flowers with a more or less inferior ovary, and circumscissile capsules. In addition, the flowers of *Hydrolea* show late sympetaly (Erbar et al. 2005), like most Solanales, while those of *Sphenoclea* show early sympetaly. *Hydrolea* is divided into two sections, i.e., sect. *Hydrolea* (placentas 2-lobed; New World species) and sect. *Attaleria* (placentas unlobed; Old World species) (Davenport 1988).

 The showy, usually sky-blue flowers are pollinated by various insects. The small seeds float, and are water dispersed.

*Gentianales*

**Gelsemiaceae** L. Struwe and V. Albert

(Yellow-jessamine Family)

*Shrubs, trees, or twining lianas*; with highly toxic indole alkaloids and plant sterols; stems with internal phloem. Hairs simple or plant glabrous. *Leaves usually opposite and decussate*, but alternate and spiral in *Pteleocarpa*, simple, *entire* to occasionally slightly dentate, with pinnate venation; *stipules interpetiolar*, sometimes reduced and forming a nodal line or sheath, *colleters often present* at base of adaxial surface of petiole. Inflorescences determinate, terminal or axillary, sometimes reduced to a solitary flower. *Flowers bisexual, radial, often heterostylous*. *Sepals 5*, basally connate, often with colleters on adaxial surface. *Petals 5, connate*, forming a funnel-shaped to trumpet-shaped corolla, **yellow** to white, the lobes imbricate. *Stamens 5*, distinct; *filaments adnate to corolla*; **anthers opening by lateral slits**; pollen grains tricolporate. Carpels 2, connate; *style 1, distally twice divided* (*Gelsemium*, *Mostuea*) *or styles 2* (*Pteleocarpa*); stigmas punctate to capitate. Ovules 2 to several per locule, with 1 integument and a thin-walled megasporangium. Nectary unclear. *Fruit a* **flattened**, *loculicidal and/or septicidal capsule* (*Gelsemium*, *Mostuea*), or **flattened**, *usually 2-winged samara* (*Pteleocarpa*); **seeds flattened**, sometimes winged or hairy.

***Floral formula***: \* , K 5 , C 5 , A 5 , G 2 ; capsule, samara

[Circle the 5 sepals; circle the 5 petals; below the formula draw a line connecting the petals and stamens; circle the 2 carpels]

***Distribution***: Temperate to tropical, North America, northern South America, Africa, eastern and southern Asia.

***Genera/species***: 3/13. ***Genera***: *Mostuea* (9 spp.), *Gelsemium* (3), and *Pteleocarpa* (1). Only *Gelsemium* occurs in the United States.

***Economic plants and products***: Both *Mostuea* and *Gelsemium* are used medicinally (but are highly poisonous, and the latter has been used for murder and suicide, and causes livestock poisoning); honey containing *Gelsemium* nectar is toxic to humans (Struwe 2018). *Gelsemium* *sempervirens* (yellow-jessamine) is commonly cultivated, because of its showy, early-blooming, fragrant, and bright yellow flowers.

***Discussion***: The monophyly of Gelsemiaceae is supported by morphology (Struwe 2018; Struwe et al. 1994, 2014; see description) and DNA sequences (Backlund et al. 2000; Jiao and Li 2007; Refulio-Rodriguez and Olmstead 2014; Savolainen et al. 2000b; Struwe et al. 1994, 2014; Yang et al. 2016). *Pteleocarpa* (with the putative apomorphies of alternate leaves and samara fruits) is sister to the *Mostuea* + *Gelsemium* clade (retaining the plesiomorphies of opposite leaves and capsular fruits, and supported by the synapomorphy of twice-divided styles). Within *Gelsemium*, the North American species (*G. sempervirens, G. rankinii*) are sister to the eastern Asian *G. elegans*. Within *Mostuea*, the Neotropical *M*. *surinamensis* and probably also *M. muricata* are sister to a clade comprising the African species. *Gelsemium* and *Mostuea* traditionally have been placed in Loganiaceae (Rogers 1981) while *Pteleocarpa* variously has been classified in Boraginaceae, Olacaceae, Sapindaceae, or in its own family (Brummitt 2011).

 The showy flowers are pollinated by various bees. The flattened seeds of the capsular species are likely wind dispersed, as are the samaras of *Pteleocarpa lampoga*.

*Lamiales*

**Calceolariaceae** Olmstead

(Slipper Flower Family)

*Herbs* or shrubs, **the wood rayless**; plants with iridoids, diterpenes, triterpenes, naphthoquinones, and phenylpropanoids. Hairs simple, eglandular or gland headed. *Leaves opposite and decussate*, sometimes in a basal rosette, simple, sometimes deeply pinnately lobed, toothed to occasionally entire, with pinnate venation; stipules lacking. Inflorescences determinate, terminal or axillary, sometimes reduced to a solitary flower. *Flowers bisexual, bilateral*. **Sepals 4***,* slightly connate, *valvate*. **Petals 4**, connate, the **corolla** with a short tube **and 2, ± rounded lobes/lips**, **so appearing as only having 2 petals**, these valvate, *the lower lobe merely cupped*, *or saccate to strongly inflated and slipper-like*, the same size to much larger than the upper lobe, **and each corolla lobe developing from a uniform meristematic ridge**; *the lower lobe usually with a median portion, infolded, and bearing a region of dense, oil-secreting, gland-headed, multicellular hairs*. **Stamens 2**; *filaments adnate to corolla*; anthers 2-locular, but the anther sacs sometimes ± confluent, opening by 2 slits or a single curved slit; pollen grains tricolporate. *Carpels 2, connate*; *ovary superior* to half-inferior, with axile placentation, the placentas undivided; stigma punctate to capitate or 2-lobed. Ovules usually numerous in each locule, with 1 integument and a thin-walled megasporangium. **Nectary absent**. *Fruit a septicidal and loculicidal capsule*.

***Floral formula***: X K 4 , C 4 , A 2 , G 2 ; capsule

[Circle the 4 sepals, circle the 4 petals, circle the 2 carpels]

***Distribution***: North America (Mexico) south through South America, and especially diverse in the Andes; New Zealand; occasionally naturalized elsewhere.

***Genera/species***: 2/260. ***Major genus***: *Calceolaria* (254 spp.). No species occur natively in the continental United States or Canada.

***Economic plants and products***: *Calceolaria* (slipper flower) is a popular ornamentals and is grown for its showy, slipper-like, usually yellow (but also red, pink, white, orange), occasionally spotted flowers. They are poisonous and occasionally used medicinally because of their various terpenoid compounds.

***Discussion***: The monophyly of Calceolariaceae is supported by morphology (Cosacov et al. 2009; Mayr and Weber 2005) and DNA-sequences (Andersson 2006; Cosacov et al. 2009; Olmstead et al. 2001; Refulio-Rodriguez and Olmstead 2014), but the familial clade until recently has been considered as a tribe within the Scrophulariaceae, as traditionally circumscribed (see discussion under Plantaginaceae). Calceolariaceae are recognized in the APG IV system (APG 2016; Stevens 2001 onward), and also recognized here, but the family was included within Gesneriaceae in Christenhusz et al. (2017). *Calceolaria* (including *Stenotria*) and *Jovellana* are sister taxa, together comprising the Calceolariaceae. Synapomorphies for *Calceolaria* include the saccate to inflated and slipper-like lower lip which produces a pad of oil-producing glandular hairs, and these likely represent key innovations leading to the evolutionary success of this species-rich genus. Three major clades are evident within *Calceolaria.* *Calceolaria* subg. *Cheiloncos* (flowers with long stamens) and subg. *Rosula* (rosette habit), both occurring in southern temperate regions, are successively sisters to the mainly tropical subg. *Calceolaria*, which is characterized by several homoplasious synapomorphies: simple hairs on both adaxial and abaxial leaf surfaces, the lack of glandular hairs on the leaves and calyx, closed flowers, and a short style (Cosacov et al. 2009). The family is most diverse in South America, but it is interesting that a long-distance dispersal event has resulted in *Jovellana* occurring in both Chile and New Zealand (Nylinder et al. 2012).

