# Familial classification of the boraginales

Familial classificatio**n of the Boraginales**

Boraginales Working Group*

*Federico Luebert[1,2], Lorenzo Cecchi[3], Michael W. Frohlich[4], Marc Gottschling[5], C. Matt Guilliams[6], Kristen E. Hasenstab-Lehman[7], Hartmut H. Hilger[8], James S. Miller[9], Moritz Mittelbach[10], Mare Nazaire[7], Massimo Nepi[11], Daniele Nocentini[11], Dietrich Ober[12], Richard G. Olmstead[13], Federico Selvi[14], Michael G. Simpson[15], Karel Sutorý[16], Benito Valdés[17], Genevieve K. Walden[18], Maximilian Weigend[1]

[1]Universität Bonn, Nees – Institut für Biodiversität der Pflanzen, Meckenheimer Allee 170, D – 53115 Bonn, Germany.
[2]Universidad de Chile, Departamento de Silvicultura y Conservación de la Naturaleza, Santiago, Chile.
[3]Università di Firenze, Museo di Storia Naturale, sezione botanica “Filippo Parlatore”, Via G. La Pira 4, 50121, Florence, Italy.
[4]Jodrell Laboratories, Kew Botanical Gardens, Richmond, Surrey, TW9 3DS, UK.
[5]Department Biologie, Systematische Botanik und Mykologie, GeoBio-Center, Ludwig-Maximilians-Universitat Munchen, Menzinger Str. 67, 80638 Munich, Germany.
[6] Santa Barbara Botanic Garden, 1212 Mission Canyon Road, Santa Barbara, CA 93105, U.S.A.
[7]Rancho Santa Ana Botanic Garden, 1500 N College Ave, Claremont, CA, 91711, U.S.A.
[8]Freie Universität Berlin, Institut für Biologie-Botanik, Altensteinstraße 6, D-14195 Berlin, Germany.
[9]Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A.
[10]Ruhr-Universität Bochum, Geobotanik - Gebäude ND 03/170, Universitätsstrasse 150, 44780 Bochum, Germany.
[11]Biodiversity and Conservation Network (BIOCONNET), Department of Environmental Sciences, University of Siena, via P.A. Mattioli 4, 53100 Siena, Italy.
[12]Botanisches Institut und Botanischer Garten, Universität Kiel, D–24098 Kiel, Germany.
[13]Department of Biology, Box 355325, University of Washington, Seattle, Washington 98195 U.S.A.
[14]Università di Firenze, Dipartimento di Scienze delle Produzioni Agroalimentari e dell’Ambiente (DISPAA), Laboratorio di Botanica, P.le delle Cascine 28, 50144 Florence, Italy.
[15]Department of Biology, San Diego State University, San Diego, CA 92182, U.S.A.
[16]Department of Botany, Moravian Museum, Hviezdoslavova streer 29a, 627 00, Brno, Czech Republic.
[17]Universidad de Sevilla, Departamento de Biología Vegetal y Ecología, Avda. Reina Mercedes s/n, 41012 Sevilla, Spain.
[18]Department of Integrative Biology, University of California, Berkeley, CA 94720, U.S.A.

Author for correspondence:
Federico Luebert (fluebert@uni-bonn.de) and Maximilian Weigend (mweigend@uni-bonn.de)

Running head: Families of Boraginales

**Abstract** The Boraginales are now universally accepted as monophyletic and firmly placed in Lamiidae. However, a consensus about familial classification has remained elusive, with some advocating recognition of a single, widely variable family, and others proposing recognition of several, distinct families. A consensus classification is proposed here, based on recent molecular phylogenetic studies, morphological characters, and taking nomenclatural stability into consideration. We suggest the recognition of eleven, morphologically well-defined and clearly monophyletic families, namely the Boraginaceae *s.str.*, Codonaceae, Coldeniaceae *fam. nov.*, Cordiaceae, Ehretiaceae, Heliotropiaceae, Hoplestigmataceae, Hydrophyllaceae, Lennoaceae, Namaceae *fam. nov.*, and Wellstediaceae. Descriptions, synonomy, a taxonomic key, and a list of genera for these eleven families are provided, including the new families Coldeniaceae (monogeneric) and Namaceae (segregated from Hydrophyllaceae and comprising *Nama*, *Eriodictyon*, *Turricula*, and *Wigandia*), the latter necessitating a revised circumscription of a more morphologically consistent Hydrophyllaceae.

**Keywords** angiosperms, Boraginaceae, Boraginales, classification, family, plant taxonomy

## INTRODUCTION

Boraginaceae in their traditional sense (de Candolle, 1845; Bentham & Hooker, 1976; Gürke, 1893; Engler, 1898; Pilger & Krause, 1915) were subdivided into five subfamilies, namely Boraginoideae, Cordioideae, Ehretioideae, Heliotropioideae and Wellstedioideae. Most workers accepted this circumscription of Boraginaceae in pre-molecular times (e.g., Chadefaud & Emberger, 1960; Melchior, 1964b; Takhtajan, 1980, 1997; Cronquist, 1981, 1988; Thorne, 1992), although some authors recognized one or the other subfamily at the family level. For example, Svensson (1925) and di Fulvio (1978) moved Cordioideae, Heliotropioideae and Ehretioideae to Heliotropiaceae based on embryological studies, while Merxmüller (1960), Dahlgren (1980), and Takhtajan (1987) treated Wellstedioideae at the family level as Wellstediaceae.

Phylogenetic studies demonstrate that Hoplestigmataceae, Hydrophyllaceae, and Lennoaceae are nested within Boraginaceae in the traditional sense (Olmstead & al. 1993; Ferguson, 1999; Gottschling & al., 2001; Nazaire & Hufford, 2012; Refulio-Rodríguez & Olmstead, 2014; Weigend & al., 2014). The close relationships of these taxa to traditional Boraginaceae had been previously acknowledged by several authors (e.g., Jussieu, 1789; Baillon, 1891; Peter, 1893; Svensson, 1925; Chadefaud & Emberger, 1960; Melchior, 1964a,c; Takhtajan, 1980; Cronquist, 1981, 1988). For example, Baillon (1891) defined the Boraginaceae as comprising nine series, which included both Boraginaceae and Hydrophyllaceae in their traditional circumscription. Moreover, Chadefaud & Emberger (1960) considered Boraginaceae, Hoplestigmataceae, Hydrophyllaceae, and Lennoaceae to form a natural group within their order Tubiflorales. Takhtajan (1980) included these same families in the suborder Boraginineae. However, Thorne (1992) palced Tetrachondraceae in his Boraginineae, and Takhtajan (1997) placed them in his order Boraginales. After removal of Tetrachondraceae to Lamiales (Savolainen & al., 2000), the remainder of the families was reunited in the order Boraginales (Takhtajan, 2009; Reveal & Chase, 2011), which was

originally proposed to include only some of these groups (Berchtold & Presl, 1820). Historical circumscriptions of Boraginaceae and related families by different authors are summarized in Appendix 1.

Phylogenetic studies further demonstrate that Hydrophyllaceae in their traditional sense are not monophyletic. *Hydrolea* L., previously treated in the Hydrophyllaceae, has been removed to the family Hydroleaceae in Solanales (Cosner & al., 1994; Soltis & al., 2000). *Codon* L., which is the sister group to a clade including *Wellstedia* Balf.f. (= Wellstedioideae) and Boraginaceae s.str. (= Boraginoideae), has been segregated to the family Codonaceae (Weigend & Hilger, 2010, Weigend & al., 2014). The remaining genera of the traditional Hydrophyllaceae form two distinct clades within Boraginales (Ferguson, 1999; Refulio-Rodríguez & Olmstead, 2014; Weigend & al., 2014; Fig. 1) and are successive sister groups to a clade comprising *Coldenia* L., Cordiaceae, Ehretiaceae, Heliotropiaceae, Hoplestigmataceae, and Lennoaceae. The first clade of the traditional Hydrophyllaceae includes the type genus of the family (*Hydrophyllum* L.) and the majority of the genera, while the second comprises *Eriodictyon* Benth., *Nama* L., *Turricula* J.F. Macbr., and *Wigandia* Kunth. Hydrophyllaceae *s.l.* is thus not monophyletic (Ferguson, 1999).

Boraginales, in this revised circumscription, is a well-supported monophyletic group (Gottschling & al., 2001; Moore & Jansen, 2006; Luebert & al., 2011a; Nazaire & Hufford, 2012; Cohen 2014; Refulio-Rodríguez & Olmstead, 2014; Weigend & al., 2014). Phylogenetic studies retrieve Boraginales in Lamiidae (Bremer & al., 2002; Soltis & al., 2011; Refulio-Rodríguez & Olmstead, 2014; Weigend & al., 2014). Monogeneric Vahliaceae have been sometimes regarded as a close relatives of Boraginales (e.g., Bremer & al., 2002), but more comprehensive molecular phylogenetic studies indicate that this family is more closely related either to Solanales (Savolainen & al., 2000; Refulio-Rodríguez & Olmstead, 2014) or Lamiales (Weigend & al., 2014). Similarly, Boraginales have been resolved as sister to Lamiales (Soltis & al., 2011; Refulio-Rodríguez & Olmstead, 2014), Solanales (Weigend & al., 2014), Gentianales (Stull & al., in press), or

Solanales+Gentianales (Moore & al., 2010), always with low to moderate support only.

Recent phylogenetic studies provide clear insights into the major lineages within Boraginales, and these are summarized in Fig. 1. Most recent authors consider Boraginales to be composed of several families (e.g., Gottschling & al., 2001; Hilger & al., 2005; Luebert & Wen, 2008; Weigend & Hilger, 2010; Luebert & al., 2011a; Cohen 2014; Refulio-Rodríguez & Olmstead, 2014; Weigend & al., 2014). Accepting the principle of monophyly in classification, the advantages of recognizing different families within the order Boraginales versus lumping all clades into a single family Boraginaceae s.l. include ease of morphological recognition, group size, and nomenclatural stability (Backlund & Bremer, 1998; Vences & al., 2013), as well as providing a classification congruent to what is accepted for other major clades of Lamiidae (Gentianales, Lamiales, Solanales).

The Angiosperm Phylogeny Group classifications (APG, 1998; APG II, 2003; APG III, 2009) opted for recognizing a single family Boraginaceae s.l., which was classified as an unplaced family (i.e., not placed in an order) within the Euasterids I (APG, 1998; APG II, 2003) or within the Lamiids (APG III, 2009). This was done in the absence of a clear phylogenetic understanding of the interrelationships among clades included within Boraginales and their relationships to other orders. While this was an understandable solution at the time, this option has the drawback of maintaining an empty level of classification (i.e., Boraginales containing only one family) and reducing the widely recognized and accepted families Hoplestigmataceae, Hydrophyllaceae and Lennoaceae to subfamily or tribe level. These families have a long history of recognition, including past taxonomic treatments (e.g., Melchior, 1964a,c; Yatskievych & Mason, 1986), major floras (e.g., Aubréville, 1959; Hepper, 1963; Howard, 1989; Liogier, 1994; Sullivan, 2001; Yatskievych, 2001, 2012; Hofmann, 2004; Sklenář & al., 2005; Zuloaga & al., 2008; Ricketson, 2012; Cecchi & Selvi, 2015a) and textbooks (e.g., Cronquist, 1988; Heywood & al., 2007; Takhtajan, 2009). In addition, Boraginales are comparable in age to Gentianales, Lamiales, and Solanales (Wikström & al., 2001,

2015; Bremer & al., 2004, Bell & al., 2010, Naumann & al., 2013, Nazaire & al., 2014), thus suggesting that recognition at the rank of order is appropriate based on the criterion of time banding (Vences & al., 2013).

Some recent treatments have followed a broad circumscription of Boraginaceae (i.e., including Hoplestigmataceae, Hydrophyllaceae, Lennoaceae) as recommended by the APG systems (e.g., Judd & al., 2008; Mabberley, 2008; Simpson, 2010; Reveal, 2011, 2012; Acevedo-Rodríguez & Strong, 2012; Nazaire & Hufford, 2012; Walden & Patterson, 2012; Walden & al., 2014). However, most recent studies on Boraginales or its subgroups favor the recognition of several families (Gasparino & Vitorino da Cruz Barros, 2009; Melo & al., 2009; Véliz Pérez & al., 2009; Luebert & al., 2010, 2011a,b; Machado & al., 2010; Melo & Semir 2010; Milet-Pinheiro & Schlindwein, 2010; Stapf & al. 2010; Weeks & al., 2010; Weigend & Hilger, 2010; Campos-Ríos & Chiang Cabrera, 2012; Miller, 2012, 2013a,b; Stutzman & al., 2012; Feuillet, 2013; Luebert, 2013; Stapf & Silva, 2013a,b; Tölke & al., 2013; Cohen, 2014; Gottschling & al., 2014a,b; Refulio-Rodríguez & Olmstead, 2014; Weigend & al., 2014; Irimia & al., 2015; Liu & al., 2015; Luebert & Hilger, 2015). This view has already been adopted in several recent floristic and taxonomic treatments, such as Flora critica d'Italia (Cecchi & Selvi, 2015a,b), Flora Mesoamericana (Davidse & al., 2012), Families and Genera of Vascular Plants (Kubitzki & al., in press), Angiosperm Phylogeny Website (Stevens 2001 onwards), and has recently been incorporated in the most important German botanical textbook (Kadereit & al., 2014). This is likely to continue and increase, because floristic treatments and taxonomic revisions are undertaken by Boraginales specialists, who, unless rigid editorial rules are enforced, used and will use a taxonomic circumscription of several families in Boraginales. For example, Flora of North America (http://floranorthamerica.org/Review/under-prod-15, accessed 21 Jul 2015), Flora of Nepal (http://padme.rbge.org.uk/floraofnepal/, accessed 22 Sep 2015), and Flora of Ecuador (http://www2.dpes.gu.se/project/ecuador/, accessed 22 Sep 2015) plan to publish their treatments of

Boraginales with several constituent families. Recognizing Boraginaceae *s.l.* therefore contradicts nomenclatural stability, reducing several long-recognized families to subfamilies.

Moreover, lack of morphological homogeneity renders Boraginaceae *s.l.* impossible to characterize: this broadly defined family would include vastly different flower and fruit morphologies (see below), apart from a whole range of vegetative characters (see Weigend & al., 2014 and Table 1). Historically, the coherence of Boraginaceae (excl. Hydrophyllaceae s.l.) was primarily based on the presence of four one-seeded compartments in the fruit, four separate nutlets in the most typical case (Bentham & Hooker, 1876; Gürke, 1893). However, it has now been shown that two major clades of the Boraginaceae s.l. independently evolved this gross fruit morphology from ancestors with multi-ovulate capsular fruits (Weigend & al., 2013, 2014). A more detailed study shows that the development of these superficially similar fruits follows different developmental trajectories and therefore does not represent a case of homology (Fig. 2). Therefore, no morphological synapomorphy has been identified for Boraginales (= "Boraginaceae *s.l.*") so far. The inner pericarp of Boraginaceae *s.str.* is not lignified and lacks transfer cells (Hilger, 1985), while in the woody clades of Boraginales (i.e., Heliotropiaceae, *Coldenia* + Cordiaceae + Hoplestigmataceae, Ehretiaceae + Lennoaceae), the hard endocarp is multi-layered functioning as effective seed protection, and specialized transfer cells in seed coat and funicle facilitate water uptake for bursting it during germination (Diane & al., 2002). In the face of this evidence, the most important historical argument for maintaining traditional Boraginaceae and Hydrophyllaceae as separate entities, or even as a single broadly circumscribed family (Boraginaceae *s.l.*), is eliminated and an updated classification appears even more justified.

Based on phylogenetic data, the two major clades of the Boraginaceae *s.l.* [Boraginales] consist of: (i) Codonaceae + Wellstediaceae + Boraginaceae *s.str.*; and (ii) Hydrophyllaceae *s.l.* + Heliotropiaceae + *Coldenia* + Cordiaceae + Hoplestigmataceae + Ehretiaceae + Lennoaceae (Fig. 1). Thus, one option is to recognize each of the two clades at the family level. However, this

solution would have the same drawbacks as recognition of Boraginaceae *s.l.*, given that neither of the two major clades has been named at any taxonomic level in previous classifications, so this would cause maximal nomenclatural disruption. Furthermore, one clade lacks any known morphological apomorphies (Fig. 1). The question is, therefore, which clades of Boraginales are best recognized and named at the family level?

Although nested within the Ehretiaceae in some analyses, Lennoaceae have been segregated (see Appendix 1) from others in the complex, not only because of their parasitism, but also because of their possessing more than five calyx and corolla lobes and more than four seeds enclosed in enodarpids developing per fruit (Yatskievych & Mason, 1986; Fig. 1), a combination of characters that is otherwise only found within Boraginales in the distantly related Codonaceae (but with capsular fruits). In addition, recognition of a separate Cordiaceae (see Appendix 1) is based on multiple apomorphies, such as presence of four stigmatic branches, undivided endocarp, and plicate cotyledons (Gottschling & al., 2005). Inclusion of *Coldenia* and *Hoplestigma* within Cordiaceae would compromise this ease of recognition.

