

# The Families and Genera of Vascular Plants

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Edited by K. Kubitzki

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*Volume XV*

## Flowering Plants Eudicots

Apiales, Gentianales (except Rubiaceae)

Joachim W. Kadereit · Volker Bittrich (Eds.)

THE FAMILIES  
AND GENERA  
OF VASCULAR PLANTS

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**XV** *Flowering Plants · Eudicots*  
*Apiales, Gentianales (except Rubiaceae)*

Volume Editors:  
Joachim W. Kadereit · Volker Bittrich

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With 85 Figures

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The Families and Genera of Vascular Plants

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## Preface

It is with great pleasure that I present a volume with family treatments of the orders Apiales and Gentianales (except Rubiaceae). An immense amount of evidence recently accrued had to be taken into account to present up-to-date treatments of these families, including evidence from taxonomic revisions of large groups, new comparative morphological studies, but also data from karyological and phytochemical findings and, above all, results from an increasing number of molecular systematic studies that have changed our concepts of relationships considerably. In the two large families Apiaceae and Apocynaceae, which comprise 466 and 378 genera respectively, the establishment of a phylogenetic framework obviously has been a comprehensive effort for many years by several authors. Although much smaller, the same is true for Loganiaceae where establishment of family limits proved to be particularly difficult. The authors of the Apiaceae treatment found it difficult to devise a single usable key to the genera of this family. Therefore, separate keys were constructed for the native and naturalized genera in seven major geographic regions of the world. The treatments of Apiaceae and Apocynaceae also include many references to various keys and taxonomic treatments of parts of the families that are difficult to find, which makes these treatments even more useful.

Altogether, the volume contains a wealth of interesting information, and I am greatly indebted to all authors for their ardent desire to complete their contributions, and to the volume editors who took care that the project was brought to an end. I am also grateful to all copyright holders who so kindly gave permission to reproduce illustrations published under their responsibility, and to all artists who contributed original illustrations. The artist Bobbi Angell, New York, again deserves our special thanks for the generosity with which she authorized the use of fine illustrations published under her authorship. Doris Franke, Mainz, is gratefully acknowledged for preparing all figures for print.

Finally, I have great pleasure in thanking the copy editor of the present volume, Dr. Monique Delafontaine, for her dedicated editorial work. My warm thanks also go to Dr. Sabine von Mering, who kindly took care of preparing the index of scientific names. As always, it is a pleasure to acknowledge the cordial collaboration with Dr. Andrea Schlitzberger from Springer Verlag.

Hamburg  
2 May 2018

Klaus Kubitzki

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# Introduction to the Orders of this Volume

V. BITTRICH AND J.W. KADEREIT

The present volume of this book series completes the treatment of the Asterids. Asterids are now contained in Vols. VI (Cornales, Ericales, 2004), VII (Lamiales, 2004), VIII (Asterales, 2007), XIV (Aquifoliales, Boraginales, Bruniales, Dipsacales, Escalloniales, Garryales, Paracryphiales, Solanales, Icacinaceae, Metteniusaceae, Vahliaceae, 2016) and the present volume, which contains the orders Apiales and Gentianales (except Rubiaceae). The only families of Asterids not treated in the series are Acanthaceae (Lamiales), Convolvulaceae (Solanales) and Rubiaceae (Gentianales).

## CONSPECTUS OF THE FAMILIES OF APIALES

1. Plants without secretory canals; leaves simple; nectary absent or present; fruit fleshy, 1-seeded 2
  - Plants with secretory canals throughout; leaves simple or composed; gynoeceal nectary mostly present; fruit fleshy or dry, sometimes schizocarpic, 1- to many-seeded 4
2. Petiole not sheathing; petals valvate; nectary absent; ovary superior, unilocular **Pennantiaceae**
  - Petiole ± sheathing; petals (sub-)imbricate, rarely induplicate-valvate; nectary present or absent; ovary inferior, 3-locular at least in upper part 3
3. Leaves distichous or subopposite, blade minutely pellucid-punctate; ovary 3-locular above, 1-locular below **Griselinaceae**
  - Leaves spiral, blade not punctate; ovary 3-locular throughout **Toricelliaceae**
4. Leaves simple, petiole not sheathing at base; inflorescences not umbellate; petals 4–40 mm long; stamen filaments straight in bud; style simple, ovary superior; nectary at base of ovary (rarely absent); fruit a capsule or berry, rarely woody indehiscent **Pittosporaceae**

- Leaves simple or compound, petiole usually sheathing at base; inflorescences or their ultimate units often umbellate; petals usually shorter; stamen filaments inflexed in bud; stylopodia 2–many, ovary inferior; nectary on ovary roof; fruit a schizocarp or drupaceous 5
- 5. Plants herbaceous, rarely woody; leaves mostly compound, rarely entire, usually membranous; petals usually clawed and with an inflexed tip; ovules 2 per locule, one abortive; fruit usually dry and schizocarpic **Apiaceae**
  - Plants mostly shrubs or small trees; leaves simple to compound, usually subcoriaceous to coriaceous; petals usually broadly inserted, rarely clawed, and without inflexed tip; ovule 1 per locule; fruit usually drupaceous, rarely dry schizocarpic 6
- 6. Calyx with evident lobes; sepals and petals 5, petal apex without pointed adaxial thickening, stamens 5, carpels 2; fruit with secretory vesicles located immediately adjacent to the endocarp **Myodocarpaceae**
  - Calyx with minute to obscure lobes, often forming a truncate rim; sepals and petals (3–)5(–12), petal apex with pointed adaxial thickening, stamens 5 (3–numerous), carpels 2–5(–100+); fruit without secretory vesicles **Araliaceae**

Seven families (about 522 genera, 6000 spp.) are currently included: Apiaceae (466 / 3820), Araliaceae (40 / 1900), Griselinaceae (1 / 7), Myodocarpaceae (2 / 17), Pennantiaceae (1 / 4), Pittosporaceae (9 / 250) and Torricelliaceae (s.l. = incl. Aralidiaceae and Melanophyllaceae; 3 / 10). The phylogeny currently accepted is (Pennantiaceae + (Toricelliaceae + (Griselinaceae + (Pittosporaceae + (Araliaceae + (Myodocarpaceae + Apiaceae)))))).

Few of the families now included in the Apiales were placed in the order before data from DNA sequencing became available. Undisputed were only Apiaceae + Araliaceae (see

below). Diversification and evolution of the order is discussed in detail in Stevens (2001 onwards), Kårehed (2003), Chandler and Plunkett (2004) and Nicolas and Plunkett (2014). The current phylogenies (e.g. Soltis et al. 2011) show the monogeneric Pennantiaceae as sister to the remainder of Apiales. Kårehed (2001), based on DNA sequence data, was the first to point out that *Pennantia* does not belong in Icacinaceae, as believed since the mid-19th century (cf. Miers 1852), but in Apiales. Because of the position of *Pennantia* in the phylogeny, recognition of the genus as a separate family had to be accepted. The next branch in the Apiales phylogeny is formed by the small but heterogeneous Torricelliaceae. The three genera of this family were often included in separate monogeneric families and only DNA sequence data suggested that they form a clade in the Apiales (Plunkett et al. 1996; Savolainen et al. 2000; Kårehed 2003). Although *Aralidium* was often included in Araliaceae in the 19th century, the lack of schizogenous secretory canals suggested different positions—for example, inclusion in Cornales (e.g. Thorne 1983). The other two genera, *Melanophylla* and *Torricellia*, were usually included in Cornales or Rosales. The monogeneric Griselinaceae, forming the next branch in the Apiales phylogeny, was usually included in Cornales or even Cornaceae (Hooker 1867; Cronquist 1981), although already Endlicher (1850) had placed *Griselinia* in Araliaceae. Chase et al. (1993), in the first large angiosperm phylogeny based on DNA (*rbcl*) sequence data, recovered a clade composed of Araliaceae, Apiaceae, Griselinaceae [as Cornaceae p.p., that family was shown to be polyphyletic] and Pittosporaceae (see also Olmstead et al. 1993). Pittosporaceae here is sister to Araliaceae + (Myodocarpaceae + Apiaceae), a large clade of Apiales, which is also morphologically well characterized. van Tieghem (e.g. 1884) had already early emphasized that schizogenic resin canals in many parts of the plants and a root anatomy with a characteristic arrangement of the canals and lateral roots suggested a close relationship among Pittosporaceae, Apiaceae and Araliaceae. The root anatomy of Myodocarpaceae apparently has not been investigated. Hegnauer (1969) was one of few who endorsed the proposal of van Tieghem and added some supporting evidence, especially chemical data (see also Judd et al.

1994). Ignorance of this evidence by most specialists in angiosperm classification suggests that these characters were given low weight. Cronquist (1981) insisted on the traditional Rosales affinity of Pittosporaceae and did not even mention root anatomical data in the family descriptions of Pittosporaceae, Apiaceae and Araliaceae, and he cited neither van Tieghem (1884) nor Hegnauer (1969). Takhtajan (1980) preferred Saxifragales for placement of Pittosporaceae, and Thorne (1983) his superorder Rosiflorae. Only Dahlgren (1983) relatively early classified Pittosporales (assessing the position of Tremandraceae and Byblidaceae in this order as highly uncertain) close to Araliales (Apiaceae and Araliaceae). The apparently considerable difference in the ovary position, inferior in Apiaceae and Araliaceae, but superior in Pittosporaceae, possibly was another reason for the resistance of many authors to accept a close relationship among these families. As Erbar and Leins (2010) pointed out, however, in this case the difference is of lesser importance than thought by most systematists, as the intercalary growth in the floral axis resulting in the inferior ovaries is only a gradual difference. Furthermore, one surely can make an argument that the superior ovary of Pittosporaceae is derived.

Apiaceae and Araliaceae were early considered closely related (e.g. Jussieu 1789; Lindley 1830). While this close relationship has long been accepted due to the obvious similarities between the two, their circumscription and delimitation has proved much less simple. Without DNA sequence data, phylogenetic relationships could not be recovered correctly (e.g. Judd et al. 1994). The two genera of Myodocarpaceae as circumscribed here were originally placed in Apiaceae (*Myodocarpus*) and Araliaceae (*Delarbrea*) respectively, and sometimes considered to link these families, and later were mostly placed in tribe Myodocarpeae of Araliaceae. The need to place the two genera in their own family has only recently been realized based on DNA sequence data (Plunkett and Lowry 2001). Nevertheless, the first attempts to clarify the delimitation of Apiaceae and Araliaceae by using DNA sequence data still gave ambiguous results (e.g. Plunkett and Lowry 2001). Especially problematic was the circumscription of subfamily Hydrocotyloideae, which apparently was polyphyletic (Plunkett et al. 1997). Based on extensive taxon sampling

and two DNA plastid markers, Nicolas and Plunkett (2009) finally could convincingly show that the subfamily as traditionally circumscribed (e.g. Drude 1898) is indeed polyphyletic and composed of several lineages dispersed among the Apiaceae and Araliaceae. Hydrocotyloideae s.str. (only four genera) appeared as sister group to the Araliaceae s.str. and today is included in that family. Some systematists, like Thorne (e.g. 1983), had complained that the taxonomic world kept Apiaceae separate from Araliaceae in spite of “numerous non-missing links”. Only the new molecular data could clarify details of the relationships between the two families.

