Introduction to the Orders and Families of Uncertain Placement of this Volume

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The present volume of this book series is the first of two to (almost) complete the treatment of the Asterids which started with Vol. VI (Cornales, Ericales, 2004), Vol. VII (Lamiales, 2004) and Vol. VIII (Asterales, 2007). It contains the orders Boraginales, Garryales and Solanales of the Lamiids (Asterids I) as well as three unplaced families of that clade, i.e. Vahliaceae, Icacinaceae and Metteniusaceae, and the orders Aquifoliales, Escalloniales, Bruniales, Dipsacales and Paracryphiales of the Campanulids (Asterids II).

Asterids I (Lamiids)

CONSPECTUS OF THE FAMILIES OF GARRYALES

1. Deciduous trees with alternate leaves. 1 genus/1 species, China **Eucommiaceae**
– Evergreen shrubs with opposite leaves 2
2. Inflorescence catkin-like, fruit a berry with 2 or 3 seeds. 1/15, N and C America, Greater Antilles **Garryaceae**
– Inflorescence not catkin-like, fruit a 1-seeded drupe. 1/8–11, E Asia **Aucubaceae**

As treated here, **Garryales** contain Garryaceae, Aucubaceae and Eucommiaceae with altogether three genera and 24 to 27 species. In APG III (2009), Aucubaceae was included in Garryaceae. Whereas a close relationship between Garryaceae and Aucubaceae had already been suspected by Baillon (1877), the relationship between Garryaceae/Aucubaceae and Eucommiaceae had not been suspected until revealed by molecular analyses (Soltis et al. 2000). Garryales at present are resolved as sister to all other Lamiids except Icacinaceae and Metteniusaceae (incl. Oncothecaceae; Refulio-Rodriguez and Olmstead 2014). All taxa in the order are dioecious woody plants with exstipulate leaves containing the iridoid aucubin. Beyond that, no obvious synapomorphy can be recognized, although the close relationship between *Garrya* and *Eucommia* (but not *Aucuba*) may be supported by the possession of gutta-percha (trans-1, 4-polyisoprene). The order is distributed in East Asia (*Aucuba*, *Eucommia*) and western North America (*Garrya*, with one species in the Greater Antilles). The stem group age of Garryales has been estimated at ca. 97 million years ago (Ma; Magallón and Castillo 2009), and the split between Garryaceae/Aucubaceae and Eucommiaceae has been dated at 20 ±8.6 Ma (Janssens et al. 2009) or 49.8 Ma (Magallón and Castillo 2009). The two families may represent remnants of a formerly more widespread north hemispherical lineage of presumably forest plants.

THREE FAMILIES OF UNCERTAIN PLACEMENT WITHIN THE LAMIIDS

Vahliaceae, **Icacinaceae** and **Metteniusaceae** (incl. Oncothecaceae) have all been associated with Garryales. However, new evidence indicates a relationship of Vahliaceae to Solanales, and Icacinaceae plus Metteniusaceae (incl. Oncothecaceae) appear to be sister to all other Lamiids (Refulio-Rodriguez and Olmstead 2014). No character is known which could support the relationship between Vahliaceae and Solanales. Whereas Vahliaceae with one genus and five species are annual or perennial herbaceous to subshrubby plants, Metteniusaceae with two genera and nine species and Icacinaceae with 35 genera

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Boraginales by M. Weigend

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and ca. 245 species are woody, sometimes lianaceous in Icacinaceae. All three families are largely tropical in distribution. Thus, Vahliaceae are found mainly in Africa (but also on the Indian subcontinent), Metteniusaceae grow on New Caledonia (*Oncotheca*) and Central to South America (*Metteniusa*), and Icacinaceae are pantropical with centres of diversity in Africa and Southeast Asia. The woody *Dendrobangia* of essentially unknown affinity with two species from Central to South America is here treated in Metteniusaceae, and this appears to be supported by new data (Greg Stull, pers. comm.). The circumscription of Icacinaceae presented here differs from past treatments of the family, and further changes in circumscription can be expected. Thus, several genera of Icacinaceae have been included in Cardiopteridaceae and Stemonuraceae of Aquifoliales and Pennantiaceae of Apiales (Kårehed 2001), and new data (Greg Stull, pers. comm.) seem to require the transfer of a number of other genera of Icacinaceae as treated here into an expanded Metteniusaceae.

If the relationships of Icacinaceae with Metteniusaceae (incl. Oncothecaceae) can be confirmed, they would represent a tropical to south hemispherical counterpart of the north hemispherical Garryaceae/Aucubaceae and Eucommiaceae. The ages of Icacinaceae and Metteniusaceae (and Oncothecaceae) have been estimated at ca. 97 Ma, and that of Vahliaceae at ca. 83.5 Ma (Magallón and Castillo 2009).

Conspectus of the families of Solanales

1. Herbs of swampy areas, cortex with large air-spaces. Flowers small in dense terminal spikes, petal lobes folded inwards. 1/1, tropical and subtropical regions of the Old World, naturalized in the Americas **Sphenocleaceae**
– Characters not as above 2
2. Plants dioecious. Leaf axils with tuft of hairs. Ovary inferior. 3/5, equatorial and southern Africa and Madagascar **Montiniaceae**
– Plants rarely dioecious. Leaf axils without tuft of hairs. Ovary superior 3
3. Plants with milky sap (sometimes inconspicuous), sepals large, free. About 57/1600, cosmopolitan **Convolvulaceae** (not in this volume)
– Plants without milky sap. Sepals of various size, united at base 4
4. Bases of filaments conspicuously broadened. Stylodia 2, spreading. 1/11, cosmopolitan, mainly tropical **Hydroleaceae**
– Bases of filaments not conspicuously broadened. Style simple. 96/2400, cosmopolitan **Solanaceae**

The **Solanales** are composed of five families: Solanaceae (94 genera; incl. Duckeodendraceae, Goetzeaceae, Nolanaceae and Sclerophylacaceae), Convolvulaceae (57 genera; incl. Cuscutaceae), Sphenocleaceae (1 genus), Hydroleaceae (1 genus) and Montiniaceae (3 genera). Vahliaceae probably should also be included in the order as they appear to be sister to Solanales (Refulio-Rodríguez and Olmstead 2014). This latter relationship, however, had high support only in the Bayesian tree and not in the ML and MP trees. The close relationship of Convolvulaceae and Solanaceae, which are sister to each other, has long been accepted (e.g. Jussieu 1789) but the presently accepted composition of the order has been proposed only rather recently. In the past, Solanales often were considered part of a larger suprafamiliar group, the “Tubiflorae”, which also included Polemoniales, Boraginales (Bartling 1830; Bessey 1915 as Polemoniales) and sometimes (Engler system, e.g. Engler 1903) also Lamiales. Until recently, Boraginaceae s.l. and Polemoniaceae (the latter now part of Ericales near the base of the asterids) were considered families closely related to Convolvulaceae/Solanaceae. The first large angiosperm phylogeny DNA sequence study (Chase et al. 1993) suggested that Montiniaceae (formerly included in Saxifragaceae, Cornaceae or Grossulariaceae) belong to Solanales. *Sphenoclea* was generally considered part of or close to Campanulaceae until Cosner et al. (1994), using *rbc*L sequence data, showed that it belonged into Solanales. *Hydrolea* had always been included in Hydrophyllaceae or in Hydroleaceae s.l., comprising various genera of Hydrophyllaceae s.l. until Di Fulvio de Basso (1990), based mainly on embryological data, showed that Hydroleaceae should include only *Hydrolea*. The *rbc*L sequence data of Cosner et al. (1994) later demonstrated that such monogeneric Hydroleaceae belong in Solanales instead of Boraginales. The placement of Polemoniaceae in Ericales, first suggested by Olmstead et al. (1992) based on *rbc*L sequence data, was unexpected (e.g. Cronquist 1981; Dahlgren 1983; Thorne 1983). This family shares with Solanales characters such as usually alternate leaves, 5-merous and usually actinomorphic perianth and androecium, plicate sympetalous corolla with adnate stamens, superior ovary, annular nectary disk frequent, and persistent calyx. On the other hand, non-DNA differences to typical Solanales are few: lack of alkaloids, internal phloem typical of Solanaceae and Convolvulaceae absent, sepals with broad membranous margins, and endosperm development nuclear (cellular in most Solanales with the exception of Convolvulaceae, but data lacking for Montiniaceae). Hufford (1992) suggested that the 3-carpellate gynoecia and loculicidal capsules of Polemoniaceae fit better in Ericales than in (core) asterids which tend to have bicarpellate gynoecia and septicidal capsules. Convolvulaceae, however, also often have loculicidal capsules, and 3-carpellate gynoecia occasionally occur in Solanales. Of the two possible morphological synapomorphies of Ericales discussed by Judd et al. (2008), i.e. theoid leaf teeth and protruding axile placentas, none is found in Polemoniaceae.