The largely woody lineages related to *Cordia* L. and *Ehretia* P. Browne comprise a monophyletic group and could be united to form Ehretiaceae *s.l.* (Kubitzki & al., in press; with Lennoaceae separate). However, monophyly of Ehretiaceae *s.l.* is verified only by molecular data at present, as no morphological apomorphy is known for this clade (Fig. 1). This solution would thus be inconsistent with the explicit aim of recognizing morphologically well-circumscribed families. Alternatively, based on the presence of multilayered endocarp in Heliotropiaceae + Cordiaceae *s.l.* + Ehretiaceae + Lennoaceae, these could potentially be united into a more broadly defined Heliotropiaceae *s.l.* This classification has not been proposed before and would therefore be a major change.

The authors of this paper favor the recognition of eleven, easily recognizable and well-defined monophyletic families (i.e., the major clades of Fig. 1, see Table 1). These entities are

characterized mostly by apomorphic characters, or at least consistent traits (Fig. 1). This classification represents only a minimal disruption of nomenclatural stability by mostly recognizing taxa with valid family names already in use; all but two have valid names at the family level. Novel changes include description of the monogeneric Coldeniaceae *fam. nov.* (*Coldenia* alone), and the splitting of the Hydrophyllaceae into two families (Refulio-Rodríguez & Olmstead, 2014; Weigend & al., 2014), creating a new family Namaceae *fam. nov.* to accommodate the genera *Eriodictyon*, *Nama*, *Turricula*, and *Wigandia*.

The consensus for this system was achieved during an international meeting on Boraginales research in 2014 in Bonn, where most of the authors attended and discussed different alternatives of classification. All participants in that meeting favored a classification of Boraginales into several separate families. Further coauthors were invited to participate in this proposal after a draft classification had been formulated by the participants. One case was left open to discussion, namely the split of Cordiaceae, Coldeniaceae, Hoplestigmataceae, Ehretiaceae, and Lennoaceae. The opinion of the specialists in this group was then adopted.

The classification of Boraginales as outlined here reflects the current knowledge about the phylogenetic relationships of the group and provides a familial classification for the order, lacking in recent angiosperm-wide classifications (APG, 1998; APG II, 2003; APG III, 2009; Reveal, 2011, 2012; Reveal & Chase, 2011). This classification attempts to fulfill APG III (2009) criteria for recognition of taxa at the family level as proposed by Backlund & Bremer (1998). Boraginales composed of eleven families is also more consistent with the classifications currently accepted for the related orders Solanales, Lamiales, and Gentianales, all of which comprise multiple families, including morphologically divergent lineages in monogeneric families (e.g., Byblidaceae, Hydroleaceae, Plocospermataceae, Sphenocleaceae, Thomandersiaceae).

There are two instances in which phylogenetic results currently available are not entirely clear. First, the relationships of Hydrophyllaceae and Namaceae (Fig. 1) to the other lineages of

Boraginales are not fully resolved. ITS phylogenies recover Hydrophyllaceae *s.l.* (excl. *Codon*) as monophyletic (Gottschling & al., 2001; Nazaire & Hufford, 2012), with our Hydrophyllaceae *s.str.* sister to our Namaceaeae, *fam. nov*., with moderate to poor support. Studies with plastid data resolve these two clades as successive sister groups to Heliotropiaceae + Cordiaceae + Coldeniaceae + Hoplestigmataceae + Ehretiaceae + Lennoaceae, albeit not always with high support (Refulio-Rodríguez & Olmstead, 2014 based on chloroplast *atpB*, *matK*, *ndhF*, *psbBTNH*, *rbcL*, *rps4*, *rps16*, *trnL-F*, *trnV-atpE*, and mitochondrial *rps3*; Weigend & al., 2014, based on chloroplast *ndhF*, *rbcL*, *rps16*, *trnL-F*). The present proposal is compatible with both plastid and ITS phylogenies. The key morphological character of the traditional Hydrophyllaceae, capsular fruit, is plesiomorphic, so the subdivision is not in conflict with morphology, but neither does morphology provide support for the separation (Table 1).

The second taxonomic uncertainty is the status of Lennoaceae and its relationship to Ehretiaceae. Morphologically, the Ehretiaceae are readily circumscribed with diagnostic features including a bifid style with 2 stigmatic branches and usually drupaceous fruits with four pyrenes (less commonly two 2-seeded pyrenes, or rarely an entire endocarp). However, monophyly has been challenged because molecular data suggest that parasitic Lennoaceae may be nested within Ehretiaceae (Gottschling & al., 2001, 2014a; Nazaire & Hufford, 2012; Weigend & al., 2014). More research is necessary to determine whether Lennoaceae constitute the sister group of Ehretiaceae or should be included in that family. Pending a more satisfactory resolution of these relationships, Lennoaceae are retained as they have historically been recognized.

## FORMAL TAXONOMY

**Boraginales** Juss. ex Bercht. & J. Presl, Přir. Rostlin: 244. 1820.

= Asperifoliae H.Rose, Elem. Bot.: 56. 1775.

= Cordiales Mart., Consp. Regn. Veg. [Martius]: 23. 1835.

= Ehretiales Mart., Consp. Regn. Veg. [Martius]: 22. 1835.

= Hydrophyllales Mart., Consp. Regn. Veg. [Martius]: 22. 1835.

= Echiales Lindl., Penny Cyclop. 10: 128. 1838.

*Annual* or perennial herbs, shrubs, trees, lianas or holoparasitic plants. *Leaves* simple, alternate or opposite, estipulate. Flowers in scorpioid inflorescences, rarely solitary. *Flowers* hermaphroditic or unisexual, actinomorphic or rarely zygomorphic, hypogynous. Perianth heterochlamydeous, (4–)5(–20)-merous. Androecium composed of (4–)5(–12 or 20–35) stamens, filaments usually united with corolla tube. Gynoecium with style insertion apical or gynobasic, style 1, rarely 2 or 4 stylodia, stigmatic branches 1, 2 or 4. Ovary 2-carpellate or rarely 5–16-carpellate. Fruit a capsule, drupe, nut or (1–)4 nutlets, dehiscence loculicidal, septicidal, eremocarpic, schizocarpic, indehiscent. Ovary locules 1–4(10–28). Ovules per locule 1–many. Placentation axile, parietal or apical. Seeds per fruit 1–many. Endosperm copious, scanty or absent.

Eleven families with 125 genera and around 2700 species.

**Key to the families of Boraginales**

**1.** Plants without chlorophyll, leaves reduced to scale-shaped cataphylls; ovary 5–16-carpellate, 10–28-locular by secondary subdivision; fruit with numerous pyrenes (i.e., individual seeds enclosed separately in lignescent endocarps) at maturity.

**Lennoaceae**

- Plants with chlorophyll, leaves with normal lamina; ovary 2-carpellate, 1–4-locular by secondary subdivision or not; fruit with 1–4 pyrenes, or without pyrenes (i.e., “nutlets” or capsules).

**2**

**2.** Ovary subdivided into four mericarpids (single-seeded parts) in flower, developing into (1–)4(–8) individual nutlets; style insertion gynobasic.

**Boraginaceae *s.str.***

- Ovary undivided 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 with stiff, white spines; calyx and corolla 10–12-merous, calyx segments unequal; fruit a many-seeded capsule.

**Codonaceae**

- Stems and leaves not spinose, but sometimes setose or with axillary thorns (*Rochefortia* Sw.); flowers usually 4–5-merous (if more, as in *Hoplestigma*, then fruit drupaceous); calyx segments equal or subequal.

**4**

**4.** Fruit a laterally flattened, obcordate capsule with 1–2 seeds; flowers always 4-merous.

**Wellstediaceae**

-Fruit ovoid, if capsular never laterally flattened and with 4–∞ seeds; flowers usually 5-merous, if tetramerous fruits then spiny nutlets.

**5**

**5.** Fruit a capsule with 4–∞ seeds, sometimes fewer by abortion.

**6**

- Fruit indehiscent or schizocarpic, fleshy or dry, often subdivided into mericarps, 4-seeded, sometimes fewer by abortion.

**7**

**6.** Shrubs or small trees, or herbaceous (only *Nama*); leaves cauline, simple; stylodia 2, or style

united for 3/4 of its length with two stigmatic branches.

**Namaceae**

- Annual or perennial herbs, leaves cauline and basal, rarely basal or cauline only, simple or - more commonly - variously divided to bipinnate; style 1 with two stigmatic branches.

**Hydrophyllaceae**

**7.** Stigma not terminal, a continuous ring around at the base of terminal non-stigmatic tissue (style-stigma complex), style undivided; flowers usually in dense, scorpioid, bracteate or ebracteate monochasia.

**Heliotropiaceae**

- Stigma(s) terminal, style entire to prominently divided; flowers otherwise arranged, often in repeatedly dichasial inflorescences.

**8**

**8.** Gynoecium bearing four stigmatic branches (if 2, then fruit completely enclosed in accrescent calyx); ovules orthotropous; cotyledons plicate.

**Cordiaceae**

- Gynoecium bearing 1–2 stigmatic branches; fruit not enclosed in accrescent calyx (except in *Bourreria grandicalyx* J.S.Mill. & Sirot); ovules anatropous; cotyledons not plicate.

**9**

**9.** Androecium composed of 20–35 stamens attached in three irregular series.

**Hoplestigmataceae**

- Androecium composed of 4 or 5 stamens, usually attached in one series.

**10**

**10.** Flowers 5-merous; mostly perennial, woody plants without adventitious roots.

**Ehretiaceae**

- Flowers 4-merous; annual plants with adventitious roots.

**Boraginaceae** Juss., Gen. Pl. [Jussieu]: 128. 1789.

Type genus: *Borago* L. (1753)

= Buglossaceae Hoffmanns. & Link, Fl. Portug. [Hoffmannsegg] 1: 63. 1809 (‘Buglossinae’).

= Anchusaceae Vest, Anleit. Stud. Bot.: 274, 302. 1818 (‘Anchusoideae’).

= Cerinthaceae Martynov, Tekhno-Bot. Slovar: 120. 1820 (‘Cerinthoides’).

= Onosmaceae Martinov, Tekhno-Bot. Slovar: 437. 1820 (‘Onosmoides’).

= Asperifoliaceae Rchb., Consp. Regn. Veg. [H.G.L.Reichenbach]: 89, 118. 1829.

= Echiaceae Raf., Fl. Tellur. 2: 61. 1837 (‘Echidia’).

= Cynoglossaceae Döll, Rhein. Fl.: 406. 1843.

*Annual* to perennial, herbs, rarely shrubs or trees, taprooted or rhizomatous, pubescent, sericeous or hispid. *Leaves* alternate, entire, sessile or petiolate, lamina mostly (ob-)ovate to elliptical. *Inflorescences* terminal or axillary, monochasial or dichasial, usually scorpioid and contracted into boragoids, sometimes congested into terminal “heads” or reduced to single flowers. *Flowers* pentamerous, bisexual; calyx united nearly to apex or divided nearly to base; corolla white, yellow, pink or often blue, sympetalous, hypocrateriform, infundibuliform to cylindrical or campanulate, lobes variously erect to spreading; stamens 5, rarely fewer, filaments various, short to very long, anthers deeply included to exserted; gynoecium bicarpellate, 4-locular by secondary subdivision at early anthesis, style gynobasic, often with pyramidal to subulate gynobase. *Fruit* with (1–2)–4 one-seeded nutlets, rarely of two, two-seeded nutlets, these variously modified, often dorsiventrally compressed, with a marginal wing or ring, often glochidiate.

Around 90 genera (Appendix 2) with some 1,600–1,700 species of worldwide distribution,

especially in extra-tropical zones.

Major clades within Boraginaceae *s.str.* are relatively well-resolved, with Echiochileae sister to the rest, where Borageneae and Lithospermeae form a clade, which is sister to Cynoglosseae *s.l.* (Weigend & al., 2013). The family is readily distinguished by its mostly herbaceous habit, generally scorpioid inflorescences, gynobasic style, and four nutlets sometimes ornamented with glochidiate spines. Traditionally, Boraginaceae have also included Cordiaceae, Ehretiaceae, Heliotropiaceae, and Wellstediaceae. However, Boraginaceae have been variously circumscribed, ranging from an inclusive taxon encompassing the whole order Boraginales to a family defined on its most strict sense as accepted here (see Appendix 1).

**Codonaceae** Weigend & Hilger, Phytotaxa 10: 27. 2010.

Type genus: *Codon* L. (1753)

= Codonoideae Retief & P.S. van Wyk, Bothalia 35(1): 79. 2005.

= Codoneae (Retief & P.S. van Wyk) Nazaire & L. Hufford, Syst. Bot. 37: 779. 2012.

*Subperennial* or perennial, densely branched, spiny shrublets with taproots. *Leaves* alternate, entire, petiolate, lamina ovate, adaxially densely spiny, abaxially with spines only on the very prominent midvein. *Inflorescences* frondose-bracteose, initially scorpioid, later straight monochasial, rarely reduced to a single terminal flower. *Flowers* with 10–12 perianth elements, bisexual; calyx divided nearly to base; corolla white or yellow, sympetalous, campanulate to saucer-shaped, lobes half-erect to spreading; stamens 10–12, filaments basally pubescent and each connected to corolla tube by septa forming a nectary chamber, anthers exserted; gynoecium bicarpellate, nearly bilocular by deeply intruding placentae, style terminal, stigmatic branches 2. *Fruit* a dry, bivalved capsule, loculicidal, seeds numerous with reticulate testa and testa cells with variously elevated anticlinal

walls.

One genus (*Codon*) and two species endemic to southwestern Africa. *Codon* is readily recognized by its peculiar spines, flowers with 10–12 perianth parts, bivalvate, capsular fruits, and the presence of a nectary chamber. Constance (1963) recommended that *Codon* "should constitute a family of its own." *Codon* was identified as a clade separate from Hydrophyllaceae (Ferguson, 1999), and as a distinct lineage in the Boraginaceae at subfamily (Retief & van Wyk, 2005) and tribal level (Nazaire & Hufford, 2012), and was segregated as Codonaceae (Weigend & Hilger, 2010).

**Coldeniaceae** J. S. Mill. & Gottschling, fam. nov.
Type genus: *Coldenia* L. (1753)

*Procumbent* annual herbs with slender, branched stems, often with adventitious roots. *Leaves* numerous, fasciculate, small, asymmetrical, bullate, margin crenate, venation unusual in that secondary veins end in the base of the sinuses of the crenations. *Flowers* solitary, axillary, small, bisexual, tetramerous; calyx deeply lobed; corolla white or yellow, aestivation imbricate, tube cylindrical, glabrous, lobes spreading; anthers included; gynoecium with two stigmatic branches. *Fruit* small, dry, ovoid-conical, 4-lobed, separating into four 1-seeded, apically beaked and spinose nutlets lacking sterile chambers.

One species (*Coldenia procumbens* L.) widespread in the Old World tropics and introduced elsewhere. Long considered congeneric with *Tiquilia* Pers. in the Ehretiaceae (e.g., Gray, 1962; Bentham & Hooker, 1976; Baillon, 1891; Gürke, 1893; Johnston, 1924; Chadefaud & Emberger, 1960; Takhtajan, 1987). Richardson (1976) demonstrated that the two genera were distantly related based on morphology and biogeography, and this is supported by recent molecular studies

(Gottschling & al., 2005; Moore & Jansen, 2006; Weigend & al., 2014). *Coldenia* had been provisionally included in Cordiaceae (Miller & Gottschling, 2007). However, *Coldenia* is distinct in its procumbent annual growth habit, its leaves with craspedodromous venation with the secondary veins ending in the sinus of serrations, and fruits separating in four apically beaked and spinose nutlets.

**Cordiaceae** R. Br. ex Dumort., Anal. Fam. Pl.: 20, 25. 1829.

Type genus: *Cordia* L. (1753)

= Sebestenaceae Vent., Tabl. Regn. Vég. 2: 380. 1799 (‘Sebestenae’).

= Cordieae Dumort., Anal. Fam. Pl.: 25. 1829.

= Cordioideae Beilschm., Flora 16 (Beibl. 7): 69, 106. 1833 (‘Cordiaceae’, p. 61; ‘Cordieae’, p. 106).

*Trees*, shrubs, or rarely lianas, often pubescent with stiff trichomes. *Leaves* alternate, rarely subopposite, entire, petiolate, lamina variable in shape. *Inflorescences* mostly terminal, basically with dichasial or monochasial paracladia, but also capitate, spicate or very shortly cymose umbellate to globose, sometimes in corymbo-thyrsoids. *Flowers* pentamerous, rarely tetramerous, or with up to 15 lobes, bisexual and often distylous, occasional unisexual and dioecious; calyx united in a tube, tubular to campanulate; corolla white, or rarely yellow, tubular to campanulate or rotate, lobes distinct or not, erect to spreading; stamens (4–)5(–15), filaments generally adnate to the corolla tube, at least at the base, sometimes puberulent at the point of insertion, anthers bilocular; gynoecium bicarpellate, tetralocular from secondary subdivision, style terminal, stigmatic branches 4, clavate to capitate. *Fruits* generally with a slightly to greatly accrescent calyx, drupaceous with 4 locules, occasionally 3 locules aborting and drupes asymmetric, or fruits ellipsoid and fibrous-walled and dispersed with the marcescent corolla.