In the phylogenies of Winkworth et al. (2008) and Soltis et al. (2011), the Apiales appear as sister to the Paracryphiales (only family Paracryphiaceae) + Dipsacales clade. These orders are part of the subclass Campanulidae.

Woodiness occurs in all families of Apiales and is certainly plesiomorphic; large trees are very rare, however, and the predominantly herbaceous Apiaceae have by far the largest number of species. Plants are evergreen or deciduous. Schizogenous canals containing ethereal oils, resin or gums occur in the large majority of species, but are restricted to the core Apiales (= Pittosporaceae, Araliaceae, Myodocarpaceae, Apiaceae) and are absent in the three basal families of the order. Vessel elements have scalariform or simple perforation plates, helical thickenings in vessels are sometimes present, and fibres are septate and non-septate. Nodes are normally 3-lacunar to multilacunar. Phyllotaxy is usually spiral, the leaves are simple to compound and their margins entire or not. Stomata are paracytic in Pennantiaceae as well as in the core Apiales, but anisocytic, anomocytic, diacytic and encyclocytic types are also reported for the order. The petiole is nearly always exstipulate and very often sheathing at the base (but not in the basal Pennantiaceae and some Pittosporaceae).

The inflorescences are mostly described as paniculate, more rarely cymose. In the Araliaceae / Myodocarpaceae / Apiaceae clade at least the ultimate units are mostly umbellate. The pedicel is often articulated, the flowers are unisexual or bisexual, typically pentamerous with the exception of the ovary. Dioecy occurs at least in some species of most families of the Apiales. The calyx often has more or less strongly reduced lobes; the

petals are mostly free at anthesis, but Erbar and Leins (2004, 2011) found early sympetaly in Araliaceae (incl. *Hydrocotyle*) and Pittosporaceae, although not (yet) in Apiaceae (only members of Saniculoideae and Apioideae studied). Stamens have free filaments and anthers open by longitudinal slits (except in a few Pittosporaceae). Pollen is nearly exclusively tricolporate and usually more or less spherical. Small flowers, nectaries or nectar-less but fragrant flowers (in *Pennantia*) suggest insect pollination for Apiales.

Superior ovaries exist in Pennantiaceae and, apparently derived from the inferior condition, in Pittosporaceae. All other members of the order have inferior ovaries. Free or only shortly connate stylodia are characteristic for the order, with the exception of Pittosporaceae, part of the Araliaceae and a few Apiaceae. Trans-septal bundles in the ovary occur in Torricelliaceae and Griselinaceae. A nectary is absent in Pennantiaceae, but it is usually present in the other families and of gynoecial origin, as also in most Asterales. At anthesis, it is situated on the lower carpel flanks in the superior ovaries of Pittosporaceae and on the ovary roof, typically in an enlarged stylopodium, in part of the Torricelliaceae (*Aralidium* and *Toricellia*, absent in *Melanophylla*), Apiaceae, Araliaceae and Myodocarpaceae. According to Erbar and Leins (2010), the different position of the nectary in most Apiales families compared with Pittosporaceae is related to the intercalary growth in the floral axis which results in the inferior ovaries in these families. The nectary is always formed, however, at the dorsal base of the carpels. Families of the basal grade of Apiales (Pennantiaceae, Torricelliaceae, Griselinaceae) apparently have a 3-carpellate gynoecium, but only one carpel is fertile. Pennantiaceae have pseudomonomerous 1-locular ovaries with a 3-lobed stigma. The bicarpellate condition is derived and is found in most core Apiales, including nearly all Apiaceae, and all carpels are fertile. In Pittosporaceae the ovary is 2(3–5)-carpellate, the placentation axile or parietal, and there are several ovules. Other core Apiales have one fertile ovule per carpel, and the ovule is unitegmic and tenuinucellate or more rarely crassinucellate.

One-seeded drupes, as in the Pennantiaceae, are common in the order and are probably the plesiomorphic condition, but schizocarpic fruits with dry mericarps on a carpophore are typical

for many Apiaceae, *Myodocarpus* and a few Araliaceae. The drupes suggest endozoochory but reports of this exist only for Pennantiaceae and some Araliaceae. The dry mericarps are dispersed either by autochory or, when winged, by wind and/or water, when with barbs or spines by epizoochory. Most Pittosporaceae have many-seeded capsules, and the sticky fluid around the seeds of *Pittosporum* (produced by multicellular epidermal hairs in the septal region (Erbar and Leins 1995)) suggests bird dispersal which may explain the wide distribution of the genus in the Indo-Pacific region. Seeds contain copious endosperm, apparently mostly oily, and a small straight embryo.

There are little phytochemical data for several families, making meaningful comparisons difficult. Fruit or seed oils containing petroselinic acid were found in *Griselinia*, Araliaceae and Apiaceae, and may occur also in Myodocarpaceae (no data). They are apparently lacking in Pittosporaceae. As Pennantiaceae and Torricelliaceae have not yet been investigated, the distribution and phylogenetic significance of this fatty acid in the Apiales is unclear. Polyacetylenes are known from *Toricellia*, Pittosporaceae, Araliaceae, Myodocarpaceae and Apiaceae. Cyanogenic compounds are very rare in the order. The lack of proanthocyanidins and ellagic acid (or their restriction to the seed coat) is also typical for Apiales. Many Pittosporaceae, Apiaceae and Araliaceae contain triterpenoid saponins and flavonoids (especially the flavonols kaempferol and quercetin). The occurrence of the iridoid glucoside griselinoside in *Aralidium*, *Toricellia* and *Griselinia* supports their close relationship, but data for Pennantiaceae are needed to conclude whether iridoids are plesiomorphic in the order. A basic chromosome number of  $x = 6$  was suggested for the order by Yi et al. (2004). The Apiaceae are extremely variable in their chromosome numbers (see Plunkett et al., this volume).

The historical biogeography of the Apiales clade has recently been analyzed in detail by Nicolas and Plunkett (2014), who also estimated the divergence times for all major clades of the order. They concluded that the order originated in Australasia in the Early Cretaceous, with Aus-

tralia as the likely centre of origin. Many palaeoendemics of the core Apiales today occur in Australia and especially New Caledonia. This island apparently offered refugia to “relictual lineages” because, unlike Australia, it suffered much less aridification and was much later colonized by humans. However, it was submerged at least partly during the Palaeogene. The early diversification of Apiales was probably due to vicariance events during the break-up of Gondwana. Younger lineages more probably developed after long-distance dispersal to Madagascar, Asia and the Americas (*Pittosporum* and Araliaceae). Apiaceae probably also originated in Australia and migrated to South America and South Africa before the complete Gondwana break-up, and later to north temperate regions.

#### CONSPECTUS OF THE FAMILIES OF GENTIANALES<sup>1</sup>

1. Ovary inferior (rarely semi-inferior and very rarely superior); plants usually with interpetiolar stipules (sometimes deciduous); internal phloem absent
  - Rubiaceae**
  - Ovary superior, rarely semi-inferior; interpetiolar stipules usually absent (often with interpetiolar ridges); internal phloem present 2
2. Latex in non-articulated laticifers present in vegetative parts, usually white, less often translucent or yellowish or reddish; ovary mostly apocarpous, less often (congenitally or postgenitally) syncarpous
  - Apocynaceae**
  - Latex absent in vegetative parts; ovary syncarpous, less often partially apocarpous (then Australian herbaceous species) 3
3. Style apically divided into 4 long stigmatic lobes, rarely with two free styles (then a tree with alternate leaves and fruit a 1-seeded samara) **Gelsemiaceae**
  - Style single, rarely two free styles (then leaves not alternate and fruit not a 1-seeded samara) 4
4. Corolla lobes mostly contorted in bud; rarely valvate or imbricate (then plants either herbaceous and from N temperate or palaeotropical regions, or shrubby with pitcher-shaped leaves, or tropical trees with very long and narrow corolla tubes); placentation usually parietal, rarely axile **Gentianaceae**

<sup>1</sup>Key to families by J.W. Kadereit and L. Struwe.

- Corolla lobes imbricate, valvate or exduplicate-valvate in bud; placentation usually axile **Loganiaceae**

As understood here, the well-supported **Gentianales**, a name first used by Lindley (1833) to rename Bartling's (1830) 'Contortae', comprise Rubiaceae (incl. Dialypetalanthaceae and Theligonaceae; 611 genera / 13150 species fide Stevens 2001 onwards; not treated in this volume), Apocynaceae (incl. Asclepiadaceae; 378 / ca. 5350), Gelsemiaceae (3 / 13), Gentianaceae (102 / ca. 1750) and Loganiaceae (16 / ca. 460).

Following the account by Backlund et al. (2000), this circumscription of the order, apart from details, was essentially established by Downie and Palmer (1992) and Olmstead et al. (1993). Whereas close relationships among Apocynaceae (incl. Asclepiadaceae), Gentianaceae and Loganiaceae (at that time incl. part of Gelsemiaceae as well as various elements since segregated; see below) had been accepted for a long time (Bentham and Hooker 1862–1883), inclusion of Rubiaceae was first suggested by Wagenitz (1959). Two families placed near (or sometimes in) Gentianales even in the more recent past (Dahlgren 1980; Takhtajan 1987), Menyanthaceae and Oleaceae, rather belong to Asterales and Lamiales respectively (Downie and Palmer 1992; Olmstead et al. 1992).