*rbc*L sequence data (Chase et al. 1993), *ndh*F sequence data (Olmstead et al. 2000), and sequence data of the 25,000 bp plastid inverted repeat (IR) region (Moore et al. 2011) weakly supported Boraginales as sister of Solanales. Soltis et al. (2011), however, identified Gentianales as sister of Solanales, but without bootstrap support. The phylogeny of Qiu et al. (2010), based on sequence data of mitochondrial genes, found Boraginales, Solanales and Gentianales as successive branches close to the base of Lamiidae. Corolla tubes with folding lines was suggested as a possible synapomorphy of Boraginales+Solanales (Judd and Olmstead 2004), but knowledge of this character, rarely mentioned in modern taxonomic literature, is rather incomplete. Alternate leaves, terminal inflorescences, and a persistent calyx are other morphological characters common to Boraginales and Solanales. Lack of iridoids has been suggested as a possible synapomorphy of Solanales and Boraginales by Judd et al. (2008), but iridoids are not completely absent from Solanales (see below). Pollen tubes with callose is another character possibly supporting a close relationship of Solanales and Boraginales. It occurs in Convolvulaceae, Solanaceae, Boraginaceae and part of Hydrophyllaceae (tribe Hydrophylleae), but not in Ehretiaceae, Heliotropiaceae and another part of Hydrophyllaceae (tribe Romanzoffieae; Prósperi and Cocucci 1979). In summary, a sister group relationship of Boraginales and Solanales seems best supported by the data currently available. The partly incomplete knowledge of morphological characters and lack of resolution at the base of Lamiidae, however, considerably complicate the evaluation of synapomorphies.

The members of Solanales are mainly herbs to shrubs or twining herbaceous or woody plants; trees, especially large trees, are rare (e.g. *Duckeodendron*, *Humbertia*). Leaves are alternate, usually simple and exstipulate. Flowers are arranged in terminal inflorescences, are normally bisexual, frequently 5-merous in perianth and androecium, with stamens adnate to the corolla tube; the ovary normally is superior and, with few exceptions (e.g. *Jaborosa*, *Nicandra*, *Nolana*), bicarpellate. The corolla is usually actinomorphic, and sympetaly is late, early only in *Sphenoclea* (Erbar 1995). A nectary often forming a disk around the ovary (always of gynoecial origin?) is rarely absent (e.g. *Solanum*, *Sphenoclea*). The endosperm is cellular (Hydroleaceae, Solanaceae, Sphenocleaceae) or nuclear (Convolvulaceae, probably an autapomorphy), unknown for Montiniaceae. Fruit types are various, but most common fruits are capsules (septicidal or septicidal-loculicidal, more rarely loculicidal or circumscissile) or berries, and the calyx is persistent.

Phytochemical data are abundant for Solanaceae and Convolvulaceae, but much less so for the three smaller families. In his detailed review, Eich (2008) characterized the former two families as follows:

General secondary metabolites: phenolics such as simple cinnamic acid derivatives, hydroxycoumarins, hydroxycinnamate conjugates, flavonoids, lignans, sterols, carotenoids, fats/oils and fatty acids.

Specific secondary metabolites: ornithine-derived alkaloids such as hygrines, N-acylpyrrolidines, nicotinoids, tropanes, calystegines. Sesquiterpenoid phytoalexins.

Absent: iridoids; essential oils, complex mixtures of lipophilic mono-/sesquiterpenes and/or phenylpropanoids secreted in oil cells, secretion ducts/cavities or glandular hairs; condensed tannins (proanthocyanidins).

While iridoids seem to be completely absent from Solanaceae and Convolvulaceae, the presence of the allochemical secoiridoid-glycosides, able to inhibit root growth of rice seedlings, has been reported by Hirai et al. (2000) for the weedy *Sphenoclea zeylanica*. An iridoid compound (Montinioside) has also been reported for *Montinia caryophyllacea* (Dahlgren et al. 1977). Alkaloids appear to be absent from *Sphenoclea*.

Phylogenetic relationships within Solanales as currently accepted are (((HYDROL-SPHENO)(MONTIN))(CONVOLV-SOLAN)). Embryological data support the sister group relationship of Hydroleaceae and Sphenocleaceae as both have endosperm haustoria at both the chalazal and micropylar ends; vestured pits occur in Montiniaceae and Hydroleaceae, but have not yet been reported from Sphenocleaceae. Convolvulaceae and Solanaceae share various supposedly apomorphic characters such as an intraxylary phloem (also common in Gentianales), lack of iridoids, similar alkaloids, flowers with oblique symmetry and similar corolla aestivation (Stevens 2001 onwards).

The stem age of Solanales was estimated to between about 80 Ma and 106 Ma (cf. Olmstead 2013). A historical biogeographical analysis based on current phylogenies suggested that the HYDROL-SPHENO-MONTIN clade arose in Africa, the Convolvulaceae in SE Asia, India and Madagascar, and the Solanaceae in South America. "Thus Solanales may present a classic case of vicariance following Gondwanan breakup, with its descendants on each of the three initial continental fragments giving rise to the three extant clades" (Olmstead 2013).

Conspectus of the families of Boraginales

1. Plants without chlorophyll, leaves reduced to scale-shaped cataphylls; ovary plurilocular by secondary subdivision, fruit with numerous "pits" (endocarpids—individual seeds enclosed separately in lignescent inner pericarp) at maturity. 2/4, SW USA and Mexico **Lennoaceae**

– Plants with chlorophyll, leaves green and with normal lamina; ovary uni- to tetralocular, fruit with only 1–4 endocarpids, or without endocarpids (nutlets, capsules) 2

2. Ovary subdivided into four mericarpids in flower, developing into (1–)4 individual nutlets, style insertion gynobasic. Ca. 85/1600–1700, subcosmopolitan, centres of diversity in the Mediterranean, western Asia and western North America, largely absent from the wet tropics **Boraginaceae** s.str.