Two genera (*Cordia* and *Varronia* P. Browne; see Appendix 2) with ca. 400 species of worldwide distribution, especially in the tropics and subtropics. The subfamilial classification of Cordiaceae has long been debated. Ivan Johnston in numerous publications in his series "Studies in the Boraginaceae" recognized a broadly defined *Cordia* with 5–7 sections (Hilger & Zippel, 2001). Recent molecular studies indicate that *Varronia* is sister to the rest of *Cordia*, and Miller & Gottschling (2007) argued for its recognition as a distinct genus. *Cordia s.str.* differs from *Varronia* in comprising multi-stemmed shrubs, with serrate leaf margins, condensed inflorescences, and porate pollen grains. Cordiaceae is the only family in Boraginales with plicate cotyledons and generally a twice-dichotomous style bearing four stigmatic branches. The family Cordiaceae was established by Dumortier (1829) to encompass both Cordieae and Ehretieae. It has been recognized as a valid family (e.g., Takhtajan, 1987) or as part of the Heliotropiaceae (e.g., Svensson, 1925) or Boraginaceae (see Appendix 1).

**Ehretiaceae** Mart., Nov. Gen. Sp. Pl. 2: 136, 138. 1827.

Type genus: *Ehretia* P. Browne (1756)

= Ehretieae Dumort., Anal. Fam. Pl.: 25. 1829.

= Ehretioideae Arn., Botany [Arnott]: 122. 1832 ('Ehretieae').

*Trees*, shrubs, perennial herbs, rarely with thorns (*Rochefortia*), often pubescent with stiff trichomes. *Leaves* alternate, entire, petiolate, lamina variable in shape, strongly dissected in the halophytic *Cortesia* Cav. *Inflorescences* terminal or axillary, thyrsoidal, sometimes congested. *Flowers* pentamerous, bisexual or unisexual with dioecious sex distribution in *Lepidocordia* Ducke and *Rochefortia*; calyx lobes united in a tube or distinct nearly to the base, tubular to campanulate, the lobes valvate, imbricate, or quincuncial; corolla white, red or blue (*Halgania* Gaudich., some

*Bourreria* P. Browne), generally tubular with spreading lobes, rotate, or campanulate to urceolate; stamens 5, the filaments generally adnate to the corolla tube at least at the base, sometimes puberulent at the point of insertion, the anthers bilocular; gynoecium bicarpellate, tetralocular from secondary subdivision, style terminal, stigmatic branches 2, clavate to capitate. *Fruits* generally drupaceous, often drying and separating into two two-seeded pyrenes, or 4 single-seeded pyrenes or schizocarps, or 4 nutlets.

Seven genera (Appendix 2) with ca. 150 species of worldwide distribution, especially in the tropics and subtropics. Generic delimitation and relationships in the Ehretiaceae are reasonably well understood as a consequence of recent molecular studies (Gottschling & al., 2014a; Weigend & al., 2014), but it is not clear at present whether they include Lennoaceae, or are the sister group of these parasites. Ehretiaceae are morphologically heterogeneous and diverse, and the only trait known at present holding them together are their bifid styles with two stigmatic branches (putatively a plesiomorphic character). Ehreatiaceae have been variously included in Boraginaceae (e.g., Bentham & Hooker, 1976), Cordiaceae (e.g., Dumortier, 1829), Heliotropiaceae (e.g., Svensson, 1925), or defined in a strict sense as a family of their own (e.g., Takhtajan, 1987).

**Heliotropiaceae** Schrad., Commentat. Soc. Regiae Sci. Gott. Recent. 4: 192. 1819.
Type genus: *Heliotropium* L. (1753)
= Heliotropieae Dumort., Fl. Belg. (Dumortier): 39. 1827.
= Tournefortieae Bartl., Ord. Nat. Pl.: 197. 1830 (‘Tournefortiea’).
= Heliotropioideae Arn., Botany [Arnott]: 122. 9. 1832 (‘Heliotropieae’).

*Annual* or perennial herbs, subshrubs, shrubs, lianas or small trees. *Leaves* alternate, petiolate or sessile, lamina linear to suborbicular. *Inflorescences* thyrsoids, terminal or axillary; partial

inflorescences scorpioid cymes. *Flowers* 5-merous, perfect, rarely unisexual; calyx tube usually short, mostly campanulate, calyx lobes linear to ovate, mostly persistent after anthesis; corolla sympetalous, with subcircular to linear lobes; stamens antesepalous and borne on corolla tube, anthers usually included; gynoecium bicarpellate, usually 4-locular with one ovule in each locule; style terminal with a conical stigmatic head having a basal ring-shaped stigma and a sterile, sometimes two-lobed apex. *Fruit* dry or fleshy, usually 4-seeded, rarely 1–2-seeded, falling apart into 1–4 mericarpids with 1–2 seeds each.

Four genera (Appendix 2) with ca. 450 species of worldwide distribution, especially in the tropics and subtropics. Comprises the type genus *Heliotropium* (incl. *Tournefortia* L.) and the genera *Euploca* Nutt., *Ixorhea* Fenzl (monotypic) and *Myriopus* Small. *Ixorhea* is sister to *Euploca* and *Myriopus* (Weigend & al., 2014). Together they form a clade sister to *Heliotropium*, which comprises four major clades: *Heliotropium* sect. *Heliothamnus* I.M. Johnst., Old-World *Heliotropium*, *Heliotropium* sect. *Cochranea* (Miers) Post & Kuntze, and the *Tournefortia*-clade, the latter comprising *Tournefortia* sect. *Tournefortia* and all remaining New World species of *Heliotropium* (Hilger & Diane, 2003; Luebert & al., 2011b). Heliotropiaceae vary from herbs to vines, shrubs, and trees, mostly with distinctly scorpioid cymose inflorescences, but are unique in the possession of conical stigmatic heads. Heliotropiaceae as here defined were established by Schrader (1819). Heliotropiaceae also have been recognized as a subfamily of Boraginaceae (Bentham & Hooker, 1876; Engler, 1898), included in Ehretieae (e.g., Endlicher, 1836) in its entirety, or split into Heliotropioideae and Ehretioideae (e.g., de Candolle, 1845).

**Hoplestigmataceae** Gilg in Engler & Gilg, Syllabus (ed. 9 & 10): 322. 1924.

Type genus: *Hoplestigma* Pierre (1899)

= Hoplestigmateae Reveal, Phytoneuron 2012-33: 2. 2012.

*Trees*. *Leaves* alternate, entire, petiolate, obovate. *Inflorescences* terminal thyrsoids, with dichasial paracladia. *Flowers* bisexual, borne in cymes with subscorpioid branches; calyx tearing into uneven lobes; corolla with 11–14 deeply divided lobes; stamens 20–30 in three irregular series, free from corolla, anthers bilocular; gynoecium bicarpellate, unilocular with four pendulous anatropous ovules, style terminal, stigmatic branches 2, capitate. *Fruits* drupaceous, borne in a slightly accrescent calyx, endocarp undivided, with two additional sterile chambers.

One genus (*Hoplestigma*) and two species endemic to central and western Africa. *Hoplestigma* is unique in having polymerous flowers and very large drupaceous fruits with large sterile chambers. *Hoplestigma* was first placed in Flacourtiaceae (Pierre, 1899), and later placed uncertainly in Ebenales (Gilg, 1908; Wagenitz, 1964), Bixales (Hutchinson, 1959), Violales (Cronquist, 1981), and in Boraginales (Dahlgren, 1980; Takhtajan, 1987, 1997, 2009).

**Hydrophyllaceae** R. Br., Bot. Reg. 3: t. 242. 1817. excl. gen.

Type genus: *Hydrophyllum* L. (1753)

= Hydrophyllineae Link, Handbuch [Link] 1: 570. 4-11. 1829.

= Romanzoffieae Dumort., Anal. Fam. Pl.: 26. 1829 (‘Romanzoviaceae’).

= Hydrophylleae Rchb., Fl. Germ. Excurs. 1(3): 347. 1831.

= Hydrophylloideae Burnett, Outlines Bot.: 1006, 1095, 1105. 1835 (‘Hydrophyllidae’).

= Ellisieae Rchb., Handb. Nat. Pfl.-Syst.: 193. 1837.

= Nemophileae Rchb., Handb. Nat. Pfl.-Syst.: 193. 1837.

= Eutocaceae Horan., Char. Ess. Fam.: 124. 1847.

= Phacelieae Bentham ex A. Gray, Proc. Amer. Acad. Arts 10: 312. 1875.

= Hydrophyllinae Reveal, Phytoneuron 2012-33: 2. 2012.

= Phaceliinae Reveal, Phytoneuron 2012-37: 218. 2012.

= Romanzoffiinae Reveal, Phytoneuron 2012-37: 218. 2012.

*Annual*, biennial, or perennial herbs. *Leaves* cauline and basal, rarely basal or cauline only, alternate, undivided or – more commonly – variously divided to bipinnate. *Inflorescences* terminal or axillary, thyrsoidal, usually of scorpioid monochasia, sometimes congested. *Flowers* (4–)5-merous, bisexual; aestivation of petals contorted or imbricate; corolla scales present, small or absent, stamens of equal or unequal length, filaments equally or unequally inserted on the corolla tube; style 1, stigmatic branches 2; ovary unilocular or bilocular, sometimes the two large, fleshy parietal placentae filling the locule at anthesis, ovary thus appearing 2- or 5-locular, or placentae narrow, cartilaginous, partially or completely dividing ovary, capsule appearing 2-celled; nectar disc present or reduced to glands at ovary base. *Fruit* a membranaceous capsule, dehiscence loculicidal with 2 valves, 2–many-seeded.

Twelve genera (Appendix 2) with about 240–260 species restricted to North and Central America and western South America. Comprises the type genus *Hydrophyllum* and the genera *Draperia* Torr., *Ellisia* L., *Emmenanthe* Benth., *Eucrypta* Nutt., *Hesperochiron* S. Watson, *Howellanthus* (Constance) Walden & R. Patt., *Nemophila* Nutt., *Phacelia* Juss., *Pholistoma* Lilja, *Romanzoffia* Cham., and *Tricardia* Torr. The circumscription of Hydrophyllaceae is here amended, excluding the entire tribe Nameae, traditionally considered part of this family. Hydrophyllaceae has three major clades (Ferguson, 1999, Walden, 2010), a clade of *Phacelia* + *Romanzoffia* (equivalent to Romanzoffieae) (Walden & al., 2014), a clade of *Hydrophyllum* + *Pholistoma* + *Nemophila* + *Emmenanthe* + *Ellisia* + *Eucrypta* (equivalent to Hydrophylleae) (Walden, 2015), and a clade (otherwise unnamed) of *Draperia* + *Tricardia* + *Howellanthus* + *Hesperochiron* (Walden, unpublished data). Brown (1810) first considered the genera *Hydrophyllum*, *Phacelia*, and *Ellisia* as

distinct from Boraginaceae, these later formalized as Hydrophyllaceae (Edwards, 1817), a circumscription followed by subsequent authors (e.g., Bentham, 1835; Endlicher, 1836–1840; de Candolle, 1846). Gray (1875) expanded the family to include Hydrophylleae, Phacelieae, Namaeae, and Hydroleae in Hydrophyllaceae, a delimitation followed by Bentham & Hooker (1876), Peter (1893), Brand (1913), Constance (1963) and most modern authors (e.g., Takhtajan, 1980, 1987, 1997; Cronquist, 1981; Thorne 1992). Hydrophyllaceae have also been regarded as a member of Boraginaceae (Jussieu, 1789; Baillon, 1891; Reveal, 2011, 2012).

**Lennoaceae** Solms, Abh. Naturf. Ges. Halle 11: 174. 1870.

Type genus: *Lennoa* Lex. (1824)

= Pholismateae Horan., Char. Ess. Fam.: 109. 1847 (‘Pholisma’).

= Lennooideae Torr., Ann. Lyceum Nat. Hist. New York 8: 56. 1854 (‘Lennoeae’).

= Lennoeae Baill., Hist. Pl. (Baillon) 11: 161, 207. 1891.

*Parasitic* herbs, without chlorophyll, leafless (cataphylls present). *Inflorescences* densely spicate or capitate cymose-thyrsoids. *Flowers* bisexual; calyx 6–10-lobed, the lobes narrow; corolla tubular with 5–10 lobes; stamens the same number as the corolla lobes, the filaments adnate to the corolla tube, the free portion very short, anthers bilocular; gynoecium 10–15-locular, style simple and undivided, stigma capitate. *Fruits* capsular, irregularly circumscissile, at maturity breaking into 12–28 nutlets.

Two genera (*Lennoa*, *Pholisma* Nutt. ex Hook.) and four species of aphyllous root holoparasites distributed in southwestern North America, Mexico, and northwestern South America. The family is distinct in its parasitic habit, 10–15-locular gynoecium, and unusual circumscissile capsular fruits. Lennoaceae have been associated with Primulaceae (La Llave & Lexarva, 1824), Orobanchaceae

(Hooker, 1844), Ericales (Solms-Laubach, 1870; Bentham & Hooker, 1876; Engler, 1898), Cuscutaceae (Conzatti & Smith, 1909), or Boraginineae (Takhtajan, 1980; Thorne, 1992), or have been treated either as a subfamily in Boraginaceae (Reveal, 2011, 2012), or a family of Boraginales (Dahlgren, 1980; Takhtajan, 1987, 1997, 2009; current treatment).

**Namaceae** Walden & Olmstead, *fam. nov.*

Type genus (here designated): *Nama* L. (1759)

Basionym: Hydrophyllaceae tribus Nameae Choisy, Prodr. [A. P. de Candolle] 10: 182. 1846.

= Namoideae A.W. Benn., J. Linn. Soc. London, Bot. 11: 266. 1870.

= Wigandieae Horan., Char. Ess. Fam.: 124. 1847. ('Wigandieae [Hydroleaceae]')

*Shrubs* or small trees, or herbaceous (only *Nama*). *Leaves* cauline, alternate, simple. *Inflorescences* terminal or axillary, thyrsoidal, usually of scorpioid monochasia, sometimes congested. *Flowers* 5-merous, bisexual; aestivation of petals imbricate; corolla scales absent; stylodia 2, or style connate 3/4 of length with 2 stigmatic branches; ovary bilocular, placentae narrow, membranaceous or cartilaginous, completely dividing ovary. *Fruit* capsule appearing 2-celled, dehiscing loculicidally or loculicidally and septicidally, with 2 or 4 valves, respectively.

Four genera (*Eriodictyon* Benth., *Nama*, *Turricula* J.F. Macbr., *Wigandia* Kunth) with a total of ca. 75 species in the Americas and the Caribbean, one species in Hawaii.

Namaceae has two major clades, the first clade comprising *Nama*, and a second clade comprising *Wigandia*, *Eriodictyon*, and *Turricula* (Ferguson, 1999; Taylor, 2012). Two species of *Nama* are in the second clade, *N. rothrockii* A. Gray and *N. lobbii* A. Gray, which are successively sister to *Turricula* (Walden, unpublished data). *Nama* was first included in Hydroleaceae along with

*Hydrolea* (Brown, 1818), with later additions by Dumortier (1829), Lindley (1831), Endlicher (1836–1840), and Bentham (1844). Hydroleaceae was later transferred to Hydrophyllaceae (Bentham & Hooker, 1976) and retained there until recent times (e.g., Davenport, 1988). Based on phylogenetic studies (Cosner & al., 1994; Soltis & al., 2000), *Hydrolea* was excluded from Hydrophyllaceae *s.l.* and placed as its own family in Solanales (Takhtajan, 2009; Reveal, 2011, 2012; Reveal & Chase, 2011).

**Wellstediaceae** Novák in S. Prát (ed.), Rostlinopis 9: 530. 1943.

Type genus: *Wellstedia* Balf. f. (1884).

= Wellstedioideae Pilg., Bot. Jahrb. Syst. 46: 558. 1912.

*Small* densely branched herbs or shrublets. *Leaves* cauline, sometimes some basal, often alternate and distichous on branches, simple, indumentum sericeous, acroscopically appressed. *Inflorescences* axillary cymes or reduced to single flowers. *Flowers* tetramerous, calyx deeply divided, corolla deeply divided into four lobes, tube inside with 4 protrusions often fused into a distinct rim, style terminal with two short stigmatic lobes. *Fruit* bivalved capsule; seeds one, rarely two, asymmetrically ovoid in lateral view, strongly laterally compressed, pubescent often with ring of longer hairs near funicular pole, exendospermous.

One genus (*Wellstedia*) and six species disjunctly distributed in arid zones of southwestern and northeastern Africa and Socotra (Thulin & Johansson, 1996; Thulin, 1998). *Wellstedia* is easily recognized by its 4-merous flowers, and unusual flattened, obcordate capsular fruits. *Wellstedia* was first considered as a subfamily of Boraginaceae (Pilger, 1912) and treated as such by most authors (e.g., Thulin & Johansson, 1996; Retief & van Wyk, 2008; Takhtajan, 2009; Reveal, 2011, 2012). However, some authors have also regarded it as its own family (e.g., Merxmüller, 1960; Dahlgren,

1980; Takhtajan, 1987).