Of all families in the order (apart from inclusion of Asclepiadaceae in Apocynaceae; Judd et al. 1994; Endress et al. 1996; for historical account and further references, see family account in this volume), most changes took place in Loganiaceae in the highly para- and polyphyletic circumscription of Leeuwenberg and Leenhouts (1980). These resulted not only in recognition (Struwe et al. 1994) and later recircumscription (Struwe et al. 2014) of Gelsemiaceae (for details, see account of Gelsemiaceae in this volume) as part of the order, but also in the exclusion of several genera (*Buddleja* – Scrophulariaceae / Lamiales; *Nuxia*, *Stilbe* (*Retzia*) – Stilbaceae / Lamiales; *Polyprenum* – Tetrachondraceae / Lamiales; *Plocosperma* – Plocospermataceae / Lamiales; *Peltanthera*, *Sanango* – Gesneriaceae / Lamiales; *Desfontainia* – Columelliaceae / Bruniales; *Anthocleista*, *Fagraea*, *Potalia* – Gentianaceae / Gentianales; generic, familial and ordinal assignment according to Stevens 2001 onwards; for details and further refer-

ences, see account of Loganiaceae in this volume).

Vegetatively, the order almost always has opposite leaves with interpetiolar lines or interpetiolar stipules (interpetiolar stipules are almost always present in Rubiaceae but far less common in the other four families), colleters, defined as multicellular secretory structures, are common and most often found in the leaf axils and on the sepals, and all families except Rubiaceae have bicollateral vascular bundles (internal phloem). Habit is very diverse in the order, ranging from annual or ephemeral herbs to large trees and lianas, and including several mycoheterotrophic and sometimes achlorophyllous genera in Gentianaceae. With very few exceptions flowers are 4- or 5-merous, tetracyclic and sympetalous with epipetalous stamens on the petal tube (Endress 2011) and a bicarpellate apo- (and then often postgenitally fused (Endress et al. 1983)) or syncarpous ovary which is superior or inferior (Rubiaceae). The corolla is often but by no means always contorted in bud. Ovules are tenuinucellar or sometimes reduced tenuinucellar (Endress 2011).

Route I iridoids, seco-iridoids and indole alkaloids, all part of one biosynthetic pathway (Jensen et al. 2002), are common in the order. The intensely bitter gentiopicrin of, amongst others, *Gentiana lutea* (Gentianaceae) represents an example for seco-iridoids, and the well-known strychnine (*Strychnos nux-vomica* / Loganiaceae) and chinine (*Cinchona* spp. / Rubiaceae) are examples for indole alkaloids. Cardenolides and steroid alkaloids are common in Apocynaceae, and xanthonones are common in Gentianaceae.

Whereas Gelsemiaceae and Loganiaceae are exclusively pantropical in distribution, Apocynaceae and Rubiaceae are predominantly pantropical but have reached temperate regions with some genera or suprageneric groups. In Rubiaceae, this is mainly tribe Rubieae (Bremer and Eriksson 2009). In Gentianaceae, the majority of tribes are tropical in distribution but its largest tribe Gentianeae, with more than half of the species diversity of the family and including *Gentiana* as the largest genus of the family, is primarily temperate-alpine (Struwe et al. 2002). Considering this distribution of the order, an origin in tropical areas appears very likely. Several estimates of the stem age of the order converge on

±100 million years ago (Bremer et al. 2004; Janssens et al. 2009; Wikström et al. 2015), but younger estimates of 83–89 (Wikström et al. 2001), 76 (56–97; Lemaire et al. 2011), 85.9 (Magallón et al. 2015) and <76.3 (Tank et al. 2015) have also been published.

Apart from the position of Rubiaceae as sister to a clade of the remaining families, already found in early molecular analyses (Downie and Palmer 1992; Olmstead et al. 1993; Bremer et al. 1999; Backlund et al. 2000), relationships among families, considering sampling of both taxa and data as well as support in various studies (e.g. Refulio-Rodriguez and Olmstead 2014; Nazaire et al. 2014; Struwe et al. 2014; Yang et al. 2016), are best considered unresolved. This, considering the taxonomic history of Loganiaceae, Gentiana-ceae and Gelsemiaceae (see above), clearly reflecting difficulties in their morphological circumscription, is not entirely surprising. Only Apocynaceae are well characterized by rather clear-cut autapomorphies, mainly the presence of latex and the usually apocarpous gynoecium.

As regards relationships of Gentianales within Asterids I (Lamiidae), the order is part of a well-supported clade also containing Boraginales, Lamiales and Solanales. However, relationships among these four orders, considering sampling of both taxa and data as well as support in various studies (Ku et al. 2013; Martínez-Alberola et al. 2013; Refulio-Rodriguez and Olmstead 2014; Weigend et al. 2014; Magallón et al. 2015; Stull et al. 2015; Chen et al. 2016), again are best considered unresolved.

For Rubiaceae, which are not included in this volume, Robbrecht and Manen (2006) and Bremer (2009) provided extensive accounts of phylogeny, evolution and classification. Whereas Robbrecht and Manen (2006) suggested subdivision into two subfamilies, Cinchonoideae and Rubioideae, of which the former is paraphyletic by inclusion of *Coptosapeltea* (containing only *Luculia*, *Acranthera* and *Coptosapelta*: Rydin et al. 2009 - these authors treated *Luculia* as the monogeneric tribe Luculieae), Bremer (2009) recognized three subfamilies, Cinchonoideae, Ixoroideae and Rubioideae with *Coptosapeltea* (+ *Luculia*) unclassified. In a more recent analysis of mitochondrial data (Rydin et al. 2017), *Coptosapeltea* (excl. *Luculia*) were found to be sister to Cinchonoideae plus Ixoroideae.

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## Apiaceae

Apiaceae Lindl., *Intr. Nat. Syst. Bot.*, ed. 2: 21 (1836), nom. cons. et nom. alt.

Umbelliferae Juss., *Gen. Pl.*: 218 (1789), nom. cons. et nom. alt.

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Annual, biennial or perennial, monocarpic or polycarpic, caulescent or acaulescent, glabrous or pubescent or glandular-pubescent herbs, rarely suffrutescent or woody subshrubs, shrubs or trees, evergreen or deciduous; with taproots, rhizomes, or unbranched to branched rootstocks, sometimes swollen and tuberiform; with schizogenous secretory canals throughout the plant. Stems erect, ascending, decumbent, prostrate or rarely creeping; branched or unbranched; with multilacunar (or rarely trilacunar) nodes, internodes sometimes fistulose. Leaves alternate, rarely opposite or verticillate; petioles usually present and typically sheathing at base, often inflated, without (or rarely with) stipules; blades ternately or pinnately compound, or pinnately, ternately, or palmately lobed, or simple and entire to toothed, to deeply divided, rarely sessile or perfoliate; venation pinnate or less commonly palmate or parallel. Plants andromonoecious or hermaphroditic, rarely gynodioecious to dioecious. Inflorescences compound-umbellate (less commonly simple-umbellate, capitulate or cymose), arranged in cymose or racemose synflorescences; umbels typically subtended by an involucre of one to many bracts at the base of the rays (secondary axes), bracts entire or dissected, or lacking; umbellules typically subtended by involucre of one to many bracteoles at the base of the pedicels, bracteoles entire or dissected, or lacking. Flowers perfect or staminate (rarely functionally pistillate), epigynous, actinomorphic (or outer flowers of the umbel or umbellule zygomorphic). Perianth and androecium 5-merous (rarely 5–6-merous). Calyx lobes linear to lanceolate, triangular, or ovate, sometimes spiny or pinnatisect, or small to obscure. Petals valvate, usually basally clawed

and having a narrowed, inflexed apex (less commonly with broad insertion and/or lacking the inflexed apex), sometimes lobed (or shortly notched to deeply bifid), dorsally glabrous or puberulent; sometimes with one to several secretory ducts. Stamens alternate with the petals; anthers dorsifixed or basifixed, tetrasporangiate, dehiscing by longitudinal slits; filaments filiform, inflexed in bud. Ovary syncarpous of 2 carpels (rarely 1 or 2–4), each carpel unilocular with apical to axile placentation; stigmas on stylodia; stylodia distinct, rarely connate, frequently reflexed in fruit, usually swollen at the base to form a nectariferous disc or stylopodium. Ovules anatropous, pendulous, two per locule (but one always abortive), unitegmic, tenuinucellate or pseudocrassinucellate. Fruits dry (rarely fleshy), usually schizocarpic with two mericarps attached by a commissural face, usually with a bifurcated or entire carpophore (becoming free from or remaining fused to the mericarps at maturity); fruits with filiform, keeled, corky, winged, dentate, spiny or obscure ribs formed over the vascular bundles (primary ribs), and sometimes formed in the furrows or valleculeae (secondary ribs); one or more secretory canals found in association with the vascular strands (rib oil ducts, sometimes obscure) and/or in the valleculeae and commissural face (vittae, sometimes arranged cyclically); endocarp parenchymatous (soft to lignified) or sclerified. Seeds straight, endosperm at commissural face plane to deeply concave or sulcate, copious and oily; embryo minute but often well differentiated.

A cosmopolitan family comprising 466 genera and about 3,820 species, most diverse in temperate Eurasia and North America.

**VEGETATIVE MORPHOLOGY.** The typical umbellifers are herbaceous annuals, biennials or perennials, but some species may become woody at the base, and a few species are truly woody trees, shrubs, or subshrubs. Most species are characterized by leafy or scapose stems, often branched and frequently hollow at the internodes. In some species, the branches may be highly reduced, or largely prostrate and rooting at the nodes, or forming a branched or unbranched caudex at or just beneath the surface of the ground; cushion plants are also known among some of the montane and alpine genera. Unbranched or sparsely branching taproots predominate in Apiaceae, ranging from slender to fleshy or tuberous; tubers may be hypocotylar or radical. The leaves of most umbellifers (especially in subfamily Apioideae) are alternate (rarely opposite, as in *Bowlesia*, *Drusa* and *Spananthe*), pinnate, ternate, decompose, or more rarely undivided. The ultimate leaf segments (leaflets or lobes) range from broad and entire, to toothed or lobed, to filiform. A “rachis-leaf” morphology (Kaplan 1970) is found in several lineages of apioids (*Lilaeopsis*, *Harperella*, *Ottoa*, *Tiedemannia*, and some species of *Oenanthe*, *Oreomyrrhis*, and *Perissocoeleum*) and saniculoids (e.g., some species of *Eryngium*), in which the leaflets are lost and the rachis is septate and either inflated or compressed. In some genera, the leaves may be spinescent (e.g., *Aciphylla*, *Echinophora*, *Eryngium*, and *Pycnocycla*), or reduced to simple or branched phyllodes (e.g., *Anginon*). Most genera of subfamilies Saniculoideae, Azorelloideae, and Mackinlayoideae have simple leaves, variously crenate, toothed or lobed (either palmately, ternately, or pinnately). Most umbellifer leaves have pinnate venation, but palmate or parallel venation is known in some genera. They are usually petiolate, but some or all leaves may be sessile or perfoliate (and in some species of *Eryngium*, the leaves may approach a monocot morphology, with a basal intercalary meristem and parallel venation in long blades that lack petioles). The petiole bases are usually sheathing and often inflated; these alate bases are generally not treated as stipules, which are therefore considered lacking in all but a few genera of Azorelloideae and Mackinlayoideae.