– Ovary entire in flower, developing into a capsule or (dry or succulent) drupe or separating into 2–4 individual nutlets at maturity, style insertion apical 3

3. Stems and leaves spinose with stiff, white spines; flowers 10–20-merous, calyx segments strongly unequal. 1/2, SW Africa **Codonaceae**

– Stems and leaves not spinose, but sometimes setose or with spinescent brachyblasts (*Rochefortia*); flowers usually 4–5-merous [if more, then fruit drupaceous]; calyx segments equal or subequal 4

4. Fruit a laterally flattened capsule, obcordate, with 1–2 seeds; flowers always tetramerous, corolla with very short tube. 1/6, SW and NE Africa **Wellstediaceae**

– Fruit never laterally flattened, ovoid, with 4–? seeds if capsular; flowers usually pentamerous, corolla tube usually distinct and tubular 5

5. Fruit capsular with 4–? seeds. 15/280–300, mainly W North America, also C America and W South America, West Indies and Hawaiian Islands **Hydrophyllaceae**

– Fruit drupaceous or dry, often subdivided into mericarpids, 4-seeded, sometimes fewer by abortion, never capsular 6

6. Style undivided with a ring-shaped subterminal stigma (style-stigma complex); flowers usually in dense, scorpioid monochasia. 4/450, pantropical, also subtropical regions, some extending into warm temperate Eurasia, South America, Australia and North America **Heliotropiaceae**

– Style entire or divided, stigma(-ta) terminal; flowers variously arranged, not in dense, scorpioid, ebracteose monochasia, often in repeatedly dichasial or strongly congested inflorescences. 10/500, pantropical, also subtropical regions, very few in warm temperate E Asia **Ehretiaceae** s.l.

As treated here, **Boraginales** contain Boraginaceae s.str. (= Boraginaceae subfam. Boraginoideae), Codonaceae (= Boraginaceae subfam. Codonoideae), Ehretiaceae s.l. (incl. Boraginaceae subfam. Ehretioideae and Cordioideae, Hoplestigmataceae, Lennoaceae), Heliotropiaceae (= Boraginaceae subfam. Heliotropioideae), Wellstediaceae (= Boraginaceae subfam. Wellstedioideae) and Hydrophyllaceae, corresponding to a total of ca. 115 genera and 2950 species. The current treatment deviates from most classical treatments which generally accepted the four families Boraginaceae s.l. (subfam. Boraginoideae, subfam. Ehretioideae, subfam. Cordioideae, subfam. Heliotropioideae; Bentham and Hooker

1883; Gürke 1893), Hydrophyllaceae (incl. *Codon*), and Lennoaceae and Hoplestigmataceae as distinct families. Baillon (1891) recognized Boraginaceae in a slightly wider definition and included Hydrophyllaceae as another subfamily. The classification provided by Takhtajan (2009) circumscribed the order Boraginales with the families Hydrophyllaceae including subfam. Hydrophylloideae and Codonoideae, Boraginaceae including subfam. Ehretioideae, Cordioideae, Heliotropioideae, Boraginoideae and Wellstedioideae, and Hoplestigmataceae plus Lennoaceae. Some genera associated with Boraginaceae/Boraginales in the past have been shown not to be close relatives of the order/family—e.g. *Vahlia* (Vahliaceae, close to Lamiales; Albach et al. 2001; Weigend et al. 2014), Tetrachondraceae (Lamiales; Wagstaff et al. 2000), pantropical *Hydrolea* L. (Solanales; Cosner et al. 1994; Soltis et al. 2000) and *Pteleocarpa* Oliv. (Geraniales; Riedl 1997; Brummitt 2011).

Detailed molecular data have revealed that Boraginales consist of two main clades, i.e. Boraginales I with Codonaceae as sister to Wellstediaceae and Boraginaceae s.str. (= subfam. Boraginoideae), and Boraginales II with doubtfully monophyletic Hydrophyllaceae as sister (when monophyletic) or successive sisters (when not monophyletic) to Heliotropiaceae and Ehretiaceae s.l. (incl. subfam. Cordioideae, Ehretiaceae, Hoplestigmataceae, Lennoaceae; Ferguson 1999, Weigend et al. 2013, 2014).

Boraginales I are a predominantly Old World group, with Codonaceae and Wellstediaceae restricted to Africa (incl. Socotra) and Boraginaceae s.str. with the bulk of its lineages, including most basal lineages, restricted to the Old World. However, all four major clades of Boraginaceae s. str. (Echiochileae, Boragineae, Lithospermeae, Cynoglosseae) have dispersed one to several times to the New World, where the latter two subgroups (Lithospermeae, Cynoglosseae) underwent massive radiations.

Codonaceae and Wellstediaceae are monogeneric families of annual to perennial herbs or small shrublets, often with an “open” life span, i.e. growing and flowering until killed by drought. They are plants from deserts and semi-deserts. Both families as here recognized have some characters which are unique in Boraginales: the two species of Codonaceae differ mainly in details of floral morphology, but share several characters such as the possession of stiff, white spines, 10–20 calyx segments of markedly differing size, 10–20 corolla lobes, red, glandular structures on the corolla and many-seeded capsules with seeds with a very irregular, reticulate testa (Weigend and Hilger 2010). The six species of Wellstediaceae differ mainly in habit and indumentum, but share very small, tetramerous flowers with a weakly developed corolla tube, laterally flattened, 1–2-seeded, obcordate capsules and asymmetrically ovoid seeds often with a ring of longer hairs near the funicular pole (Thulin and Johansson, 1996).

All Boraginaceae s.str. have an ovary subdivided into four mericarpids with gynobasic style insertion. With a total of ca. 1600—1700 species in ca. 85 genera, the family is highly variable in its vegetative and generative morphology. However, Echiochileae, sister to the remainder of Boraginaceae s.str., are similar in ecology to Codonaceae and Wellstediaceae, with the bulk of species being shrubs from semi-desert and desert habitats; they are more species-rich (ca. 30 spp.) and more widespread than the former two families and range from western Asia to north-western Africa and are distributed with one genus with 10–15 spp. in the Americas. Core Boraginaceae—tribes Boragineae, Cynoglosseae and Lithospermeae—are the most species-rich clade in the order. They are predominantly herbaceous, with shrubs largely restricted to some subgroups of Lithospermeae, and are the only group of Boraginales where relatively complex flowers with both basal and faucal corolla scales occur. The three tribes of core Boraginaceae are particularly diverse in the warm-temperate and Mediterranean ecosystems of the northern hemisphere.

In contrast to Boraginales I, Boraginales II are predominantly New World in distribution, with Hydrophyllaceae restricted to the Americas. However, several isolated genera (*Hoplestigma*, *Coldenia*) und numerous species in Heliotropiaceae and Ehretiaceae (in *Euploca*, *Heliotropium*, *Cordia* and *Ehretia*) are found in the Old World. Hydrophyllaceae are a vegetatively and ecologically heterogeneous group, with a centre of diversity in south-western North America. They comprise 280–300 spp. in 17 genera. The majority of species are herbs and shrubs from seasonally arid habitats. Only a handful of taxa (e.g.