**LITERATURE CITED**


**Acevedo-Rodríguez, P. & Strong, M. T.** 2012. *Catalogue of seed plants of the West Indies.* Washington, D.C.: Smithsonian Institution Scholarly Press.

**Al-Shehbaz, I. A. Al-**. 1991. The genera of Boraginaceae in the southeastern United States. *J. Arnold Arbor.* 1: 1–169.

**APG**. 1998. An ordinal classification for the families of flowering plants. *Ann. Missouri Bot. Gard.* 85: 531–553.

**APG II**. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Bot. J. Linn. Soc.* 141: 399–436.

**APG III**. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot. J. Linn. Soc.* 161: 105–121.

**Aubréville, A.** 1959. *La flore forestière de la Côte d'Ivoire.* 2nd edn. Nogent-sur-Marne: Centre Technique Forestier Tropical.

**Backlund, A. & Bremer, K.** 1998. To be or not to be. Principles of classification and monotypic plant families. *Taxon* 47: 391–400.

**Baillon, H. E.** 1891. *Histoire des Plantes*, vol. 10. Paris: Librairie Hachette.

**Bell, C. D., Soltis, D. E. & Soltis P. S.** 2010. The age and diversification of the angiosperms re-revisited. *Amer. J. Bot.* 97: 1296–1303.

**Bentham, G.** 1835. Review of the order of Hydrophylleae. *Trans. Linn. Soc. London* 17: 267–282.

**Bentham, G.** 1844. *The botany of the voyage of H.M.S. Sulphur*. London: Smith, Elder.

**Bentham, G. & Hooker, J. D.** 1876. *Genera Plantarum*, vol. 2. London: Reeve & Co., Williams & Norgate.

**Berchtold, F. & Presl, J. S.** 1820. *O přirozenosti rostlin.* Praha: Krala Wiljma Endersa.

**Brand, A.** 1913. Hydrophyllaceae. Pp. 1–210 in: Engler, A. (ed.), *Das Pflanzenreich* IV.251.

Leipzig: W. Engelmann.

**Bremer, B., Bremer, K., Heidari, N., Erixon, P., Olmstead, R. G., Anderberg, A. A., Källersjö, M. & Barkhordarian, E.** 2002. Phylogenetics of asterids based on 3 coding and 3 non-coding chloroplast DNA markers and the utility of non-coding DNA at higher taxonomic levels. *Molec. Phylogenet. Evol.* 24: 274–301.

**Bremer, K., Friis, E. M. & Bremer B.** 2004. Molecular phylogenetic dating of asterid flowering plants shows early Cretaceous diversification. *Syst. Biol.* 53:496–505.

**Brown, R.** 1810. *Prodromus florae Novae Hollandiae et insulae Van-Diemen*. London: J. Johnson & Co.

**Brown, R.** 1818. *Observations systematical and geographical on the herbarium collected by Professor Christian Smith, in the vicinity of the Congo*. London: W. Bulmer & Co.

**Campos-Ríos, M.G., & Chiang-Cabrera, F.** 2012. El género *Varronia* P. Browne (Cordiaceae, Boraginales) en México. *Polibotanica* 33: 1–32.

**Cecchi, L. & Selvi, F.** 2015a. Hydrophyllaceae. Pp. 1–20 in: L. Peruzzi, L. Cecchi, G. Cristofolini, G. Domina, W. Greuter, E. Nardi, F. M. Raimondo, F. Selvi, & A. Troìa (eds.), *Flora Critica d'Italia*, Florence: Fondazione per la Flora Italiana. http://www.floraditalia.it/

**Cecchi, L. & Selvi, F.** 2015b. Heliotropiaceae. Pp. 1-35 in: L. Peruzzi, L. Cecchi, G. Cristofolini, G. Domina, W. Greuter, E. Nardi, F. M. Raimondo, F. Selvi, & A. Troìa (eds.), *Flora Critica d'Italia*, Florence: Fondazione per la Flora Italiana. http://www.floraditalia.it/

**Chadefaud, M. & Emberger, L.** 1960. *Traité de botanique systématique.* Paris: Masson.

**Cohen, J. I.** 2014. A phylogenetic analysis of morphological and molecular characters of Boraginaceae: Evolutionary relationships, taxonomy, and patterns of character evolution. *Cladistics* 30: 139–169.

**Constance, L.** 1963. Chromosome number and classification in Hydrophyllaceae. *Brittonia* 15: 273–285.

**Conzatti, C. & Smith, L. C.** 1909. *Flora sinóptica mexicana*, vol. 2. 2nd ed. Mexico: Imprenta y fototipia de la secretaria de fomento.

**Cosner, M. E., Jansen, R. K. & Lammers, T. G.** 1994. Phylogenetic relationships in the Campanulales based on *rbcL* sequences. *Plant Syst. Evol.* 190: 79-95.

**Cronquist, A.** 1981. *An integrated system of classification of flowering plants.* New York: Columbia University Press.

**Cronquist, A.** 1988. *The evolution and classification of flowering plants.* New York: New York Botanical Garden.

**Dahlgren, R. M. T.** 1980. A revised system of classification of the angiosperms. *Bot. J. Linn. Soc.* 80: 91–124.

**Davenport, L. J.** 1988. A monograph of *Hydrolea* (Hydrophyllaceae). *Rhodora* 90: 169–208.

**Davidse, G., Sousa Sánchez, M., Knapp, S. & Chiang Cabrera, F. (eds.)**. 2012. *Flora Mesoamericana*, vol. 4(2). St. Louis: Missouri Botanical Garden Press.

**de Candolle, A. L. P. P.** 1845. *Prodromus systematis naturalis regni vegetabilis*, vol. 9. Paris: Fortin, Masson et Sociorum.

**de Candolle, A. L. P. P.** 1846. *Prodromus systematis naturalis regni vegetabilis*, vol. 10. Paris: Masson.

**de Candolle, A.** 1873. *Prodromus systematis naturalis regni vegetabilis*, vol. 17. Paris: Masson.

**Diane, N., Hilger, H. H. & Gottschling, M.** 2002. Transfer cells in the seeds of Boraginales. *Bot. J. Linn. Soc.* 140: 155–164.

**di Fulvio, T. E.** 1978. Sobre la vasculatura floral, embriología y chromosomas de *Ixorhea tschudiana* (Heliotropiaceae). *Kurtziana* 11: 75–105.

**Dumortier, B.-C.** 1829. *Analyse des familles des plantes*. Tournay: J. Casterman.

**Edwards, S.** 1817. *Hydrophyllum canadense*. *Bot. Reg*. 3: 242.

**Endlicher, S.** 1836–1840. *Genera plantarum secundum ordines naturales disposita*. Vienna: F.

Beck.

**Engler, A. (ed).** 1893. *Die natürlichen Pflanzenfamilien*, vol. 4(3a). Leipzig: W. Engelmann.

**Engler, A.** 1898. *Syllabus der Pflanzenfamilien*. 2nd ed. Berlin: Gebrüder Borntraeger.

**Engler, A. (ed).** 1908. *Die natürlichen Pflanzenfamilien*, suppl. 2. Leipzig: W. Engelmann.

**Engler, A. (ed).** 1915. *Die natürlichen Pflanzenfamilien*, suppl. 3. Leipzig: W. Engelmann.

**Ferguson, D. M.** 1999. Phylogenetic analysis and relationships in Hydrophyllaceae based on ndhF sequence data. *Syst. Bot.* 23: 253–268.

**Feuillet, C.** 2013. The typification of *Cordia flavescens* Aubl., the transfer of *Firensia* Scop. from *Cordia* L. (Cordiaceae, Boraginales) to the synonymy of *Ocotea* Aubl. (Lauraceae), and the identity of the species of *Firensia*. *PhytoKeys* 23: 19–24.

**Gasparino, E. C., & Vitorino da Cruz Barros, M. A.** 2009. Palinotaxonomia das espécies de Cordiaceae (Boraginales) ocorrentes no Estado de São Paulo. *Revista Brasil. Bot.* 32: 33–55.

**Gilg, E.** 1908. Die systematische Stellung der Gattung *Hoplestigma* und einiger anderer zweifelhafter Gattungen. *Bot. Jahrb. Syst.* 40: 76–84.

**Gottschling, M., Hilger, H. H., Wolf, M. & Diane, N.** 2001. Secondary structure of the ITS1 transcript and its application in a reconstruction of the phylogeny of Boraginales. *Plant Biol.* 3: 629–636.

**Gottschling, M., Miller, J. S., Weigend, M. & Hilger, H. H.** 2005. Congruence of a phylogeny of Cordiaceae (Boraginales) inferred from ITS1 sequence data with morphology, ecology, and biogeography. *Ann. Missouri Bot. Gard.* 92: 425–437.

**Gottschling, M., Luebert, F., Hilger, H. H. & Miller, J. S.** 2014a. Molecular delimitations in the Ehretiaceae (Boraginales). *Molec. Phylogenet. Evol.* 72: 1–6.

**Gottschling, M., Nagelmüller, S. & Hilger, H. H.** 2014b. Generative ontogeny in *Tiquilia* (Ehretiaceae: Boraginales) and phylogenetic implications. *Biol. J. Linn. Soc.* 112:

520–534.

**Gray, A.** 1862. Characters of new or obscure species of plants of monopetalous orders in the collection of the United States South Pacific Exploring Expedition under Captain Charles Wilkes, U. S. N. with occasional remarks, &c. *Proc. Amer. Acad. Arts Sci.* 5: 321–352.

**Gray, A.** 1875. A conspectus of the North American Hydrophyllaceæ. *Proc. Amer. Acad. Arts Sci.* 10: 312–332.

**Gürke, M.** 1893. Boraginaceae (Asperifoliaceae). Pp. 71–131 in: Engler, A. (ed.), *Die natürlichen Pflanzenfamilien*, vol. 4(3a). Leipzig: W. Engelmann.

**Hepper, F. N.** 1963. Hoplestigmataceae. Pp. 15–16 in: F. N. Hepper (eds.), *Flora of West Tropical Africa*, vol. 2. London: Crown Agents for Oversea Governments and Administrations.

**Heywood, V. H.** 2007. *Flowering plant families of the world.* Kew: Royal Botanic Gardens.

**Hilger, H. H.** 1985. Ontogenie, Morphologie und systematische Bedeutung geflügelter und glochidientragender Cynoglosseae- und Eritrichieae-Früchte (Boraginaceae). *Bot. Jahrb. Syst.* 105: 323–378.

**Hilger, H. H.** 1987. Flower and fruit development in *Wigandia caracasana* (Hydrophyllaceae). *Amer. J. Bot.* 74: 250–259.

**Hilger, H. H.** 2014. Ontogeny, morphology, and systematic significance of glochidiate and winged fruits of Cynoglosseae and Eritrichieae (Boraginaceae). *Plant Diversity Evol.* 131: 167–214.

**Hilger, H. H. & Diane, N.** 2003. A systematic analysis of Heliotropiaceae (Boraginales) based on trnL and ITS1 sequence data. *Bot. Jahrb. Syst.* 125: 19–51.

**Hilger, H. H. & Zippel, E.** 2001. “Studies in the Boraginaceae”: An index to the publications of Ivan M. Johnston dealing with the Borage family. *Haussknechtia Beiheft* 11: 1–151.

**Hilger, H. H., Gottschling, M., Selvi, F., Bigazzi, M., Långström, E., Zippel, E., Diane, N. & Weigend, M.** 2005. The Euro+Med treatment of Boraginaceae in Willdenowia 34 – a response. *Willdenowia* 35: 43–48.

**Hofmann, M.** 1999. Flower and fruit development in the genus *Phacelia* (Phacelieae, Hydrophyllaceae): Characters of systematic value. *Syst. Geogr. Plants* 68: 203–212.

**Hofmann, M.** 2004. Hydrophyllaceae. Pp. 190–191 in: N. Smith, S. A. Mori, A. Henderson, D. W. Stevenson, & S. V. Heald (eds.), *Flowering plants of the Neotropics*, Princeton: Princeton University Press.

**Hooker, W. J.** 1844. *Icones plantarum*, vol. 7. London: Hippolyte Baillière.

**Howard, R. A.** 1989. Boraginaceae Pp. 188–211 in: Howard, R.A. (ed.), *Flora of the Lesser Antilles*, vol. 6. Jamaica Plain, Massachusetts: Arnold Arboretum, Harvard University.

**Hutchinson, J.** 1959. *The families of flowering plants: Dicotyledons.* Oxford: Clarendon Press.

**Irimia, R.-E., Pérez-Escobar, O. A. & Gottschling, M.** 2015. Strong biogeographic signal in the phylogenetic relationships of *Rochefortia* Sw. (Ehretiaceae, Boraginales). *Plant Syst. Evol.* 301: 1509–1516.

**Johnston, I. M.** 1924. A tentative classification of the South American Coldenias. *Contr. Gray Herb.* 70: 55–61.

**Judd, W. S., Campbell, S., Kellogg, E. A., Stevens, P. F. & Donoghue, M. J.** 2008. *Plant systematics: A phylogenetic approach*. 3rd Ed. Massachusetts: Sinauer Associates.

**Jussieu, A. L. de.** 1789. *Genera plantarum secundum ordines naturales disposita*. Paris: Herissant & Barrois.

**Kadereit, J. W., Körner, C., Kost, B. & Sonnewald, U.** 2014. *Strasburger − Lehrbuch der Pflanzenwissenschaften.* Berlin, Heidelberg: Springer.

**Kubitzki, K., Kadereit, J. W. & Bittrich, V. (eds.)**. in press. *The families and genera of vascular*

*plants.* vol. XVI [including Boraginales]. Berlin: Springer-Verlag.

**La Llave, P. & Lexarza, J. J. M.** 1824. *Novorum vegetabilium descriptiones*, vol. 1. Mexico: Martino Rivera.

**Lindley, J.** 1831. *An introduction to the natural system of botany*. New York: G. & C. & H. Carvill.

**Liu, B.,Ye, J., Liu, S., Wang, Y., Yang, Y., Lai, Y., Zeng, G. & Lin, Q.** 2015. Families and genera of Chinese angiosperms: A synoptic classification based on APG III (in Chinese). *Biodivers. Sci.* 23: 225–231.

**Liogier, H. A.** 1994. *La flora de la Española.* San Juan: Editorial de la Universidad de Puerto Rico.

**Luebert, F.** 2013. A revision of *Heliotropium* sect. *Cochranea* (Heliotropiaceae). *Kew Bull.* 68: 1–54.

**Luebert, F. & Hilger, H. H.** 2014. Typification of *Heliotropium* and *Tournefortia* (Heliotropiaceae) species described by Ruiz and Pavón. *Anales J. Bot. Madrid* 71: e012.

**Luebert, F. & Wen, J.** 2008. Phylogenetic analysis and evolutionary diversification of *Heliotropium* sect. *Cochranea* (Heliotropiaceae) in the Atacama Desert. *Syst. Bot.* 33: 390–402.

**Luebert, F., Weigend, M. & Hilger, H. H.** 2010. Epitypification of *Heliotropium arborescens* L. (Heliotropiaceae). *Taxon* 59: 1263–1266.

**Luebert, F., Hilger, H. H. & Weigend, M.** 2011a. Diversification in the Andes: Age and origins of South American *Heliotropium* lineages (Heliotropiaceae, Boraginales). *Molec. Phylogenet. Evol.* 61: 90–102.

**Luebert, F., Brokamp, G., Wen, J., Weigend, M. & Hilger, H. H.** 2011b. Phylogenetic relationships and morphological diversity in Neotropical *Heliotropium* (Heliotropiaceae). *Taxon* 60: 663–680.

**Mabberley, D. J.** 2008. *Mabberley's plant book. A portable dictionary of plants, their classification and uses.* Cambridge: Cambridge University Press.

**Machado, I.C., Lopes, A.V., & Sazima, M.** 2010. Contrasting bee pollination in two co-occurring distylic species of *Cordia* (Cordiaceae, Boraginales) in the Brazilian semi-arid Caatinga: Generalist in *C. globosa* vs. specialist in *C. leucocephala*. *An. Acad. Bras. Cienc.* 82: 881–891.

**Melchior, H.** 1964a. Hydrophyllaceae. Pp. 430–431 in: Melchior, H. (ed.), *A. Engler's Syllabus der Pflanzenfamilien*, vol. 2. Berlin: Gebrüder Borntraeger.

**Melchior, H.** 1964b. Boraginaceae. Pp. 431–434 in: Melchior, H. (ed.), *A. Engler's Syllabus der Pflanzenfamilien*, vol. 2. Berlin: Gebrüder Borntraeger.

**Melchior, H.** 1964c. Lennoaceae. Pp. 434–434 in: Melchior, H. (ed.), *A. Engler's Syllabus der Pflanzenfamilien*, vol. 2. Berlin: Gebrüder Borntraeger.

