Familial classification of the Boraginales

Boraginales Working Group
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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, and Wellstediaceae. Descriptions, synonomy, a taxonomic key, and a list of genera for these eleven families are provided, including the new family Coldeniaceae (monogeneric) and Namaceae (segregated from Hydrophyllaceae and comprising *Nama*, *Eriodictyon*, *Turricula*, and *Wigandia*), the latter necessitating a revised circumscription of a more morphologically coherent Hydrophyllaceae.

Keywords angiosperms; Boraginaceae; Boraginales; classification; family; plant taxonomy

■ INTRODUCTION

Boraginales are a plant group of the Lamiidae comprising about 125 genera and around 2700 species of herbs, shrubs, trees and lianas distributed worldwide. The classification of this order has changed dramatically over time, especially since molecular data and phylogenetic analyses became available. The purpose of this paper is to provide a familial classification of the order Boraginales compatible with phylogenetic data and adequately reflecting the morphological heterogeneity within this group. The core of the species of Boraginales belongs to the family Boraginaceae in the traditional sense.

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Boraginaceae in this traditional sense (Candolle, 1845; Bentham & Hooker, 1876; Gürke, 1893; Engler, 1898; Pilger & Krause, 1915) were subdivided into five subfamilies, namely Boraginoideae, Cordioideae, Ehretioideae, Heliotropioideae and Wellstedioideae. In pre-molecular times most scientists accepted this circumscription of Boraginaceae (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) removed 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. Conversely, Hoplestigmataceae, Hydrophyllaceae, and Lennoaceae were generally accepted as distinct families. However, the close relationships of these taxa to traditional Boraginaceae has been widely 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 circumscriptions. Chadefaud & Emberger (1960) considered Boraginaceae, Hoplestigmataceae, Hydrophyllaceae, and Lennoaceae to form a natural group within the order Tubiflorales. Takhtajan (1980) included these same families in the suborder Boraginineae.

On the other hand, three groups historically associated to Boraginaceae have been clearly shown to be only distantly related: Thorne (1992) placed Tetrachondraceae in Boraginineae, and Takhtajan (1997) placed them in the order Boraginales. After Savolainen & al. (2000) demonstrated that Tetrachondraceae are phylogenetically closer to Lamiales, the remainder of the families was reunited in the order Boraginales (Takhtajan, 2009; Reveal & Chase, 2011). Monogeneric Vahliaceae have been sometimes been regarded as 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). Phylogenetic studies further demonstrate that *Hydrolea* L., previously treated in the Hydrophyllaceae, is more closely related to Solanales (Cosner & al., 1994; Soltis & al., 2000). Historical circumscriptions of Boraginaceae and related families by different authors are summarized in Appendix 1.

Phylogenetic studies demonstrate that Boraginaceae in the traditional sense are paraphyletic with respect to Hoplestigmataceae, Hydrophyllaceae, and Lennoaceae, and that Hydrophyllaceae in the traditional sense are not monophyletic (Olmstead & al., 1993; Ferguson, 1999; Gottschling & al., 2001; Nazaire & Hufford, 2012; Refulio-Rodríguez & Olmstead, 2014; Weigend & al., 2014). *Codon* L., traditionally accepted in Hydrophyllaceae, is the sister group to a clade including *Wellstedia* Balf.f. (= Wellstedioideae) and Boraginaceae s.str. (= Boraginoideae), and has been segregated to the family Codonaceae (Weigend & Hilger, 2010; Weigend & al., 2014). The remaining genera of the traditional Hydrophyllaceae (after removal of *Hydrolea*) form two distinct clades within Boraginales (Ferguson, 1999; Refulio-Rodríguez & Olmstead, 2014; Weigend & al., 2014) (Fig. 1). The first clade 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. These clades are successive sister groups to a clade comprising *Coldenia* L., Cordiaceae, Ehretiaceae, Heliotropiaceae, Hoplestigmataceae, and Lennoaceae (Fig. 1).

Boraginales, in this revised circumscription (i.e., after exclusion of Vahliaceae, Hydroleaceae, and Tetrachondraceae and inclusion of Hoplestigmataceae, Hydrophyllaceae, and Lennoaceae), is a well-supported monophyletic group in Lamiidae (Gottschling & al., 2001; Bremer & al., 2002; Moore & Jansen, 2006; Luebert & al., 2011a; Soltis & al., 2011; Nazaire & Hufford, 2012; Cohen 2014; Refulio-Rodríguez & Olmstead, 2014; Weigend & al., 2014). However, Boraginales have been variously resolved as sister to Lamiales (Soltis & al., 2011; Refulio-Rodríguez & Olmstead, 2014), Solanales (Weigend & al., 2014), Gentianales (Stull & al., 2015), or Solanales+ Gentianales (Moore & al., 2010), always with low to moderate support only.

Recent phylogenetic studies provide clear insights into the major lineages of Boraginales, and these are summarized in Fig. 1. Most recent authors recognize several distinct families in Boraginales (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 Boraginales versus lumping all clades into a single family Boraginaceae s.l. include the ease of morphological recognition, moderate group size, and increased nomenclatural stability (Backlund & Bremer, 1998; Vences & al., 2013).

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 understanding of the phylogenetic interrelationships among clades included within Boraginales and their relationships to other orders. This option has the drawback of reducing the 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; Ricketson, 2012; Cecchi & Selvi, 2015a) and angiosperm classification systems (e.g., Cronquist, 1988; Heywood & al., 2007; Takhtajan, 2009).

Some recent treatments have followed a broad circumscription of Boraginaceae (i.e., including traditional Boraginaceae, Hoplestigmataceae, Hydrophyllaceae, and Lennoaceae) as recommended by the APG systems (e.g., Judd & al., 2008; Mabberley, 2008; Stapf, 2009; Simpson, 2010; Reveal, 2011,

2012; Acevedo-Rodríguez & Strong, 2012; Nazaire & Hufford, 2012; Walden & Patterson, 2012; Walden & al., 2014). However, most recent studies of 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; Melo & Semir 2010; Stapf & al., 2010; Weeks & al., 2010; Weigend & Hilger, 2010; Campos-Ríos & Chiang Cabrera, 2012; Miller, 2012, 2013a, b; Stutzman & al., 2012; 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, 2014). This view has 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* (Kadereit & Bittrich, 2016), Angiosperm Phylogeny Website (Stevens, 2001–), and has recently been incorporated in the most important German botanical textbook (Kadereit & al., 2014). 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. Although we acknowledge that views may differ, we believe that recognizing Boraginaceae s.l. does not serve nomenclatural stability, reducing several long-recognized families to subfamilies.

Historically, the coherence of Boraginaceae was primarily based on the presence of four one-seeded compartments in the fruit, separating into four nutlets in the most typical case (Bentham & Hooker, 1876; Gürke, 1893). However, it has now been shown that this fruit morphology evolved independently in the two major clades of Boraginales from ancestors with many-seeded, capsular fruits (Weigend & al., 2013, 2014). A more detailed study (Fig. 2) shows that the development of superficially similar fruits with four separate nutlets follows different trajectories and therefore does not represent a case of phylogenetic homology (Fig. 2). Capsular fruits, as characteristic of polyphyletic Hydrophyllaceae appear to represent