Hydrophyllum) are found as perennials in mesic forest habitats. The bulk of the genera are restricted to western North America, and only *Nama*, *Phacelia* and *Wigandia* extend into western South America. Ehretiaceae s.l. (500 spp. in 10 genera) and Heliotropiaceae (450 spp. in 4 genera) are larger and much more widespread groups than Hydrophyllaceae. Both families have their centres of diversity in seasonally arid subtropical habitats and both groups range into the humid tropics with only a handful of species. Ehretiaceae s.l. have their centre of diversity in the New World, but some isolated genera (*Hoplestigma*, *Coldenia*) and many species in the larger genera (e.g. *Cordia*, *Ehretia*) are restricted to the Old World. The family is almost exclusively woody, with some genera (*Coldenia*, *Tiquilia*) forming dwarf shrubs in dry, sandy habitats and the majority of taxa (*Cordia*, *Ehretia*, *Hoplestigma*) forming large, sometimes scandent shrubs or even tall trees. The only notable exception to this are the American former Lennoaceae (*Lennoa*, *Pholisma*), a group of parasitic herbs. Heliotropiaceae have all their basal lineages (*Myriopus*, *Ixorhea*) restricted to the Americas, but *Heliotropium* (incl. *Tournefortia*) has numerous species in the Old World tropics and subtropics. Unlike Ehretiaceae, Heliotropiaceae are vegetatively highly diverse and include a wide range of growth forms, ranging from ephemeral and perennial herbs (sometimes with stolons, rhizomes or root tubers), sub-shrubs and shrubs to small trees and lianas (Luebert et al. 2011a, 2011b). Superficially, Heliotropiaceae are similar to Boraginaceae, with mostly infundibuliform corollas with narrow tubes uncommon in the other groups. However, they differ profoundly in ovary (ovary entire, style apical) and corolla morphology (basal and faucal scales absent).

There are several characters which are widespread in Boraginales and have been used to characterize individual subgroups, but characters uniting the entire order or its two subgroups Boraginales I and Boraginales II so far have not been identified. Phytochemically, the presence of pyrrolizidine alkaloids (PAs) had been considered as characteristic for Boraginaceae s.str. and Heliotropiaceae (Hegnauer 1966) and they have since also been reported from some Ehretiaceae s. l. (Suri et al. 1980; Fu et al. 2002). However, PAs are absent from the Hydrophyllaceae studied so far and also from most Ehretiaceae, and detailed phytochemical data have not been published for either Codonaceae or Wellstediaceae. The available evidence thus fails to clarify the evolutionary history of PAs in Boraginales, but documents their absence in several groups. Also, PAs occur outside Boraginales and are not a unique substance class for the order.

Fruit morphology traditionally has been used to diagnose the constituent families, with four one-seeded mericarpids in the Boraginaceae s.l., multiple mericarpids in Lennoaceae and capsular fruits in Hydrophyllaceae. Recent data clearly retrieve clades with capsular fruits at the base of both Boraginales I (Codonaceae, Wellstediaceae) and Boraginales II (Hydrophyllaceae), implying the independent origin of fruits with four one-seeded mericarpids in Boraginales I and II (Weigend et al. 2014). A more detailed view further shows that the formation of "nutlets" is morphologically different between Boraginales I (Boraginaceae s.str. with nutlets separating from a persistent central column (= gynobase) and Boraginales II (mericarpids usually without a central column). This underscores the non-homology of the four one-seeded mericarpids found in these two clades. Moreover, representatives of Boraginales II with mericarpids (Ehretiaceae, Heliotropiaceae) have been shown to share a complex, derived pericarp anatomy with a multi-layered endocarp and specialized transfer cells in the seed coat which are absent in Hydrophyllaceae and Boraginales I (Diane et al. 2002).

Flower morphology provides relatively few informative characters at family level in Boraginales. Flowers are essentially tetracyclic, heterochlamydeous, synsepalous and sympetalous and with epipetalous filament insertion. The ovary is superior and consists of two united carpels with an apical (most) or gynobasic style (only Boraginaceae). The bulk of Boraginales have campanulate or infundibuliform corollas without conspicuous modifications of the corolla. Secondary increase of the number of perianth elements, irregular calyx aestivation, and an increased number of anthers (10 or more) are restricted to Lennoaceae, *Hoplestigma*, and some *Cordia* in Ehretiaceae s.l. Derivations from the pentamerous perianth are also found in Codonaceae (10–20), Lennoaceae (4–10) and Wellstediaceae (4). Boraginales I and

Hydrophyllaceae share a trend towards corolla tube modifications in the form of scale-shaped basal ingrowths, sometimes united into a ring of 5–10 distinct scales arching over the disk nectary. These basal scales are indistinct in Codonaceae and Wellstediaceae, variously present or absent in Hydrophyllaceae and absent in individual groups of Boraginaceae s.str. (e.g. Echiochileae), but very well developed in most groups of the latter family. Most Boraginaceae s.str. additionally have faucal scales, i.e. petal intrusions near the mouth of the tube, which are absent or indistinct in some taxa (e.g. hair tufts in Echiochileae) but very prominent in the majority of species (e.g. Boragineae, most Cynoglosseae with hypocrateriform flowers). The presence of some type of corolla tube invagination may thus be the ancestral character state for Boraginales, with several losses in Boraginales I (individual genera or species of Boraginaceae s.str.) and the crown group of Boraginales II.

An unequivocal fossil record of Boraginales is limited to Boraginaceae, Heliotropiaceae and Ehretiaceae s.l., and consists mainly of fruit remnants of Ehretiaceae s.l. from the Eocene and Miocene (Eocene of Europe: Chandler 1964; Gottschling et al. 2002; Miocene of Tasmania: Ettingshausen 1888), and of Boraginaceae s.str. from the Late Miocene (Texas to South Dakota in North America: Thomasson 1979, 1987). Putative fossil pollen has been recorded for Heliotropiaceae (Oligocene to Pliocene of Mexico and Puerto Rico: Graham and Jarzen 1969; Graham and Dilcher 1998; Muller 1981) and Boraginaceae s.str. (upper Miocene of Spain: Van Campo 1976). Dated phylogenies generally place the origin of the stem group of Boraginales (Boraginaceae s.l.) into the late Cretaceous (81 Ma: Wikström et al. 2004; 77.47 Ma: Magallón and Castillo 2009) or mid-Cretaceous (Bell et al. 2010). Gottschling et al. (2004) postulated an early diversification of Boraginales predating the late Cretaceous. Their data support the divergence of several modern genera in Ehretiaceae and Heliotropiaceae before 80–100 Ma, which would imply that the divergence of families of the order would have taken place no later than the mid-Cretaceous.

Different from the above circumscription of relationships (Weigend et al. 2014), Lennoaceae, clearly nested in Ehretiaceae s.l., are here treated as a separate family for practical reasons. Also, doubtfully monophyletic Hydrophyllaceae are retained in their classical circumscription until their relationships are better resolved based on a wider sampling.