**Melo, J. I. M. de, Alves, M., & Semir, J.** 2009. Padrões de distribuição geográfica das espécies de *Euploca* e *Heliotropium* (Heliotropiaceae) no Brasil. *Rodriguésia* 60: 1025–1036.

**Melo, J. I. M. de & Semir, J.** 2010. Taxonomia do gênero *Euploca* Nutt. (Heliotropiaceae) no Brasil. *Acta Bot. Brasil.* 24: 111–132.

**Merxmüller, H.** 1960. Wellstediaceae. *Mitt. Bot. Staatssamml. München* 3: 619–622.

**Milet-Pinheiro, P., & Schlindwein, C.** 2010. Mutual reproductive dependence of distylic *Cordia leucocephala* (Cordiaceae) and oligolectic *Ceblurgus longipalpis* (Halictidae, Rophitinae) in the Caatinga. *Ann. Bot.* 106: 17–27.

**Miller, J.S.** 2012. New Boraginales from tropical America 7: A new species of *Cordia* from Bolivia and nomenclatural notes on Neotropical Cordiaceae. *Brittonia* 64:359–362.

**Miller, J. S.** 2013a. A revision of *Cordia* section *Gerascanthus* (Boraginales: Cordiaceae). *J. Bot. Res. Inst. Texas* 7: 55–83.

**Miller, J. S.** 2013b. New Boraginales from tropical America 8: Nomenclatural notes on *Varronia* (Cordiaceae: Boraginales). *Brittonia* 65: 342–344.

**Miller, J. S. & Gottschling, M.** 2007. Generic classification in the Cordiaceae (Boraginales):

Resurrection of the genus *Varronia* R. Br. *Taxon* 56: 163–169.

**Moore, M. J. & Jansen, R. K.** 2006. Molecular evidence for the age, origin, and evolutionary history of the American desert plant genus *Tiquilia* (Boraginaceae). *Molec. Phylogenet. Evol.* 39: 668–687.

**Moore, M. J., Soltis, P. S., Bell, C. D., Burleigh, J. G. & Soltis, D. E.** 2010. Phylogenetic analysis of 83 plastid genes further resolves the early diversification of Eudicots. *Proc. Natl. Acad. Sci. U.S.A.* 107: 4623–4628.

**Naumann, J., Salomo, K., Der, J. P., Wafula, E. K., Bolin, J. F., Maass, E., Frenzke, L., Samain, M.-S., Neinhuis, C., dePamphilis, C. W. & Wanke, S.** 2013. Single-copy nuclear genes place haustorial Hydnoraceae within Piperales and reveal a Cretaceous origin of multiple parasitic angiosperm lineages. *PLoS ONE* 8: e79204.

**Nazaire, M. & Hufford, L.** 2012. A broad phylogenetic analysis of Boraginaceae: Implications for the relationships of *Mertensia*. *Syst. Bot.* 37: 758–783.

**Nazaire, M., Wang, X.-Q. & Hufford, L.** 2014. Geographic origins and patterns of radiation of *Mertensia* (Boraginaceae). *Amer. J. Bot.* 101: 104–118.

**Olmstead, R. G., Bremer, B., Scott, K. M. & Palmer, J. D.** 1993. A parsimony analysis of the Asteridae sensu lato based on rbcL sequences. *Ann. Missouri Bot. Gard.* 80: 700–722.

**Peter, A.** 1893. Hydrophyllaceae. Pp. 54–71 in: Engler, A. (ed.), *Die natürlichen Pflanzenfamilien*, vol. 4(3a). Leipzig: W. Engelmann.

**Pierre, L.** 1899. Observations sur quelques Bixacées (suite). *Bull. Mens. Soc. Linn. Paris* 2: 113–119.

**Pilger, R.** 1912. Die Gattung *Wellstedia* in Südwestafrika. *Bot. Jahrb. Syst.* 46: 558–561.

**Pilger, R. & Krause, K.** 1915. *Die Natürlichen Pflanzenfamilien*, Ergänzungsheft 3. Leipzig: W. Engelmann.

**Refulio-Rodríguez, N. F. & Olmstead, R. G.** 2014. Phylogeny of Lamiidae. *Amer. J. Bot.* 101: 287–299.

**Retief, E. & van Wyk, A. E.** 2005. Boraginaceae. Codonoideae, a new subfamily based on *Codon*. *Bothalia* 35: 78–80.

**Retief, E. & van Wyk, A. E.** 2008. The genus *Wellstedia* (Boraginaceae: Wellstedioideae) in southern Africa. *Bothalia* 38: 57–63.

**Reveal, J. L.** 2011. Summary of recent systems of angiosperm classification. *Kew Bull.* 66: 5–48.

**Reveal, J. L.** 2012. An outline of a classification scheme for extant flowering plants. *Phytoneuron* 2012: 1–221.

**Reveal, J. L. & Chase, M. W.** 2011. APG III: Bibliographical information and synonymy of Magnoliidae. *Phytotaxa* 19: 71–134.

**Richardson, A.** 1976. Reinstatement of the genus *Tiquilia* (Boraginaceae: Ehretioideae) and descriptions of four new species. *Sida* 6: 235-240.

**Ricketson, J. M.** 2012. Hydrophyllaceae. Pp. 291–294 in: G. Davidse, M. Sousa Sánchez, S. Knapp, & F. Chiang Cabrera (eds.), *Flora Mesoamericana*, vol. 4(2). St. Louis: Missouri Botanical Garden Press.

**Savolainen, V., Fay, M. F., Albach, D. C., Backlund, A., van der Bank, M., Cameron, K. M., Johnson, S. A., Lledó, M. D., Pintaud, J.-C., Powell, M., Sheahan, M. C., Soltis, D. E., Soltis, P. S., Weston, P., Whitten, W. M., Wurdack, K. J. & Chase, M. W.** 2000. Phylogeny of the Eudicots: A nearly complete familial analysis based on rbcL gene sequences. *Kew Bull.* 55: 257–309.

**Schrader, H. A.** 1819. De Asperifoliis Linnei Commentatio Recitata. *Commentat. Soc. Regiae Sci. Gott. Recent*. 4: 175–196.

**Simpson, M. G.** 2010. *Plant systematics.* 2nd edn. Burlington: Academic Press.

**Sklenář, P., Luteyn, J. L., Ulloa Ulloa, C., Jørgensen, P. M. & Dillon, M. O.** 2005. Flora

genérica des los Páramos: Guía ilustrada de las plantas vasculares. *Mem. New York Bot. Gard.* 92: 1–499.

**Solms-Laubach, H.** 1870. *Die Familie der Lennoaceen*. Halle: H.S. Schmidt.

**Soltis, D. E., Soltis, P. S., Chase, M. W., Mort, M. E., Albach, D. C., Zanis, M., Savolainen, V., Hahn, W. H., Hoot, S. B., Fay, M. F., Ax$^{TEL}$l, M., Swensen, S. M., Prince, L. M., Kress, W. J., Nixon, K. C. & Farris, J. S.** 2000. Angiosperm phylogeny inferred from 18S rDNA, rbcL, and atpB sequences. *Bot. J. Linn. Soc.* 133: 381–461.

**Soltis, D. E., Smith, S. A., Cellinese, N., Wurdack, K. J., Tank, D. C., Brockington, S. F., Refulio-Rodriguez, N. F., Walker, J. B., Moore, M. J., Carlsward, B. S., Bell, C. D., Latvis, M., Crawley, S., Black, C., Diouf, D., Zhenxiang, X., Rushworth, C. A., Gitzendanner, M. A., Sytsma, K. J., Qiu, Y.-L., Hilu, K. W., Davis, C. C., Sanderson, M. J., Beaman, R. S., Olmstead, R. G., Judd, W. S., Donoghue, M. J. & Soltis, P. S.** 2011. Angiosperm phylogeny: 17 genes, 640 taxa. *Amer. J. Bot.* 98: 704–730.

**Stapf, M. N. S.** 2009. Neotropical Boraginaceae. in: W. Milliken, B. Klitgård, & A. Baracat (eds.), *Neotropikey - Interactive key and information resources for flowering plants of the Neotropics*, Kew: Royal Botanic Gardens. http://www.kew.org/science/tropamerica/neotropikey/families/Boraginaceae.htm (accessed 7 Sep 2015).

**Stapf, M. N. S. de & Silva, T. dos S.** 2013a. Four new species of genus *Cordia* (Cordiaceae, Boraginales) from Brazil. *Brittonia* 65: 191–199.

**Stapf, M. N. S. de & Silva, T. dos S.** 2013b. Typifications in *Cordia* (Cordiaceae), with an assessment of the status of *Cordia blanchetii*. *Kew Bull.* 68: 355–359.

**Stapf, M. N. S., Ranga, N. T. & Silva, T. R. S.** 2010. A new species of *Cordia* (Cordiaceae, Boraginales) from Brazil. *Novon* 20: 212–214.

**Stevens, P. F.** 2001 onwards. Angiosperm Phylogeny Website. Version 9, June 2008 [and more or less continuously updated since]. http://www.mobot.org/mobot/research/apweb/welcome.html (accessed 16 Oct 2015).

**Stull, G. W., de Stefano, R. D., Soltis, D. E., Soltis, P. S.** in press. Resolving basal lamiid phylogeny and the circumscription of Icacinaceae with a plastome-scale dataset. *Amer. J. Bot.*

**Stutzman, J. K., Lickey, E. B., Weeks, A., & McMullen, C. K.** 2012. A taxonomic study of the Galapagos endemic *Varronia* (Cordiaceae) species with nomenclatural notes. *J. Bot. Res. Inst. Texas* 6: 75–99.

**Sullivan, G. A.** 2001. Hydrophyllaceae. Pp. 1154–1156 in: W. D. Stevens, C. Ulloa Ulloa, A. Pool, & M. Montiel (eds.), *Flora de Nicaragua*, vol. 2. St. Louis, Missouri: Missouri Botanical Garden.

**Svensson, H. G.** 1925. Zur Embryologie der Hydrophyllaceen, Borraginaceen und Heliotropiaceen mit besonderer Rücksicht auf die Endospermbildung. *Uppsala Univ. Årsskr.* 2: 3–175.

**Takhtajan, A. L.** 1980. Outline of the classification of flowering plants (Magnoliophyta). *Bot. Rev* 46: 225–359.

**Takhtajan, A.** 1987. *Systema Magnoliophytorum* (in Russian). Leningrad: Oficina Editoria NAUKA.

**Takhtajan, A.** 1997. *Diversity and classification of flowering plants.* New York: Columbia University Press.

**Takhtajan, A.** 2009. *Flowering Plants.* 2nd edn. New York: Springer.

**Taylor, S. E.** 2012. *Molecular systematics and the origins of gypsophily in* Nama *L. (Boraginaceae)*. Dissertation, University of Texas, Austin, Texas, U.S.A.

**Thorne, R. F.** 1992. Classification and geography of the flowering plants. *Bot. Rev* 58: 225–327.

**Thorne, R. F. & Reveal, J. L.** 2007. An updated classification of the class Magnoliopsida ("Angiospermae"). *Bot. Rev.* 73: 67–181.

**Thulin, M.** 1998. A new species of *Wellstedia* (Boraginaceae) from Somalia. *Nordic J. Bot.* 18: 663–665.

**Thulin, M. & Johansson, N. B.** 1996. Taxonomy and biogeography of the anomalous genus *Wellstedia*. Pp. 73–86 in: L. J. G. van der Maesen, X. M. van der Burgt, & J. M. van Madenbach de Rooy (eds.), *The biodiversity of African plants*, Dordrecht: Kluwer Academic Publishers.

**Tölke, E. E. A. D., Melo, J. I. M. de., Carmello-Guerreiro, S. M. & Lacchia, A. P. S.** 2013. Leaf anatomy with emphasis on separation of two species of *Varronia* P.Br. (Cordiaceae) of the Brazilian semi-arid region. *Braz. J. Bot* 36: 189–201.

**Véliz Pérez, M. E., Campos-Ríos, M. G., & Miller, J. S.** 2009. Especie nueva del género *Bourreria* (Ehretiaceae, Boraginales) de Mesoamérica. *Brittonia* 61: 237–240.

**Vences, M., Guayasamin, J. M., Miralles, A. & de la Riva, I.** 2013. To name or not to name: Criteria to promote economy of change in Linnaean classification schemes. *Zootaxa* 3636: 201–244.

**Venkateswarlu, J., & Atchutaramanurti, B.** 1955. Embryological Studies in Boraginaceæ. I. — *Coldenia procumbens* Linn. *J. Indian Bot. Soc.* 34: 235–247.

**Wagenitz, G.** 1964. Ebenales. Pp. 396–403 in: Melchior, H. (ed.), *A. Engler's Syllabus der Pflanzenfamilien*, vol. 2. Berlin: Gebrüder Borntraeger.

**Walden, G. K.** 2010. *Phylogeny of infrageneric relationships within* Phacelia *(Boraginaceae) inferred from chloroplast sequence data*. MSc Thesis, San Francisco State University, San Francisco, California, U.S.A.

**Walden, G. K.** 2015. *Systematics of* Emmenanthe, Eucrypta, *and* Phacelia *sect.* Ramosissimae *(Hydrophyllaceae; Boraginales)*. Dissertation, University of California, Berkeley,

San Francisco, California, U.S.A.

**Walden, G. K. & Patterson, R.** 2012. Nomenclature of subdivisions within *Phacelia* (Boraginaceae: Hydrophylloideae). *Madroño* 59: 211–222.

**Walden, G. K., Garrison, L. M., Spicer, G. S., Cipriano, F. W. & Patterson, R.** 2014. Phylogenies and chromosome evolution of *Phacelia* (Boraginaceae: Hydrophylloideae) inferred from nuclear ribosomal and chloroplast sequence data. *Madroño* 61: 16–47.

**Watson, L. & Dallwitz, M. J.** 1992 onwards. The families of flowering plants: descriptions, illustrations, identification, and information retrieval. http://delta-intkey.com/angio/ (accessed 16 Oct 2015).

**Weeks, A., Baird, K. E. & McMullen, C. K.** 2010. Origin and evolution of endemic Galápagos *Varronia* species (Cordiaceae). *Molec. Phylogenet. Evol.* 57: 948–954.

**Weigend, M. & Hilger, H. H.** 2010. Codonaceae—a newly required family name in Boraginales. *Phytotaxa* 10: 26–30.

**Weigend, M., Luebert, F., Selvi, F., Brokamp, G. & Hilger, H. H.** 2013. Multiple origins for Hound's tongues (*Cynoglossum* L.) and Navel seeds (*Omphalodes* Mill.) – The phylogeny of the borage family (Boraginaceae s.str.). *Molec. Phylogenet. Evol.* 68: 604–618.

**Weigend, M., Luebert, F., Gottschling, M., Couvreur, T. L. P., Hilger, H. H. & Miller, J. S.** 2014. From capsules to nutlets – Phylogenetic relationships in the Boraginales. *Cladistics* 30: 508–518.

**Wikström, N., Savolainen, V. & Chase, M. W.** 2001. Evolution of the angiosperms: Calibrating the family tree. *Proc. Roy. Soc. B* 268: 2211–2220.

**Wikström, N., Kainulainen, K., Razafimandimbison, S. G., Smedmark, J. E. E. & Bremer, B.** 2015. A revised time tree of the Asterids: Establishing a temporal framework for

evolutionary studies of the coffee family (Rubiaceae). *PLoS ONE* 10: e0126690.

**Yatskievych, G.** 2001. Lennoaceae. Pp. 1213–1214 in: W. D. Stevens, C. Ulloa Ulloa, A. Pool, & M. Montiel (eds.), *Flora de Nicaragua*, vol. 2. St. Louis: Missouri Botanical Garden.

**Yatskievych, G.** 2012. Lennoaceae. Pp. 309–310 in: G. Davidse, M. Sousa Sánchez, S. Knapp, & F. Chiang Cabrera (eds.), *Flora Mesoamericana*, vol. 4(2). St. Louis: Missouri Botanical Garden Press.