**VEGETATIVE ANATOMY.** The stems of umbellifers are often ribbed and fistulose, with the pith lost

at the internodes, or the pith may be present and spongy. Strands of collenchyma are often found in the cortex (under or within the ribs), but these may be lacking, or sometimes replaced by a ring of sclerenchyma (Hoar 1915). Vascular strands are usually arranged in a ring of isolated bundles (or less commonly fused and continuous); cortical and medullary bundles are also common (Hoar 1915). Most species are herbaceous, but the woody habit may result from conventional or anomalous secondary growth in some taxa. The xylem is characterized by libriform fibers and diffuse pores, scanty vasicentric parenchyma, heterogeneous IIB rays (uniseriate or biseriate), vessel elements with almost exclusively simple, elliptical or nearly round perforations (rarely also scalariform) that are nearly at right angles to the lateral walls, simple and bordered pits, and sometimes other modifications, such as helical thickenings (Hoar 1915; Rodríguez 1971; Watson and Dallwitz 1992). Schizogenous secretory canals are found associated with vascular strands, originating from the intercellular space formed by 3 or 4 adjacent cells, and expanding to form elongated, circular canals surrounded by an endothelium of 10–20 cells in transverse section (Mittal 1961), which secrete essential oils, mucilage, balsam, gums and resins. In the roots, concentric rings of amphicribal bundles may be present (as in species of *Angelica*, *Anthriscus*, *Apium*, *Carum*, *Chaerophyllum*, *Cicuta*, *Daucus*, *Oenanthe*, and *Sium*; Metcalfe and Chalk 1983). The sieve-tube plastids of Apiaceae belong to the S-type (see Wagenitz 1992).

The nodes are usually multilacunar, with 7 to 15–17 traces per leaf (Mittal 1961), but trilacunar nodes have also been reported for *Bowlesia* and *Drusa* (Pimenov and Sdobnina 1984).

The petioles may be solid or fistulose, glabrous or pubescent, grooved or ungrooved on the adaxial side; with or without medullary vascular bundles; with collenchyma strands that may or may not be lignified. Petiolar anatomy may vary considerably in some polymorphic genera (e.g., *Angelica*, *Seseli*), where it may be useful for infrageneric taxonomy, whereas in some large genera (e.g., *Ferula*) the petioles are much less variable, and in some unrelated genera, the petioles may be quite similar (Pimenov et al. 1982, 1986).

The primary roots of most Apiaceae exhibit a typical dicot development, in which the central xylem core is diarch to polyarch (with 2–many protoxylem ridges) developing centripetally and alternating with areas of primary phloem, surrounded by 1–2 layers of parenchyma (from which the pericycle develops) and an endodermis (Courchet 1884; Solereder 1908; Havis 1939; Esau 1940; Metcalfe and Chalk 1950). Schizogenous secretory canals are located just interior of the endodermis, opposite both the xylem archs and phloem groups, leading to a peculiar development of lateral roots from the pericycle regions but between the resin canals (and thus between the xylem archs and phloem groups), a feature shared with both Araliaceae and Pittosporaceae (van Tieghem 1872; Solereder 1908; Esau 1940). Secondary growth is initiated from the vascular cambium, after which the cortex and endodermis are shed and the periderm (which develops from the pericycle) becomes the protective layer (Warning 1934; Esau 1940). Schizogenous secretory canals are present in the secondary phloem of older roots (and rarely also in secondary xylem in some species of *Myrrhis* and *Opopanax*) (Metcalfe and Chalk 1950). In the tuberous roots of some species (esp. *Oenanthe*, but also in *Angelica*, *Anthriscus*, *Apium*, *Carum*, *Chaerophyllum*, *Cicuta*, *Daucus*, *Ferula*, *Magydaris*, and *Sium*), numerous centric bundles are found in concentric rings, each with central xylem (Metcalfe and Chalk 1950).

The indumentum is rarely taxonomically important, and many species of Apiaceae are entirely glabrous. In those taxa having an indumentum, it ranges from scarcely puberulent to densely tomentose, and the trichomes range from short papillae to thin and slender hairs, and may be unicellular or multicellular, multi-seriate, glandular, and/or stellate (including hairs, scales or glochids); many taxa are glaucescent, which may be associated with different types of wax crystalloids on adjacent epidermal cells, as in *Bupleurum* (Barthlott et al. 1998). The stomata are anomocytic, hemiparacytic, paracytic, and/or diacytic (Guyot 1966, 1971, 1978; Ostroumova 1987, 1990; Ostroumova and Kljuykov 1991, 2007), and in some cases there is a mixture of stomatal types on a single leaf blade. For those groups in which it has been studied, the dominant stomatal type can be useful as a taxo-

nomic character at the generic or sectional level. Bicytic stomata are relatively rare, but they are known from some species of *Carum*, *Chaerophyllum*, *Ostericum*, and *Vanasushava* (in proportions of 10–50%) and in *Daucus*, *Pimpinella*, *Pternopetalum* and infrageneric groups of *Angelica*, *Laserpitium*, and *Scandix* (in proportions > 50%).

**INFLORESCENCE STRUCTURE AND FLORAL MORPHOLOGY.** Umbellate inflorescences predominate in Apiaceae, although capitulate and cymose inflorescences are also found, particularly in Saniculoideae, Azorelloideae, and Mackinlayoideae. In Apioideae, the inflorescence is most commonly a compound umbel. The peduncles may be terminal, axillary, or both, terminating in one to many secondary axes known as rays. Each ray terminates in one or more pedicels, forming umbellules. The umbels are often subtended by one or more variously shaped bracts, forming an involucre, and the umbellules by one or more bracteoles, forming an involucl. Bracts and/or bracteoles may be entire or dissected, herbaceous, membranaceous, or spiny. Pseudanthia (anthoids) may be formed by the enlargement of the marginal petals of the outer umbellules or flowers (especially in compound-umbellate species of genera such as *Orlaya*, *Lisaea*, *Coriandrum*, *Tordylium*, *Artemisia*, and *Scandix*), or by the enlargement of the involucl bracts (especially in simple-umbellate and capitulate species, as in *Astrantia*, *Actinolema*, *Hacquetia*, *Alepidea*, *Hymenolaena*, *Bupleurum*, *Xanthosia*). Rarely, umbellules may be uniflorous (as in some species of *Centella*, *Xanthosia*, *Bupleurum* and *Lagoecia*). The plants are frequently andromonoecious (with perfect and functionally staminate flowers variously arranged), or completely hermaphroditic, or less commonly gynodioecious or dioecious.

The flowers are epigynous, and development proceeds acropetally through a variety of initiation patterns, but generally ending in the same number and positions of the floral organs (Erbar and Leins 1997; Leins and Erbar 2004). The calyx may be represented by a rim of 5 (4–6) variously sized lobes or teeth, often rather small or sometimes obscure, or linear to lanceolate, triangular or ovate, and sometimes spiny or pinnatisect (*Lagoecia*) or rarely petaloid (*Hermas*). The corolla appears choripetalous at maturity, but

the petals are initiated from a continuous ring primordium (“early sympetaly”; Erbar and Leins 1996, 2004), and comprises 5 (4–6) white, yellow, greenish to rose or purple, valvate petals. The petal bases are usually clawed and the apices are typically narrowed and strongly inflexed; this inflexion may also result in the appearance of a shallow notch or deep cleft, and the apex may be further connate to the body of the petal through a midrib “bridge”. Less commonly, the petals have a broader base and/or a plane to merely recurved apex, or may be deeply dissected (*Sinocarum*), have attenuate hornlets (*Lagoecia*), or a long attenuate apex (*Acronema*); they may also be filiform (resembling staminodes, as in *Hermas*), or sepaloid (as in the female flowers of *Arctopus*). They are typically equal to subequal, but the marginal petals may become enlarged and radiate.

The androecium is formed by 5 (4–6) stamens, alternate with the petals and opposite to the calyx lobes. The filaments are typically long and slender, strongly inflexed in bud but ascending at anthesis. The anthers are basifixed to dorsifixed and longitudinally dehiscent, with two thecae (tetrasporangiate).

The syncarpous gynoecium is almost always bicarpellate and bilocular (rarely unilocular through carpel abortion, or up to 4-carpellate and 4-locular in *Apiopetalum*). The apex of the ovary and the bases of the styles are frequently enlarged into a nectariferous disc or stylopodium (Erbar and Leins 2010) of various shapes and colors, terminating in two (rarely up to 4) styles with wet, non-papillate stigmas. In many New World Umbellifers, the stylopodia (or their upper apocarpic part) may be reduced. The placentation is axile (but appears apical). Each locule encloses a single functional pendulous ovule and a second entirely abortive ovule.

**EMBRYOLOGY.** The endothecium of the anther walls develops fibrous thickenings, but the middle layer is ephemeral (Davis 1966). The cells of the tapetum are glandular, becoming binucleate. Cell wall formation after meiosis is simultaneous. The microspore tetrads are tetrahedral, isobilateral, or decussate, and the pollen, when shed, is 3-celled (Davis 1966).

The ovules are non-arillate, epitropous (with a ventral raphe), anatropous, unitegmic, and

tenuinucellate or pseudocrassinucellate, with a differentiated endothelium. The micropyle is very long due to a massive integument and small nucellus. Several megaspore mother cells may form, but generally only one develops to maturity. Meiosis and cytokinesis of the megaspore mother cell usually occur together. The resulting tetrads are linear, with the chalazal megaspore usually developing into a Polygonum-type embryo sac, although the tetrasporic 16-nuclear Drusa-type (*Drusa* and related genera in Azorelloideae) and Penaea-type (*Azorella trifurcata*) are also represented; in *Sanicula* and *Bupleurum aureum*, the Allium-type and Adoxa-type have been observed alongside the Polygonum-type. The synergids are broad and short, the polar nuclei fuse during or before fertilization, and the 3–11 antipodal cells persist into the early stages after fertilization. Embryogeny is of the solanad type and long suspensors are common (Davis 1966).