Asterids II (Campanulids)

Conspectus of the families of Aquifoliales

1. Inflorescences epiphyllous 2
– Inflorescences not epiphyllous 3
2. Flowers unisexual and plants dioecious. 1/4, E Asia **Helwingiaceae**
– Flowers bisexual. 1/4, New World tropics **Phyllonomaceae**
3. Gynoecium pluriloculate. 1/>600, cosmopolitan **Aquifoliaceae**
– Gynoecium uniloculate (probably pseudomonomerous) 4
4. Petals fused at least at base, stamens epipetalous (not *Citronella*). 5/ca. 45, Old World tropics and subtropics, rarely America (*Citronella*) **Cardiopteridaceae**
– Petals free, stamens not epipetalous. 12/ca. 90, mainly Old World tropics, rarely America (*Discophora*) **Stemonuraceae**

Aquifoliales, sister to all other Campanulids (Tank and Donoghue 2010), comprise Cardiopteridaceae, Stemonuraceae, Aquifoliaceae, Helwingiaceae and Phyllonomaceae. The order Aquifoliales in this circumscription was first resolved by Soltis et al. (2000) and has been recovered since in several other studies (Bremer et al. 2002; Winkworth et al. 2008; Tank and Donoghue 2010; Soltis et al. 2011). Before Soltis et al. (2000), Aquifoliales were considered to consist of Aquifoliaceae, Helwingiaceae and Phyllonomaceae only (APG 1998). No morphological synapomorphy of this clade is known. Aquifoliales consist of two subclades. The first contains Cardiopteridaceae and Stemonuraceae, of which all genera except *Cardiopteris* had previously been included in Icacinaceae. Detailed reallocation of genera of Icacinaceae to Cardiopteridaceae and the newly erected Stemonuraceae was first suggested by Kårehed (2001). Stevens (2001 onwards) lists entire leaf margins, adaxial carpel alone fertile and integument vascularized as possible synapomorphies of the two families, but toothed or lobed leaves can be found in Cardiopteridaceae, and gynoecium structure is well known only for *Cardiopteris* (Kong et al. 2014) and *Gonocaryum* (Fagerlind 1945). Tobe (2012) suggested that a pseudomonomerous gynoecium may represent a synapomorphy for the two families, but no detailed data on gynoecium structure appear to be available for Stemonuraceae. The second subclade contains Aquifoliaceae, Helwingiaceae and Phyllonomaceae, of which the latter two are sister to each other in more recent analyses (Tank and Donoghue 2010; Soltis et al. 2011). Following Stevens (2001 onwards), nodes 1:1, the presence of stipules, the absence of a style, and one ovule/carpel may be synapomorphies of this clade, but there are more than one ovule/carpel in Phyllonomaceae, and short styles have been described for most members of these three families. The sister group relationship between Helwingiaceae and Phyllonomaceae is well supported by the shared possession of epiphyllous inflorescences. The stem group age of the order has been estimated at ca. 100 Ma (Magallón and Castillo 2009).

Conspectus of the families of Escalloniales

1. Glandular annual herbs. 1/1, western Australia **Eremosynaceae**
– Plants woody at least at base 2
2. Leaves opposite to subopposite, flowers 4-merous. 1/80, India, New Caledonia, Australia **Polyosmaceae**
– Leaves alternate, flowers 5-merous 3
3. Creeping subshrubs, entirely glabrous, leaf apices tridentate. 1/1, Southern Andes **Tribelaceae**
– Mostly shrubs or small trees, variously pubescent at least in flowers, leaf apices not tridentate. 4/45, S America, Australia and Tasmania, Réunion **Escalloniaceae**

Escalloniales, a clade first identified by Lundberg (2001) and confirmed by, for example, Winkworth et al. (2008; as *Escallonia* clade), Tank and Donoghue (2010; as Escalloniaceae) and Soltis et al. (2011; as Escalloniaceae), are here treated to comprise Eremosynaceae, Escalloniaceae, Polyosmaceae and Tribelaceae. These four largely south hemispherical families were all included in a broader Escalloniaceae in APG III (2009). Although the order is clearly monophyletic, relationships within it are still essentially unresolved (Lundberg 2001; Bremer et al. 2002; Winkworth et al. 2008; Tank and Donoghue 2010), so that treatment as four separate families does not contradict the molecular data available. Escalloniales are herbaceous to more often woody plants with mostly alternate and exstipulate leaves. Flowers are bisexual and actinomorphic with free petals. The mostly inferior ovary often consists of two carpels, ovules are mostly tenuinucellate, and fruits often are capsules, more rarely drupes. No clear synapomorphy uniting these four families has been identified. In historical systems, and before the advent of molecular analyses, they had been associated with Saxifragaceae in Engler's (1928) circumscription. The stem group age of the order (Escalloniaceae and Polyosmaceae) has been estimated at ca. 97 Ma (Magallón and Castillo 2009). Escalloniales are sister to all other Campanulids except Aquifoliales and Asterales (Tank and Donoghue 2010).

Conspectus of the families of Bruniales

1. Ericoid shrubs or small trees, leaves alternate, stipulate, petals free. 6/81, S Africa **Bruniaceae**
– Trees or shrubs, leaves opposite, exstipulate, petals fused. 2/5 C to S America **Columelliaceae**

Bruniaceae, with six genera and 81 species mainly in the western and eastern Cape of South Africa, and Columelliaceae, with two genera and five species in the Andes of South America, are reasonably well supported as sister families (Winkworth et al. 2008; Tank and Donoghue 2010; Soltis et al. 2011) and have been treated as **Bruniales** by APG III (2009). The order is sister to Apiales, Paracryphiales and Dipsacales (Tank and Donoghue 2010). Apart from being woody and having bisexual flowers with a mostly half-inferior ovary of mostly two and rarely five (*Desfontainia*) fused carpels, there is little to connect the two families. Whereas Bruniaceae are ericoid shrubs without iridoids, have alternate and stipulate or exstipulate leaves, free petals, weakly crassinucellate ovaries and 1-seeded dry fruits, Columelliaceae, with *Columellia* and *Desfontainia* as rather divergent elements, are trees or shrubs with iridoids, have exstipulate opposite leaves, fused petals, tenuinucellate ovules and capsules or berries. Earlier analyses of 109 non-DNA characters and of a combined matrix of the non-DNA and *rbc*L sequence data both indicated Columelliaceae to be part of Dipsacales. Bruniaceae were sister to such an expanded order in the combined analysis and very closely related to the order in the other analysis (Backlund and Donoghue 1996). Stem group ages of Columelliaceae and Bruniaceae have been estimated at ca. 97 and 94 Ma respectively (Magallón and Castillo 2009). The sister group relationship of the South African Bruniaceae and the South American Columelliaceae may represent an ancient vicariance event.

Conspectus of the families of Dipsacales

1. Corolla usually actinomorphic; nectary of various types (on the ovary roof, adaxially on the petal bases, urceolate in the inflorescences, or a nectarine stigma) or absent; stylodia 3–5, short or absent. 5/175-210, mainly N hemisphere, centred in E Asia, also S America, Africa and SE Australia **Adoxaceae**
– Corolla usually zygomorphic; trichome nectary basally within the flower tube; style simple, elongated 2
2. Mainly herbs, sometimes subshrubs. Calyx variously modified; corolla with strong, mostly single transpetal veins 3
– Shrubs or lianas, rarely perennial herbs (*Triosteum*). Calyx not modified; corolla without transpetalar veins or more than one 4
3. Inflorescences forming dense involucrate heads, rarely thyrsoidal (*Triplostegia*); epicalyx present, simple or double (*Triplostegia*). 14/300 (+1/2 *Triplostegia*), mainly extratropical Old World, especially E Mediterranean and Irano-Turanian region, rare in C and S Africa and C and E Asia **Dipsacaceae** (incl. ***Triplostegia***)
– Inflorescences not forming involucrate heads, epicalyx absent. 5/400, mainly in the N hemisphere and mountainous regions of S America (especially Andes) **Valerianaceae**
4. Flowers in "verticillasters", involucel (epicalyx) formed by four fused bracteoles with spiny margin present, enclosing the achene. 2/12, Balkans to China, centred in E Asia **Morinaceae**
– Inflorescences different, epicalyx with spiny margin absent, but sometimes supernumerary bracts at the base of the inferior ovary present. 13/230, (+ 1/6 *Zabelia*), mainly temperate to boreal N hemisphere **Caprifoliaceae** (+ ***Zabelia*** inc. sed.)