**Yatskievych, G. & Mason, C. T.** 1986. A revision of the Lennoaceae. *Syst. Bot.* 11: 531–548.

**Table 1.** Comparative morphological characterization of the families of Boraginales recognized here [Gürke (1893), Peter (1893), Gilg (1908), Venkateswarlu & Atchutaramanurti (1955), Hilger (1985, 1987, 2014), Yatskievych & Mason (1986), Al-Shehbaz (1991), Thulin & Johansson (1996), Hofmann (1999), Diane & al. (2002), Gottschling & al. (2005, 2014b), Weigend & Hilger (2010)].

| Family | Habit | Perianth merosity | Stigmatic branches | Style insertion | Stigma form | Fruit type | Fruit dehiscence | Ovary locules | Placentation | Ovules per locule | Seeds per fruit | Testa transfer cells | Endosperm |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Boraginaceae *s.str.* | herbs and shrubs | 5 | (1) | gynobasic | capitate to bilobate | nutlet | eremocarpic | 4 | axile | 1 | 4 | absent | scanty or absent |
| Codonaceae | shrubs | 10–20 | 2 | apical | punctiform | capsule | loculicidal | 2 | axile | many | many | absent | copious |
| Coldeniaceae | herbs | 4 | 2 | apical | capitate | nutlet | schizocarpic | 2 | axile | 2 | 4 | present | scanty |
| Cordiaceae | trees to shrubs | (4)5 or up to 10 | 4 | apical | capitate to linear | drupe, rarely nut | indehiscent | 4 | axile | 1 | 4 or less | present | scanty or absent |
| Ehretiaceae | trees to shrubs | 5 | (1), 2[1] | apical[2] | capitate | drupe, rarely nutlet | indehiscent or schizocarpic | 1–4 | axile | 1–4 | 4 or less | present | copious |
| Heliotropiaceae | herbs and trees | 5 | (1) | apical | conically elongated | nutlet or drupe | indehiscent or schizocarpic | 1–4 | axile | 1 | 4 | present | scanty |
| Hoplestigmataceae | trees | 10–15 | 2 | apical | capitate | drupe | indehiscent | 1 | (intrusive) parietal | 4 | 4 | present | scanty |
| Hydrophyllaceae | herbs | (4)5 | 2[1] | apical | capitate | capsule | loculicidal | 1 or 2 (secondary subdivision) | (intrusive) parietal | 2 to many | 1 to many | absent | copious |
| Lennoaceae | herbaceous parasites | (4)5–9(10) | (1) | apical | capitate | nut | circumscissile -schizocarpic | 10–28 | axile, appearing free central in fruit | 2 | 4 to many | present | copious |
| Namaceae | shrubs | 5 | 2[1] | apical | bilobate | capsule | loculicidal or septicidal | 2 | (intrusive) parietal | 2 to many | 2 to many | absent | copious |
| Wellstediaceae | shrubs | 4 | (1) | apical | bilobate | capsule | septicidal | 2 | apical | 1–2 | 2–4 | absent | absent |

[1] sometimes free to base = 2 stylodia; [2] sometimes anacrostylous in species of *Tiquilia*.

**Fig. 1**. Major clades of the Boraginales. One clade with + is well-supported (Bayesian posterior probability > 0.95, maximum likelihood bootstrap value > 80) only in Refulio-Rodríguez & Olmstead (2014). One clade with # is moderately supported (Bayesian posterior probability = 0.9, maximum likelihood bootstrap value = 60) only in Weigend & al. (2014) and is not present in Refulio-Rodríguez & Olmstead (2014). Clades with * indicate well-supported groups (Bayesian posterior probabilities > 0.95, maximum likelihood bootstrap values > 80) in the phylogenies of Refulio-Rodríguez & Olmstead (2014) and Weigend & al. (2014). Putative apomorphic character states for major clades are indicated.

**Fig. 2.** Flower and fruit development in *Cynoglossum australe* R. Br. (A–F, Boraginaceae s.str., *Joßberger 062*, BONN) and *Heliotropium europaeum* L. (G–L, Heliotropiaceae, *Lobin & Weigend 233-14*, BONN). The species depicted correspond to the two major clades of Boraginales, where nutlets evolved independently. In the Boraginaceae s.str., the four nutlets become distinct very early in the ontogeny (A), with the style gynobasically inserted (A–C); fruit develops into four nutlets (D–F). In Heliotropiaceae, the ovary is essentially undivided at anthesis (G), with the style apically inserted on the ovary (H–K); nutlets become distinct once fruit maturation starts (J–K); mature fruit may overtop the base of the style (L). All scale bars = 200 μm. Material cultivated at the Botanical Garden in Bonn (accession numbers 37351 and 35823). Pictures by Hans Jürgen Ensikat.

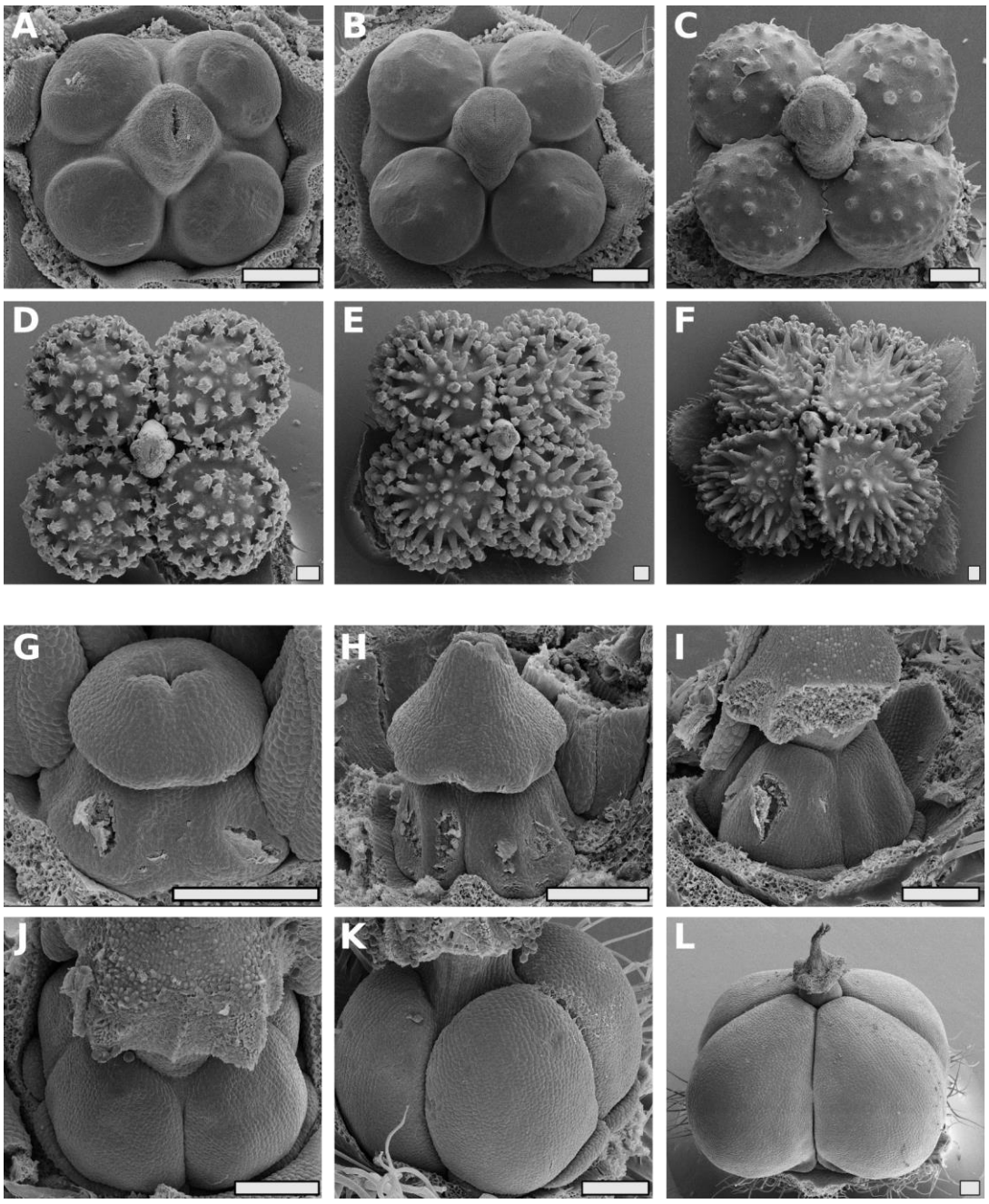


FIG. 1

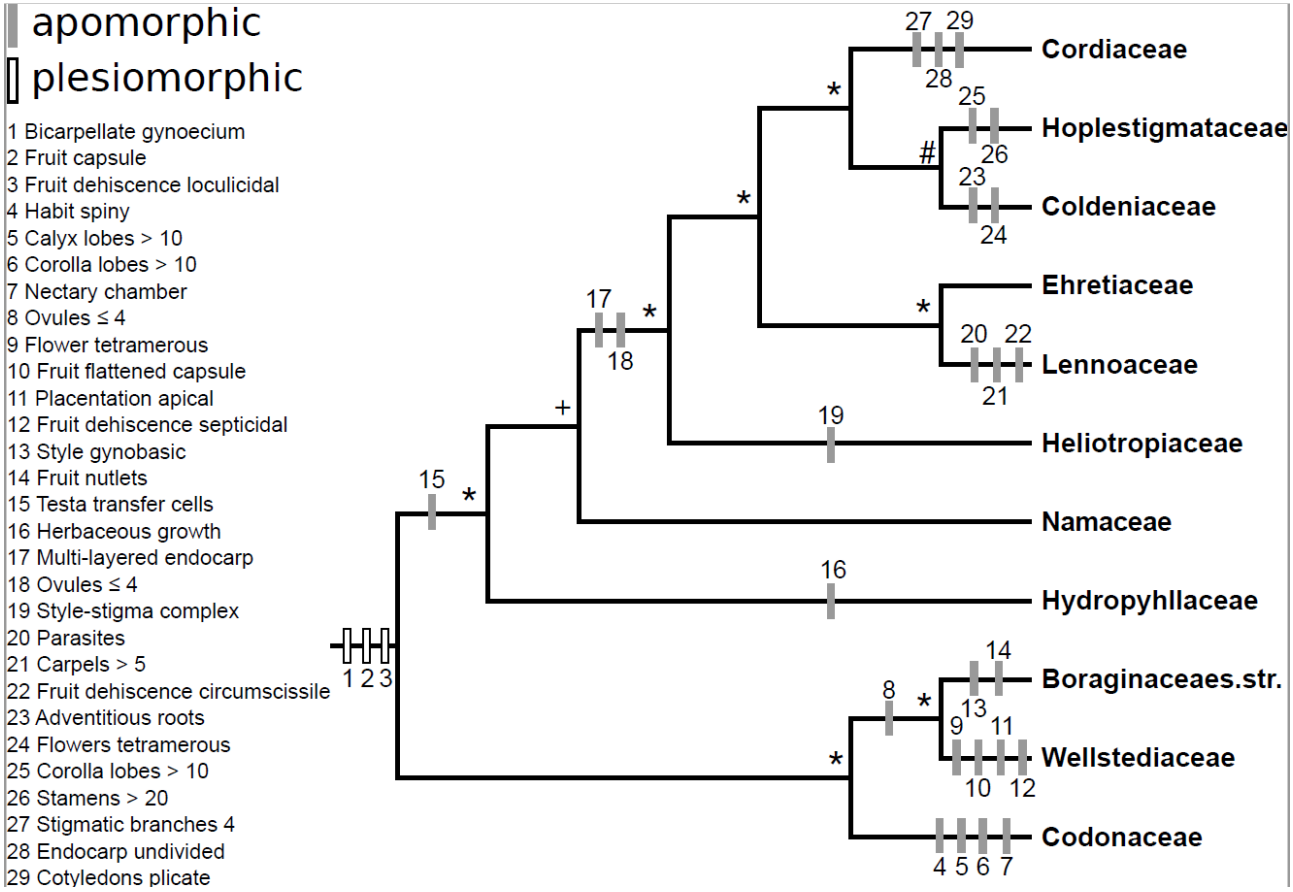
apomorphic
plesiomorphic
1 Bicarpellate gynoecium
2 Fruit capsule
3 Fruit dehiscence loculicidal
4 Habit spiny
5 Calyx lobes > 10
6 Corolla lobes > 10
7 Nectary chamber
8 Ovules ≤ 4
9 Flower tetramerous
10 Fruit flattened capsule
11 Placentation apical
12 Fruit dehiscence septicidal
13 Style gynobasic
14 Fruit nutlets
15 Testa transfer cells
16 Herbaceous growth
17 Multi-layered endocarp
18 Ovules ≤ 4
19 Style-stigma complex
20 Parasites
21 Carpels > 5
22 Fruit dehiscence circumscissile
23 Adventitious roots
24 Flowers tetramerous
25 Corolla lobes > 10
26 Stamens > 20
27 Stigmatic branches 4
28 Endocarp undivided
29 Cotyledons plicate
Cordiaceae
Hoplestigmataceae
Coldeniaceae
Ehretiaceae
Lennoaceae
Heliotropiaceae
Namaceae
Hydropyhllaceae
Boraginaceaes.str.
Wellstediaceae
Codonaceae

FIG. 2

Appendix 1. Systematics of Boraginales according to different authors.

| **This work** | **Jussieu (1789)** | **Berchtold & Presl (1820)** | **Dumortier (1829)** | **Lindley (1830)** | **Endlicher (1836)** | **de Candolle (1845, 1846, 1873 )** |
|---|---|---|---|---|---|---|
| Codonaceae | ? | ? | - | - | Hydroleaceae (Tubiflorae) | ?Hydroleaceae |
| Wellstediaceae | - | - | - | - | - | - |
| Boraginaceae | Boraginaceae II, III, IV | Boraginales | Boraginaceae – Lithospermeae, Boraginaceae – Cerintheae, Boraginaceae – Echieae (Boraginales) | Boraginaceae | Asperifoliaceae – Borageineae (Nuculiferae) | Boraginaceae – Borageineae, Cerintheae, Echieae, Lithospermeae, Craniospermeae, Anchuseae, Cynoglosseae |
| Hydrophyllaceae | Boraginaceae II | Ellisiales | Hydrophyllaceae (Boraginales) | Hydrophyllaceae | Hydrophyllaceae (Tubiflorae) | Hydrophyllaceae |
| Namaceae | Convolvulaceae | Hydroleales | Hydroleaceae (Convolvulales) | Hydroleaceae | Hydroleaceae (Tubiflorae) | Hydroleaceae – Nameae |
| Heliotropiaceae | Boraginaceae I, II, III | Boraginales | Boraginaceae – Heliotropieae (Boraginales) | Heliotropiaceae / Ehretiaceae | Asperifoliaceae – Ehretieae (Nuculiferae) | Boraginaceae – Ehretieae, Boraginaceae – Heliotropieae |
| Ehretiaceae | Boraginaceae I | Boraginales | Cordiaceae – Ehretieae (Boraginales) | Ehretiaceae | Asperifoliaceae – Ehretieae (Nuculiferae) | Boraginaceae – Ehretieae |
| Lennoaceae | - | - | - | - | dubiae sedis | Lennoaceae |
| Coldeniaceae | Boraginaceae III | Boraginales | Boraginaceae – Heliotropieae (Boraginales) | ? | Asperifoliaceae – Ehretieae (Nuculiferae) | Boraginaceae – Heliotropieae |
| Hoplestigmataceae | - | - | - | - | - | - |
| Cordiaceae | Boraginaceae I | Sebestanales | Cordiaceae – Cordieae (Boraginales) | Cordiaceae | Cordiaceae (Nuculiferae) | Boraginaceae – Cordieae |
| [Hydroleaceae (Solanales)] | Convolvulaceae | Hydroleales | Hydroleaceae (Convolvulales) | Hydroleaceae | Hydroleaceae (Tubiflorae) | Hydroleaceae – Hydroleae |
| [Tetrachondraceae (Lamiales)] | | | | | | |

Appendix 1. (continued)

| This work | Bentham & Hooker (1876) | Baillon (1891) | Engler (1898) | Engler (1893, 1908, 1915) | Chadefaud & Emberger (1960) | Takhtajan (1980) |
|---|---|---|---|---|---|---|
| Codonaceae | Hydrophyllaceae – Phacelieae (Polemoniales) | Boraginaceae – Phacelieae | Hydrophyllaceae – Phacelieae (Boraginineae) | Hydrophyllaceae – Phacelieae | Hydrophyllaceae (Tubiflorales) | Hydrophyllaceae (Boraginineae – Polemoniales) |
| Wellstediaceae | | | | Boraginaceae – Wellstedioideae | Boraginaceae – Wellstedioideae (Tubiflorales) | Boraginaceae (Boraginineae – Polemoniales) |
| Boraginaceae | Boraginaceae – Boragineae (Polemoniales) | Boraginaceae – Boragineae, Boraginaceae – Echieae, Boraginaceae – Harpagonelleae | Boraginaceae – Boraginoideae (Boraginineae) | Boraginaceae – Boraginoideae | Boraginaceae – Boraginoideae (Tubiflorales) | Boraginaceae (Boraginineae – Polemoniales) |
| Hydrophyllaceae | Hydrophyllaceae – Hydrophylleae, Hydrophyllaceae – Phacelieae (Polemoniales) | Boraginaceae – Hydrophylleae, Boraginaceae – Phacelieae | Hydrophyllaceae – Hydrophylleae, Hydrophyllaceae – Phacelieae (Boraginineae) | Hydrophyllaceae – Hydrophylleae, Hydrophyllaceae – Phacelieae | Hydrophyllaceae (Tubiflorales) | Hydrophyllaceae (Boraginineae – Polemoniales) |
| Namaceae | Hydrophyllaceae – Nameae (Polemoniales) | Boraginaceae – Phacelieae | Hydrophyllaceae – Nameae (Boraginineae) | Hydrophyllaceae – Nameae | Hydrophyllaceae (Tubiflorales) | Hydrophyllaceae (Boraginineae – Polemoniales) |
| Heliotropiaceae | Boraginaceae – Heliotropieae (Polemoniales) | Boraginaceae – Heliotropieae | Boraginaceae – Heliotropioideae (Boraginineae) | Boraginaceae – Heliotropioideae | Boraginaceae – Heliotropioideae (Tubiflorales) | Boraginaceae (Boraginineae – Polemoniales) |
| Ehretiaceae | Boraginaceae – Ehretieae (Polemoniales) | Boraginaceae – Ehretieae | Boraginaceae – Ehretioideae (Boraginineae) | Boraginaceae – Ehretioideae | Boraginaceae – Ehretioideae (Tubiflorales) | Boraginaceae (Boraginineae – Polemoniales) |
| Lennoaceae | Lennoaceae (Ericales) | | Lennoaceae (Ericales) | Lennoaceae | Lennoaceae (Tubiflorales) | Lennoaceae (Boraginineae – Polemoniales) |
| Coldeniaceae | Boraginaceae – Ehretieae (Polemoniales) | Boraginaceae – Ehretieae | Boraginaceae – ?Ehretioideae (Boraginineae) | Boraginaceae – Ehretioideae | Boraginaceae – Ehretioideae (Tubiflorales) | Boraginaceae (Boraginineae – Polemoniales) |
| Hoplestigmataceae | - | - | - | Hoplestigmataceae | Hoplestigmataceae (Tubiflorales) | Hoplestigmataceae (Boraginineae – Polemoniales) |
| Cordiaceae | Boraginaceae – Cordieae (Polemoniales) | Boraginaceae – Cordieae | Boraginaceae – Cordioideae (Boraginineae) | Boraginaceae – Cordioideae | Boraginaceae – Cordioideae (Tubiflorales) | Boraginaceae (Boraginineae – Polemoniales) |
| [Hydroleaceae (Solanales)] | Hydrophyllaceae – Hydroleae (Polemoniales) | Boraginaceae – Hydroleae | Hydrophyllaceae – Hydroleae (Boraginineae) | Hydrophyllaceae – Hydroleae | Hydrophyllaceae – Hydroleae (Tubiflorales) | Hydrophyllaceae (Boraginineae – Polemoniales) |
| [Tetrachondraceae (Lamiales)] | | | | | Tetrachondraceae (Tubiflorales) | ?Lamiaceae (Lamiales) |