**POLLEN MORPHOLOGY.** The pollen grains of Apiaceae are isopolar, tricolporate, small to large (polar axis 15–70  $\mu\text{m}$ ), prolate or perprolate (P/E 1.3 to 2.5), rarely subspheroidal, and triangular in polar view. Cerceau-Larrival (1971) distinguished five pollen types: subrhomboidal, subcircular, ovoid, sub-rectangular, and equatorially constricted. The exine comprises a tectum that appears smooth using light microscopy but is typically striate (or rugulate or psilate) using SEM, and smooth in cross-section. The underlying columellae are arranged in a reticulate pattern and are usually straight (rarely branched). Umbelliferous pollen is triaperturate, with three longitudinal colpi (ectoapertures) and three endoapertures; the furrows are angular or interangular. The pores have distinct costae and may be circular, or elliptical to rectangular, and are arranged perpendicularly to the longitudinal axis of the grain (Cerceau-Larrival 1971; Punt 1984).

**KARYOLOGY.** Chromosome counts have been completed for nearly 75% of umbellifer genera and 45% of species, and these data have been treated at length by Pimenov et al. (2003). With the transfer of *Hydrocotyle*, *Neosciadium*, and *Trachymene* to Araliaceae, haploid chromosome numbers in the remaining Apiaceae range from  $n = 3$  (in *Sium suave* and *Zosima korovinii*) to

$n = 77$  (in *Lomatium columbianum*). Among members of subfamily Apioideae,  $n = 11$  is most common (53%); haploid numbers based on  $x = 11$  ( $n = 22, 33, 44, 55, 66,$  and  $77$ ) together account for an additional 8%. A dysploid or aneuploid series extends without interruption down to  $n = 3$ ; each of these numbers also represents the base of an additional polyploid series (Pimenov et al. 2003; see also Moore 1971). In Saniculoideae, the haploid number ranges from  $n = 4$  to  $n = 48$ . The most common number is  $n = 8$  (44%), followed by  $n = 7$  (17%). Among the genera assigned to Azorelloideae and Mackinlayoideae, haploid numbers range from  $n = 5$  to  $n = 48$ ; although  $n = 10$  and  $n = 8$  are most common (16% each). Together with their polyploid series (i.e.,  $x = 8, x = 10$ ), these numbers account for 65% of chromosome counts in these subfamilies. Some large genera are uniform in chromosome numbers (e.g., *Ferula* with  $2n = 22$ ), but other (even some small) genera exhibit dysploidy (e.g., *Bupleurum* and *Bunium*) or polyploidy.  $C$ -values in Apiaceae have been determined for 46 species in 24 genera, ranging from  $C = 0.63$  pg in *Oenanthe fistulosa* ( $n = 11$ ) to  $C = 5.48$  pg in *Daucus montanus* ( $n = 3x = 33$ ); a similar value of  $C = 5.18$  pg was found in *Astrodaucus littoralis* ( $n = 10$ ; Pimenov et al. 2003; Bennett and Leitch 2005).  $B$ -chromosomes have been documented from 40 species in 24 genera (Pimenov et al. 2003).

**POLLINATION AND REPRODUCTIVE SYSTEMS.** Apiaceae are largely insect pollinated (Koul et al. 1993). The apparent “monotony” of floral morphology among umbellifers, together with the wide range of insect visitors (Diptera, Coleoptera, Hymenoptera, Hemiptera, Lepidoptera) suggested promiscuous pollination, but for those taxa studied more intensively, relatively few of the visitors, mostly Hymenopterans, are effective pollinators (Bell 1971; Bell and Lindsey 1982). Pollinators are attracted by nectar (produced by the stylopodium) and pollen, and presumably by the coloration of the petals and stylopodia; in at least one species (*Angelica triquinata*), the nectar also has a narcotic effect (Bell 1971). Where studied, floral fragrance is dominated by volatile monoterpene hydrocarbons (especially  $\alpha$ -pinene,  $\beta$ -pinene, *cis*- $\beta$ -ocimene, *trans*- $\beta$ -ocimene, limonene, sabinene, and myrcene), which is consistent

with hymenopteran pollinators (Borg-Karlson et al. 1994).

Most apioids are andromonoecious; the distribution of staminate flowers varies widely, but they are most commonly distributed in the center of the outer umbellules and become progressively predominant in the inner umbellules, often with entirely staminate central umbellule(s) (Bell 1971; Webb 1981). The flowering sequence is usually centripetal, with the outer flowers (and outer umbellules) opening before the inner flowers (and inner umbellules; Webb 1981). Protandry also dominates in Apiaceae. If this is strongly developed, it may provide complete outcrossing or at least geitonogamy; when weakly developed, some self-pollination (within flowers) is possible, especially from late-dehiscing anthers (Bell 1971; Webb 1981; Bell and Lindsey 1982; Koul et al. 1993), and self-compatibility seems to be widespread (Lindsey 1982). Protogyny, while less common, has been described for many North American taxa (e.g., *Thaspium* and *Zizia*), but even among protogynous taxa, the distribution and sequence of staminate flowers (predominating in earlier-developing umbels) and hermaphrodite flowers (concentrated in late-developing umbels) provides an overall protandrous development to the entire plant (Webb 1981; Schlessman and Graceffa 2002). Less common still are gynodioecy (as in *Scandia*, *Gingidia*, and *Lignocarpa*) and dioecy (e.g., *Aciphylla*, *Arctopus*, *Anisotome*, and *Trinia*), in which the pistillate flowers often have only rudimentary or non-functional staminodes (Dawson 1971). Even more complex patterns can be found (as in *Centella*), with monoecious, androdioecious and andromonoecious species having umbellules of exclusively staminate, pistillate, or hermaphrodite umbellules.

**FRUITS AND SEEDS.** The fruit is a cremocarp, developing from an inferior, syncarpous ovary usually formed by two carpels (Figs. 1–5). At maturity, the fruits are dry (rarely fleshy, as in *Apiopetalum* and *Mackinlaya*) and indehiscent, usually schizocarpic, splitting along a central commissure and yielding two mericarps. The two mericarps are usually equal, but in some taxa, they may be heteromericarpic (e.g., *Heteromorpha*, *Komarovia*, and some species of *Tordylium*), and in others pseudo-monocarpellate (e.g., *Lagoecia*, *Petagnaea*, *Echinophora*, *Symphyloloma* and

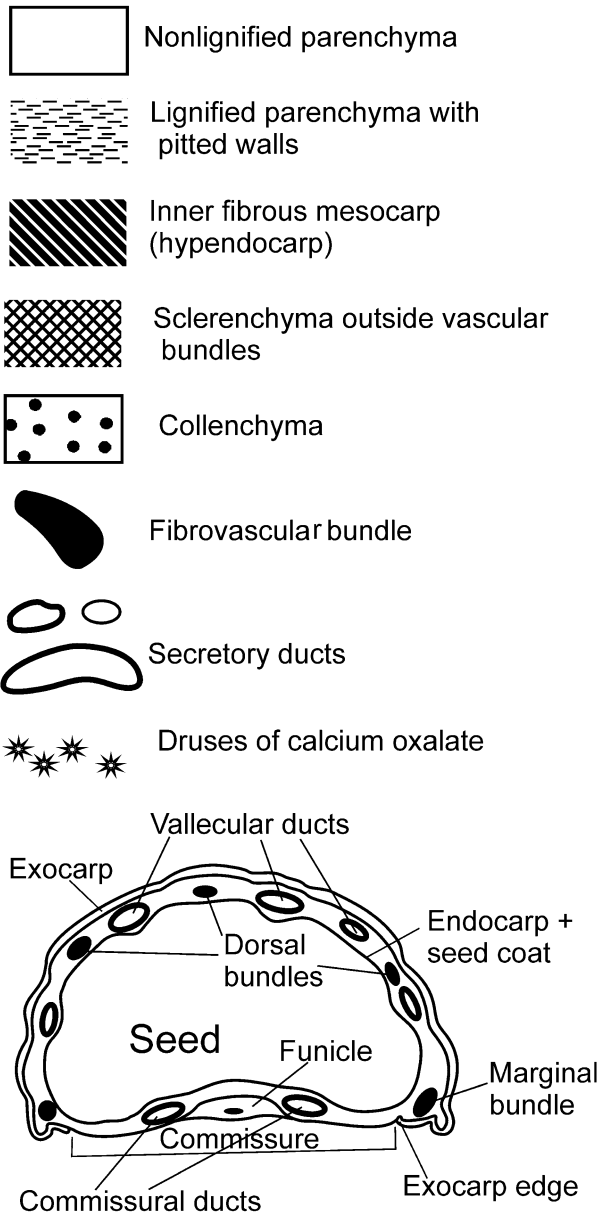


Fig. 1. Apiaceae. Line drawings of a generalized mericarp transverse section, highlighting major features illustrated in Figs. 2 and 3. (Orig., illustrations by Tatiana Ostroumova)

*Schtschurowskia*) (Baumann-Bodenheim 1955). The commissure ranges from very broad (as wide as the mericarps themselves) to very narrow (less than 5% of the mericarp width). Fruits in which the commissure is narrow and the two mericarps are almost spherical are said to be didymous. One or two vascular bundles in the center of the pistil lead to the formation of the

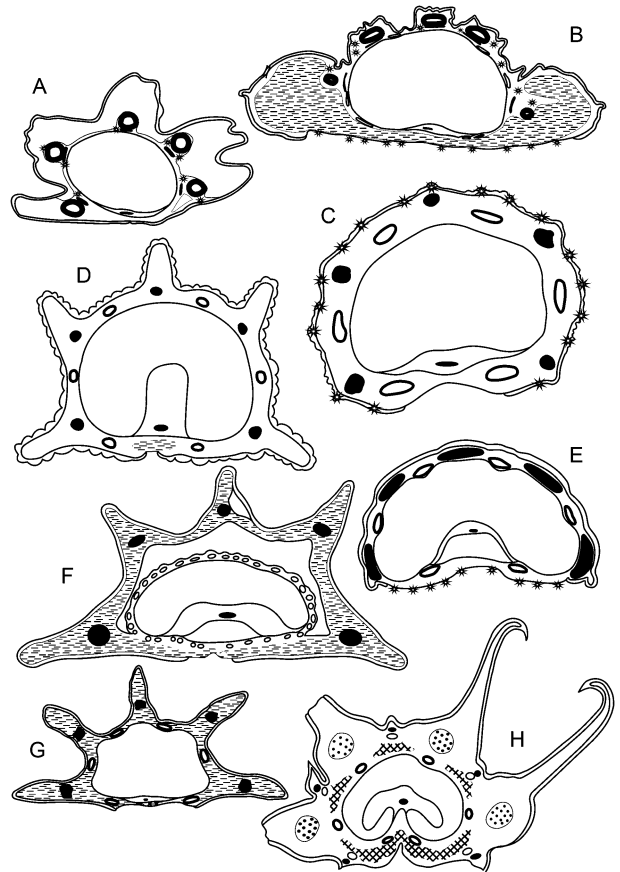


Fig. 2. Apiaceae. Line drawings highlighting major features of the transverse sections of mericarps of the following species: A *Astrantia major*. B *Eryngium maritimum*. C *Ammi majus*. D *Aulacospermum anomalum*. E *Chaerophyllum prescottii*. F *Angelica decurrens*. G *Cnidium monnieri*. H *Caulalis platycarpus*. Scale bars = 1 mm. (Orig., illustrations by Tatiana Ostroumova)

carpophore. In many species, the mericarps are borne at the apex of free carpophores (which may be entire, partially bifid, or entirely bifurcating), but in other species, the carpophores remain fused to the mericarps (or the carpophores may be absent and represented by small vascular bundles in the commissure). The fruits range from transversely terete to strongly compressed, either dorsally or laterally. In some taxa, the upper part of the mericarp is extended into a narrow beak (e.g., *Scandix* and *Anthriscus*). Each mericarp typically has five (or rarely more) primary ribs, of which three are dorsal (one median rib and two laterals) and two are closest to the commissure (marginal ribs). The primary ribs are separated by furrows called valleculae. Secondary ribs