 The flowers of *Calceolaria* are mainly pollinated by oil-gathering bees (Renner and Schaefer 2010; Sérsic 2004) but oil-producing glandular hairs have been lost several times, and such species are pollinated by pollen-gathering bees or are selfing. Two species, *C. uniflora* and *C. fothergillii*, are bird pollinated. They have lost oil-producing glands and instead the lower lip of the corolla is modified to form a white, strongly contrasting, structure – a food body – which attracts and is eaten by birds (Sérsic and Cocucci 1996). The tiny seeds of *Calceolaria* are dispersed by wind or rain-wash.

***Additional reference***: Fischer 2004.

**Linderniaceae** Borsch, K. Müller & Eb. Fischer

(Wishbone-flower Family)

*Herbs*, sometimes soft-woody, occasionally of aquatic or wetland habitats; autotrophic, lacking haustoria; with triterpenoid saponins, and often unusual compounds, e.g., the sugar 2-octulose, involved in desiccation resistance, but lacking iridoids; roots sometimes orange or red; stems often square. Hairs simple or branched, eglandular or glandular, in the latter the head with vertical partitions. *Leaves opposite and decussate*, *simple*, entire to variously toothed or dissected, with pinnate or palmate venation; stipules lacking. Inflorescences indeterminate, terminal or axillary, sometimes reduced to a solitary, axillary flower. *Flowers bisexual and bilateral*. Sepals usually 5, ± connate, sometimes winged. *Petals usually 5, connate, the corolla usually ± 2-lipped, with glandular hairs on the inside*,the lobes imbricate. *Stamens 4, strongly didynamous, the lower stamens different from the upper, sometimes reduced to 2, and then with 2 staminodes,* **the stamens/staminodes often curved, bent, or Z-shaped***, and often variously appendaged, sometimes with glandular hairs*; *filaments adnate to corolla*; *anthers often sticking together in pairs*, usually 2-locular, locules distinct, opening by 2 longitudinal slits, the pollen sacs ± divergent; **pollen grains usually tricolpate**. *Carpels 2, connate; ovary superior with axile placentation*, the placentas moderate to large, *not divided*; **stigma** *2 lobed*, **expanded and sensitive**. Ovules numerous in each locule, with 1 integument and a thin-walled megasporangium. Nectar disk present. *Fruit usually a septicidal or septifragal capsule*; **seeds usually with rounded pits or longitudinal furrows**; **endosperm ruminate** (**±** **star-shaped in cross section**).

***Floral formula***: X K 5 , C 2 + 3 , A 2 + 2 or 2 + 2**.** , G 2 , capsule

[Circle the 5 sepals, circle the 2+3 petals, draw a line connecting stamens to petals, as in formula for Plantaginaceae, and circle the 2 carpels]

***Distribution and ecology***: Pantropical with temperate extensions in North America, Europe, and Eastern Asia; many are wetland plants and some are desiccation tolerant, e.g., *Chamaegigas intrepidus*, *Craterostigma* *plantagineum*.

***Genera/species***: 28/265. Major genera: *Vandella* (55 spp.), *Torenia* (51), *Crepidorhopalon* (30), and *Lindernia* (30). *Micranthemum* occurs natively and *Lindernia* has both native and naturalized species in the continental United States and/or Canada; *Torenia* is introduced in the southeastern United States and *Bonnaya* in Louisiana and Florida.

***Economic plants and products***: A few species of *Torenia* (wishbone flower, bluewings) are popular ornamentals; *Micranthemum umbrosum* (mudflower) is an aquarium plant.

***Discussion***: The monophyly of Linderniaceae is supported by DNA-sequence data (Albach et al. 2005l Biffin et al. 2018; Fischer et al. 2013; Oxelman et al. 2005; Rahmanzadeh et al. 2004), although there are also a few putative morphological synapomorphies (see description, and Stevens 2001 ongoing). The genera of Linderniaceae were traditionally included within a broadly circumscribed, and non-monophyletic Scrophulariaceae (Fischer 2004; see also discussion under Plantaginaceae). The *Stemodiopsis* + *Cubitanthus* clade is sister to the remaining genera. Members of Linderniaceae are easily confused with the Phrymaceae (see key), Plantaginaceae (but this familial clade has glandular hairs lacking vertical partitions, non-sensitive stigma lobes, and homogeneous endosperm), and Gesneriaceae (but this clade has parietal placentation and non-sensitive stigma lobes).

The variously colored flowers are usually pollinated by nectar-gathering bees. Nectar guides are common. A few have cleistogamous flowers and are selfing, e.g., species of *Micranthemum*.

***Additional references***: Almeida et al. 2019; Fischer 2004; Lewis et al. 2019; Tank et al. 2006.

**Martyniaceae** Horaninow

(Unicorn-plant Family)

*Usually herbs*, but shrubs in *Holoregmia*; with phenolic glycosides, iridoids, and sometimes cornoside; *roots often tuberous*. Hairs simple, nonglandular *or gland-headed*, with the cells of the head separated by vertical partitions, **viscid/sticky, and fetid**. *Leaves usually opposite and decussate*, but occasionally alternate and spiral, *simple*, entire to variously toothed or lobed, *with palmate or pinnate venation*, *often cordate at base*; stipules lacking. Inflorescences indeterminate, terminal. *Flowers bisexual and bilateral*. *Sepals 5*, ± distinct, or connate, and then with a vertical slit. *Petals 5, connate, the corolla ± 2-lipped*, the lobes imbricate. *Stamens 4, didynamous*, sometimes reduced to 2, along with 2 staminodes, the fifth stamen present as a staminode; *filaments adnate to corolla*; anthers 2-locular, the locules distinct, opening by 2 longitudinal slits, *the pollen sacs very divergent, spreading at an angle of 180 degrees*, **the anthers sticking together in pairs**; **pollen grains without apertures, the exine made up of 20-40 platelets**. *Carpels 2, connate*; *ovary superior*, **terminated by an incurved-beak-beak** (**sterile upper portion of ovary**), **with parietal placentation, the placentas intruded, T-shaped**, with ovules attached at ends of the cross-bar; stigma 2-lobed, *usually sensitive*. Ovules 2 to many per carpel, with 1 integument and a thin-walled megasporangium. Nectar disk present (around base of ovary). **Fruit a drupaceous, loculicidal capsule, with paired, short to elongate spurs or hooks, developed from sterile upper part of ovary**, *and usually having the appearance of the tusks of an elephant or mammoth*, but ± lacking in *Holoregmia*; **the outer portion of fruit ± fleshy, sloughing off, revealing the woody endocarp, with spines, crests, and/or ridges**. **Seeds large**, ± *globose, unwinged*; endosperm present but thin.