Dipsacales, with the Adoxaceae s.l. (incl. *Sambucus* and *Viburnum*), Caprifoliaceae, Dipsacaceae, Morinaceae and Valerianaceae, were recognized as a "natural" group as early as the 19th century. The assignment of certain genera (e.g. *Heptacodium*, *Triplostegia*, *Viburnum*, *Zabelia*) to families and the circumscription of families varied through the years, and in some cases discussion continues until today. Dipsacales are ancestrally woody (mainly shrubs) although herbs are common, the opposite leaves lack true stipules, nodal anatomy is mainly 3:3 (also in the closely related Paracryphiales and Apiales) but also often 5:5 in the Morinaceae-Dipsacaceae-Valerianaceae clade (Neubauer 1978); flowers are arranged in mostly terminal, cymose or paniculate inflorescences which often are corymbiform, monotelic or frequently lack terminal flowers, corollas are tubular at the base with early sympetaly (excl. *Adoxa* with late sympetaly; Erbar 1994), there are (1–)3–5 (the unithecal split stamens of *Adoxa* should not be counted as two, see below) stamens which are adnate to the corolla, and ovaries are (semi)inferior with unitegmic, mostly tenuinucellate ovules. Route 1 secoiridoids are commonly present.

The present volume treats Dipsacales as containing the following families: Adoxaceae s.l. (incl. Sambucaceae and Viburnaceae), Caprifoliaceae (incl. Diervillaceae and Linnaeaceae), Dipsacaceae (incl. *Triplostegia*), Morinaceae and Valerianaceae. According to various recent studies, however, the phylogeny of the Dipsacales is Adoxaceae [Diervillaceae [Caprifoliaceae [Linnaeaceae [Morinaceae [Dipsacaceae + Valerianaceae]]]]]. For a monophyletic Caprifoliaceae s.l., Caprifoliaceae s.str. (incl. Linnaeaceae), Morinaceae, Dipsacaceae and Valerianaceae must be combined into one family as already suggested by Judd et al. (1994). Alternatively, Caprifolieae, Diervilleae and Linnaeeae could each be raised to family rank (with Adoxaceae, Morinaceae, Dipsacaceae and Valerianaceae as remaining families of the order) in order to have monophyletic taxa (Backlund and Pyck 1998), as recently done in Flora of China (2011). Judd et al. (1994) and later APG II (2003) and III (2009) argued in favour of the first option (combining several families in Caprifoliaceae) in order to escape problems with the monophyly of Caprifoliaceae in a more restricted circumscription and to keep the number of families in APG classifications at bay (Stevens 1998). Indeed, the position of *Zabelia* is still unclear (Landrein et al. 2012) and conceivably an additional family will be needed for this genus. Adoxaceae were not included in the expanded Caprifoliaceae by Landrein et al. (2012) although *Sambucus* and *Viburnum*, now members of Adoxaceae s.l., were included in Caprifoliaceae

s. str. in most earlier classifications because of their similarity to that family.

Whatever the best solution for the classification of Dipsacales, the order has 100% bootstrap support in Soltis et al. (2011), and infraordinal relationships are well understood for most parts. Stevens (2001 onwards) suggested pollen grains trinucleate when shed and a vascularised testa as possible synapomorphies of the order. Bud scales (reduced in herbaceous taxa), the typically multicellular club-shaped glandular hairs (Weberling 1977), and the position of the ovule (basically apotropous but turned lateral in the mature flower; Lagerberg 1909) may be other candidates for possible synapomorphies. Paracryphiales (Sphenostemonaceae + Paracryphiaceae) were resolved as a sister group of Dipsacales in the phylogenies of Tank and Donoghue (2010, strongly supported) and Soltis et al. (2011, no bootstrap support). Stevens (2001 onwards) suggested that the presence of true tracheids, serrate laminas and terminal inflorescences may represent synapomorphies of Dipsacales + Paracryphiales.

Of *Adoxa*, *Viburnum* and *Sambucus* as major genera of Adoxaceae s.l., the latter two were mostly included in Caprifoliaceae in the past (e.g. Fritsch 1892; Höck 1897; Bessey 1915; Wagenitz 1964; Fukuoka 1972; Takhtajan 1980; Cronquist 1981; Goldberg 1986). Among recent authors, only Thorne (1983) included both *Sambucus* and *Viburnum* in Adoxaceae. Earlier in the 19th century, however, a close relationship between *Adoxa*, *Sambucus* and *Viburnum* was frequently accepted: Röper (1834, cited in Meissner's Plantarum vascularium genera, pt. 2: p. 111, 1838), Koch (1837: 323) and Meissner (1838) favoured an inclusion of *Adoxa* in Caprifoliaceae close to or together with *Sambucus* and *Viburnum*. Also Payer (1857: p. 413) suggested a close relationship of *Sambucus* and *Adoxa*, and Röper (1860: p. 4) stated: "... one is almost inclined to name *Adoxa*, *Sambucus Moschatellina*" ["... man fast dazu neigen möchte, *Adoxa* als *Sambucus Moschatellina* zu bezeichnen"]. Ascherson (1864), following the system of Alexander Braun (1864), included *Adoxa*, *Sambucus* and *Viburnum* in Caprifoliaceae subfamily Sambucoideae (Adoxaceae s.l. of today) with actinomorphic rotate and campanulate flowers, distinct stylodia or sessile stigmas and one ovule per locule; also Hooker (1873) included these three genera in Caprifoliaceae tribe Sambuceae, and Eichler (1875) concluded that *Adoxa* belonged to Caprifoliaceae close to *Sambucus*.

While a close relationship of *Adoxa* to *Sambucus* and *Viburnum* (and of these three genera to other Dipsacales) was frequently accepted in the 19th century, this was only exceptionally the case up to the 1980s. This is somewhat surprising considering Lagerberg's (1909) detailed embryological studies in support of a close relationship of *Adoxa* and *Sambucus*. He explicitly rejected monogeneric Adoxaceae. The embryological studies by Moissl (1941) of Caprifoliaceae s.l. emphasized the similarities between Sambucus and Viburnum, especially the shared presence of a glandular tapetum and of strongly reduced sterile ovules. Otherwise, the distinctness of *Sambucus* and *Viburnum* from other Caprifoliaceae (in their traditional circumscription) was mostly acknowledged, but the Adoxaceae s.str. were rarely considered. This changed in the last decades of the 20th century when various new characters were used. Donoghue (1983), in a formal cladistic analysis using morphological characters, obtained evidence supporting Ascherson's (1864) classification. Wagenitz and Laing (1984) used the morphology of floral nectaries as argument in support of the view that *Viburnum* and *Sambucus* differ from Caprifoliaceae, and for the monophyly of Caprifoliaceae s.l. sensu APG III (= Dipsacales excl. Adoxaceae s.l.): the flowers of all genera investigated have a nectary in the floral tube composed of unicellular epidermal hairs and an underlying nectary tissue. In contrast, Adoxaceae s.l. have various types of nectaries: *Adoxa* has multicellular hairs on the corolla, *Viburnum* has a disk nectary on the roof of the inferior ovary with nectary slits, and in *Sambucus*, nuptial nectaries are normally absent (only *S. javanica* has urceolate nectaries in the inflorescence, probably modified from extrafloral nectaries common in the genus, and *S. ebulus* has a nectarine stigma; Vogel 1997).