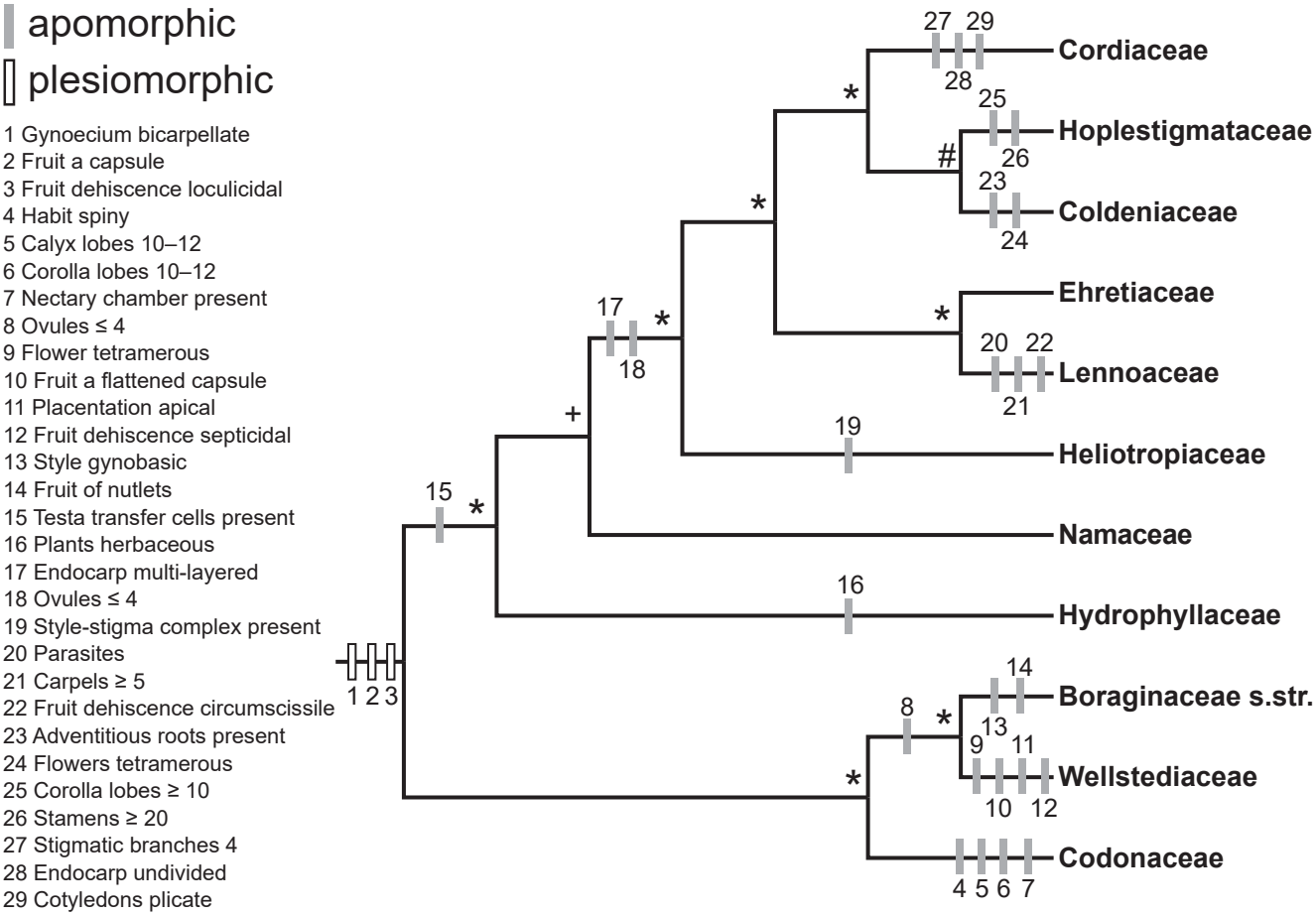

Fig. 1. Major clades of the Boraginales based on Refulio-Rodríguez & Olmstead (2014) and Weigend & al. (2014). The clade with + is well supported (Bayesian posterior probability >0.95, maximum likelihood bootstrap value >80) only in Refulio-Rodríguez & Olmstead (2014). The clade with # is moderately 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. These are not based on a explicit ancestral state reconstruction.

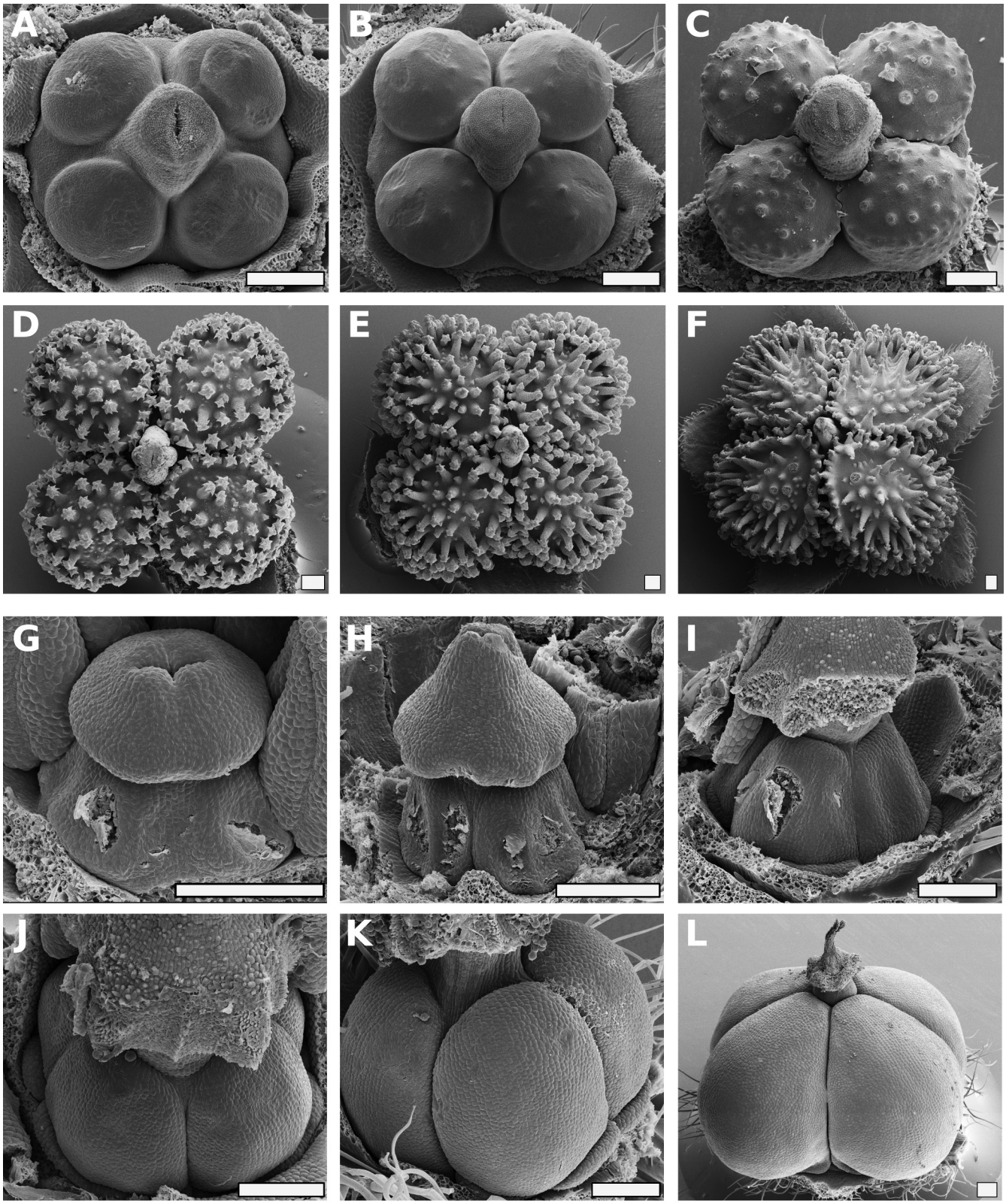

Fig. 2. Flower and fruit development in *Cynoglossum australe* R.Br. (**A–F,** Boraginaceae s.str., *Joßberger 062*, BONN) and *Heliotropium europaeum* L. (**G–L,** Heliotropiaceae, *Lobin & Weigend 233-14*, BONN). The species depicted correspond to the two major clades of Boraginales, in which nutlets evolved independently. In the Boraginaceae s.str., the four nutlets become distinct very early in 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.

the plesiomorphic condition for both clades (Fig. 1). Thus, no fruit morphological synapomorphy for Boraginales can be recognized. 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 (Refulio-Rodríguez & Olmstead, 2014; Weigend & al., 2014; Stull & al., 2015), the two major clades of the Boraginaceae s.l. [Boraginales] consist of: (1) Codonaceae+Wellstediaceae+Boraginaceae s.str.; and (2) Hydrophyllaceae+Namaceae+Heliotropiaceae+Lennoaceae+Ehretiaceae+*Coldenia*+Hoplestigmataceae+Cordiaceae (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.

Lennoaceae are here recognized at family level, because of the combination of a parasitic life form, polymerous perianth and a unique fruit morphology (circumscissile capsule enclosing pyrenes; Yatskievych & Mason, 1986) (Fig. 1). The recognition of Cordiaceae (see Appendix 1) is based on multiple apomorphies, such as the presence of four stigmatic branches, an undivided endocarp, and plicate cotyledons (Gottschling & al., 2005).

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. (Kadereit & Bittrich, 2016; with Lennoaceae separate). However, monophyly of Ehretiaceae s.l. is verified only by molecular data at present, as no morphological apomorphy has been proposed 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 a multilayered endocarp in Heliotropiaceae+Lennoacea+Ehretiaceae+*Coldenia*+Hoplestigmataceae+Cordiaceae, these could be united into a more broadly defined Heliotropiaceae s.l. This has not been proposed before and would therefore be a major change in classification.

The authors of this paper favor the recognition of eleven easily recognizable and morphologically well-defined monophyletic families (i.e., the major clades of Fig. 1, see Table 1). These entities are characterized mostly by apomorphic characters (Fig. 1). This classification represents only a minimal disruption of nomenclatural stability in mostly recognizing taxa with valid family names already in use; all but one have valid names at the family level. Taxonomic novelties are the 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), with Namaceae accommodating the genera *Eriodictyon*, *Nama*, *Turricula*, and *Wigandia*.

The consensus for this system was achieved during an international meeting on Boraginales 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 Lennoaceae, Ehretiaceae, Coldeniaceae, Hoplestigmataceae, and Cordiaceae. 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 in 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).

There are two instances in which phylogenetic results currently available are not entirely conclusive. 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 the Hydrophyllaceae s.str. sister to Namaceaeae with moderate to poor support. Studies using plastid data resolve these two clades as successive sister groups to Heliotropiaceae+Lennoacea+Ehretiaceae+Coldeniaceae+Hoplestigmataceae+Cordiaceae, 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, the capsular fruit, is plesiomorphic, so the subdivision is not in conflict with morphology, but neither does morphology provide strong support for their separation (Table 1).