Appendix 1. (continued)

| **This work** | **Dahlgren (1980)** | **Cronquist (1981, 1988)** | **Takhtajan (1987)** | **Thorne (1992)** | **Takhtajan (1997)** | **APG (1998, 2003); Mabberley (2008)** |
|---|---|---|---|---|---|---|
| Codonaceae | Hydrophyllaceae (Boraginales) | Hydrophyllaceae (Solanales) | Hydrophyllaceae (Boraginales) | Hydrophyllaceae (Boraginineae – Solanales) | Hydrophyllaceae (Boraginales) | Boraginaceae (Euasterids I unplaced) |
| Wellstediaceae | Wellstediaceae (Boraginales) | Boraginaceae (Lamiales) | Wellstediaceae (Boraginales) | Boraginaceae (Boraginineae – Solanales) | Boraginaceae (Boraginales) | Boraginaceae (Euasterids I unplaced) |
| Boraginaceae | Boraginaceae (Boraginales) | Boraginaceae (Lamiales) | Boraginaceae (Boraginales) | Boraginaceae (Boraginineae – Solanales) | Boraginaceae (Boraginales) | Boraginaceae (Euasterids I unplaced) |
| Hydrophyllaceae | Hydrophyllaceae (Boraginales) | Hydrophyllaceae (Solanales) | Hydrophyllaceae (Boraginales) | Hydrophyllaceae (Boraginineae – Solanales) | Hydrophyllaceae (Boraginales) | Boraginaceae (Euasterids I unplaced) |
| Namaceae | Hydrophyllaceae (Boraginales) | Hydrophyllaceae (Solanales) | Hydrophyllaceae (Boraginales) | Hydrophyllaceae (Boraginineae – Solanales) | Hydrophyllaceae (Boraginales) | Boraginaceae (Euasterids I unplaced) |
| Heliotropiaceae | Boraginaceae (Boraginales) | Boraginaceae (Lamiales) | Boraginaceae (Boraginales) | Boraginaceae (Boraginineae – Solanales) | Boraginaceae (Boraginales) | Boraginaceae (Euasterids I unplaced) |
| Ehretiaceae | Ehretiaceae (Boraginales) | Boraginaceae (Lamiales) | Ehretiaceae (Boraginales) | Boraginaceae (Boraginineae – Solanales) | Boraginaceae (Boraginales) | Boraginaceae (Euasterids I unplaced) |
| Lennoaceae | Lennoaceae (Boraginales) | Lennoaceae (Lamiales) | Lennoaceae (Boraginales) | Lennoaceae (Boraginineae – Solanales) | Lennoaceae (Boraginales) | Boraginaceae (Euasterids I unplaced) |
| Coldeniaceae | Ehretiaceae (Boraginales) | Boraginaceae (Lamiales) | Ehretiaceae (Boraginales) | Boraginaceae (Boraginineae – Solanales) | Boraginaceae (Boraginales) | Boraginaceae (Euasterids I unplaced) |
| Hoplestigmataceae | Hoplestigmataceae (Boraginales) | Hoplestigmataceae (Violales) | Hoplestigmataceae (Boraginales) | Hoplestigmataceae (Boraginineae – Solanales) | Hoplestigmataceae (Boraginales) | Hoplestigmataceae (unplaced) |
| Cordiaceae | Ehretiaceae (Boraginales) | Boraginaceae (Lamiales) | Cordiaceae (Boraginales) | Boraginaceae (Boraginineae – Solanales) | Boraginaceae (Boraginales) | Boraginaceae (Euasterids I unplaced) |
| [Hydroleaceae (Solanales)] | Hydrophyllaceae (Boraginales) | Hydrophyllaceae (Solanales) | Hydrophyllaceae (Boraginales) | Hydrophyllaceae (Boraginineae – Solanales) | Hydrophyllaceae (Boraginales) | Hydroleaceae (Solanales) |
| [Tetrachondraceae (Lamiales)] | ? | Lamiaceae (Lamiales) | Lamiaceae (Lamiales) | Tetrachondraceae (Boraginineae – Solanales) | Tetrachondraceae (Boraginales) | Tetrachondraceae (Lamiales) |

Appendix 1. (continued)

| This work | Takhtajan (2009) | APG (2009) | Reveal & Chase (2011) | Reveal (2011, 2012) |
|---|---|---|---|---|
| Codonaceae | Hydrophyllaceae – Codonoideae (Boraginales) | Boraginaceae (lamiids unplaced) | Boraginaceae (Boraginales) | Boraginaceae – Codonoideae (Boraginineae - Solanales) |
| Wellstediaceae | Boraginaceae – Wellstedioideae (Boraginales) | Boraginaceae (lamiids unplaced) | Boraginaceae (Boraginales) | Boraginaceae – Wellstedioideae (Boraginineae - Solanales) |
| Boraginaceae | Boraginaceae – Boraginoideae (Boraginales) | Boraginaceae (lamiids unplaced) | Boraginaceae (Boraginales) | Boraginaceae – Boraginoideae (Boraginineae - Solanales) |
| Hydrophyllaceae | Hydrophyllaceae – Hydrophylloideae (Boraginales) | Boraginaceae (lamiids unplaced) | Boraginaceae (Boraginales) | Boraginaceae – Hydrophylloideae (Boraginineae - Solanales) |
| Namaceae | Hydrophyllaceae – Hydrophylloideae (Boraginales) | Boraginaceae (lamiids unplaced) | Boraginaceae (Boraginales) | Boraginaceae – Hydrophylloideae (Boraginineae - Solanales) |
| Heliotropiaceae | Boraginaceae – Heliotropioideae (Boraginales) | Boraginaceae (lamiids unplaced) | Boraginaceae (Boraginales) | Boraginaceae – Heliotropiodeae (Boraginineae - Solanales) |
| Ehretiaceae | Boraginaceae – Ehretioideae (Boraginales) | Boraginaceae (lamiids unplaced) | Boraginaceae (Boraginales) | Boraginaceae – Ehretioideae (Boraginineae - Solanales) |
| Lennoaceae | Lennoaceae (Boraginales) | Boraginaceae (lamiids unplaced) | Boraginaceae (Boraginales) | Boraginaceae – Lennooideae (Boraginineae - Solanales) |
| Coldeniaceae | Boraginaceae – Ehretioideae (Boraginales) | Boraginaceae (lamiids unplaced) | Boraginaceae (Boraginales) | Boraginaceae (Boraginineae - Solanales) |
| Hoplestigmataceae | Hoplestigmataceae (Boraginales) | Boraginaceae (lamiids unplaced) | Boraginaceae (Boraginales) | Boraginaceae – Cordioideae (Boraginineae - Solanales) |
| Cordiaceae | Boraginaceae – Cordioideae (Boraginales) | Boraginaceae (lamiids unplaced) | Boraginaceae (Boraginales) | Boraginaceae – Cordioideae (Boraginineae - Solanales) |
| [Hydroleaceae (Solanales)] | Hydroleaceae (Solanales) | Hydroleaceae (Solanales) | Hydroleaceae (Lamiales) | Hydroleaceae (Solanineae – Solanales) |
| [Tetrachondraceae (Lamiales)] | Tetrachondraceae (Lamiales) | Tetrachondraceae (Lamiales) | Tetrachondraceae (Lamiales) | Tetrachondraceae (Gesneriineae – Lamiales) |

Appendix 2. Accepted genera of Boraginales (bold case) and generic synonyms (regular case). Number of species and distribution are indicated for each accepted genus. Number of genera/number of species is indicated for families and supra-generic names. Only valid generic names are included. Orthographic variations and genera originally published under a family of Boraginales, but currently in a different order, are excluded. * indicates genera or synonyms so far not supported by molecular data. Abbreviations: Afr: Africa; Am: America; Arab: Arabian Peninsula; Aus: Australia; Cal: California; Eur: Europe; Ind: India; Med: Mediterranean region; Neotrop: Neotropical; NZ: New Zealand; pantrop: pantropical; subcsmop: subcosmopolitan; trop: tropical

Boraginaceae Juss. (~90/~1600–1700)

- Echiochileae Långström & M.W. Chase (3/26)
  - Amblynotopsis Macbr. = *Antiphytum*
  - Amphibologyne Brand = *Antiphytum*
  - ***Antiphytum*** DC. ex Meisn. (10) N & S Am
  - Chamissoniophila Brand = *Antiphytum*
  - Chilechium Pfeiff. = *Echiochilon*
  - Chilochium Raf. = *Echiochilon*
  - ***Echiochilon*** Desf. (15) N Afr to SW Asia, Macaronesia, Pakistan & W Ind
  - Echiochilopsis Caball. = *Echiochilon*
  - Exioxylon Raf. = *Echiochilon*
  - Leurocline S. Moore = *Echiochilon*
  - Megastoma (Benth. & Hook. f.) Coss. & Durieu ex Bonnet & Barratte = *Ogastemma*
  - ***Ogastemma*** Brummitt (1) N Afr to Arab
  - Sericostoma Stocks (1) = *Echiochilon*
  - Tetraedrocarpus O. Schwartz = *Echiochilon*
- Boragineae Rchb. (17/~150)
  - ***Anchusa*** L. (~35) Afr, Eur, W Asia
  - ***Anchusella*** Bigazzi, Nardi & Selvi (2) Med
  - Bessera Schult. = *Pulmonaria*
  - ***Borago*** L. (5) W Med
  - ***Brunnera*** Steven (3) W Asia & SE Med
  - Buglossa Gray = *Lycopsis*
  - Buglossites Moris = *Borago*
  - Buglossum Mill. = *Anchusa*
  - Caryolopha Fisch. & Trautv. = *Pentaglottis*
  - ***Cynoglottis*** (Guşul.) Vural & K. Tan (2) Eur & Anatolia
  - Echioides Fabr. = *Lycopsis*
  - Elizaldia Willk. = *Nonea*
  - ***Gastrocotyle*** Bunge (2) N Afr, Arab, S Balkans
  - ***Hormuzakia*** Guşul. (2) SE Med
  - ***Lycopsis*** L. (2) W Asia & Eur
  - Massartina Maire = *Nonea*
  - ***Melanortocarya*** Selvi, Bigazzi, Hilger & Papini (1) SE Med
  - Meratia A. DC. = *Moritzia*
  - ***Moritzia*** DC. ex Meisn. (3) S Am
  - Nephrocarya P. Candargy = *Nonea*
  - ***Nonea*** Medik. (~35) N Afr, W Asia, Eur
  - Nordmannia Ledeb. ex Nordm. = *Trachystemon*
  - Oskampia Baill. = *Lycopsis*

Paraskevia W. Sauer & G. Sauer = *Pulmonaria*
***Pentaglottis*** Tausch (1) SW Eur
***Phyllocara*** Guşul. (1) Irano-Turanian
Procopiania Guşul. = *Symphytum*
Procopiphytum Pawł. = *Symphytum*
Psilostemon A. DC. = *Trachystemon*
***Pulmonaria*** L. (~17) E Asia & Eur
***Symphytum*** L. (~35) W Asia & Eur
***Thaumatocaryon*** Baill. (3) S Am
***Trachystemon*** D. Don (1) E Med

Lithospermeae Dumort. (25/~460)
***Aegonychon*** Gray (3) Asia & Eur
***Alkanna*** Tausch (~40) Med & SW Asia
***Ancistrocarya*** Maxim. (1) Japan & Korea
Aipyanthus Steven = *Huynhia*
Argyrexias Raf. = *Echium*
***Arnebia*** Forssk. (~30) NE Afr, SE Eur, SW & C Asia
Arnebiola Chiov. = *Arnebia*
Baphorhiza Link = *Alkanna*
Batschia J.F. Gmel. = *Lithospermum*
***Buglossoides*** Moench (2) Eur, N Afr & W Asia
Camptocarpus Decne. = *Alkanna*
Campylocaryum DC. ex A. DC. = *Alkanna*
***Cerinthe*** L. (7–10) Eur, NW Afr to W Asia
Colsmannia Lehm. = *Onosma*
Choriantha Riedl = *Onosma*
Cyphorima Raf. = *Lithospermum*
***Cystostemon*** Balf. f. (~15) SW Arab, trop Afr
Dioclea Spreng. = *Arnebia*
Echioides Moench = *Myosotis*
Echioides Ortega = *Huynhia*
Echiopsis Rchb. = *Lobostemon*
***Echiostachys*** Levyns (3) S Afr
***Echium*** L. (~60) N Afr, Eur, Macaronesia, W Asia
***Glandora*** D.C. Thomas, Weigend & Hilger (8) N Afr & S Eur
Gymnoleima Decne. = *Moltkia*
***Halacsya*** Dörfl. (1) Balkans
***Huynhia*** Greuter (2) Turkey & Caucasus area
Isoplesion Raf. = *Echium*
Isorium Raf. = *Lobostemon*
Larephes Raf. = *Echium*
Lasiarrhenum I.M. Johnst. = *Lithospermum*
Leptanthe Klotzsch = *Arnebia*
***Lithodora*** Griseb. (3–5) N Afr, W & SE Eur, SW Asia
***Lithospermum*** L. (~80) Afr, N & S Am, Eur
Lobostema Spreng. = *Lobostemon*
***Lobostemon*** Lehm. (~30) S Afr
Macromeria D. Don = *Lithospermum*
Macrotomia DC. = *Arnebia*
***Maharanga*** DC. (9) C & E Asia

***Mairetis*** I.M. Johnst. (1) NW Afr
Margarospermum (Rchb.) Opiz = *Aegonychon*
Megacaryon Boiss. = *Echium*
Meneghinia Endl. = *Arnebia*
***Moltkia*** Lehm. (6) S Eur & SW Asia
***Moltkiopsis*** I.M. Johnst. (1) NE Afr & SW Asia
Munbya Boiss. = *Arnebia*
***Neatostema*** I.M. Johnst. (1) Med & Macaronesia
Nomosa I.M. Johnst. = *Lithospermum*
Onochilis Mart. = *Alkanna*
***Onosma*** L. (~150) NW Afr, Eur, Asia
Onosmodium Michx. = *Lithospermum*
Oplexion Raf. = *Lobostemon*
Osmodium Raf. = *Lithospermum*
***Paramoltkia*** Greuter (1) Balkans
Pentalophus A. DC. = *Lithospermum*
Penthysa Raf. = *Lobostemon*
Perittostema I.M. Johnst. = *Lithospermum*
***Podonosma*** Boiss. (3) NE Afr, E Med & SW Asia
***Pontechium*** U.-R. Böhle & Hilger (1) E Eur to W Asia
Psilolaemus I.M. Johnst. = *Lithospermum*
Purshia Spreng. = *Lithospermum*
Rhytispermum Link = *Aegonychon*
Sava Adans. = *Onosma*
****Stenosolenium*** Turcz. (1) NE Asia
Stomotechium Lehm. = *Echium*
Strobila G. Don = *Arnebia*
Tetaris Lindl. = *Arnebia*
Toxostigma A. Rich. = *Arnebia*
Traxara Raf. = *Lobostemon*
Ulugbekia Zakirov = *Lithospermum*
Vaupelia Brand = *Cystostemon*
Zwackhia Sendt. = *Halacsya*