When listing characters separating Adoxaceae s.l. from other Dipsacales, Wagenitz and Laing (1984) included the glandular tapetum as typical for the family (incorrectly scored as amoeboid by Judd et al. 1994), as well as a superficial cork cambium (*Sambucus* and *Viburnum*; Solereder 1899) and the armpalisade cells of the mesophyll. Corolla vascularization (Gustafsson 1995; Backlund and Donoghue 1996) and karyological data (Jianquan et al. 1999; Benko-Iseppon and Morawetz 2000) further supported the close relationship of *Adoxa* to *Viburnum* and *Sambucus*. Donoghue et al. (1992) and Judd et al. (1994), based on morphological cladistic analyses, Backlund and Bremer (1997), based on a taxonomically more restricted *rbc*L analysis, and Eriksson and Donoghue (1997), based on ITS sequences and morphology, found relationships in Adoxaceae as basically still accepted today: (*Viburnum* (*Adoxa*/*Sambucus*)). Interestingly, while evidence for removing *Viburnum* and *Sambucus* from Caprifoliaceae and linking them to *Adoxa* instead (as variously accepted earlier, see above) kept accumulating, it was considered unclear whether the *Adoxa*/*Sambucus*/*Viburnum* group and the Caprifoliaceae (plus Dipsacaceae, Morinaceae and Valerianaceae) were closely related at all (cf. Donoghue 1983; Wagenitz and Laing 1984; Wagenitz 1992).

The basic phylogeny of the Dipsacales (Adoxaceae [Diervillaceae [Caprifoliaceae [Linnaeaceae [Morinaceae [Dipsacaceae + Valerianaceae]]]]]) as recently found by Soltis et al. (2011) was first correctly recovered by Donoghue et al. (2003) based on a combined ITS and chloroplast DNA sequence dataset. In principle, this made possible the identification of synapomorphic characters of various subclades, but the relationships of certain problematic genera (especially *Heptacodium* and *Zabelia*; see Jacobs et al. 2011) and different options of character optimization influence the interpretation of various supposed synapomorphies. Judd et al. (1994) suggested reduced calyx lobes with one vascular trace, rotate corollas, semi-tectate-reticulate pollen grains (Reitsma and Reuves 1975; Böhnke-Gütlein and Weberling 1981), short stylodia and drupaceous fruits as possible synapomorphies for Adoxaceae.

For the Caprifoliaceae s.l. (sensu APG III), on the other hand, Judd et al. (1994) suggested long zygomorphic corolla tubes (only slightly zygomorphic in the basal Diervilleae and part of Caprifolieae), nectaries with unicellular hairs, large pollen grains, fully inferior ovaries with capitate stigmas on long styles, reduced carpel vasculature (Wilkinson 1949), and small chromosomes (Sax and Kribs 1930) as possibly apomorphic. The study of corolla vascularisation provided another character (Gustaffsson 1995; Backlund and Donoghue 1996): in nearly all Caprifoliaceae s.l. sensu APG, the main petal veins show lateral connections (“transpetalar veins”) which are lacking in Adoxacaeae s.l. and all studied outgroups (Paracryphiales not included).

Above the basal Diervilleae/Diervillaceae, Caprifoliaceae s.l. sensu APG, i.e. Caprifoliaceae s.s. + Linnaeeae/Linnaeaceae + Morinaceae + Dipsacaceae + Valerianaceae, have no clear synapomorphies (Stevens 2001 onwards). As shown by Jacobs et al. (2011), three related fruit characters (fruit an achene, two sterile carpels, pericarp as outermost mechanical layer) either are synapomorphic for this clade with a reversal within Lonicereae or evolved in parallel in *Heptacodium* and at the base of the Linnaeaceae-Morinaceae-Dipsacaceae-Valerianaceae clade (see below). *Heptacodium* has also been suspected, however, of being of hybrid origin (Zhang et al. 2002; Jacobs et al. 2011).

Linnaeeae/Linnaeaceae+Morinaceae+Dipsacaceae+Valerianaceae (clade “Linnina” of Donoghue et al. 2001) typically have two of the three carpels aborted and achenes (cypselas; Bell et al. 2011). Supernumerary inflorescence bracts are possibly synapomorphic for this clade (Donoghue et al. 2001), or alternatively for the less inclusive Morinaceae/Dipsacaceae/Valerianaceae clade (Zhang et al. 2003). Four didynamous stamens were added by Stevens (2001 onwards). Morinaceae/Dipsacaceae/Valerianaceae (clade “Valerina” of Donoghue et al. 2001) share various morphological characters—e.g. herbaceous habit (and bud scales absent) with basal rosette and a taproot, vascular flank-bridge between lateral bundles in stem (see Neubauer 1979), nodes 5:5, epicalyx (modified or absent in Valerianaceae), enlarged embryo, and the occurrence of monoterpenoids and alkaloids (Donoghue et al. 2001; Stevens 2001 onwards; Zhang et al. 2003; Jacobs et al. 2011). In Dipsacaceae/Valerianaceae young shoots have an endodermis (Solereder 1899), but data for Morinaceae seem to be lacking.

Inflorescences are basically cymose, mostly thyrses, often corymbiform, but also complex panicles, sometimes pseudo-umbellate in Adoxaceae s.l., and condensed into capitula (e.g. *Adoxa*, *Heptacodium*, Dipsacaceae), among other modifications (Troll and Weberling 1966; Landrein and Prenner 2013). In Adoxaceae s.l., terminal flowers are normally present, in Caprifoliaceae s. l. sensu APG typically absent (truncated monotelic to polytelic), with the exception of the basal Diervilleae/Diervillaceae (Wagenitz and Laing 1984; Landrein and Prenner 2013). In the *Adoxa* clade, elongated thyrses (*Sinadoxa*) or raceme-like inflorescences (*Tetradoxa*) are probably plesiomorphic (Donoghue et al. 2001). The peculiar cube-like inflorescence of *Adoxa*, a condensed depauperate thyrse (Weberling 1966 cited in Wagenitz and Laing 1984), is derived from these. Concerning the capituliform inflorescences of Dipsacaceae, however, Hofmann and Göttmann (1990) pointed out that their internal structure could easily be described as racemose with the lateral flowers lacking prophylls. Only the phylogenetic position of the family would favour the interpretation of an evolutionary reduction to their terminal flowers of the dichasial paracladia of an original thyrse. Supernumerary bracts below the flowers (*Abelia* spp., *Dipelta*, *Linnaea*, *Patrinia*; in some spp. forming a 3-lobed wing in fruit, as in some *Valeriana* spp.) and the homologous development of an epicalyx (*Morina*, Dipsacaceae incl. *Triplostegia*) are conspicuous features in many genera of Caprifoliaceae s.l. sensu APG (Hofmann and Göttmann 1990).