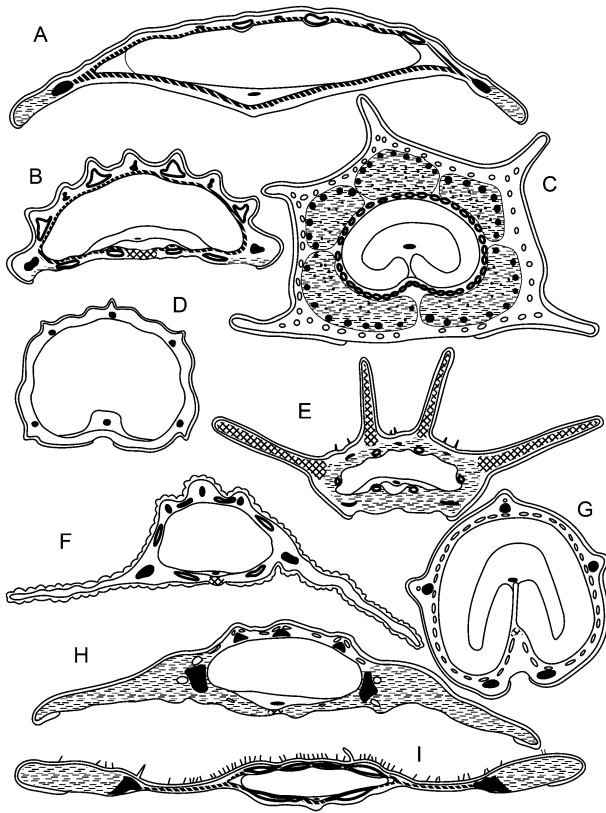


Fig. 3. Apiaceae. Line drawings highlighting major features of the transverse sections of mericarps of the following species: A *Heracleum chorodanum*. B *Laser trilobum*. C *Prangos ferulacea*. D *Bupleurum rotundifolium*. E *Laserpitium latifolium*. F *Ostericum tenuifolium*. G *Smyrniolum olusatrum*. H *Rhizomatophora aegopodioides*. I *Zosima absinthiifolia*. Scale bars = 1 mm. (Orig., illustrations by Tatiana Ostroumova)

develop from the valleculeae in some groups. Either set of ribs may be filiform to very broad, or develop narrow to broad wings, or be variously ornamented (e.g., with hairs, barbs or scales), or obscure. Each primary rib encloses one to several vascular bundles and often one to several associated schizogenous secretory canals called rib oil ducts (also known as intrajugal oil ducts or companion canals). Rib oil ducts are usually well developed in Saniculoideae (where they are typically rather large), Azorelloideae, and Mackinlayoideae; in most Apioideae, they are small to absent, but may be quite large in some apioids (e.g., *Johrenia*, *Oreoselinum*, and some species of *Peucedanum* s. lat.). Exceptions are found in *Steganothaenia* and *Polemanniopsis* (where they are replaced by large cavities in the wings), in *Phlyc-*

*tidocarpa* (where they co-occur with vittae), in *Lichtensteinia* and *Marlothiella* (where they are large and characteristically surrounded by concentric rings of cells), and in *Choritaenia* (where the segments of the four marginal rib oil ducts are uniquely separated to form rows of globose vesicles) (Van Wyk et al. 2013). A second set of schizogenous secretory canals, not associated with the vasculature, are called vittae and are found in the valleculeae and/or the commissural face of the fruits (less commonly cyclical, forming a near-continuous ring, as in *Berula*) in Apioideae, and they are often septate, and rarely anastomosing. More rarely, the vittae of Apioideae may be represented by very short, vesicular oil cavities dispersed in the mesocarp (known only in *Bilacunaria* and *Smyrniopsis*), or lacking altogether (as in *Polemanniopsis*, *Steganothaenia*, *Lichtensteinia*, *Marlothiella*, *Choritaenia*, and the mature fruits of *Aegopodium* and *Conium*). Vittae are also lacking in the fruits of Saniculoideae (but rarely found in *Alepidea*), Azorelloideae, and Mackinlayoideae (although small, vittae-like oil ducts may be scattered in the mesocarp in these subfamilies).

Three layers of pericarp are usually distinguished, but their delimitation can be rather complicated in Apiaceae. The exocarp is derived from the epidermis; it is usually a single layer of small cells with thickened outer walls, but in some genera, the cells may be rather large (30–40  $\mu\text{m}$ ; e.g., *Physotrichia*, *Taeniopetalum*). The mesocarp has several layers and is parenchymatous (although the cells of the inner layers may be thickened with lignified cell walls). Transformed parenchyma may be variously localized in the fruits of many apioids, especially aquatic and xerophytic species. The mesocarp may also be crystalliferous. When present, the crystals of Azorelloideae and Mackinlayoideae are rhomboidal (and found only in the inner layer of the mesocarp, often forming a continuous ring around the endocarp), but druses in Saniculoideae and Apioideae (either scattered throughout the mesocarp, as in Saniculoideae and some early diverging Apioideae, or on the commissural face only, sometimes localized around the carpophore, as in some Apioideae). The endocarp/inner pericarp of Apioideae and Saniculoideae may be parenchymatous, but in some apioids (e.g., in *Heracleum*, *Pastinaca*, *Leiotulus*, *Ferula*



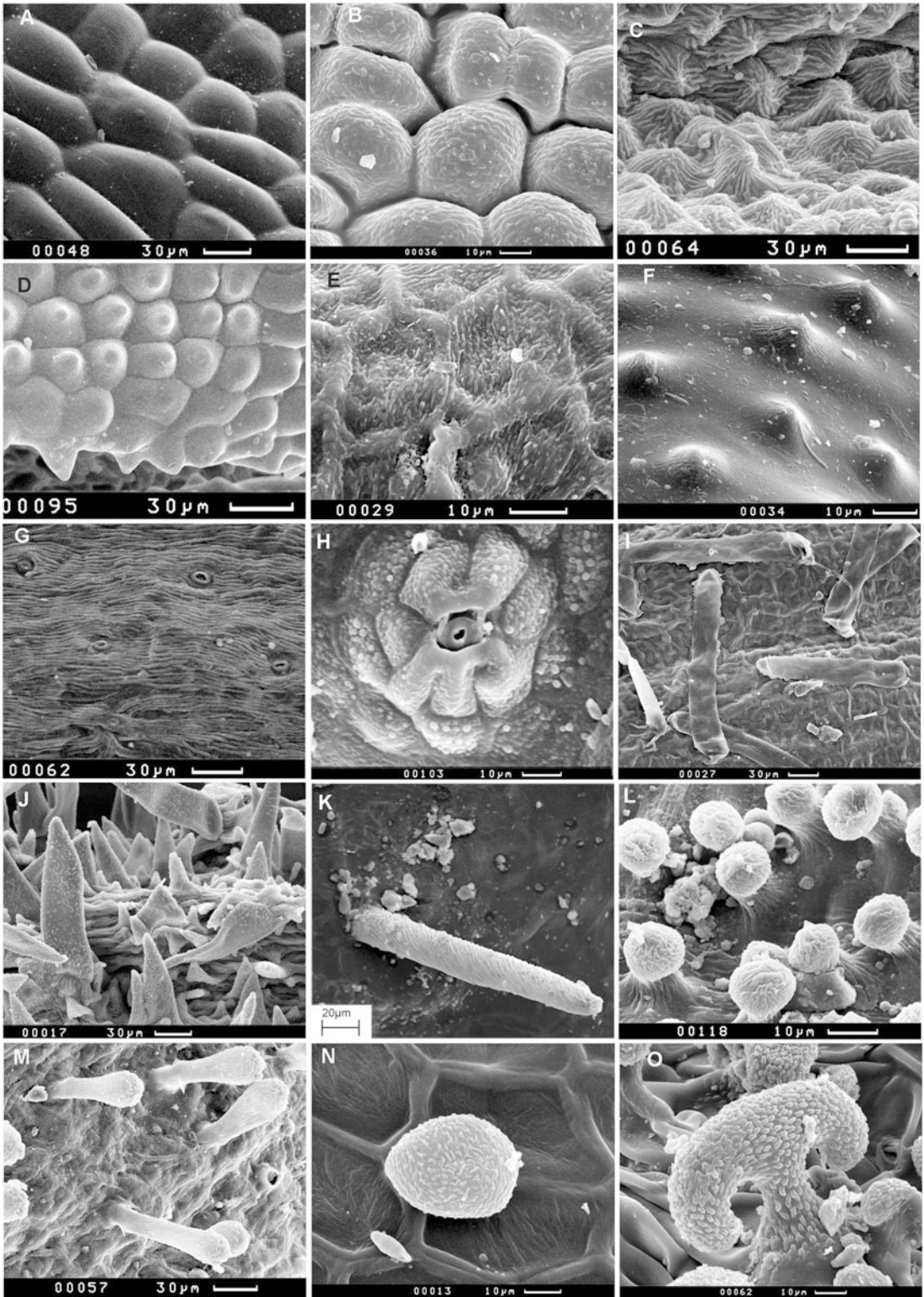


Fig. 4. Apiaceae. Variation in fruit micromorphology. A–D Cells with distinctly sunken borders, outer periclinal walls convex. A *Ostericum palustre*. B *Taeniopetalum are-*

*narium*. C *Katapsuxis silaifolia*. D *Eryngium planum*. E Cells with raised borders (*Pastinaca pimpinellifolia*). F, G Cells with indistinct borders. F *Geocaryum macrocarpum*.