The second 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 two stigmatic branches and usually drupaceous fruits with four pyrenes (less commonly two 2-seeded pyrenes, or rarely an entire endocarp). However, monophyly has been questioned because molecular data suggest that Lennoaceae may be nested in Ehretiaceae (Gottschling & al., 2001, 2014a; Nazaire & Hufford, 2012; Weigend & al., 2014). Additional data are required to resolve detailed relationships of Lennoaceae and Ehretiaceae. Lennoaceae are therefore here retained as historically 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.: 23. 1835.
= Ehretiales Mart., Consp. Regn. Veg.: 22. 1835.
= Hydrophyllales Mart., Consp. Regn. Veg.: 22. 1835.
= Echiales Lindl. in Penny Cyclop. 10: 128. 1838.

Table 1. Comparative morphological characterization of the families of Boraginales recognized here.

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 or trees	5	(1)	gynobasic	capitate to bilobate	nutlet	eremocarpic	4	axile	1	4	absent	scanty or absent
Codonaceae	shrubs	10–12	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	clavate to capitate	drupe, rarely nut	indehiscent	4	axile	1	4 or less	present	scanty or absent
Ehretiaceae	trees to shrubs	5	(1), 2[a]	apical[b]	clavate to capitate	drupe, rarely nutlet	indehiscent or schizocarpic	1–4	axile	1–4	4 or less	present	copious
Heliotropiaceae	herbs to trees	5	(1)	apical	conically elongated	nutlet or drupe	indehiscent or schizocarpic	1–4	axile	1	4 or less	present	scanty
Hoplestigmataceae	trees	10–15	2	apical	capitate	drupe	indehiscent	1	(intrusive) parietal	4	4	present	scanty
Hydrophyllaceae	herbs	(4)5	2[a]	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	capsule	circumscis-sile-schizo-carpic	10–32	axile, ap-pearing free central in fruit	2	10 to many	present	copious
Namaceae	shrubs, rarely herbs	5	2[a]	apical	bilobate	capsule	loculicidal or septicidal	2	(intrusive) parietal	2 to many	2 to many	absent	copious
Wellstediaceae	shrubs or herbs	4	(1)	apical	bilobate	capsule	septicidal	2	apical	1–2	1–2	absent	absent

Morphological information based on Gürke (1893), Peter (1893), Gilg (1908), Pilger (1912), Brand (1913), 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).

[a] Sometimes free to base = 2 stylodia

[b] Sometimes anacrostylous in species of *Tiquilia*

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(–15)-merous, calyx lobes free nearly to the base to united nearly completely, corolla usually united for at least half of its length. Androecium composed of (4–)5(–12 or 20–35) stamens, filaments usually united with corolla tube, anthers bilocular. Gynoecium with style insertion apical or gynobasic, style 1, rarely 2 or 4 stylodia, stigma undivided or with 2 or 4 branches. Ovary 2-carpellate or rarely 5–16-carpellate. Fruit a capsule, drupe, nut or (1–)4 nutlets, dehiscence loculicidal, septicidal, eremocarpic (see Glossary), schizocarpic, or indehiscent. Ovary locules 1–4(10–32). 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 cataphylls; ovary 5–16-carpellate, 10–32-locular by secondary subdivision; fruit a depressed capsule with circumscissile dehiscence…… **Lennoaceae**
1. Plants with chlorophyll, leaves with well-developed lamina; ovary 2-carpellate, 1-locular or 2–4-locular by secondary subdivision; fruit with 1–4 pyrenes, or 4-seeded, but undivided, or capsular with loculicidal or septicidal dehiscence…… 2
2. Ovary subdivided into (1–)4(–8) uni-ovulate eremocarps in flower developing into corresponding number of individual nutlets; style insertion gynobasic …… ..... **Boraginaceae s.str.**
2. Ovary entire in flower, developing into a capsule or a (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**
3 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**
4. 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
5. 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 ¾ of its length with two stigmatic branches ……**Namaceae**
6. Annual or perennial herbs, leaves cauline and basal, rarely basal or cauline only, simple or–more commonly–variously divided to bipinnate; style 1 with 2 stigmatic branches ……**Hydrophyllaceae**
7. Stigma not terminal, style undivided, terminal with a conical stigmatic head having a basal ring-shaped stigma and a sterile, sometimes 2-lobed apex (style-stigma complex); flowers usually in dense, scorpioid, bracteate or ebracteate monochasia…… **Heliotropiaceae**
7. Stigma(s) terminal, style entire to deeply divided; flowers not in scorpioid monochasia, often in repeatedly dichasial inflorescences …… 8
8. Gynoecium with 4 stigmatic branches (if 2, then fruit completely enclosed in accrescent calyx); ovules orthotropous; cotyledons plicate …… **Cordiaceae**
8. Gynoecium with 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. Stamens 20–35 in three irregular series…… …… **Hoplestigmataceae**
9. Stamens 4 or 5 in one series…… 10
10. Flowers 5-merous; mostly perennial, woody plants without adventitious roots …… **Ehretiaceae**
10. Flowers 4-merous; annual plants with adventitious roots ……**Coldeniaceae**

Family descriptions

Note: In the following descriptions, apomorphic characters of the families are highlighted in bold (compare Fig. 1).

Boraginaceae Juss., Gen. Pl.: 128. 1789, nom. cons. – Type: *Borago* L.

= Buglossaceae Hoffmanns. & Link, Fl. Portug. 1: 63. 1809 (“Buglossinae”).

= Anchusaceae Vest, Anleit. Stud. Bot.: 274, 302. 1818 (“Anchusoideae”).

= Cerinthaceae Bercht. & J.Presl, Přir. Rostlin: 244. 1820.

= Onosmaceae Martinov, Tekhno-Bot. Slovar: 437. 1820 (“Onosmoides”).

= Asperifoliaceae Rchb., Consp. Regn. Veg.: 89, 118. 1829.

= Echiaceae Raf., Fl. Tellur. 2: 61. 1837 (“1836”) (“Echidia”).

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

Annual to perennial herbs, rarely shrubs or trees, tap-rooted or rhizomatous, indumentum 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 (see Glossary), sometimes congested into terminal “heads” or reduced to single flowers. *Flowers* pentamerous, bisexual; calyx united nearly to apex or divided nearly to base, lobes mostly narrowly ovate-acuminate, sometimes linear or broadly ovate-acuminate with a cordate base, with a more or less pronounced scabrid to lanate or uncinate indumentum, aestivation apert to valvate; corolla white, yellow, pink or often blue, sympetalous,

hypocrateriform, infundibuliform to cylindrical or campanulate, lobes variously erect to spreading, aestivation imbricate or contorted; stamens 5, rarely fewer, filaments various, short to very long, anthers deeply included to exserted; gynoecium bicarpellate, ovary 4-locular by secondary subdivision at early anthesis, **style gynobasic,** often with pyramidal to subulate gynobase, stigma capitate to bilobate; nectar disc present at ovary base. *Fruit* with (1–2)–4 1-seeded **nutlets,** rarely of two 2-seeded nutlets, these variously modified, often dorsiventrally compressed, with a marginal wing or ring, often glochidiate.

Around 90 genera (Appendix 2) with some 1600–1700 species of worldwide distribution, especially in extratropical zones.

Major clades within Boraginaceae s.str. are relatively well-resolved, with Echiochileae sister to the rest, where Borageineae 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. Boraginaceae have been variously circumscribed, ranging from an inclusive taxon encompassing the whole order Boraginales to a family defined in its most strict sense as accepted here (see Appendix 1).

Codonaceae Weigend & Hilger in Phytotaxa 10: 27. 2010 – Type: *Codon* L.

= Codonoideae Retief & A.E.van Wyk in Bothalia 35(1): 79. 2005.

= Codoneae Nazaire & L.Hufford in Syst. Bot. 37: 778. 2012.

Subperennial or perennial, densely branched, **spiny shrublets** with tap-roots, indumentum of white spines, stiff unicellular trichomes and 2–5-celled gland-tipped trichomes. *Leaves* alternate, entire, petiolate, lamina ovate, adaxially densely spiny, abaxially with spines only on the very prominent midvein. *Inflorescences* terminal, 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, lobes unequal in width, narrow and wide calyx lobes alternating, densely spinose and pubescent, aestivation valvate; corolla white or yellow, sympetalous, campanulate to saucer-shaped, lobes half-erect to spreading, aestivation imbricate; stamens 10–12, filaments basally pubescent and each connected to corolla tube by septa forming a **nectary chamber,** anthers exserted; gynoecium bicarpellate, ovary nearly bilocular by deeply intruding placentae, style terminal, stigmatic branches 2, stigma punctiform; nectar disc present at ovary base. *Fruit* a dry, bivalved capsule, loculicidal, seeds numerous.

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: *Coldenia* L.