***Floral formula***: X , K 5 , C 2 + 3 , A 2 + 2 , G 2 ; drupaceous capsule with spurs/hooks

[Put a dashed line around 5 sepals; circle the 2+3 petals; draw a line below the formula connecting the petals and stamens; circle the 2 carpels]

***Distribution and ecology***: Temperate and tropical North and South America (although widely naturalized elsewhere). Typically, they are plants of weedy, disturbed, and/or arid habitats.

***Genera*/*species***: 5/16. ***Major genera***: *Proboscidea* (8 spp.), *Craniolaria* (3), and *Ibicella* (3). Only *Proboscidea* is native in the United States and Canada; *Martynia*, however, is introduced in the United States.

***Economic plants and products***: *Proboscidea louisianica* (unicorn-plant, devil’s claw, cow-catcher, mule-grab) and *Ibicella lutea* (yellow unicorn-plant) are grown as ornamentals. The young fruits and seeds of *Proboscidea* and *Ibicella* are eaten. The unusual fruits of various species of *Proboscidea* are used in dried flower arrangements or in weaving baskets. *Martynia annua* (tiger’s claw, cat’s claw) is a medicinal herb.

***Discussion***: The monophyly of Martyniaceae is supported by DNA sequences (Gormley et al. 2015; Gutierrez 2008, 2011; Oxelman et al. 2005) and morphology, especially the distinctive pollen grains and drupaceous capsules (Bretting and Nilsson 1988; Ihlenfeldt 2004; Stevens 2001 onward; Thieret 1977; see also description). Phylogenetic patterns within the family are still unclear, although *Proboscidea* may be related closely to *Martynia*. *Holoregmia* is morphologically distinctive (shrubby habit, fruit with very short spurs) and may be related to *Craniolana*, and the near absence of apical spurs in *Holoregmia* may represent an evolutionary loss (but see also Harley et al. 2003). The Martyniaceae sometimes have been combined with Pedaliaceae (Brummitt 1992; Cronquist 1981), an Old-World clade that also has fruits that are hooked or spiny, but its floral pedicels have paired, extrafloral nectaries, the pollen grains are aperturate, and the ovary has axile placentation.

 Insects frequently get caught in the glandular hairs of Martyniaceae, but the plants are not carnivorous. The hairs, however, probably are protective against herbivory.

 The showy flowers of Martyniaceae are pollinated by various bees or moths. The unusual 2-spurred or 2-hooked fruits are trample burrs, attaching to the feet of large mammals, e.g., horses, cattle, sheep, bison). The seeds of *Proboscidea* and *Ibicella* are gradually shed as the fruits are carried around by the animals, while in the few-seeded *Craniolaria* and *Martynia* the seeds remain in the fruits. The fruits of *Holoregmia* are not trample burrs, and their dispersal is unknown.

***Additional references***: Phillippi and Tyrl 1979; Thieret 1976.

**Mazaceae** Reveal

(Mazus Family)

*Herbs*, often with rhizomes or rooting at the nodes; with iridoids, phenolic glycosides, triterpene saponins, and alkaloids. Hairs simple, eglandular or glandular. *Leaves usually opposite and decussate*, but upper leaves occasionally alternate and spiral, *simple*, toothed to entire, or lobed, with pinnate venation; stipules lacking. Inflorescences indeterminate, usually terminal, sometimes scapose. *Flowers bisexual, bilateral*. *Sepals 5*, connate. *Petals 5, connate, the corolla 2-lipped, the lower lip well developed, usually with 2 longitudinal raised ridges*, the tube short to long, the lobes imbricate. *Stamens 4, didynamous*, a staminode lacking; *filaments adnate to corolla*; *anthers sagittate*, **often ± connate in pairs**; pollen grains tricolpate or tricolporate. *Carpels 2, connate; ovary superior, with axile placentation*, *the placentas not lobed*; style 1; **stigma** *± capitate*, **with 2 ridge-like lobes, these sensitive**. Ovules numerous, with 1 integument and a thin-walled megasporangium. Nectar disk at base of stamens. *Fruit a ± globose or ovoid, loculicidal capsule*, surrounded by persistent calyx, or rarely a berry. Seeds ellipsoid, tiny, not winged, with a reticulate testa; endosperm present.

***Floral formula***: X , K 5 , C 2 + 3 , A 2 + 2 , G 2 ; capsule

[Circle the 5 sepals, circle the 2+3 petals; draw a line below formula connecting the stamens and petals; circle the 2 carpels]

***Distribution***: Turkey and central Asia to eastern Asia and south to Australia, Tasmania, and New Zealand; also widely naturalized.

***Genera/species***: 3/38. ***Major genus***: *Mazus* (35 spp.). Two species of *Mazus* are naturalized in the United States.

***Economic plants and products***: *Mazus* is sometimes used medicinally, and it is a popular ornamental (a groundcover).

***Discussion***: The monophyly of Mazaceae has been supported by several recent DNA-based phylogenetic analyses (Albach et al. 2009; Deng et al. 2019; Schäferhoff et al. 2010; Xia et al. 2009); unfortunately, support from morphology is weak (see description; Reveal 2011) as is the case with several of the families of Lamiales. The Mazaceae are most closely related to Phrymaceae, Orobanchaceae, and Paulowniaceae, but the familial clade is probably most easily confused with Plantaginaceae (as both share many pleisiomorphic characters; compare descriptions). Plantaginaceae, however, lack sensitive stigmas, and their anthers are not connate in pairs. Both Phrymaceae and Mazaceae have sensitive stigmas, but the shape of their stigmatic lobes differs (see descriptions). Paulowniaceae are trees, with branched hairs, and winged seeds, while Orobanchaceae are hemi- to holoparasites (with root haustoria). *Mazus*, *Lancea*, and *Dodartia* historically were included in the Scrophulariaceae s.l. (in the tribe Mimuleae).

 The showy, blue to violet flowers of *Mazus* are pollinated by various bees (Jin et al. 2017). The small seeds are dispersed by raindrop-splash (Amador et al. 2012).

***Additional references***: Pringle 2018; Rawat et al. 1988.

**Paulowniaceae** Nakai

(Princess-tree Family)

**Trees**; with iridoids, phenolic glycosides and acids, quinones, lignans, terpenoids, and prenulated flavonoids; *young branches with conspicuous white lenticels*. **Hairs uniseriate-branched to stellate**, and also simple, gland-headed. *Leaves usually opposite and decussate*, sometimes whorled, *simple*, entire to serrate, occasionally lobed, with pinnate venation, often with extrafloral nectaries; stipules lacking. Inflorescences determinate, terminal. *Flowers bisexual, bilateral*, **with an open space between calyx and corolla**. *Sepals 5, connate* but deeply lobed, valvate, *densely covered with brown hairs*. *Petals 5, connate, the corolla ± 2-lipped, large, the tube elongate*, the lobes imbricate. *Stamens 4, didynamous*, the fifth stamen sometimes represented by a staminode; *filaments adnate to corolla*; *anthers sagittate*, **the endothecium massive, extending across the connective**; pollen grains tricolpate. *Carpels 2 connate*; *ovary superior, with axile placentation*, the placentas circular, not lobed; style 1, **hollow**; stigma punctate to capitate. Ovules numerous, with 1 integument and a thin-walled megasporangium. Nectar disk present. *Fruit a ± ovoid, loculicidal capsule*. **Seeds with several wings, the largest lateral, their margins ± sinuous, with cells elongated anticlinally**; endosperm present.