Cynoglosseae W.D.J. Koch (~45/~950–1040)
Actinocarya Benth. = *Microula*
****Adelinia*** J.I. Cohen (1) N Am
Adelocaryum Brand = *Cynoglossum*
****Afrotysonia*** Rauschert (3) E Afr
Allocarya Greene = *Plagiobothrys*
Allocaryastrum Brand = *Plagiobothrys*
Amblynotus I.M. Johnst. = *Eritrichium*
Amphibologyne Brand = *Amsinckia*
***Amsinckia*** Lehm. (~15) N & S Am
Anchusopsis Bisch. = *Cynoglossum*
****Andersonglossum*** J.I. Cohen (3) N Am
Anisanthera Raf. = *Caccinia*
***Anoplocaryum*** Ledeb. (5) C Asia
***Antiotrema*** Hand.-Mazz. (1) W China
***Asperugo*** L. (1) Asia & Eur
Austrocynoglossum Popov ex R.R. Mill = *Hackelia*

Bilegnum Brand = *Cynoglossum*
Boraginella Siegesb. ex Kuntze = *Trichodesma*
Boraginodes Post & Kuntze = *Trichodesma*
Borraginoides Moench = *Trichodesma*
***Bothriospermum*** Bunge (5) C & E Asia
***Brachybotrys*** Maxim. ex Oliv. (1) NE Asia
Brandella R.R. Mill = *Microparacaryum*
***Caccinia*** Savi (~6) Iran to S & C Asia
Casselia Dum. = *Mertensia*
Cerinthopsis Kotschy ex Paine = *Cynoglossum*
Cerinthodes Kuntze = *Mertensia*
Cervia Rodrig. ex Lag. = *Rochelia*
***Chionocharis*** I.M. Johnst. (1) C Asia
***Craniospermum*** Lehm. (4–5) C & E Asia
Crucicaryum O. Brand = *Cynoglossum*
***Cryptantha*** Lehm. ex G. Don (~160) N & S Am
Cynoglossopsis Brand = *Cynoglossum*
Cynoglossospermum Kuntze = *?Lappula*
***Cynoglossum*** L. (180–200) subcosmop
Cyphomattia Boiss. = *Cynoglossum*
***Dasynotus*** I.M. Johnst. (1) N Am
***Decalepidanthus*** Riedl (7) Himalayas
Diploloma Schrenk = *Craniospermum*
Echidiocarya A. Gray ex Benth. & Hook. f. = *Plagiobothrys*
Echinoglochin Brand = *Plagiobothrys*
Echinospermum Sw. ex Lehm. = *Lappula*
Embadium J.M. Black = *Hackelia*
Endogonia Lindl. = *Trigonotis*
****Eremocarya*** Greene = *Cryptantha*
***Eritrichium*** Schrad. ex Gaudin (~50) N Am, Asia, Eur
Exarrhena R. Br. = *Myosotis*
Friedrichsthalia Fenzl = *Trichodesma*
Glochidocaryum W.T. Wang = *Microula*
Glyptocaryopsis Brand = *Plagiobothrys*
****Greeneocharis*** Gürke & Harms = *Cryptantha*
Gruvelia A. DC. = *Pectocarya*
Gymnomyosotis (A. DC.) O.D. Nikif. = *Myosotis*
****Gyrocaryum*** Valdés (1) Spain
***Hackelia*** Opiz (~45) N & S Am, Asia, Aus, Eur
***Harpagonella*** A. Gray (1) N Am
Havilandia Stapf = *Trigonotis*
Heliocarya Bunge = *Caccinia*
Hemisphaerocarya Brand = *Cryptantha*
Henryettana Brand = *Antiotrema*
***Heterocaryum*** A. DC. (~6) W Asia
Hippoglossum Hartm. = *Mertensia*
Ivanjohnstonia Kazmi = *Cynoglossum*
****Johnstonella*** Brand = *Cryptantha*
Krynitzkia Fisch. & Mey. = *Cryptantha*
Ktenospermum Lehm. = *Pectocarya*

Kuschakewiczia Regel & Smirnow = *Cynoglossum*
Lacaitaea Brand = *Trichodesma*
***Lappula*** Moench (50–60) N Am, N Afr, Asia, Aus, Eur
***Lasiocaryum*** I.M. Johnst., (3) C Asia
Leiocarya Hochst. = *Trichodesma*
***Lepechiniella*** Popov (~6) NE Afr to SW Asia
*Lindelofia Lehm. = *Cynoglossum*
Maccoya F. Muell. = *Plagiobothrys*
Mattia Schult. = *Cynoglossum*
*Mattiastrum (Boiss.) Brand = *Cynoglossum*
***Memoremea*** Otero, Jim.-Mejías, Valcárcel & P. Vargas (1) Eur
***Mertensia*** Roth (~40) N Am, E Asia, NW Eur
Metaeritrichium W.T. Wang = *Microula*
***Microcaryum*** I.M. Johnst. (1) C Asia
***Microparacaryum*** (Popov ex Riedl) Hilger & Podlech (3) SW Asia
***Microula*** Benth. (30) C Asia
*Mimophytum Greenm. = *Omphalodes*
***Myosotidium*** Hook. (5) S Am, Juan Fernández, NZ
***Myosotis*** L. (80–100) subcosmop
***Nesocaryum*** I.M. Johnst. (1) San Ambrosio
***Nihon*** Otero, Jim.-Mejías, Valcárcel & P. Vargas (5) Japan
Octosomatium Gagnep. = *Trichodesma*
Omphalium Wallr. = *Omphalodes*
***Omphalodes*** Mill. (20–30) N Am, Asia, Eur
Omphalolappula Brand = *Lappula*
****Omphalotrigonotis*** W.T. Wang (1) E Asia
***Oncaglossum*** Sutorý (1) Mexico
****Oreocarya*** Greene = *Cryptantha*
Oreocharis Lindl. = *Mertensia*
Oreogenia I.M. Johnst. = *Lasiocaryum*
****Paracaryopsis*** (Riedl) R.R. Mill (3) Arab & Ind
*Paracaryum Boiss. = *Cynoglossum*
Paracynoglossum Popov = *Cynoglossum*
Pardoglossum Barbier & Mathez = *Cynoglossum*
***Pectocarya*** DC. ex Meisn. (15) N & S Am
Pedinogyne Brand = *Trigonotis*
Picotia Roem. & Schult. = *Omphalodes*
Piptocalyx Torr. = *Cryptantha*
***Plagiobothrys*** Fisch. & C.A. Mey. (~70) N & S Am, NE Asia, Aus
Platynema Schrad. = *Mertensia*
Pneumaria J. Hill = *Mertensia*
Pollichia Medik. = *Trichodesma*
Pseudomertensia Riedl = *Decalepidanthus*
Raclathris Raf. = ?*Rochelia*
*Rindera Pall. = *Cynoglossum*
***Rochelia*** Rchb. (~15) Asia to W Eur
Sauria M.S. Bajtenov = *Eritrichium*
Scapicephalus Ovcz. & Czukav. = *Decalepidanthus*
Schistocaryum Franch. = *Microula*

Sclerocaryopsis Brand = *Lappula*
Scorpioides Gilib. = *Myosotis*
Selkirkia Hemsl. = *Myosotidium*
Setulocarya R.R. Mill & D.G. Long = *Lasiocaryum*
***Sinojohnstonia*** Hu (1) E Asia
*Solenanthus Ledeb. = *Cynoglossum*
Sonnea Greene = *Plagiobothrys*
Spiroconus Stev. = *Trichodesma*
Steenhammera Rchb. = *Mertensia*
Stephanocaryum Popov = *Trigonotis*
Streblanthera Steud. = *Trichodesma*
Strophiostoma Turcz. = *Myosotis*
***Suchtelenia*** Karel. ex Meisn. (1) C Asia
***Thyrocarpus*** Hance (3) Asia
*Tianschaniella B. Fedtsch. = *Eritrichium*
*Trachelanthus Kunze = *Cynoglossum*
Tretocarya Maxim. = *Microula*
***Trichodesma*** R. Br. (40–50) S Afr to S & SE Asia & Aus
Trigonocaryum Trautv. = *Myosotis*
***Trigonotis*** Steven (~60) E & SE Asia to SE Russia
Tysonia Bolus = *Afrotysonia*
Umbilicaria Heist. ex Fabr. = *Omphalodes*
Wheelerella G.B. Grant = *Cryptantha*
Winkleria Rchb. = *Mertensia*
Zoelleria Warb. = *Trigonotis*

Codonaceae Weigend & Hilger (1/2)
***Codon*** L. (2) SW Afr

Coldeniaceae J. S. Mill. & Gottschling (1/1)
***Coldenia*** L. (1) trop Afr, S Asia & N Aus
Lobophyllum F. Muell. = *Coldenia*

Cordiaceae R. Br. ex Dumort. (2/~350)
Acnadena Raf. = *Cordia*
Ascania Crantz = *Cordia*
Auxemma Miers = *Cordia*
Bourgia Scop. = *Cordia*
Calyptracordia Britton = *Cordia*
Carpiphea Raf. = *Cordia*
Catonia Raf. = *Varronia*
Cerdana Ruiz & Pav. = *Cordia*
Cienkowskya Regel & Rach = *Cordia*
Coilanthera Raf. = *Cordia*
Collococcus P. Browne = *Cordia*
***Cordia*** L. (~250) pantrop
Cordiada Vell. = *Cordia*
Cordiopsis Desv. ex Ham. = *Varronia*
Diacoria Endl. = *Cordia*
Ectemis Raf. = *Cordia*
Firensia Scop. = *Cordia*
Gerascanthus P. Browne = *Cordia*
Gynaion A. DC. = *Cordia*

Hemigymnia Griff. = *Cordia*
Hymenesthes Miers = *Cordia*
Lithocardium Kuntze = *Cordia*
Macielia Vandelli = *Cordia*
Macria Ten. = *Cordia*
Montjolya Friesen = *Varronia*
Myxa (Endl.) Lindl. = *Cordia*
Novella Raf. = *Cordia*
Paradigma Miers = *Cordia*
Patagonula L. = *Cordia*
Physoclada (DC.) Lindl. = *Cordia*
Pilicordia (A. DC.) Lindl. = *Cordia*
Piloisia Raf. = *Varronia*
Plethostephia Miers = *Cordia*
Rhabdocalyx (A. DC.) Lindl. = *Cordia*
Quarena Raf. = *Cordia*
Saccellium Humb. & Bonpl. = *Cordia*
Salimori Adans. = *Cordia*
Sebestena Boehm. = *Cordia*
Topiaris Raf. = *Varronia*
Toquera Raf. = *Cordia*
Ulmarronia Friesen = *Varronia*
***Varronia*** P. Browne (~100) Neotrop
Varroniopsis Friesen = *Varronia*

Ehretiaceae Mart. (7/~160)

Antrophora I.M. Johnst, = *Lepidocordia*
***Bourreria*** P. Browne (48) Neotrop, E Afr
Carmona Cav. = *Ehretia*
***Cortesia*** Cav. (1) W Argentina
Crematomia Miers = *Bourreria*
Desmophyla Raf. = *Rochefortia*
Diplostylus H. Karst. & Triana = *Rochefortia*
Eddya Torrey & A. Gray = *Tiquilia*
***Ehretia*** P. Browne (~50) pantrop
Galapagoa Hook. f. = *Tiquilia*
Gaza Terán & Berland. = *Ehretia*
***Halgania*** Gaudich. (~20) Aus
Hilsenbergia Tausch ex Meisn = *Bourreria*
***Lepidocordia*** Ducke (2) C & S Am
Lithothamnus Zipp. ex Span. = *Ehretia*
Lutrostylis G. Don = *Rochefortia*
Menais Loefl. = *Ehretia*
Monomesia Raf. = *Tiquilia*
Morelosia Lex. = *Bourreria*
Ptilocalyx Torrey & A. Gray = *Tiquilia*
Rhabdia Mart. = *Ehretia*
***Rochefortia*** Sw. (9) Neotrop
Rotula Lour. = *Ehretia*
Stegnocarpus Torrey & A. Gray = *Tiquilia*
Subrisia Raf. = *Bourreria*

Tetracoccus Griseb. = *Bourreria*
***Tiquilia*** Pers. (28) N & S Am
Tiquiliopsis (A. Gray) A. Heller = *Tiquilia*
Traxilum Raf. = *Ehretia*
Zombiana Baill. = *Ehretia*

Heliotropiaceae Schrad. (4/~450)

Argusia Böhm. = *Heliotropium*
Beruniella Zakirov & Nabiev = *Heliotropium*
Bourjotia Pomel = *Heliotropium*
Bucanion Steven = *Heliotropium*
Cochranea Miers = *Heliotropium*
Ceballosia Kunkel ex Förther = *Heliotropium*
Dialion Raf. = *Heliotropium*
Eliopia Raf. = *Heliotropium*
***Euploca*** Nutt. (~100) subcosmop
Heliophytum (Cham.) A. DC. = *Heliotropium*
***Heliotropium*** L. (~325) subcosmop
Hieranthemum (Endl.) Spach = *Heliotropium*
Hilgeria Förther = *Euploca*
***Ixorhea*** Fenzl (1) NW Argentina
Lithococca Small ex Rydb. = *Euploca*
Mallotonia (Griseb.) Britton = *Heliotropium*
Meladendron Molina = *Heliotropium*
Messerschmidia L. ex Hebenstr. = *Heliotropium*
Messerschmidia Roem. & Schult. = *Heliotropium*
***Myriopus*** Small (~25) Neotrop
Nogalia Verdc. = *Heliotropium*
Notonerium Benth. = *Euploca*
Orthostachys (R. Br.) Spach = *Euploca*
Oskampia Raf. = ?*Myriopus*
Oxyosmyles Speg. = *Ixorhea*
Pentacarya DC. ex Meisn. = *Euploca*
Peristima Raf. = *Heliotropium*
Pioctonon Raf. = *Euploca*
Piptoclaina G. Don = *Heliotropium*
Pittonia Mill. = *Heliotropium*
Preslaea Mart. = *Euploca*
Sarcanthus Andersson = *Euploca*
Schleidenia Endl. = *Euploca*
Schobera Scop. = *Heliotropium*
Scorpianthes Raf. = *Heliotropium*
Scorpiurus Heist ex Fabr. = *Heliotropium*
Synzistachium Raf. = *Heliotropium*
Tetrandra (A. DC & DC.) Miq. = *Heliotropium*
Tiaridium Lehm. = *Heliotropium*
Tournefortia L. = *Heliotropium*
Valentina Speg. = *Heliotropium*
Valentinella Speg. = *Heliotropium*
Verrucaria Medik. = *Myriopus*

Hydrophyllaceae R. Br. (12/250)

Aldea Ruiz & Pav. = *Phacelia*
Capnorea Raf. = *Hesperochiron*
Colpophyllos Ehret ex C.J. Trew = *Ellisia*
Cosmanthus Nolte ex A. DC. = *Phacelia*
Decemium (A. Gray) Brand = *Hydrophyllum*
***Draperia*** Torr. ex A. Gray (1) Cal
***Ellisia*** L. (1) w N Am
***Emmenanthe*** Benth. (2) sw N Am
Endiplus Raf. = *Phacelia*
****Eucrypta*** Nutt. (2) sw N Am
Eutoca R. Br. = *Phacelia*
***Hesperochiron*** S. Wats. (2) w N Am
Heteryta Raf. = *Phacelia*
***Howellanthus*** (Constance) Walden & R. Patt. (1) Cal
***Hydrophyllum*** L. (11) N Am
Macrocalyx C.J. Trew = *Ellisia*
Microgenetes A. DC. = *Phacelia*
Miltitzia DC. ex A. DC. = *Phacelia*
***Nemophila*** Nutt. (19) w & se N Am
Nyctelea (L.) Scop. = *Ellisia*
***Phacelia*** Juss. (210) w & e N Am, S Am
***Pholistoma*** Lilja (3) sw N Am
***Romanzoffia*** Dumort. (5) w N Am
***Tricardia*** Torr. ex S. Wats. (1) sw N Am
Viticella Mitch. = *Nemophila*
Whitlavia Harvey = *Phacelia*

Hoplestigmataceae Gilg (1/2)

***Hoplestigma*** Pierre (2) W Afr

Lennoaceae Solms (2/4)

Ammobroma Torrey ex A. Gray = *Pholisma*
Corallophyllum Kunth = *Lennoa*
***Lennoa*** Lex. (1) N to S Am
***Pholisma*** Nutt. ex Hook. (3) N Am

Namaceae Walden & Olmstead (4/71)

Andropus Brand = *Nama*
Conanthus S. Wats. = *Nama*
***Eriodictyon*** Benth. (8) sw N Am
Ernstamra Kuntze = *Wigandia*
Lemmonia A. Gray = *Nama*
Marilaunidium Kuntze = *Nama*
***Nama*** L. (56) sw N Am & trop Am, Hawaii
***Turricula*** J.F. Macbr. (1) sw N Am
***Wigandia*** Kunth (6) trop Am

Wellstediaceae Novák (1/6)

***Wellstedia*** Balf. f. (6) SW & NE Afr & Socotra