Procumbent annual herbs with slender, branched stems, often with **adventitious roots,** indumentum densely, softly pubescent with simple, unicellular white trichomes. *Leaves* numerous, alternate, shortly petiolate, fasciculate, small, asymmetrical, bullate, margin serrate to crenate, venation pinnate with secondary veins deeply immersed and ending in sinuses of the crenations, obovate in outline, pubescent only between veins adaxially and across the entire surface abaxially. *Inflorescences* axillary, frondose monochasia, these often elongating and anthocladal (see Glossary). *Flowers* **tetramerous,** bisexual, minute; calyx lobes free nearly to base, ovate, long-pubescent, aestivation valvate; corolla white or yellowish, sympetalous, tube urceolate, glabrous, lobes oblong, porrect, aestivation imbricate; stamens 4, filaments short, adnate to the corolla tube, anthers deeply included; gynoecium bicarpellate, ovary ovoid, densely covered with moniliform trichomes, style terminal, apically with two minute, papillose stylodia, stigma capitate; nectar disc possibly present at ovary base. *Fruit* small, dry, broadly pear-shaped in lateral view, deeply 4-lobed, apically beaked from sterile apex of ovary, coarsely and irregularly pubescent, sparsely and irregularly verrucose to spinose, largely enclosed into strongly accrescent calyx, tardily (post-dispersal) separating into four 1-seeded, oblique pear-shaped nutlets, sterile chambers absent, pericarp weakly lignified and cork-like in structure.

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, 1862; Bentham & Hooker, 1976; Baillon, 1891; Gürke, 1893; Johnston, 1924; Chadefaud & Emberger, 1960; Takhtajan, 1987). Richardson (1976) demonstrated that the two genera are distantly related based on morphology, 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 habit, frondose inflorescences, flat (not plicate) cotyledons, and fruits separating in four apically beaked and spinose nutlets.

Cordiaceae R.Br. ex Dumort., Anal. Fam. Pl.: 20, 25. 1829, nom. cons. – Type: *Cordia* L.

= Sebestenaceae Vent., Tabl. Règn. Vég. 2: 380. 1799 ("Sebestenae").

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

= Cordioideae Beilschm. in Flora 16(1, Beibl.): 69, 106. 1833 ("Cordiaceae", p. 69; "Cordieae", p. 106).

Trees, shrubs, or rarely lianas, indumentum often pubescent with stiff trichomes, sometimes hispid or glabrescent. *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 corymbo-thyrsoid. *Flowers* pentamerous, rarely tetramerous, rarely more perianth elements, bisexual and often distylous, occasional unisexual and dioecious; calyx united in a tube,

tubular to campanulate, lobes lanceolate to ovate, aestivation valvate; corolla white, or rarely yellow, sympetalous, tubular to campanulate or rotate, lobes distinct or not, erect to spreading, aestivation imbricate; stamens (4–)5(–15), filaments generally adnate to the corolla tube, at least at the base, sometimes puberulent at the point of insertion, anthers usually exerted; gynoecium bicarpellate, ovary tetralocular from secondary subdivision, style terminal, **stigmatic branches 4,** stigma clavate to capitate; nectar disc usually present at ovary base. *Fruits* drupaceous with 4 locules, each 1-seeded, occasionally 3 locules aborting and drupes asymmetric, or fruits ellipsoid and fibrous-walled and dispersed with the marcescent corolla, generally with a slightly to greatly accrescent calyx.

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 of his series "Studies in the Boraginaceae" (Johnston, 1930, 1935, 1949, 1950, 1951) recognized a broadly defined *Cordia* with 5–7 sections (see also 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. Cordiaceae is the only family in Boraginales with **plicate cotyledons** and generally a twice-dichotomous style with four stigmatic branches. Cordiaceae have been recognized as a family or as part of the Heliotropiaceae or Boraginaceae (see Appendix 1).

Ehretiaceae Mart., Nov. Gen. Sp. Pl. 2: 136, 138. 1827, nom. cons. – Type: *Ehretia* P.Browne.
= Ehretieae Dumort., Anal. Fam. Pl.: 25. 1829.
= Ehretioideae Arn., Botany [preprint from Encycl. Brit., ed. 7, 5]: 122. 1832 ("Ehretieae").

Trees, shrubs, perennial herbs, rarely with thorns (*Rochefortia*), indumentum variable, hirsute to glabrescent. *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 and dioecious in *Lepidocordia* Ducke and *Rochefortia*; calyx lobes united in a tube or distinct nearly to the base, tubular to campanulate, aestivation imbricate (mostly quincuncial); corolla white, red or blue (*Halgania* Gaudich., some *Bourreria* P.Browne), sympetalous, generally tubular with spreading lobes, rotate, or campanulate to urceolate, aestivation imbricate; stamens 5, the filaments generally adnate to the corolla tube at least at the base, sometimes puberulent at the point of insertion, anthers usually exerted; gynoecium bicarpellate, ovary one to tetralocular from secondary subdivision, style terminal, stigmatic branches (1)2, stigma clavate to capitate; nectar disc usually present at ovary base. *Fruits* generally drupaceous, often drying and separating into two two-seeded pyrenes, or 4 1-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 this parasitic family. 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). Ehretiaceae have been variously included in Boraginaceae, Cordiaceae, Heliotropiaceae, or defined in a strict sense as a family of their own (see Appendix 1).

Heliotropiaceae Schrad. in Commentat. Soc. Regiae Sci. Gott. Recent. 4: 192. 1819, nom. cons. – Type: *Heliotropium* L.
= Heliotropieae Dumort., Fl. Belg.: 39. 1827.
= Tournefortieae Bartl., Ord. Nat. Pl.: 197. 1830 ("Tournefortiea").
= Heliotropioideae Arn., Botany [preprint from Encycl. Brit., ed. 7, 5]: 122. 1832 ("Heliotropieae").

Annual or perennial herbs, subshrubs, shrubs, lianas or small trees, indumentum pubescent, often strigose, sericeous or glandular. *Leaves* alternate, usually entire, very rarely crenate or dentate, often revolute, petiolate or sessile, lamina linear to suborbicular. *Inflorescences* terminal or axillary, thyrsoids, partial inflorescences scorpioid cymes. *Flowers* pentamerous, bisexual, rarely unisexual; calyx mostly divided nearly to base, lobes linear to ovate, usually pubescent, tube usually short, mostly campanulate, aestivation valvate; corolla white, yellow, blue, pink or orange, sympetalous, with subcircular to linear lobes, aestivation (sub-)valvate, apert-duplicative, imbricate (quincuncial or cochlear); stamens 5, filaments adnate to the corolla tube, anthers usually included; gynoecium bicarpellate, ovary usually 4-locular, **style terminal with a conical stigmatic head having a basal ring-shaped stigma and a sterile, sometimes 2-lobed apex;** nectar disc present at ovary base. *Fruit* dry or fleshy, usually 4-seeded, rarely 1–2-seeded, sometimes with sterile chambers, separating into 1–4 nutlets with 1–2 seeds each.

Four genera (Appendix 2) with ca. 450 species of worldwide distribution, especially in the tropics and subtropics. The family comprises the type genus *Heliotropium* (incl. *Tournefortia* L.) and the genera *Euploca* Nutt., *Ixorhea* Fenzl (monospecific) 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, which is a synapormorphy for this family. Heliotropiaceae also have been recognized as a subfamily of Boraginaceae, included in Ehretieae in its entirety, or split into Heliotropioideae and Ehretioideae (see Appendix 1).

Hoplestigmataceae Gilg in Engler & Gilg, Syllabus, ed. 9 & 10: 322. 1924, nom. cons. – Type: *Hoplestigma* Pierre.
= Hoplestigmateae Reveal in Phytoneuron 2012-33: 2. 2012.

Trees, indumentum pubescent to glabrescent. *Leaves* alternate, entire, petiolate, obovate, abaxially hirsute. *Inflorescences* terminal thyrsoids, with dichasial paracladia. *Flowers* 10–15-merous, bisexual, borne in cymes with subscorpioid branches; calyx torn into uneven lobes, united in a tube, lobes ovate, densely villous, irregularly rupturing at anthesis; corolla white, sympetalous, **with 11–14 deeply divided lobes,** aestivation imbricate; **stamens 20–30** in three irregular series, free from corolla, anthers included; gynoecium bicarpellate, ovary unilocular with four pendulous anatropous ovules, style terminal, stigmatic branches 2, stigma capitate; nectar disc possibly present at ovary base. *Fruits* drupaceous included in a slightly accrescent calyx, endocarp undivided, with four seeds and two additional sterile chambers.

A single 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, with some uncertainty, in Ebenales (Gilg, 1908; Wagenitz, 1964), Bixales (Hutchinson, 1959), Violales, and in Boraginales (see Appendix 1).

Hydrophyllaceae R.Br. in Bot. Reg. 3: ad t. 242. 1817, excl. gen., nom. cons. – Type: *Hydrophyllum* L.
= Hydrophyllineae Link, Handbuch 1: 570. 1829.
= Romanzoffieae Dumort., Anal. Fam. Pl.: 26. 1829 ("Romanzoviaceae").
= Hydrophylleae Rchb., Fl. Germ. Excurs.: 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 Benth. ex A.Gray in Proc. Amer. Acad. Arts 10: 312. 1875.
= Hydrophyllinae Reveal in Phytoneuron 2012-33: 2. 2012.
= Phaceliinae Reveal in Phytoneuron 2012-37: 218. 2012.
= Romanzoffiinae Reveal in Phytoneuron 2012-37: 218. 2012.