***Floral formula***: X , K 5 , C 2 + 3 , A 2 + 2 , G 2 ; capsule

[Circle the 5 sepals; circle the 2+3 petals; below the formula draw a line connecting petals and stamens; circle the 2 carpels]

***Distribution***: Eastern Asia.

***Genera/species***: 1/7. ***Genus***: *Paulownia* (7 spp., incl. *Shiuyinghua*). The genus is naturalized in the United States (and also in Europe).

***Economic plants and products***: *Paulownia* (princess-tree), especially *P. tomentosa*, is grown as an ornamental because of its showy, blue to violet or light purple to white flowers. Species of *Paulownia* are also used for timber, and their leaves are used for animal fodder, and also used medicinally.

***Discussion***: The family has only recently been widely recognized as a result of DNA-based phylogenetic analyses (Beardsley and Olmstead 2002; Luna et al. 2019; Olmstead et al. 2001; Oxelman et al. 2005; Refulio-Rodriguez and Olmstead 2014; Wortley et al. 2005; Xia et al. 2009). Traditionally *Paulownia* was placed either in the Bignoniaceae (Campbell 1930; Cronquist 1981; Takhtajan 1980) or Scrophulariaceae s.l. (Bentham and Hooker 1876; Takhtajan 1997), as it is woody and with winged seeds like the former, but has simple leaves, unlobed placentas, ovoid capsules, and seeds with endosperm like the latter. DNA-sequence data indicate that it belongs to neither familial clade (see Fig. 8.124)! The monophyly of Paulowniaceae is supported by DNA sequences (Li et al. 2020; Xia et al. 2019; Zhao et al. 2019) and morphology (Stevens 2001 onward), especially the seed morphology. The genus *Wightia* is sometimes placed in Paulowniaceae, but its inclusion likely would make the family non-monophyletic (Xia et al. 2019). Species relationships within *Paulownia* are still rather unclear, and interspecific hybridization is common. More study of the poorly known *Shiuyinghua* is needed, but it probably belongs within *Paulownia*.

 The colorful flowers with nectar guides are pollinated by various insects, especially bees, and the winged seeds are wind dispersed.

***Additional reference***: Paclt 1962.

**Tetrachondraceae** Wettstein

(Rustweed Family)

Herbs; **tissues with sorbitol** (a sugar alcohol), cornoside and verbascoside (phenylethanoid glycosides), and conandroside (a bitter glycoside), but iridoids lacking; roots adventitious, or not, and then with a taproot. Hairs simple, gland-headed or eglandular. *Leaves opposite and decussate*, *simple*, **± sessile**, entire to obscurely toothed, sometimes ciliolate, with obscurely pinnate venation; *leaf bases connected by stipule-like sheath*; **blade with stomates on both adaxial and abaxial surfaces**. Inflorescences determinate, axillary, or reduced to solitary flower. *Flowers bisexual, radial*, **quite small**. *Sepals usually 4, connate*. *Petals usually 4, connate*, white, ± wheel-shaped (rotate) to bell-shaped (campanulate), with or without hairs in the throat, the lobes imbricate. *Stamens usually 4, distinct; filaments adnate to corolla*; pollen grains tricolporate. *Carpels 2, connate*; ovary superior to partly inferior, 2-loculate (*Polypremum*) or 4-loculate, due to each carpel divided by a false septum (*Tetrachondra*), with axile placentation (*Polypremum*) or basal placentation (*Tetrachondra*); style gynoterminal (*Polypremum*) or gynobasic (*Tetrachondra*); stigma truncate to capitate. Ovules 2 per carpel and 1 in each locule (*Tetrachondra*) or numerous per carpel (*Polypremum*), with 1 integument and a thin-walled megasporangium. **Nectary** **absent**. *Fruit a ± flattened, loculicidal* (and septicidal) *capsule* (*Polypremum*) *or a schizocarp of 4 nutlets* (*Tetrachondra*).

***Floral formula***: \* , K 4 , C 4 , A 4 , G -2- ; capsule, schizocarp

[Circle the 4 sepals; circle the 4 petals; below the formula draw a line connecting the 4 petals to the 4 stamens; circle the 2 carpels]

***Distribution and ecology***: Patagonia and New Zealand (*Tetrachondra*) and the eastern United States to Mexico and south to the West Indies, northern South America (*Polypremum*). Plants of open, aquatic to dry, upland habitats.

***Genera/species***: 2/3. ***Genera***: *Tetrachondra* (2 spp.) and *Polypremum* (1). *Polypremum* occurs in the United States.

***Economic plants and products***: *Polypremum procumbens* (Rustweed, juniperleaf) provides groundcover, especially in poor soils.

***Discussion***: The monophyly of Tetrachondraceae is supported by chemistry and morphology (see description; Jensen 1992, 2000; Stevens 2001 onward; Wagstaff 2004) and also by DNA sequences (Oxelman 1999; Refulio-Rodriguez and Olmstead 2014; Savolainen et al. 2000b; Schäferhoff et al. 2010; Wagstaff et al. 2000; Wikström et al. 2015). Within the family, there is strong support for the monophyly of *Tetrachondra*, which is sister to *Polypremum*. *Polypremum* was placed traditionally in Gentianales, especially Loganiaceae s.l. or the segregate Buddlejaceae (Cronquist 1981; Rogers 1986), while *Tetrachondra* was included in either Boraginaceae or Lamiaceae (Cheesman 1906; Cronquist 1981). It is not surprising that these two genera historically were placed in different families, given their pronounced differences in floral and fruit characters (see description).

 The small, white flowers are pollinated by bees, wasps, flies, and thrips. The tiny seeds of *Polypremum* likely are dispersed by wind or rainwash, although fruits are also dispersed along roadsides and rights-of-way by mowing equipment.

 ***Additional reference***: Rogers 1986.

**Bruniales**

**Bruniaceae** de Candolle

(Brunia Family)

*Shrubs or small trees*, **with *Erica*-like appearance**; tannins and resin-like substances present, **but lacking iridoids**. Hairs simple, nonglandular. *Leaves alternate and spiral*, **small**, **closely spaced and overlapping, entire**, *shortly petiolate to sessile*, **the blade linear to scale-like**, **with a black tip**, **with parallel venation**, **the stomata cyclocytic**, transversely oriented, and the epidermal cells are often papillate or dome-shaped; stipules present and minute, colleters-like, or absent. Inflorescences indeterminate, usually terminal, *usually bracteate heads or less commonly spikes*, but sometimes flowers solitary. Flowers bisexual, radial, *often small*. *Sepals 4 or 5*, distinct or slightly connate, imbricate. *Petals 4 or 5, distinct*, *often clawed*, **usually with various adaxial swellings or ridges**, imbricate. *Stamens 4 or 5*; filaments distinct and free or adnate to the petal bases, incurved in bud; anthers dorsifixed or versatile; pollen grains tricolporate to polycolporate. *Carpels 2-3, or 1*, and then possibly pseudomonomerous, connate; *ovary usually inferior* or half-inferior, with usually apical-axile placentation; styles 1-3, basally fused or not; stigmas capitate. Ovules 1-4 per carpel, with a single integument. Nectaries associated with gynoecium or lacking. *Fruit a loculicidal capsule*, *schizocarp of achenes, or an achene* (if only a single carpel present); seeds sometimes with an aril.