The evolution of reproductive characters has been analyzed based on the mostly well-resolved and stable phylogeny of the order (Donoghue et al. 2002; Jacobs et al. 2010a, 2010b). Numbers of stamens and petals were found to have evolved independently in the usually zygomorphic flowers of Caprifoliaceae s.l. sensu APG clade. They mostly covary in the sister clade Adoxaceae with typically actinomorphic flowers. In Caprifoliaceae s.l. the number of stamens varies from one to five and the number of petals from three and five. With very few exceptions (cf. *Valeriana* p.p.: former genera *Belonanthus* and *Phyllactis*) flowers with 1–4 stamens have five petals (e.g. *Fedia*, *Centranthus*, *Morina*, *Triplostegia*, *Valerianella*). In Adoxaceae, however, the 3–5 corolla lobes correlate with 3–5 stamens, although the stamens are split more or less deeply into two halves in *Adoxa*, *Tetradoxa* and *Sinadoxa*, resulting in apparently twice the number of unithecal stamens (e.g. Yang et al. 2011). The ancestral condition of the gynoecium in the order probably is 3-carpellate as present in *Viburnum*, *Sambucus* p.p. and part of the Caprifoliaceae s.l. sensu APG. In the Adoxaceae an increase of carpel number to up to five (in *Adoxa*, *Tetradoxa* and *Sambucus* p. p.) as well as a reduction (*Sinadoxa*: bicarpellate, unilocular and uniovular) can be observed. Of the three locules in *Viburnum*, only one has a single ovule and the other locules are sterile, while in *Sambucus* all 3–5 locules are fertile. In the Caprifoliaceae s.l. sensu APG, a bicarpellate ovary with many ovules is present in the basal Diervilleae (Diervillaceae) clade (an apomorphic condition). In the following Caprifolieae clade, some genera lack compressed sterile locules (*Leycesteria* has five or more and *Lonicera* 2–5 locules), while the others (*Heptacodium*, *Symphoricarpos*, *Triosteum*) may have one or two sterile locules with aborted ovules. Two sterile locules are also typical for the clade Linnaeaceae+Morinaceae+Dipsacaceae+Valerianaceae, and in Dipsacaceae the ovary is pseudomonomerous. Thus, there is a tendency in Dipsacales to a reduction in number of fertile locules, which took place in parallel in *Viburnum* and one or more times in the Caprifoliaceae sensu APG. While in the Caprifoliaceae s.l. sensu APG the progressive reduction of ovules is well visible in the extant genera, in the ovary of Adoxaceae s.l. only vestigial archesporial tissue as a remnant of aborted ovules above the fertile ovule can be found (see Moissl 1941; Wilkinson 1949; Erbar 1994). Drupes with one or more pyrenes are typical for Adoxaceae s.l., and the Caprifoliaceae-Valerianaceae clade is more variable. The basal Diervilleae (Diervillaceae) have septicidal capsules with wind-dispersed seeds, which is unique in Dipsacales. Drupes with pyrenes occur only in *Heptacodium*, *Symphoricarpos* and *Triosteum* in tribe Caprifolieae. The other two genera of this tribe, *Leycesteria* and *Lonicera*, have baccate fruits with three to several seeds, probably a derived condition. In the clade comprising the rest of Caprifoliaceae s.l. sensu APG (Linnaeeae, Morinaceae, Dipsacaceae and Valerianaceae), the fruits are achenes with 1(2) seeds. This is correlated with the reduction of two of the locules (see above). Jacobs et al. (2010a, 2011) stated that evolution took place from small embryos and copious endosperm in the basal clades of Caprifoliaceae s.l. sensu APG to larger embryos in Morinaceae, Dipsacaceae and basal Valerianaceae (*Patrinia*, *Nardostachys*). The endpoint of this evolution is the condition seen in most

Valerianaceae where endosperm is basically absent and the embryos fill the entire seed. Furthermore, the embryo in the basal clades is protected by the sclerified seed coat (Diervilleae) or endocarp (Caprifolieae), while in the derived clades the protection is transferred to the pericarp or the epicalyx (Dipsacaceae).

The stem group age of the order is probably Mid Cretaceous, and the basal split into two clades occurred in the Tertiary, but estimates vary considerably (see Stevens 2001 onwards). Bremer et al. (2004) estimated the stem group age of Dipsacales as 111 Ma, and the crown group age as 101 Ma. Bell and Donoghue (2005a) suggested that major lineages with considerable morphological differences only appeared in the Eocene and more recently in the Miocene (especially in the herbaceous clades Valerianaceae and Dipsaceae), and that further diversification in these families took place even more recently in the Mediterranean region in Dipsacaceae and in alpine habitats of western S America in Valerianaceae. Disjunctions between the Old and New Worlds are common in the order. According to the study of Adoxaceae and Valerianaceae by Moore and Donoghue (2007), species diversification correlated less with morphological innovations but rather with shifts to mountainous habitats. The evolution from shrubs to herbs occurred three or more times in the order: in the clade of Morinaceae/Dipsacaceae/Valerianaceae, in *Adoxa* and related genera, and in *Sambucus* where several species are rhizomatous perennial herbs, a condition which evolved possibly more than once in this genus (cf. phylogeny in Eriksson and Donoghue 1997). Jacobs et al. (2010b) speculated that ovary position, seed characters and fruit colour suggest paedomorphosis in the evolution from *Sambucus*-like ancestors to *Adoxa*.

Backlund (1996), using Bremer's ancestral area and DIVA analyses, concluded that the origin of the Apiales-Dipsacales clade is located in SE Asia. Donoghue et al. (2003) confirmed a probable origin in eastern Asia, with the plants originally inhabiting the understorey of temperate forests (but see Clement and Donoghue 2011). From there, the order spread into both hemispheres of the Old and New World. Herbaceous lineages occupy alpine habitats with considerable diversification especially in western South America (Bell and Donoghue 2005a, 2005b). The sister group of Dipsacales, the Paracryphiales, is centred in the tropical western Pacific region (New Guinea, Queensland and New Caledonia). The past distribution of members of this order is disputed due to ambiguous fossils from Sweden possibly close to *Quintinia* (see Stevens 2001 onwards); Friis et al. (2013) even question that *Quintinia* belongs into Paracryphiales in spite of the data of Soltis et al. (2011).

CONSPECTUS OF THE FAMILIES OF PARACRYPHIALES

1. Fruit a berry with 1 or 2 seeds, filaments very short to absent. 1/9, New Caledonia, N Queensland, New Guinea, Moluccas, Celebes **Sphenostemonaceae**
– Fruit a capsule with several seeds, filaments distinct, sometimes short. 2/25, New Caledonia, tropical Australia, New Guinea, Philippines, Vanuatu, New Zealand **Paracryphiaceae**

Paracryphiaceae with two genera and ca. 25 species in New Guinea, the Philippines, Vanuatu, New Caledonia, tropical Australia and New Zealand, and Sphenostemonaceae with one genus of nine species in New Guinea, the Moluccas, Celebes, New Caledonia and northern Queensland, were recovered as a well-supported clade by Tank and Donoghue (2010) and Soltis et al. (2011) and are regarded as the only family (Paracryphiaceae) of the **Paracryphiales** by APG III (2009). Such treatment is justified by the fact that *Paracryphia* seems to be more closely related to *Sphenostemon* than to *Quintinia* as second genus of Paracryphiaceae as treated here. Both families contain woody plants with alternate and exstipulate leaves and, as far as presently known, free petals. Apart from that, few similarities and no obvious synapomorphies have been identified. However, in both families both bi- and unisexual flowers with or without petals can be found, and an almost verticillate leaf arrangement has been described for some species of both. Considering their essentially identical distribution range and the characters discussed, their close relationships to each other appears plausible although it had never been suggested before. The age of both families has been estimated at ca. 97 Ma (Magallón and Castillo 2009), and the order is sister to Dipsacales (Tank and Donoghue 2010).

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