Annual, biennial, or perennial **herbs,** indumentum usually scabrid to hispid, often glandular. *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; calyx lobes united at base or nearly to apex, linear to cordate, aestivation valvate; corolla commonly blue to purple, but also white, pink or yellow, sympetalous, corolla scales present, small or absent, aestivation contorted or imbricate; stamens 5 of equal or unequal length, filaments equally or unequally adnate to the corolla tube, anthers usually included; gynoecium bicarpellate, ovary unilocular or bilocular, sometimes the two large, fleshy parietal placentae filling the locule at anthesis, ovary thus appearing 2- or 5-celled, or placentae narrow, cartilaginous, partially or completely dividing ovary, style 1, terminal, stigmatic branches 2, stigma capitate; nectar disc present or reduced to glands at ovary base. *Fruit* a membranaceous capsule appearing 2-celled, dehiscence loculicidal with 2 valves, 1–many-seeded.

Twelve genera (Appendix 2) with about 240–260 species restricted to North and Central America and western South America. The family comprises the type genus *Hydrophyllum* and *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, unpub. data). Gray (1875) defined Hydrophyllaceae to include Hydrophylleae, Phacelieae, Namaeae, and Hydroleae in Hydrophyllaceae, a delimitation followed by most modern authors, but Hydrophyllaceae have also been regarded as a member of Boraginaceae (see Appendix 1).

Lennoaceae Solms in Abh. Naturf. Ges. Halle 11: 174. 1870, nom. cons. – Type: *Lennoa* Lex.
= Pholismateae Horan., Char. Ess. Fam.: 109. 1847 ("Pholisma").
= Lennooideae Torr. in Ann. Lyceum Nat. Hist. New York 8: 56. 1854 ("Lennoeae").
= Lennoeae Baill., Hist. Pl. (Baillon) 11: 161, 207. 1891.

***Parasitic* herbs,** without chlorophyll, indumentum shortly pubescent, often glandular. *Leaves* reduced to cataphylls. *Inflorescences* terminal, densely spicate or capitate cymose-thyrsoids. *Flowers* (4)5–9(10)-merous, bisexual; calyx tubular or divided nearly to base, 6–10-lobed, the lobes narrow, puberulent to tomentose, with glandular trichomes, aestivation valvate; corolla lilac to bluish purple, rarely pink or mauve, sympetalaous, tubular with 5–10 lobes, aestivation imbricate; stamens the same number as the corolla lobes, filaments adnate to the corolla tube, the free portion very short, anthers included; gynoecium **5–16-carpellate**, ovary 10–32-locular, style terminal, simple and undivided, stigma capitate; nectar disc absent. *Fruits* capsular, irregularly **circumscissile,** releasing 10–32 pyrenes.

Two genera (*Lennoa*, *Pholisma* Nutt. ex Hook.) and four species of achlorophyllous root holoparasites distributed in southwestern North America, Mexico, and northwestern South America. The family is distinct in its parasitic habit and 10–32-locular gynoecium. Its fruits are highly unusual, with circumscissile dehiscence and the seeds enclosed in hardened tissue and released as pyrenes. Lennoaceae have been associated with Primulaceae (La Llave & Lexarza, 1824), Orobanchaceae (Hooker, 1844), Ericales (Bentham & Hooker, 1876; Engler, 1898), Cuscutaceae (Conzatti & Smith, 1909), or Boraginineae, or have been treated either as a subfamily in Boraginaceae, or a family of Boraginales (see Appendix 1).

Namaceae Molinari in Weberbauerella 1(7): 2. 2016 – Type: *Nama* L.
= Nameae Choisy in Candolle, Prodr. 10: 182. 1846.
= Namoideae A.W.Benn. in J. Linn. Soc., Bot. 11: 266. 1870.

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

Shrubs or small, soft-wooded trees, or herbaceous (only *Nama*), erect, or decumbent, with well-developed tap-root, rarely rhizomatous (only *Eriodictyon*), usually densely pubescent with uni-cellular and pluricellular, glandular trichomes, sometimes with stinging hairs and/or resinous, rarely tomentose or glabrate. *Leaves* cauline only, alternate, simple, subsessile to distinctly long-petiolate, margin entire to coarsely serrate or lobed, usually densely pubescent. *Inflorescences* terminal or axillary, thyrsoidal, usually of boragoids (see Glossary), sometimes congested, bracteose or frondose. *Flowers* pentamerous, bisexual; calyx lobes united at base or nearly to apex, aestivation valvate; corolla white to purple or lavender, sympetalous, tubular, infundibuliform to campanulate, usually pubescent, aestivation imbricate; stamens 5, equal or unequal in length, equally or unequally adnate to the corolla tube, staminal appendages present or absent sometimes only filament bases dilated, anthers included; gynoecium bicarpellate, ovary bilocular, placentae narrow, membranaceous or cartilaginous, completely dividing ovary, style terminal, stylodia 2, distinct to base or connate ¾ of length (= stylar branches, only *Nama* sect. *Conanthus*), stigma bilobate; nectar disc present at ovary base. *Fruit* a capsule appearing 2-celled, dehiscing loculicidally or loculicidally and septicidally, with 2 or 4 valves, respectively, 2–many-seeded.

Four genera (*Eriodictyon* Benth., *Nama*, *Turricula* J.F. Macbr., *Wigandia* Kunth) with a total of ca. 75 species in the Americas and the Caribbean, and 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 successive sisters to *Turricula* (Walden, unpub. data). *Nama* was first included in Hydroleaceae along with *Hydrolea* (Brown, 1818). Hydroleaceae was later transferred to Hydrophyllaceae (Bentham & Hooker, 1976) and retained there until recently (e.g., Davenport, 1988). Based on phylogenetic studies (Cosner & al., 1994; Soltis & al., 2000), *Hydrolea* was excluded from Hydrophyllaceae and placed as a monogeneric family in Solanales (see Appendix 1).

Wellstediaceae Novák in Prát, Rostlinopis 9: 530. 1943 – Type: *Wellstedia* Balf.f.

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

Small densely branched herbs or shrublets, indumentum sericeous, acroscopically appressed. *Leaves* cauline, sometimes some basal, often alternate and distichous on branches, simple, sessile or petiolate, oblanceolate, ovate or obovate. *Inflorescences* axillary cymes or reduced to single flowers. *Flowers* **tetramerous,** bisexual; calyx deeply divided, lobes linear-lanceolate, abaxially pubescent, aestivation valvate; corolla pink to white or yellowish, sympetalous, deeply divided into four lobes, tube inside with 4 protrusions often fused into a distinct rim, aestivation imbricate; stamens 4, filaments free, anthers included; gynoecium bicarpellate, ovary bilocular, style terminal with two short stigmatic lobes, stigma bilobate; nectar disc absent. *Fruit* a bivalved capsule; seeds one, rarely two, asymmetrically ovoid in lateral view, **strongly laterally compressed,** pubescent, often with ring of longer hairs near funicular pole.

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 a subfamily of Boraginaceae and treated as such by most authors, although some authors have also regarded it as an independent family (see Appendix 1).

■ GLOSSARY

Anthoclade: Frondose inflorescences with extended growth and elongating internodes, resembling vegetative branches of the plant.

Boragoid: A modified cincinnus with the consecutive branches aligned more or less in the direction of the main axis causing the flowers to be pushed aside and appearing like solitary axillary flowers borne on a main axis (Buys & Hilger, 2003).

Drupe: A fruit where the—usually single—seed is enclosed in a hardened (sclerenchymatic or lignescent) inner layer of the fruit wall (endocarp), whereas the outer layers of the fruit wall (ovary wall in Boraginales) are parenchymatic, often soft and succulent, sometimes spongiose or fibrous.

Endocarp: The inner, sometimes undifferentiated, sometimes hardened (sclerenchymatic or lignescent) layers of the fruit wall enclosing the seed or seeds.

Eremocarp: A nutlet going back to part of the (united) ovary via *ab initio* separate development, i.e., not arising via secondary subdivision during fruit development (= schizocarp). It consists of one, very rarely two seeds enclosed by a dry pericarp and showing a basal or adaxial abscission line (forming a closed-line figure: circular, elliptical, triangular). Part of the ovary, called replum or gynobase, remains attached to the mother plant (Hilger, 2014).

Pyrene: Descriptive term for the (central) part of a fruit comprising a hardened (sclerenchymatic or lignescent) endocarp and the seed(s) enclosed. Usually a single one per fruit, rarely several seeds are separately enclosed in endocarps (e.g., Lennoaceae). The pyrene wall is ruptured during germination to release the seedling.

Schizocarp: A fruit separating completely into individually dispersed seed-bearing units, typically comprising part of the fruit wall and seeds (mericarps).

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Appendix 1. Systematics of Boraginales according to different authors.