***Floral formula***:

\* K 4-5 , C 4-5 , A 4-5 , G 1-3 , capsule, schizocarp, achene

[Put a dashed line around the 4-5 sepals. Draw a line above the 1-3 carpels to indicate inferior ovary; circle the 1-3 carpels to indicate connation.]

***Distribution and ecology***: South Africa, mainly limited to the Cape region, but one species in KwaZulu-Natal; plants of the Mediterranean-type, fynbos vegetation. Most species are fire-adapted, with some reseeding after fire and others resprouting from a woody base. Many species are rare and/or endangered.

***Genera/species***: 6/81. ***Major genera***: *Brunia* (40 spp.) and *Berzelia* (15). None is native to North America.

***Economic plants and products***: *Berzelia* and *Brunia* are cultivated as ornamentals (and used as cut flowers).

***Discussion***: Bruniaceae are the only family of Bruniales, and they represent an early divergent lineage of the campanulids. Their phylogenetic position was ambiguous until the advent of molecular data; Cronquist (1981) placed the family in his heterogeneous order Rosales. Within Bruniaceae, *Linconia* likely is sister to the remaining genera. It is placed in its own tribe (Linconieae), the monophyly of which is supported by the apically sterile anthers. The remaining genera form two clades: Audouineae (*Audouinia*, *Thamnea*; anthers with thecae attached to connective along their entire length) and Brunieae (*Berzelia*, *Brunia*, *Staavia*; anthers versatile, with thecae free at base) (Classen-Bockhoff 2016; Classen-Bockhoff et al. 2011; Quint and Classen-Bockhoff 2008).

 The flowers of Bruniaceae are pollinated by various insects (beetles, flies, ants, bees, and even butterflies), which are attracted by pollen or nectar (Classen-Bockhoff 2016). The fruits or seeds are dispersed by wind, rain-wash, or (when arils are present) by ants.

***Additional references***: Carlquist 2008; Stevens 2001 onward.

*Aquifoliales*

**Helwingiaceae** Decaisne

(Flowering-rafts Family)

*Shrubs to small trees*; with iridoids, cinnamic and chlorogenic acid (the latter a polyphenolic compound in coffee); **wood with silica grains**. Hairs absent. *Leaves alternate and spiral, simple, serrate to crenate*, the teeth with a glandular apex, with pinnate venation; *stipules present*, often dissected, borne on the petiole. Inflorescences determinate (*fasciculate*), *borne on the midvein of the adaxial leaf surface* (*epiphyllous*). **Flowers unisexual** (**plants dioecious**), *radial*. **Sepals very reduced, merely a rim outside petals in carpellate flowers**. *Petals* (appearing as tepals) *3-5, distinct*, *valvate-imbricate*, with ± incurved apex. *Stamens 3-5 distinct*; filaments short; pollen grains tricolporate, the surface spinulate. *Carpels 3-5*, connate; *ovary inferior*, with apical-axile placentation; *style 1, short; stigma with recurved lobes*. Ovules 1 in each locule, with 1 integument an a thin-walled megasporangium. *Nectar disk atop ovary*, with stomata. Fruit a drupe with 3-5 pits. Seeds with weakly ruminate endosperm.

***Floral formula***:

Staminate: \* , K 0 , C 3-5 , S 3-5 , G 0

Carpellate: \* , K rim , C 3-5 , A 0 , G 3-5 ; drupe

[Circle the word “rim”; circle the 3-5 carpels; draw a line above the 3-5 carpels]

***Distribution***: Eastern Asia, from the Himalayas eastward to Japan.

***Genera/species***: 1/4. ***Genus***: *Helwingia* (4 spp.). Group is not native in North America.

***Economic plants and products***: *Helwingia* (flowering-rafts) is occasionally used medicinally; the young leaves are edible. *Helwingia japonica* is used as a curiosity ornamental because of its epiphyllous flowers.

***Discussion***: The monophyly of Helwingiaceae (only *Helwingia*) is supported by morphology (see description; Stevens 2001 onward; Xiang 2016) and its isolated phylogenetic position – and related to Phyllonomaceae, of the Neotropics (Albach et al. 2001; Morgan and Soltis 1993; Savolainen et al. 2000a, b; Soltis et al. 1997, 2011). Both Helwingiaceae and Phyllonomaceae (only *Phyllonoma*) share the apomorphy of epiphyllous inflorescences (see Rodriguez 1971) – also supporting a sister group relationship between the two clades. In *Helwingia* the inflorescence is initiated adjacent to the leaf axil on the adaxial side of the leaf primordium. The action of a basal, intercalary meristem shifts the mature inflorescence to the midvein of the adaxial leaf surface. The inflorescence has its own vascular bundle, which departs from the leaf bundle at the base of the petiole (Dickinson and Sattler 1975; Xiang 2016). Ao and Tobe (2015) consider the floral perianth to be a calyx (instead of a corolla, as we have done here). Cronquist (1981) placed *Helwingia* within the Cornaceae, and *Phyllonoma* in Grossulariaceae, considering the epiphyllous inflorescences in each to have evolved independently.

 The small flowers of *Helwingia*, borne upon the leaves, probably are pollinated by generalized insect visitors (perhaps along with wind), and the leaves may provide a landing platform (Sun et al. 2014). The red to black drupes likely are bird dispersed,

***Additional reference***: Yao et al. 2016.

**Phyllonomaceae** Small

(Flowering-leaf Family)

*Shrubs or small trees*; accumulating aluminum. *Hairs absent*, except on stipules and calyx margins, then simple. *Leaves alternate and 2-ranked, simple*, entire to serrate or dentate, with pinnate venation, and sometimes with a constriction between blade and its acuminate apex; *stipules present*, with glandular hairs. Inflorescences determinate (*fasciculate*), *borne on the midvein of the adaxial leaf surface* (*epiphyllous*), *and positioned ± distally on blade*. *Flowers bisexual, radial*, **without bracteoles**. *Sepals 4-5*, distinct to very slightly connate, *with marginal, glandular hairs*, **each sepal with only 1 vascular trace**. *Petals 4-5, distinct, valvate*. *Stamens 4-5*, distinct; filaments shorter than or equaling the anthers; pollen grains tricolporate, the surface spinulate, granulose or smooth. *Carpels usually 2*, connate; *ovary* *inferior*, **with intruded-parietal placentation**; *style 1 and strongly branched or styles 2; stigmas terete, recurved*. **Ovules 6 or 7 per carpel, campylotropous**, with 1 integument and a thin-walled megasporangium. *Nectar disk atop ovary*, with stomata. **Fruit a berry**. **Seeds with testa multilayered, the exotestal cells large, thick-walled, mucilaginous**, forming irregular papillae.