and *Oenanthe*) it consists of lignified fibers or prosenchyma cells (often called the inner mesocarp or hypendocarpium; Koso-Poljansky 1916) or 2–3 layers of sclerified longitudinal fibers (as in *Hacquetia* of Saniculoideae). In Azorelloideae and Mackinlayoideae, however, the inner pericarp is usually referred to as endocarp (e.g., Tseng 1967) and is sclerified. The testa is thinly membranous, but tends to be thicker when the endocarp is parenchymatous. The seed may be adnate to the wall of the locule to entirely free, sometimes occupying only the upper part of the locule (as in *Ligusticum* s.str. and *Haloselinum*). In transverse section, seeds vary from terete to strongly compressed either dorsally or laterally, and are sometimes sulcate under the vittae; the commissural face may be convex to plane or strongly concave to deeply sulcate (rarely with revolute margins, in *Caucalis*, *Turgenia*). The endosperm is copious, oily, rich in starch, and smooth or ruminant, starting as nuclear but maturing into cellular endosperm with thick cell walls. The embryo is small and germination is usually dicotyledonous, with equal to unequal, ovate (“round”) or linear cotyledons (known as R- and L-types, respectively) (Cerceau-Larrival 1962) (Fig. 6). In some taxa (e.g., *Acronema*, *Astomaea*, *Bunium*, *Conopodium*, *Erigenia*, *Geocaryum*, *Hellenocarum*, *Kozlovia*, *Orogenia*, *Stefanoffia* and some species of *Elaeosticta*, *Neomuretia*, *Scaligeria* and *Sinocarum*), the embryo and seedlings are pseudo-monocotyledonous, in which the single cotyledon is usually entire and narrowly linear to ovate (but in some species of *Acronema*, it is more leaf-like, with a deeply dissected lamina) (Kljuykov et al. 2014). The radicle is usually short and always superior (Lubbock 1892).

**DISPERSAL.** Modifications to the schizocarp in Apiaceae are generally interpreted as adaptations for dispersal. Many taxa have winged ribs or exhibit compressed and/or winged mericarps, which apparently serve as adaptations for wind

dispersal (but see Jongejans and Telenius 2001); another adaptation for wind dispersal includes the thick but very light and corky pericarps of *Prangos*. In some taxa, the primary or secondary ribs may be spiny or barbed, indicating ectozoochory (e.g., *Daucus* and relatives), or the fruits may be fleshy (*Apiopetalum* and *Mackinlaya*), suggesting endozoochory. In other cases, the dispersal unit may be the umbellule or entire inflorescence (umbel or capitulum), as in *Petagnaea* and *Thecocarpus* (see Rodríguez 1971), or even entire lax synflorescences (e.g., *Eriosynaphe* and some species of *Seseli*). Dispersal through vegetative means is also known in Apiaceae, especially by creeping rhizomes, stoloniferous roots, and bulbules (e.g., *Sium ninsi* and *Cicuta bulbifera*).

**PHYTOCHEMISTRY.** The distinctive phytochemistry of Apiaceae makes the family easily recognizable (Crowden et al. 1969; Hegnauer 1971, 1973, 1989; Stuhlfauth et al. 1985; Holub et al. 1987; Reduron and Muckensturm 2007–2008). Mono- and sesquiterpenoids are well represented and are at the origin of essential oils (some important for medicinal or perfumery uses). Higher molecular-weight lactones that are not steam volatiles (e.g., archangelolide, gradolide, isomontanolide, laserolide, polhovolide, thapsigargin, and trilobolide) are specific markers of Apiaceae. Diterpenoids are generally absent, but kaurene-type diterpenoids are found rarely (as in *Alepidea* and *Arctopus*). Non-volatile sesquiterpenoids (e.g., sesquiterpene lactones) are found in some apioid genera (e.g., *Ferula* and *Laserpitium*). Phtalides are restricted to only a few genera (e.g., *Apium*, *Ligusticum* s.l., *Angelica* and *Levisticum*). Phenylpropanoids are often encountered, most commonly apiole, asarone, dillapiole, elemicin, estragole, eugenol, and myristicin (plus pseudoeugenol derivatives in *Pimpinella* only). Many coumarins occur in the family, but especially characteristic are the furanocoumarins and pyranocoumarins, whose presence is limited mainly to Apiaceae and one other family

← **Fig. 4.** (Continued) G *Chaerophyllum aureum*. H A stoma on a multicellular bulge, *Astrantia pontica*; such multicellular bulges can be 50–100 microns high in *Astrantia* and some other genera in the family. I–O Unicellular trichomes. I Thin-walled and strap-like, *Pastinaca pimpinellifolia*. J Thick-walled, solitary and tufted, *Seseli petraeum*.

K Thick-walled with helical striations, *Ferula rutbaensis*. L Capitulate, *Astrodaucus littoralis*. M Clavate, *Lagoecia cuminoides*. N Vesicular, *Tordylium lanatum*. O T-shaped, *Trachyspermum paktianum*. (Orig., SEM photographs by Tatiana Ostroumova)

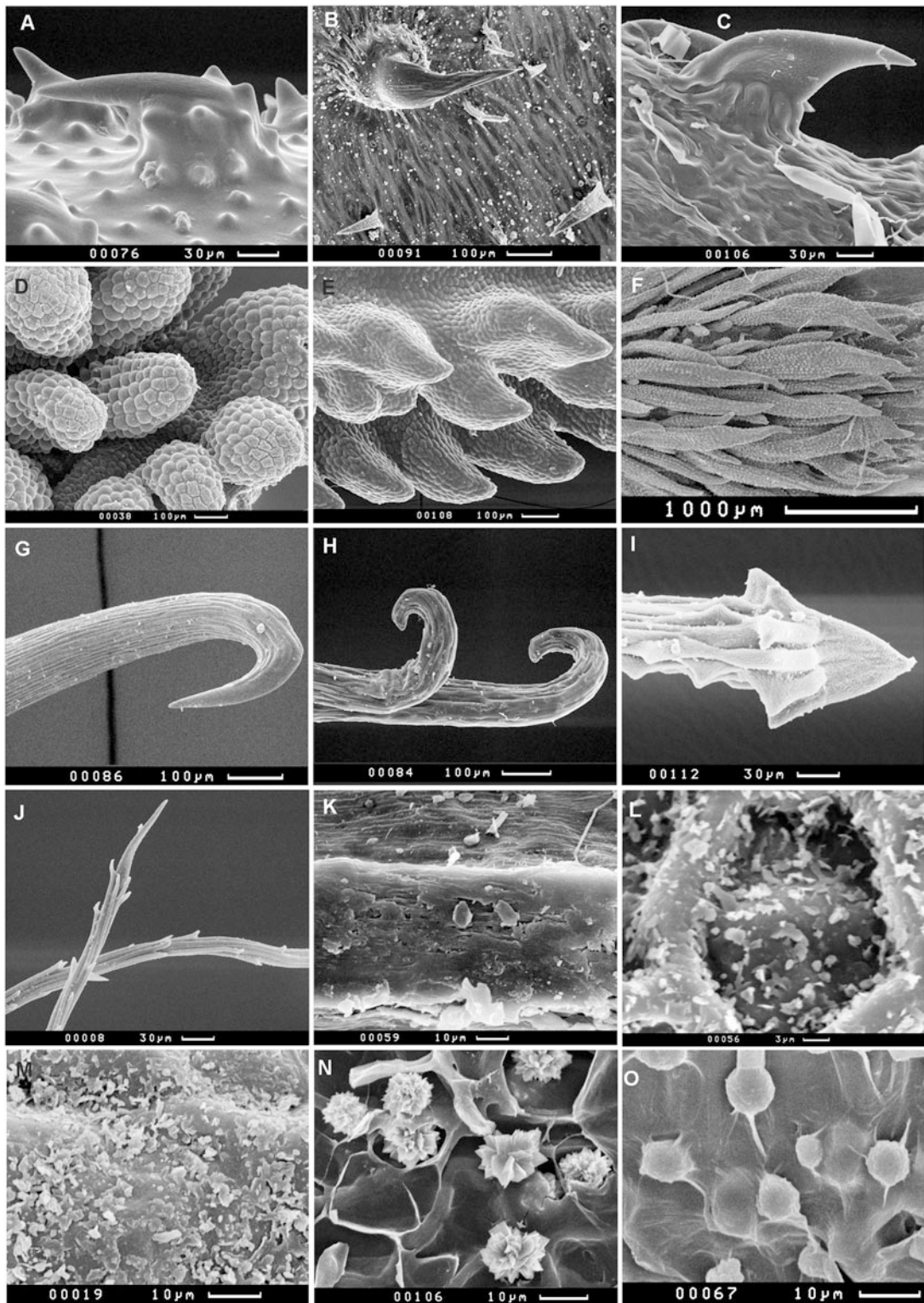


Fig. 5. (in the Apiaceae treatment). Variation in fruit micromorphology. A-C Trichomes with multiserial bases. A *Anthriscus sylvestris*. B *Heracleum grandiflorum*. C *Heracleum sosnowskyi*. D-F Multicellular



Fig. 6. Apiaceae. Seedlings, highlighting cotyledon variation. A–D Typical dicotyledonous seedlings. A *Ferula tingitana*, with narrowly oblong cotyledons. B *Oenanthe pimpinelloides*, with narrowly lanceolate cotyledons. C *Scandix grandiflora*, with linear cotyledons. D *Mediasia macrophylla*, with ovate-lanceolate cotyledons. E–G Pseudo-monicotyledonous seedlings. E *Scaligeria napi-formis*, with a single ovate cotyledon, bilobed at the tip. F *Acronema commutatum*, with a single leaf-like, ternately dissected cotyledon. G *Bunium microcarpum*, with a single narrowly oblong cotyledon. (Orig., illustrations by Svetlana Petrova)

(Rutaceae). These substances are known for their phototoxicity (inducing dermatitis) but also for their antifungal, bacteriostatic, insect antifeedant and generally repulsive properties. The most representative compounds of these classes are angelicin, byakangelicol, bergapten, imperatorin, peucedanin, pimpinellin, psoralen and xanthotoxin. Chromones are also represented, for example khellin, an important medicinal source from *Visnaga daucooides*. Polyacetylenes are present in more than 100 species, including useful compounds such as falcarinol and falcarindiol (often present in the roots, and apparently beneficial to humans in small amounts), as well as toxic compounds such as aethusin (*Aethusa*), cicutoxin (*Cicuta virosa*), oenanthotoxin (*Oenanthe crocata*), responsible for the poisonous properties of these taxa. Alkaloids are rarely found in the genera of Apiaceae, but the toxic coniine (and related compounds) from poison hemlock (*Conium maculatum*) is a famous exception. Other constituents include saponins (noticeably present in certain genera, including *Bupleurum*, *Centella*, *Eryngium*, and *Sanicula*), sugars such as the pentose sugar apiose (first isolated from parsley) and the trisaccharide umbelliferose (specific to umbellifers), and fatty acids such as petroselinic acid (also found in Araliaceae). Flavonoids are present in most Apiaceae (especially kaempferol, luteolin and quercetin), and sometimes have taxonomic value. Several species are sources of oleo-gum-resins, particularly in the genus *Ferula*. Umbellifers lack iridoids, cyanogenic compounds, proanthocyanidins and ellagic acid.