This work	Jussieu (1789)	Berchtold & Presl (1820)	Dumortier (1829)	Lindley (1831)
Codonaceae	?	?	–	–
Wellstediaceae	–	–	–	–
Boraginaceae	Boraginaceae II, III, IV	Boraginales	Boraginaceae – Lithospermeae, Boraginaceae – Cerintheae, Boraginaceae – Echieae (Boraginales)	Boraginaceae
Hydrophyllaceae	Boraginaceae II	Ellisiales	Hydrophyllaceae (Boraginales)	Hydrophyllaceae
Namaceae	Convolvulaceae	Hydroleales	Hydroleaceae (Convolvulales)	Hydroleaceae
Heliotropiaceae	Boraginaceae I, II, III	Boraginales	Boraginaceae – Heliotropieae (Boraginales)	Heliotropiaceae/Ehretiaceae
Ehretiaceae	Boraginaceae I	Boraginales	Cordiaceae – Ehretieae (Boraginales)	Ehretiaceae
Lennoaceae	–	–	–	–
Coldeniaceae	Boraginaceae III	Boraginales	Boraginaceae – Heliotropieae (Boraginales)	?
Hoplestigmataceae	–	–	–	–
Cordiaceae	Boraginaceae I	Sebestanales	Cordiaceae – Cordieae (Boraginales)	Cordiaceae
[Hydroleaceae (Solanales)]	Convolvulaceae	Hydroleales	Hydroleaceae (Convolvulales)	Hydroleaceae
[Tetrachondraceae (Lamiales)]	–	–	–	–

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Appendix 1. Continued.

This work	Endlicher (1836)	Candolle (1845, 1846, 1873)	Bentham & Hooker (1876)	Baillon (1891)
Codonaceae	Hydroleaceae (Tubiflorae)	?Hydroleaceae	Hydrophyllaceae – Phacelieae (Polemoniales)	Boraginaceae – Phacelieae
Wellstediaceae	–	–	–	–
Boraginaceae	Asperifoliaceae – Borageineae (Nuculiferae)	Boraginaceae – Borageineae, Cerintheae, Echieae, Lithospermeae, Craniospermeae, Anchuseae, Cynoglosseae	Boraginaceae – Borageineae (Polemoniales)	Boraginaceae – Borageineae, Boraginaceae – Echieae, Boraginaceae – Harpagonelleae
Hydrophyllaceae	Hydrophyllaceae (Tubiflorae)	Hydrophyllaceae	Hydrophyllaceae – Hydrophylleae, Hydrophyllaceae – Phacelieae (Polemoniales)	Boraginaceae – Hydrophylleae, Boraginaceae – Phacelieae
Namaceae	Hydroleaceae (Tubiflorae)	Hydroleaceae-Nameae	Hydrophyllaceae – Nameae (Polemoniales)	Boraginaceae – Phacelieae
Heliotropiaceae	Asperifoliaceae – Ehretieae (Nuculiferae)	Boraginaceae – Ehretieae, Boraginaceae – Heliotropieae	Boraginaceae – Heliotropieae (Polemoniales)	Boraginaceae – Heliotropieae
Ehretiaceae	Asperifoliaceae – Ehretieae (Nuculiferae)	Boraginaceae – Ehretieae	Boraginaceae – Ehretieae (Polemoniales)	Boraginaceae – Ehretieae
Lennoaceae	dubiae sedis	Lennoaceae	Lennoaceae (Ericales)	
Coldeniaceae	Asperifoliaceae – Ehretieae (Nuculiferae)	Boraginaceae – Heliotropieae	Boraginaceae – Ehretieae (Polemoniales)	Boraginaceae – Ehretieae
Hoplestigmataceae	–	–	–	–
Cordiaceae	Cordiaceae (Nuculiferae)	Boraginaceae – Cordieae	Boraginaceae – Cordieae (Polemoniales)	Boraginaceae – Cordieae
[Hydroleaceae (Solanales)]	Hydroleaceae (Tubiflorae)	Hydroleaceae – Hydroleae	Hydrophyllaceae – Hydroleae (Polemoniales)	Boraginaceae – Hydroleae
[Tetrachondraceae (Lamiales)]	–	–	–	–

Appendix 1. Continued.

This work	Engler (1893, 1908, 1915)	Engler (1898)	Chadefaud & Emberger (1960)	Takhtajan (1980)
Codonaceae	Hydrophyllaceae – Phacelieae	Hydrophyllaceae – Phacelieae (Boraginineae)	Hydrophyllaceae (Tubiflorales)	Hydrophyllaceae (Boraginineae – Polemoniales)
Wellstediaceae	Boraginaceae – Wellstedioideae	–	Boraginaceae – Wellstedioideae (Tubiflorales)	Boraginaceae (Boraginineae – Polemoniales)
Boraginaceae	Boraginaceae – Boraginoideae	Boraginaceae – Boraginoideae (Boraginineae)	Boraginaceae – Boraginoideae (Tubiflorales)	Boraginaceae (Boraginineae – Polemoniales)
Hydrophyllaceae	Hydrophyllaceae – Hydrophylleae, Hydrophyllaceae – Phacelieae	Hydrophyllaceae – Hydrophylleae, Hydrophyllaceae – Phacelieae (Boraginineae)	Hydrophyllaceae (Tubiflorales)	Hydrophyllaceae (Boraginineae – Polemoniales)
Namaceae	Hydrophyllaceae – Nameae	Hydrophyllaceae – Nameae (Boraginineae)	Hydrophyllaceae (Tubiflorales)	Hydrophyllaceae (Boraginineae – Polemoniales)
Heliotropiaceae	Boraginaceae – Heliotropioideae	Boraginaceae – Heliotropioideae (Boraginineae)	Boraginaceae – Heliotropioideae (Tubiflorales)	Boraginaceae (Boraginineae – Polemoniales)
Ehretiaceae	Boraginaceae – Ehretioideae	Boraginaceae – Ehretioideae (Boraginineae)	Boraginaceae – Ehretioideae (Tubiflorales)	Boraginaceae (Boraginineae – Polemoniales)
Lennoaceae	Lennoaceae	Lennoaceae (Ericales)	Lennoaceae (Tubiflorales)	Lennoaceae (Boraginineae – Polemoniales)
Coldeniaceae	Boraginaceae – Ehretioideae	Boraginaceae – ?Ehretioideae (Boraginineae)	Boraginaceae – Ehretioideae (Tubiflorales)	Boraginaceae (Boraginineae – Polemoniales)
Hoplestigmataceae	Hoplestigmataceae	–	Hoplestigmataceae (Tubiflorales)	Hoplestigmataceae (Boraginineae – Polemoniales)
Cordiaceae	Boraginaceae – Cordioideae	Boraginaceae – Cordioideae (Boraginineae)	Boraginaceae – Cordioideae (Tubiflorales)	Boraginaceae (Boraginineae – Polemoniales)
[Hydroleaceae (Solanales)]	Hydrophyllaceae – Hydroleae	Hydrophyllaceae – Hydroleae (Boraginineae)	Hydrophyllaceae – Hydroleae (Tubiflorales)	Hydrophyllaceae (Boraginineae – Polemoniales)
[Tetrachondraceae (Lamiales)]	–	–	Tetrachondraceae (Tubiflorales)	?Lamiaceae (Lamiales)

This work	Dahlgren (1980)	Cronquist (1981, 1988)	Takhtajan (1987)	Thorne (1992)
Codonaceae	Hydrophyllaceae (Boraginales)	Hydrophyllaceae (Solanales)	Hydrophyllaceae (Boraginales)	Hydrophyllaceae (Boraginineae – Solanales)
Wellstediaceae	Wellstediaceae (Boraginales)	Boraginaceae (Lamiales)	Wellstediaceae (Boraginales)	Boraginaceae (Boraginineae – Solanales)
Boraginaceae	Boraginaceae (Boraginales)	Boraginaceae (Lamiales)	Boraginaceae (Boraginales)	Boraginaceae (Boraginineae – Solanales)
Hydrophyllaceae	Hydrophyllaceae (Boraginales)	Hydrophyllaceae (Solanales)	Hydrophyllaceae (Boraginales)	Hydrophyllaceae (Boraginineae – Solanales)
Namaceae	Hydrophyllaceae (Boraginales)	Hydrophyllaceae (Solanales)	Hydrophyllaceae (Boraginales)	Hydrophyllaceae (Boraginineae – Solanales)
Heliotropiaceae	Boraginaceae (Boraginales)	Boraginaceae (Lamiales)	Boraginaceae (Boraginales)	Boraginaceae (Boraginineae – Solanales)
Ehretiaceae	Ehretiaceae (Boraginales)	Boraginaceae (Lamiales)	Ehretiaceae (Boraginales)	Boraginaceae (Boraginineae – Solanales)
Lennoaceae	Lennoaceae (Boraginales)	Lennoaceae (Lamiales)	Lennoaceae (Boraginales)	Lennoaceae (Boraginineae – Solanales)
Coldeniaceae	Ehretiaceae (Boraginales)	Boraginaceae (Lamiales)	Ehretiaceae (Boraginales)	Boraginaceae (Boraginineae – Solanales)
Hoplestigmataceae	Hoplestigmataceae (Boraginales)	Hoplestigmataceae (Violales)	Hoplestigmataceae (Boraginales)	Hoplestigmataceae (Boraginineae – Solanales)
Cordiaceae	Ehretiaceae (Boraginales)	Boraginaceae (Lamiales)	Cordiaceae (Boraginales)	Boraginaceae (Boraginineae – Solanales)
[Hydroleaceae (Solanales)]	Hydrophyllaceae (Boraginales)	Hydrophyllaceae (Solanales)	Hydrophyllaceae (Boraginales)	Hydrophyllaceae (Boraginineae – Solanales)
[Tetrachondraceae (Lamiales)]	?	Lamiaceae (Lamiales)	Lamiaceae (Lamiales)	Tetrachondraceae (Boraginineae – Solanales)

Appendix 1. Continued.