***Floral formula***: \* , K 4-5 , C 4-5 , A 4-5 , G 2 ; berry

[Circle the 2 carpels; draw a line above the 2 carpels]

***Distribution and ecology***: Neotropical (Mexico south to Bolivia; in moist montane forests.

***Genera/species***: 1/4. ***Genus***: *Phyllonoma* (4 spp.). The genus does not occur in the United States or Canada.

***Economic plants and products***: The leaves are occasionally used medicinally.

***Discussion***: The monophyly of Phyllonomaceae is well supported by morphology (see description; Bittrich 2016; Mori and Kallunki 1977; Stevens 2001 onward; Tobe 2015) an its isolated phylogenetic position (sister to Helwingiaceae, of eastern Asia) (Savolainen et al. 2000b; Soltis et al. 2011). Both Phyllonomaceae and Helwingiaceae (only *Helwingia*) share the apomorphy of epiphyllous inflorescences (Bittrich 2016; Dickinson and Sattler 1974, 1975; Stork 1956; Tobe 2013; Weber 2004). In *Phyllonoma* the inflorescence primordium is initiated on the adaxial side of the leaf primordium and at about the same time a vegetative bud is formed at the base of the leaf primordium. At maturity the inflorescence vascular trace departs from the midvein at the point of inflorescence insertion, so there is not an inflorescence vascular bundle running through the petiole and leaf midvein, as in *Helwingia* (Dickinson and Sattler 1974). *Phyllonoma* and *Helwingia* also share the putative apomorphies of an inferior ovary and epigynous nectar disk (Tobe 2013). *Phyllonoma* can easily be distinguished from *Helwingia* by its 2-ranked (vs. spiral) leaves, bisexual (vs. unisexual) flowers, with a calyx (vs. calyx reduced or absent), ovary with parietal (vs. axile) placentation, with several ovules (vs. one ovule) per carpel, and berry (vs. drupe) fruits.

 Pollination of *Phyllonoma* probably is by various small insects; the berries are bird dispersed.

*Apiales*

**Myodocarpaceae** Doweld

(Myodocarpus Family)

*Shrubs or small trees*, *the trunk often thick, unbranched to well branched*; *tissues aromatic* *with secretory canals* *containing ethereal oils and resins*, coumarins, falcarinone polyacetylenes, monoterpenes and sesquiterpenes, and various terpenoid oils. Hairs simple. *Leaves alternate and spiral*, **pinnately compound** or occasionally simple, entire to serrate, with pinnate venation; *petioles sheathing at base*; *stipules lacking*. Inflorescences determinate, *forming simple umbels, and these arranged in panicles or racemes*, terminal. **Flowers bisexual and staminate** (andromonoecious; *with umbels of perfect flowers terminating lower order inflorescence axes, and subtended by small umbels of staminate flowers*) or occasionally all bisexual, radial. *Sepals 5, distinct or basally connate, small*, usually valvate. *Petals 5, distinct*, **usually imbricate**, the bases broad to clawed, and in *Myodocarpus* falling as a calyptra and falsely connate (by interlocking of epidermal papillae and cuticular ledges on distal petal surfaces). *Stamens 5; filaments distinct*, inflexed in bud; pollen grains tricolporate. *Carpels 2, connate*; *ovary inferior, with apical-axile placentation*; *styles recurved*, *swollen at base to form a nectar-secreting structure* (*stylopodium*) *atop ovary*; stigmas 2, elongate. Ovules 2 in each locule but only 1 developing, with 1 integument. *Fruit a ± flattened schizocarp, the 2 dry and winged segments attached basally to an undivided central stalk* (carpophore); *elongated oil canals* (vittae) *present in fruit wall* (associated with vascular bundles), also anastomosing canals in mesocarp, **and large secretory vesicles in innermost layer of mesocarp**, in *Myodocarpus*; *or a globose/ovoid drupe with 2 pits*, **and large secretory vesicles in the innermost layer of mesocarp**, adjacent to the endocarp, in *Delarbrea*.

***Floral formula***: \* , K 5 , C 5 , A 5 , G 2 ; schizocarp, drupe

[Put a dashed line around the 5 sepals; circle the 2 carpels; put a line above the 2 carpels]

***Distribution***: New Caledonia, eastern Malesia, and Australia (Queensland), but clade most diverse in New Caledonia.

***Genera/species***: 2/17. ***Genera***: *Myodocarpus* (10 spp.) and *Delarbrea* (7, including *Pseudosciadium*). Neither genus occurs in North America.

***Economic plants and products***: A few species of *Delarbrea* are occasionally grown as ornamentals.

***Discussion***: The monophyly of Myodocarpaceae is supported by most analyses of DNA sequences (Nicolas and Plunkett 2009; Plunkett and Lowry 2001; Plunkett et al. 2004; Soltis et al. 2011; Clarkson et al. 2021) and morphology, especially fruit and wood anatomy (Baumann 1946; Konstantinova and Yembaturova 2010; Liu et al. 2010; Oskolski et al. 1997; Stevens 2001 onward). Within *Myodocarpus*, the species with simple leaves form a clade sister to those with compound leaves. Morphologically, *Myodocarpus* and *Delarbrea* are intermediate between typical Araliaceae and Apiaceae. Their woody habit is like Araliaceae. The flowers of *Myodocarpus* have broadly inserted petals, like Araliaceae, but their schizocarpic fruits with carpophores and vittae are similar to Apiaceae. In contrast, the flowers of *Delarbrea* have clawed petals, characteristic of Apiaceae, but they have fleshy drupes, like most Araliaceae (Judd et al. 1994; Lowry and Plunkett 2018; Thorne 1973). In fact, the morphological intermediacy of *Myodocarpus* and *Delarbrea* has led some botanists, e.g., Judd et al. (1994, 1999) and Thorne (1973), to recognize the Araliaceae + Myodocarpaceae + Apiaceae clade as Apiaceae s.l., although each of the three here are recognized at familial rank, following APG (2016). Myodocarpus and Delarbrea have been considered to represent a reminant of the ancestral complex that gave rise to Araliaceae and Apiaceae, and in that regard it is of interest that *Delarbrea* is placed sister to Araliaceae while *Myodocarpus* sister to Apiaceae (Baker et al. 2022; Kew Tree of Life Explorer)

 The flowers of *Myodocarpus* and *Delarbrea* likely attract a variety of pollinating insects. The winged schizocarps of *Myodocarpus* are wind dispersed, while the dark purple (or in one species, iridescent blue) drupes of *Delarbrea* are dispersed by birds or mammals. The iridescent blue color of the drupes of *D. michieana* is structural, i.e., the epidermal cells contain multilayered structures that interfere constructively with light, producing the brilliant color (Lee et al. 2000).

*Ecalloniales*

**Escalloniaceae** Dumortier

(Currybush Family)

*Trees, shrubs to subshrubs*, or rarely herbs, with triterpenes, iridoids, tannins, alkaloids, and often accumulating aluminum; *often with a curry-like odor* (especially when dried). Hairs simple, gland-headed or eglandular. *Leaves alternate and spiral*, *or opposite and decussate*, *simple*, rarely lobed, entire to variously toothed, usually pinnately veined; stipules lacking. Inflorescences indeterminate or determinate, terminal or axillary, sometimes reduced to a solitary flower. *Flowers bisexual, radial*. *Sepals usually 4 or 5, ± connate*. **Petals** *usually 4 or 5*, **distinct**, *but sometimes ± sticking together* (and appearing connate), imbricate or valvate. *Stamens usually 4 or 5, distinct*; **filaments free**, **i.e., not adnate to petals**; pollen grains usually tricolporate or triporate. *Carpels usually 2, connate*; *ovary inferior to superior*, **with usually intruded-parietal placentation**; styles 1 or 2; stigma(s) punctate or capitate, often lobed. Ovules 1 to many per carpel, usually anatropous or orthotropous, with 1 integument and usually a thin-walled megasporangium. Nectar disk usually present. *Fruit usually a septicidal capsule, drupe, or indehiscent pod*, rarely a loculicidal capsule. Seeds usually with starchy endosperm.