SUBDIVISION AND RELATIONSHIPS WITHIN THE FAMILY.

The systems of the 19th and early 20th centuries (e.g., Koch 1824; Bentham 1867; Drude 1898; Koso-Poljansky 1916) differed dramatically in their intergeneric treatments of Apiaceae, but only that of Drude (1898) has had a lasting influence on umbellifer taxonomy. Drude recognized three subfamilies: Apioideae, Saniculoideae, and Hydrocotyloideae. These were further divided into 12 tribes (eight in Apioideae and two each

Fig. 5. (Continued) tubercles and scales. D *Bupleurum papillosum*. E *Astrantia maxima*. F *Eryngium planum*. G–J Spines and bristles. G *Orlaya daucooides*. H *Sanicula rubriflora*. I *Astrodaucus littoralis*. J *Chaetosciadium trichospermum*. K–M Epicuticular waxes. K

*Angelica czernaevia*. L *Bupleurum lophocarpum*. M *Bupleurum sibiricum*. N, O Calcium oxalate crystals on the commissural face. N *Eryngium planum*. O *Chaerophyllum aureum*. (Orig., SEM photographs by Tatiana Ostroumova)

in Saniculoideae and Hydrocotyloideae). This system has been updated and enhanced by Pimenov and Leonov (1993), who expanded the number of tribes to 16 with the addition of four new apioid tribes. Subfamilies Apioideae and Saniculoideae have largely held up as natural groups, although some taxonomic transfers (e.g., the transfer of *Lagoecia* and *Oligocladus* to Apioideae) were necessary to restore monophyly. Magee et al. (2010), however, have shown that several, mostly African genera form a grade at the base of Apioideae. Almost all of these “protoapioids” have druse crystals scattered around the mesocarp. Given the placement of the protoapioids relative to Saniculoideae, these authors suggested the inclusion of Saniculoideae within an expanded Apioideae, providing a more accurate reflection of the major morphological discontinuities, but the recognition of the two subfamilies is maintained in the current treatment until greater consensus emerges. Even more difficult have been the Hydrocotyloideae, which are grossly polyphyletic. The type genus *Hydrocotyle*, along with *Trachymene* (including *Uldinia*) and *Neosciadium* have been transferred to Araliaceae, while other members have been transferred to Apioideae (e.g., *Naufraga* and *Notiosciadium*) or Saniculoideae (viz., *Arctopus*). The remaining genera are currently treated in two new subfamilies, Azorelloideae and Mackinlayoideae (Plunkett et al. 2004; Nicolas and Plunkett 2009). Subfamily Mackinlayoideae unites *Centella*, *Micropleura*, *Xanthosia*, *Actinotus*, and several other “former hydrocotyloids” with two genera transferred to Apiaceae from Araliaceae (*Mackinlaya* and *Apiopetalum*). The majority of genera, however, are now placed in subfamily Azorelloideae, which most closely resembles Drude’s (1898) circumscription of Hydrocotyloideae, and includes (among others) the large genera *Azorella*, *Bowlesia*, and *Eremocharis*. *Hermas* and *Klotzschia* remain *incertae sedis*; they are tentatively assigned here to Azorelloideae, but new subfamilies may be needed to accommodate one or both genera.

The four subfamilies recognized here are distinguished primarily on the basis of fruit characters. Apioideae have vittae in the valliculae and on the commissure, but rib oil ducts are usually very small or lacking (rarely large). The inner pericarp of Apioideae and Saniculoideae is typi-

cally parenchymatous, but when “sclerified”, the inner fiber-like cells are always arranged transversely and the outer fiber-like cells (if present) longitudinally. Saniculoideae typically have distinct (and often very large) rib oil ducts, and usually lack vallicular vittae (although small, branched, vittae-like rib oil ducts may be found scattered in the mesocarp). In addition, they often have outgrowths on their exocarps (e.g., scales, bristles, or prickles) and druse crystals scattered throughout the mesocarps. Druses surrounding the seeds are also found in the protoapioids; otherwise, druses are rare in Apioideae, and are then found only on the commissural side of the mericarp. Subfamilies Azorelloideae and Mackinlayoideae share many features, notably an endocarp of fiber-like sclereids (with the inner fibers longitudinal and the outer fibers transverse), rhomboidal crystals limited to the inner layer of the mesocarp (and often forming a ring around the endocarp). Like Saniculoideae, vallicular vittae are lacking (and likewise, if vittae are present, they are scattered in the mesocarp). Rib oil ducts are usually present and distinct (but not generally large). The mericarps of most Azorelloideae are compressed dorsally, typically by a broadening of the two lateral ribs (or less commonly of the marginal ribs, as in *Azorella* sect. *Laretia*), or rarely terete (*Oschatzia*). In Mackinlayoideae, the fruits are laterally compressed.

Few of the tribes and subtribes recognized by Drude (1898) have proved monophyletic, although Tordyliinae and the small Echinophorae are notable exceptions. Downie et al. (2001, 2010) provided synopses of currently recognized “tribes and clades” in Apioideae, but the assignment of genera to molecular clades remains incomplete, with several groups recognized only informally, and many genera left unsampled or non-monophyletic. In Saniculoideae, after the transfer of *Lagoecia* to Apioideae, the remaining genera of tribe Lagoecieae have been united with those of tribe Saniculeae. Calviño and Downie (2007) transferred two protoapioids (*Steganotaenia* and *Polemanniopsis*) to Saniculoideae, which they recognized as a new tribe, Steganotaenieae, but Magee et al. (2010) have more recently proposed several additional tribes for other protoapioids (see also Van Wyk et al. 2013). The tribes (and subtribes) of Drude’s Hydrocotyloideae, like the subfamily itself, are largely polyphyletic, and

no new tribes have yet been proposed for subfamilies Azorelloideae or Mackinlayoideae (see Nicolas and Plunkett 2009). The difficulty in circumscribing tribes in Apioideae is connected with the lack of morphological discontinuities in many characters across a great many taxa, coupled with the frequent occurrence of convergences and parallelisms for many other morphological characters. Given that the recognition and circumscription of tribes remains largely unsettled, the genera of Apiaceae are organized herein by subfamily, and thence alphabetically. Unless otherwise noted, phylogenetic relationships cited in the generic treatments below follow Downie et al. (2010) for Apioideae, Calviño and Downie (2007) for Saniculoideae, and Nicolas and Plunkett (2009) for Azorelloideae and Mackinlayoideae.

**AFFINITIES.** In groups known variously as Umbelliflorae, Umbellales or Apiales, the Apiaceae have traditionally been allied with Araliaceae, with which they share many floral features, such as frequently pentamerous perianths, reduced calyces, free petals and stamens, inferior ovaries, nectariferous discs or stylopodia, a single pendant, anatropous, functional ovule, seeds with copious endosperms and small, straight embryos, and frequently umbellate inflorescences (Rodríguez 1971). Additionally, the families share schizogenous secretory canals with essential oils and resins, and a host of other phytochemical similarities (e.g., the shared presence of polyacetylenes, seed fats with petroselinic acid, oleanene- and ursene-type triterpenic sapogenins, and the lack of iridoids and true tannins) (Hegnauer 1971). The current circumscription of the order Apiales (Plunkett et al. 2004) also includes Pittosporaceae, which shares with Apiaceae and Araliaceae schizogenous secretory canals (van Tieghem 1884), a similar ovule structure (Jurica 1922), phytochemistry (Jay 1969; Hegnauer 1971), and “early sympetalous” corolla development (Erbar and Leins 2004), although Pittosporaceae differ in several characters, notably large and showy petals, superior ovaries, and the complete lack of umbels. Several other small families have been added to Apiales, including the araliad segregate family Myodocarpaceae, plus Torricelliaceae (defined broadly to include *Torricellia*, *Melanophylla*, and *Aralidium*), Griselinaceae,

and Pennantiaceae. The order is placed in subclass Asteridae near Dipsacales and Asterales, with which it shares early sympetaly, unitegmic and mostly tenuinucellate ovules, S-type sieve-tube plastids, and a series of phytochemical characters (e.g., similar alkaloids, sesquiterpene lactones, falcarinone-type polyacetylenes, acetate-derived anthraquinones, triterpenic sapogenins, flavonols, isopentenyl-substituted coumarins, and ethereal oils, plus the absence of iridoids and tannins; reviewed in Plunkett 2001; Erbar and Leins 2004).

**DISTRIBUTION AND HABITATS.** Umbellifers are nearly cosmopolitan, but biogeographic studies (based on time-dated molecular phylogenies; Nicolas and Plunkett 2014) suggest that Apiaceae had an Australasian origin dating to the late Cretaceous/early Eocene (median minimum crown age of ~87 Ma). The major clades corresponding to subfamilies Mackinlayoideae, Azorelloideae, and Saniculoideae+Apioideae all originated at roughly the same time (median minimum crown ages of ~66 Ma), but in different regions (Australasia, southern South America, and southern Africa, respectively). Today, they are most diverse in the temperate (and especially arid) regions of the Northern Hemisphere. By comparison, they are relatively rare in the humid tropics, where they are typically restricted to higher elevations. Habitats vary widely from dry, rocky fields to aquatic environments, from open to woodland settings, and from low elevations (sea level) to high-alpine sites.

Asia has the greatest number of genera (289) and the largest number of endemics (177 genera). Geographic connections of the Asian genera are greatest with Europe (with 101 shared genera) and Africa (55 genera), and much less so with the New World (22 genera shared with North and South America combined). Europe and Africa have a comparable number of genera. Europe has a total of 126 genera, but only 17 are endemic. Europe shares the greatest number of genera with Asia (101) and Africa (58), and relatively few with the New World (16 genera). Africa has a total of 121 genera, of which 24 are shared between northern and sub-Saharan Africa. Northern Africa (with a total of 82 genera and 13 endemics) shares the greatest number of genera with Europe (56) and Asia (52), but only