This work	Takhtajan (1997)	APG (1998, 2003); Mabberley (2008)	Takhtajan (2009)	APG (2009)
Codonaceae	Hydrophyllaceae (Boraginales)	Boraginaceae (Euasterids I unplaced)	Hydrophyllaceae – Codonoideae (Boraginales)	Boraginaceae (lamiids unplaced)
Wellstediaceae	Boraginaceae (Boraginales)	Boraginaceae (Euasterids I unplaced)	Boraginaceae – Wellstedioideae (Boraginales)	Boraginaceae (lamiids unplaced)
Boraginaceae	Boraginaceae (Boraginales)	Boraginaceae (Euasterids I unplaced)	Boraginaceae – Boraginoideae (Boraginales)	Boraginaceae (lamiids unplaced)
Hydrophyllaceae	Hydrophyllaceae (Boraginales)	Boraginaceae (Euasterids I unplaced)	Hydrophyllaceae – Hydrophylloideae (Boraginales)	Boraginaceae (lamiids unplaced)
Namaceae	Hydrophyllaceae (Boraginales)	Boraginaceae (Euasterids I unplaced)	Hydrophyllaceae – Hydrophylloideae (Boraginales)	Boraginaceae (lamiids unplaced)
Heliotropiaceae	Boraginaceae (Boraginales)	Boraginaceae (Euasterids I unplaced)	Boraginaceae – Heliotropioideae (Boraginales)	Boraginaceae (lamiids unplaced)
Ehretiaceae	Boraginaceae (Boraginales)	Boraginaceae (Euasterids I unplaced)	Boraginaceae – Ehretioideae (Boraginales)	Boraginaceae (lamiids unplaced)
Lennoaceae	Lennoaceae (Boraginales)	Boraginaceae (Euasterids I unplaced)	Lennoaceae (Boraginales)	Boraginaceae (lamiids unplaced)
Coldeniaceae	Boraginaceae (Boraginales)	Boraginaceae (Euasterids I unplaced)	Boraginaceae – Ehretioideae (Boraginales)	Boraginaceae (lamiids unplaced)
Hoplestigmataceae	Hoplestigmataceae (Boraginales)	Hoplestigmataceae (unplaced)	Hoplestigmataceae (Boraginales)	Boraginaceae (lamiids unplaced)
Cordiaceae	Boraginaceae (Boraginales)	Boraginaceae (Euasterids I unplaced)	Boraginaceae – Cordioideae (Boraginales)	Boraginaceae (lamiids unplaced)
[Hydroleaceae (Solanales)]	Hydrophyllaceae (Boraginales)	Hydroleaceae (Solanales)	Hydroleaceae (Solanales)	Hydroleaceae (Solanales)
[Tetrachondraceae (Lamiales)]	Tetrachondraceae (Boraginales)	Tetrachondraceae (Lamiales)	Tetrachondraceae (Lamiales)	Tetrachondraceae (Lamiales)

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

Appendix 2. Accepted genera of Boraginales (bold) and generic synonyms (regular). Number of species and distribution are indicated for each accepted genus. Number of genera/number of species is indicated for families. 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 not yet verified by molecular data. Abbreviations: Afr: Africa; Am: America; Arab: Arabian Peninsula; Aus: Australia; Cal: California; Eur: Europe; Ind: India; Med: Mediterranean region; Neotrop: Neotropical; pantrop: pantropical; subcsmop: subcosmopolitan; trop: tropical.

BORAGINACEAE Juss. (~90/~1600–1700)
Actinocarya Benth. = *Microula*
***Adelinia** J.I.Cohen (1) N Am
***Adelocaryum** Brand (3) Arab & Ind
Aegonychon Gray (3) Asia & Eur
***Afrotysonia** Rauschert (3) E Afr
Aipyanthus Steven = *Huynhia*
Alkanna Tausch (~40) Med & SW Asia
Allocarya Greene = *Plagiobothrys*
Allocaryastrum Brand = *Plagiobothrys*
Amblynotopsis J.F.Macbr. = *Antiphytum*
Amblynotus I.M.Johnst. = *Eritrichium*
Amphibologyne Brand = *Antiphytum*
Amsinckia Lehm. (~15) N & S Am
Anchusa L. (~35) Afr, Eur, W Asia
Anchusella Bigazzi, Nardi & Selvi (2) Med
Anchusopsis Bisch. = *Cynoglossum*
Ancistrocarya Maxim. (1) Japan & Korea
***Andersonglossum** J.I.Cohen (3) N Am
Anisanthera Raf. = *Caccinia*
Anoplocaryum Ledeb. (5) C Asia
Antiotrema Hand.-Mazz. (1) W China
Antiphytum DC. ex Meisn. (10) N & S Am
Argyrexias Raf. = *Echium*
Arnebia Forssk. (~30) NE Afr, SE Eur, SW & C Asia
Arnebiola Chiov. = *Arnebia*
Asperugo L. (1) Asia & Eur
Austrocynoglossum Popov ex R.R.Mill = *Hackelia*
Baphorhiza Link = *Alkanna*
Batschia J.F.Gmel. = *Lithospermum*
Bessera Schult. = *Pulmonaria*
Bilegnum Brand = *Cynoglossum*
Boraginella Siegesb. ex Kuntze = *Trichodesma*
Boraginodes T.Post & Kuntze = *Trichodesma*
Borago L. (5) W Med
Borraginoides Moench = *Trichodesma*
Bothriospermum Bunge (5) C & E Asia
Brachybotrys Maxim. ex Oliv. (1) NE Asia
Brandella R.R.Mill = *Microparacaryum*
Brunnera Steven (3) W Asia & SE Med
Buglossa Gray = *Lycopsis*
Buglossites Moris = *Borago*
Buglossoides Moench (2) Eur, N Afr & W Asia
Buglossum Mill. = *Anchusa*
Caccinia Savi (~6) Iran to S & C Asia
Camptocarpus Decne. = *Alkanna*
Campylocaryum DC. ex A.DC. = *Alkanna*
Caryolopha Fisch. & Trautv. = *Pentaglottis*
Casselia Dumort. = *Mertensia*
Cerinthe L. (7–10) Eur, NW Afr to W Asia
Cerinthodes Kuntze = *Mertensia*
Cerinthopsis Kotschy ex Paine = *Cynoglossum*
Cervia Rodrig. ex Lag. = *Rochelia*
Chamissoniophila Brand = *Antiphytum*
Chilechium Pfeiff. = *Echiochilon*
Chilochium Raf. = *Echiochilon*
Chionocharis I.M.Johnst. (1) C Asia
Choriantha Riedl = *Onosma*
Colsmannia Lehm. = *Onosma*
Craniospermum Lehm. (4–5) C & E Asia
Crucicaryum Brand = *Cynoglossum*
Cryptantha Lehm. ex G.Don (~160) N & S Am
Cynoglossopsis Brand = *Cynoglossum*
Cynoglossospermum Kuntze = *Lappula*
Cynoglossum L. (180–200) subcosmop
Cynoglottis (Guşul.) Vural & Kit Tan (2) Eur & Anatolia
Cyphomattia Boiss. = *Cynoglossum*
Cyphorima Raf. = *Lithospermum*
Cystostemon Balf.f. (~15) SW Arab, trop Afr
Dasynotus I.M.Johnst. (1) N Am
Decalepidanthus Riedl (7) Himalayas
Dioclea Spreng. = *Arnebia*
Diploloma Schrenk = *Craniospermum*
Echidiocarya A.Gray ex Benth. & Hook.f. = *Plagiobothrys*
Echinoglochin Brand = *Plagiobothrys*
Echinospermum Sw. ex Lehm. = *Lappula*
Echiochilon Desf. (15) N Afr to SW Asia, Macaronesia, Pakistan & W Ind
Echiochilopsis Caball. = *Echiochilon*
Echioides Fabr. = *Lycopsis*
Echioides Moench = *Myosotis*
Echioides Ortega = *Huynhia*
Echiopsis Rchb. = *Lobostemon*
Echiostachys Levyns (3) S Afr
Echium L. (~60) N Afr, Eur, Macaronesia, W Asia
Elizaldia Willk. = *Nonea*
Embadium J.M.Black = *Hackelia*
Endogonia Lindl. = *Trigonotis*
***Eremocarya** Greene = *Cryptantha*
Eritrichium Schrad. ex Gaudin (~50) N Am, Asia, Eur
*Exarrhena R.Br. = *Myosotis*
Exioxylon Raf. = *Echiochilon*
Friedrichsthalia Fenzl = *Trichodesma*
Gastrocotyle Bunge (2) N Afr, Arab, S Balkans
Glandora D.C.Thomas, Weigend & Hilger (8) N Afr & S Eur
Glochidocaryum W.T.Wang = *Microula*
Glyptocaryopsis Brand = *Plagiobothrys*
***Greeneocharis** Gürke & Harms = *Cryptantha*
Gruvelia A.DC. = *Pectocarya*
Gymnoleima Decne. = *Moltkia*
*Gymnomyosotis (A.DC.) O.D.Nikif. = *Myosotis*
***Gyrocaryum** Valdés (1) Spain
Hackelia Opiz (~45) N & S Am, Asia, Aus, Eur
Halacsya Dörfl. (1) Balkans
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*
Hormuzakia Guşul. (2) SE Med
Huynhia Greuter (2) Turkey & Caucasus area
Iberodes M.Serrano, R.Carbajal & S.Ortiz (~7) W Med
Isoplesion Raf. = *Echium*
Isorium Raf. = *Lobostemon*
Ivanjohnstonia Kazmi = *Cynoglossum*
***Johnstonella** Brand = *Cryptantha*
Krynitzkia Fisch. & Mey. = *Cryptantha*
Ktenospermum Lehm. = *Pectocarya*
Kuschakewiczia Regel & M.Smirn. = *Cynoglossum*
Lacaitaea Brand = *Trichodesma*
Lappula Moench (50–60) N Am, N Afr, Asia, Aus, Eur
Larephes Raf. = *Echium*
Lasiarrhenum I.M.Johnst. = *Lithospermum*
Lasiocaryum I.M.Johnst., (3) C Asia
Leiocarya Hochst. = *Trichodesma*
Lepechiniella Popov (~6) NE Afr to SW Asia
Leptanthe Klotzsch = *Arnebia*
Leurocline S.Moore = *Echiochilon*
*Lindelofia Lehm. = *Cynoglossum*
Lithodora Griseb. (3–5) N Afr, W & SE Eur, SW Asia
Lithospermum L. (~80) Afr, N & S Am, Eur
Lobostemon Lehm. (~30) S Afr
Lycopsis L. (2) W Asia & Eur
Maccoya F.Muell. = *Plagiobothrys*
Macromeria D.Don = *Lithospermum*
Macrotomia DC. = *Arnebia*
Maharanga DC. (9) C & E Asia
Mairetis I.M.Johnst. (1) NW Afr
Mapuchea M.Serrano, R.Carbajal & S.Ortiz = *Selkirkia*
Margarospermum (Rchb.) Opiz = *Aegonychon*
Massartina Maire = *Nonea*
Mattia Schult. = *Cynoglossum*
*Mattiastrum (Boiss.) Brand = *Cynoglossum*
Megacaryon Boiss. = *Echium*
Megastoma (Benth. & Hook.f.) Coss. & Durieu ex Bonnet & Barratte = *Ogastemma*
Melanortocarya Selvi, Bigazzi, Hilger & Papini (1) SE Med
Memoremea A.Otero, Jim.-Mejías, Valcárcel & P.Vargas (1) Eur
Meneghinia Endl. = *Arnebia*
Meratia A.DC. = *Moritzia*
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*
Moltkia Lehm. (6) S Eur & SW Asia
Moltkiopsis I.M.Johnst. (1) NE Afr & SW Asia
Moritzia DC. ex Meisn. (3) S Am
Munbya Boiss. = *Arnebia*
Myosotidium Hook. (1) Chatham Islands
Myosotis L. (80–100) subcosmop
Neatostema I.M.Johnst. (1) Med & Macaronesia
Nephrocarya P.Candargy = *Nonea*
Nesocaryum I.M.Johnst. (1) San Ambrosio
Nihon A.Otero, Jim.-Mejías, Valcárcel & P.Vargas (5) Japan
Nomosa I.M.Johnst. = *Lithospermum*
Nonea Medik. (~35) N Afr, W Asia, Eur
Nordmannia Ledeb. ex Nordm. = *Trachystemon*
Octosomatium Gagnep. = *Trichodesma*
Ogastemma Brummitt (1) N Afr to Arab
Omphalium Wallr. = *Omphalodes*
Omphalodes Mill. (20–25) N Am, Asia, Eur
Omphalolappula Brand = *Lappula*
***Omphalotrigonotis** W.T.Wang (1) E Asia
Oncaglossum Sutorý (1) Mexico