***Floral formula***: \* , K 4-5 , C 4-5 , A 4-5 , G 2 ; capsule, drupe, indehiscent pod

[Circle the 4-5 sepals; circle the 2 carpels; draw a line above the carpels]

***Distribution***: Central and South America, Réunion, southern Asia to Australia, New Caledonia, and Tasmania.

***Genera/species***: 7/126. ***Major genera***: *Polyosma* (80 spp.) and *Escallonia* (40). *Escallonia rubra* is naturalized in the United States (Oregon, California).

***Economic plants and products***: Several species and hybrids of *Escallonia* (currybush) are grown as ornamentals.

***Discussion***: The monophyly of Escalloniaceae is supported by DNA sequences (Bremer et al. 2004; Lundberg 2001; Sede et al. 2013; Tank and Donoghue 2010; Winkworth et al. 2008), although morphological support is weak (see description; also, Stevens 2001 onward). Phylogenetic relationships within the family are unclear, but support for the *Escallonia* + *Forgesia* + *Valdivia* clade is strong (Zapata 2013). These three genera are phenetically distinctive, having alternate leaves, 5-merous flowers, and tricolporate pollen. In contrast, the large genus *Polyosma* has opposite or subopposite leaves, 4-merous flowers, and triporate pollen. Two small genera are taxonomically isolated: *Eremosyne* stands apart in being an annual herb, and *Tribeles* in being a subshrub, rooting from the nodes. Both have loculicidal capsules (in contrast, *Escallonia* and relatives have septicidal capsules, while *Polyosma* has drupes). All these plants traditionally were placed in Saxifragaceae (Engler 1928). They are morphologically heterogeneous and are sometimes divided into several families, i.e., Polyosmaceae, Eremosynaceae, Tribelaceae, and Escalloniaceae s.s. (Backlund 2016; Conran and MacFarlane 2016; Lundberg 2016a, b). Escalloniaceae, when broadly circumscribed, is the only family of Escalloniales, and the ordinal clade is related to Apiales, Dipsacales, and Asterales.

 The flowers of Escalloniaceae are pollinated by insects, especially bees, and also birds. The small seeds of *Escallonia* may be wind dispersed. The drupes of *Polyosma* are eaten by flying-foxes.

*Asterales*

**Calyceraceae** Richard

(Balsam-leaf Family)

*Herbs*; storing carbohydrate as the oligosaccharide inulin, also with iridoids. Hairs simple, but often lacking. *Leaves alternate and spiral, often in a basal rosette*, *simple*, but sometimes pinnately dissected, entire to variously toothed, with pinnate venation; stipules lacking. *Inflorescences determinate*, **the flowers in involucrate heads**, terminal, on ± scape-like axes. Flowers usually perfect (but also with staminate flowers, in *Acicarpha*), *radial*, and each flower associated with a bract. *Sepals usually 5, connate, with hyaline to membranous lobes or teeth, often thickened or spine-like*. *Petals usually 5, forming a cylindrical to funnel-shaped corolla, the lobes valvate*. *Stamens usually 5***; filaments connate***, and adnate to corolla tube; anthers basally connate, and with the filaments forming a tube around the style, into which the pollen is shed, and he style then growing through this tube, pushing out pollen and presenting it to the floral visitors, after which the stigma becomes receptive* (i.e., with a plunger pollination mechanism); pollen grains tricolporate. *Carpels 2, connate*; *ovary inferior*, **with apical placentation**; style not branched; **stigma usually capitate**. **Ovule 1 per ovary**, with 1 integument and a thin-walled megasporangium. **Nectaries at base of filament tube and alternating with vascular bundles of the filaments**. **Fruit an achene, often crowned by calyx lobes** **and a conical body** (persistent style base).

***Floral formula***: \* , K 5 , C 5 , A 5 , G 2 ; achene

[Circle the 5 sepals; circle the 5 petals; circle the 5 stamens; circle the 2 carpels; below the formula draw a line connecting the petals and stamens; draw a line above the 2 carpels]

***Distribution and ecology***: Southern South America; mainly plants of high altitude, arid habitats, such as open grasslands and meadows.

***Genera/species***: 8/46. ***Major genera***: *Gamocarpha* (13 spp.), *Moschopsis* (10), *Acicarpha* (7), *Leucocera* (7), and *Calycera* (6). *Acicarpha tribuloides* has been reported from the United States (at ballast sites) but has not persistent (DeVore 1991).

***Economic plants and products***: None.

***Discussion***: The monophyly of Calyceraceae is supported by DNA sequences (Denham et al. 2016; Gustafsson and Bremer 1995; Hansen 1992; Lundberg 2009; Lundberg and Bremer 2003; Pozner et al. 2012, 2021) and morphology (Denham et al. 2016; Hellwig 2007; Stevens 2001 onward; and description). Calyceraceae are comprised of two major clades, which may be diagnosed by different base chromosome numbers, i.e., one with x = 8 or 9 (*Acicarpha*, *Anachoretes*, *Asynthema*, *Boopsis*, and *Moschopsis*) and the other with x = 7 (*Calycera*, *Gamocarpha*, and *Leucocera*). DNA-based phylogenies do not correlate well with morphological variation, and the traditionally recognized genera are non-monophyletic except for *Acicarpha*. Pozner et al. (2021) have proposed a new generic system based on their DNA-based phylogeny, although these generic clades are difficult to characterize morphologically. Flower morphology is quite variable but highly homoplasious and likely reflects selection for pollination or fruit dispersal (rather than phylogeneticv affinity). These plants can be confused with members of Asteraceae (their sister family), but differ in having determinate (vs. indeterminate) heads, filaments connate (vs. distinct), gynoecia with apical (vs. basal) placentation, and capitate (vs. elongate) stigmas. They are also chemically distinctive, i.e., with iridoids and lacking sesquiterpene lactones in Calyceraceae (vs. lacking iridoids and with sesquiterpene lactones in Asteraceae). It is of interest that Calyceraceae is species-poor and geographically restricted, while the morphologically similar Asteraceae is species-rich and cosmopolitan in distribution.

 The flowers of Calyceraceae are pollinated by various insects. Their achenes are wind or water dispersed.

**Menyanthaceae** Berchtold & J. Presl

(Bogbean Family)

**Wetland or aquatic herbs** often with rhizomes, with adventitious roots, these sometimes fleshy, banana-shaped; **leaf blades and petioles with intercellular air-canals**, **and usually with branched sclereids**; iridoids present. **Hairs** **absent**. *Leaves alternate*, spiral or 2-ranked, *simple or trifoliolate*, sometimes dimorphic, **the base usually broad**, entire to variously toothed, **with palmate venation,** the blade held erectly above water’s surface or petioles flexuous and blade floating; petiole often sheathing at base; stipules absent. Inflorescences determinate or indeterminate, terminal or axillary, sometimes reduced to a solitary flower. *Flowers usually bisexual, radial*, **often heterostylous**. Sepals usually 5, connate. *Petals usually 5, connate*, the lobes valvate or imbricate, *and with a differentiated marginal region, i.e., petal-wing or marginal fringe*, *sometimes with adaxial surface fimbriate or crested*. *Stamens usually 5, distinct*; filaments adnate to the base of corolla; anthers usually sagittate; pollen grains tricolporate or with furrows ± fused; *secondary pollen presentation mechanism absent*. *Carpels 2, connate*; **ovary ± superior, with parietal placentation;** stigma bilobed. Ovules numerous on each placenta, with 1 integument and a thin-walled megasporangium. Nectar disk or glands around ovary. *Fruit a loculicidal or irregularly dehiscent capsule*, or rarely a berry. Seeds often hairy, papillate, or with various projections, occasionally arillate.