Appendix 2. Continued.

Onochilis Mart. = *Alkanna*
Onosma L. (~150) NW Afr, Eur, Asia
Onosmodium Michx. = *Lithospermum*
Oplexion Raf. = *Lobostemon*
****Oreocarya*** Greene = *Cryptantha*
Oreocharis Lindl. = *Mertensia*
Oreogenia I.M.Johnst. = *Lasiocaryum*
Oskampia Baill. = *Lycopsis*
Osmodium Raf. = *Lithospermum*
Paracaryopsis (Riedl) R.R.Mill = *Adelocaryum*
*Paracaryum Boiss. = *Cynoglossum*
Paracynoglossum Popov = *Cynoglossum*
Paramoltkia Greuter (1) Balkans
Paraskevia W.Sauer & G.Sauer = *Pulmonaria*
Pardoglossum Barbier & Mathez = *Cynoglossum*
Pectocarya DC. ex Meisn. (15) N & S Am
Pedinogyne Brand = *Trigonotis*
Pentaglottis Tausch (1) SW Eur
Pentalophus A.DC. = *Lithospermum*
Penthysa Raf. = *Lobostemon*
Perittostema I.M.Johnst. = *Lithospermum*
Phyllocara Guşul. (1) Irano-Turanian
Picotia Roem. & Schult. = *Omphalodes*
Piptocalyx Torr. = *Cryptantha*
Plagiobothrys Fisch. & C.A.Mey. (~70) N & S Am, NE Asia, Aus
Platynema Schrad. = *Mertensia*
Pneumaria Hill = *Mertensia*
Podonosma Boiss. (3) NE Afr, E Med & SW Asia
Pollichia Medik. = *Trichodesma*
Pontechium Böhle & Hilger (1) E Eur to W Asia
Procopiania Guşul. = *Symphytum*
Procopiphytum Pawł. = *Symphytum*
Pseudomertensia Riedl = *Decalepidanthus*
Psilolaemus I.M.Johnst. = *Lithospermum*
Psilostemon DC. = *Trachystemon*
Pulmonaria L. (~17) E Asia & Eur
Purshia Spreng. = *Lithospermum*
Raclathris Raf. = *Rochelia*
Rhytispermum Link = *Aegonychon*
*Rindera Pall. = *Cynoglossum*
Rochelia Rchb. (~15) Asia to W Eur
Sauria Bajtenov = *Eritrichium*
Sava Adans. = *Onosma*
Scapicephalus Ovcz. & Czukav. = *Decalepidanthus*
Schistocaryum Franch. = *Microula*
Sclerocaryopsis Brand = *Lappula*
Scorpioides Gilib. = *Myosotis*
Selkirkia Hemsl. (4) S Am, Juan Fernández
Sericostoma Stocks = *Echiochilon*
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*
****Stenosolenium*** Turcz. (1) NE Asia
*Stephanocaryum Popov = *Trigonotis*
Stomotechium Lehm. = *Echium*
Streblanthera Steud. = *Trichodesma*
Strobila G.Don = *Arnebia*
*Strophiostoma Turcz. = *Myosotis*
Suchtelenia Karel. ex Meisn. (1) C Asia
Symphytum L. (~35) W Asia & Eur
Tetaris Lindl. = *Arnebia*
Tetraedrocarpus O.Schwartz = *Echiochilon*
Thaumatocaryon Baill. (3) S Am
Thyrocarpus Hance (3) Asia
*Tianschaniella B.Fedtsch. = *Eritrichium*
Toxostigma A.Rich. = *Arnebia*
*Trachelanthus Kunze = *Cynoglossum*
Trachystemon D.Don (1) E Med
Traxara Raf. = *Lobostemon*
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*
Ulugbekia Zakirov = *Lithospermum*
Umbilicaria Heist. ex Fabr. = *Omphalodes*
Vaupelia Brand = *Cystostemon*
Wheelerella G.B.Grant = *Cryptantha*
Winkleria Rchb. = *Mertensia*
Zoelleria Warb. = *Trigonotis*
Zwackhia Sendt. = *Halacsya*

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 Torr. & 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 Torr. & A.Gray = *Tiquilia*
Rhabdia Mart. = *Ehretia*
Rochefortia Sw. (9) Neotrop
Rotula Lour. = *Ehretia*
Stegnocarpus Torr. & 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*

Appendix 2. Continued.

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*

HOPLESTIGMATACEAE Gilg (1/2)
Hoplestigma Pierre (2) W Afr

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. (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.Watson (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 Cham. (5) w N Am
Tricardia Torr. (1) sw N Am
Viticella Mitch. = *Nemophila*
Whitlavia Harvey = *Phacelia*

LENNOACEAE Solms (2/4)
Ammobroma Torr. ex A.Gray = *Pholisma*
Corallophyllum Kunth = *Lennoa*
Lennoa Lex. (1) N to S Am
Pholisma Nutt. ex Hook. (3) N Am

NAMACEAE Molinari (4/71)
Andropus Brand = *Nama*
Conanthus S.Watson = *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