***Floral formula***: \* K 5 , C 5 , A 5 , G 2 , capsule

[Circle the 5 sepals, circle the 5 petals, and circle the 2 carpels]

***Distribution and ecology***: Nearly cosmopolitan; plants of wetland or aquatic habitats.

***Genera/species***: 6/70. ***Major genus***: *Nymphoides* (50 spp.). *Nymphoides*, *Menyanthes*, and *Nephrophyllidium* occur in the continental United States and/or Canada.

***Economic plants and products***: *Menyanthes* (bogbean) and *Nymphoides* (floating-hearts, water-snowflake) are occasionally cultivated in ornamental ponds and aquaria.

***Discussion***: Menyanthaceae are well supported as monophyletic by morphology (Kadereit 2007; Stevens 2001 onward; see description) and DNA-sequences (Tippery et al. 2008; Tippery and Les 2009). If plunger-pollination is a synapomorphy for Asterales, then the loss of this secondary pollen presentation mechanism may be an additional synapomorphy for Menyanthaceae. *Menyanthes* and *Nephrophyllidium* (seeds smooth and glossy) are sister taxa, and they form a clade that is the sister-group of a species-rich *Nymphoides* + *Liparophyllum* + *Villarsia* + *Ornduffia* clade (seed coat usually slightly roughened to papillate, hairy, or variously ornamented), within which generic limits are difficult. *Nymphoides* stands apart from its relatives in having floating leaves that support the lax inflorescence, and phylogenetic relationships within this genus are reticulate due to hybridization and allopolyploid speciation (Tippery and Les 2011; Tippery et al. 2018). *Nymphoides* is superficially similar to the only distantly-related *Nymphaea* (Nymphaeaceae); both aquatics have similarly-shaped floating leaves with air-canals and branched sclereids.

 The showy, white, pink, or yellow flowers of Menyanthaceae are mainly pollinated by bees. The corolla fringe or wing may assist in keeping the flowers above the water surface (Armstrong 2002). Asexual reproduction also occurs by vegetative fragmentation. The small seeds usually float and can be dispersed by water, but they also are eaten (and dispersed) by mammals and birds. Some Australian species have seeds with an oily aril and may be ant dispersed.

***Additional references***: Chuang and Ornduff 1992; Wood 1983.

**Stylidiaceae** R. Brown

(Triggerplant Family)

*Herbs, subshrubs or cushion plants*; storing carbohydrate as inulin (an oligosaccharide), sometimes with iridoids; stems with vascular bundles in a ring or scattered, often with unusual secondary growth (i.e., cambium developing just inside the endodermis, and secondary tissue developing only towards the inside). Hairs simple, *often gland-headed and producing mucilage* (and plants then ± carnivorous). *Leaves alternate and spiral, often clustered into false whorls or in a basal rosette*, simple, entire, with midvein visible but other veins obscure; petiole and stipules lacking, **but with axillary hairs**. Inflorescences determinate, usually terminal, *often on a scape*, sometimes reduced to a solitary flower. *Flowers usually bisexual*, *bilateral to less commonly radial*, *often twisting ± 90 degrees in development* (semi-resupinate). *Sepals usually 5, connate*, often with gland-headed hairs. *Petals usually 5*, distinct (*Donatia*) *or connate* (in other genera) *and forming a tube with 5 ± equal lobes, or 4 lobes in 2 pairs and a specialized, often inconspicuous, abaxial lobe* (the labellum, which is sensitive in *Levenhookia*), **and** **imbricate. Stamens usually 2**; filaments free (*Donatia*) *or adnate to style to form a column* (other genera); **anthers extrorse**, *with locules usually set end to end*; pollen 2- to 8-colpate. *Carpels usually 2, connate; ovary inferior*, with axile or free-central placentation, or 1 carpel reduced and then placentation apparently parietal; styles 2 (rarely 3) (*Donatia*) *or stylar column 1 and usually bent to the labellar side of flower and pressed against the labellum, rapidly snapping to an oppositely bent position when touched by a pollinator* (in *Stylidium*); stigma(s) capitate to minute. Ovules numerous, with 1 integument and a thin-walled megasporangium. Nectary a disk (*Donatia*) or 1- or 2-lobed (other genera). *Fruit a septicidal capsule or a small, indehiscent pod*; embryo with 1 or 2 cotyledons.

***Floral formula***: \* or X , K 5 , C 5 or 4 + 1 , A 2 , G 2 ; capsule, indehiscent pod

[Circle the 5 sepals; circle the 4+1 petals; draw a dashed line above formula connecting 2 stamens to the 2 carpels; circle the 2 carpels, draw a line above the 2 carpels]

***Distribution and ecology***: Mainly Australia, Tasmania, and New Zealand, but also Sri Lanka to southeastern Asia and Malesia, and also in southern South America and the Falkland Islands. Plants often of open, sandy heathlands on acidic, low nutrient soils.

***Genera/species***: 4/240. ***Genera***: *Stylidium* (220 spp.), *Forestera* (9), *Levenhookia* (8), and *Donatia* (2). The clade does not occur in North America.

***Economic plants and products***: A few species of *Stylidium* (triggerplants) are occasionally grown as ornamentals.

***Discussion***: The monophyly of Stylidiaceae is supported by DNA sequences (Gustafsson and Bremer 1995; Laurent et al. 1999; Lundberg 2001; Soltis et al. 2011; Wagstaff and Wege 2002), but morphological support is weak (Stevens 2001 onward; see description) although morphological support for the *Stylidium* + *Levenhookia* + *Forestera* clade is strong (Carlquist 1981; Carolin 1960, 2007; Erbar 1992; Laurent et al. 1999; Stevens 2001 onward). Within Stylidiaceae, *Donatia* (Donatioideae; putative synapomorphies: flowers solitary, with distinct petals, and distinct styles; retaining the ancestral character of the lack of a column) is sister to the remaining genera – the Stylidioideae (putative synapomorphies: unusual secondary growth, ± resupinate flowers, flowers ± bilateral, with the stamens adnate to style, forming a column, the anther locules set end to end, and free-central placentation; retaining the plesiomorphic character of connate petals). Within Stylidioideae, *Forestera* (flower only slightly bilateral, the anthers opening horizontally) is sister to the *Levenhookia* + *Stylidium* clade (flowers strongly bilateral, column with apex inside sac-like labellum). *Stylidium* has a sensitive column, while *Levenhookia* has a sensitive labellum. *Oreostylidium* *subulatum* has nearly radial flowers and has lost the sensitive, trigger-style; it is well nested within the phylogenetic structure of *Stylidium*, and thus is included here within that genus (Laurent et al. 1999). *Donatia* is phenetically distinctive, and it is often treated as its own family, Donatiaceae (see for example, Cronquist 1981). Stylidiaceae is sister to a clade including Menyanthaceae + Goodeniaceae + Calyceraceae + Asteraceae (see references cited under Asterales).

 The showy, trigger flowers of Stylidiaceae are insect pollinated. Their tiny seeds are dispersed by wind, rain-wash, or carried in mud on the feet of birds.

***Additional reference***: Darnowski et al. 2006.

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