Heliotropiaceae

Heliotropiaceae Schrad., Commentat. Soc. Regiae Sci. Gott. Recent. 4: 192 (1819), nom. cons.

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Annual or perennial herbs, subshrubs, shrubs, lianas or small trees; hermaphrodite or rarely unisexual and dioecious; indumentum of simple, unicellular, eglandular trichomes, sometimes with glandular cells. Leaves alternate, petiolate or sessile, exstipulate; lamina linear to suborbicular, margin usually entire, very rarely crenate or dentate, often revolute; apex mostly acute or acuminate; base cuneate or decurrent. Inflorescences thyrsoids, terminal or axillary; partial inflorescences scorpioid cymes. Flowers perfect, rarely unisexual, actinomorphic, chasmogamous, sessile or shortly pedicellate; calyx tube usually short, mostly campanulate, calyx lobes often unequal, linear to ovate, glabrous to densely hairy, mostly persistent after anthesis; corolla sympetalous, with subcircular to linear lobes; androecium haplostemonous, stamens antesepalous and borne on corolla tube, usually included, filaments short, linear; anthers dorsifixed, usually linear, tetrasporangiate; gynoecium superior, syncarpous, bicarpellate, usually 4-loculate with one ovule in each locule; ovule anatropous to hemitropous, unitegmic, tenuinucellate; style terminal with a conical stigmatic head with a basal ring-shaped stigma and a sterile, sometimes two-lobed apex; nectary disk at the base of the ovary. Fruit dry or fleshy, usually 4-seeded, rarely 1–2-seeded, falling apart into 1–4 mericarpids with 1–2 seeds each. Embryo minute, straight to curved, embedded in thin endosperm, cotyledons linear to ovoid.

Four genera with ca. 450 species in the tropical, subtropical and temperate zones of all continents, most diverse in seasonally dry habitats.

Vegetative Morphology. The family comprises predominantly woody species, i.e. shrubs or subshrubs, but annual or perennial herbs are also common. Tall shrubs and small trees are common in Neotropical *Heliotropium* species. Tall, woody lianas are typical of *Myriopus* and rare in *Heliotropium*. Some species in both *Euploca* and *Heliotropium* are very small (<10 cm), ephemeral herbs in semiarid areas. The leaves are usually evergreen in perennial taxa. Phyllotaxy is alternate, rarely pseudo-opposite or pseudo-alternate in some *Heliotropium* species (Figs. 39A, G, N, 40A, I). The primary root is always well developed and persistent, sometimes secondarily thickened into a root tuber (Fig. 39G). Rhizomes and underground stolons are occasionally found in *Heliotropium*. Adventitious roots are profusely developed in some *Euploca*.

Vegetative Anatomy. The leaves are usually bifacial. Isobilateral leaves occur in *Ixorhea*, *Euploca* and *Heliotropium*. Kranz chlorenchyma organisation is found in *Euploca* (Diane et al. 2003). Calcium oxalate crystals in the leaves are widespread (Diane et al. 2003). The indumentum consists of mostly unicellular, eglandular trichomes, rarely interspersed with uniseriate gland-tipped trichomes with a few-celled stalk which can secrete resinous exudates covering the surface of stems and leaves (DiFulvio 1982). Trichome surface varies from smooth to sculptured with papillae. The primary cortex is composed of chlorenchymatic, collenchymatic and parenchymatic layers, frequently with isolated sclerenchymatic strands. The xylem is mostly dif-

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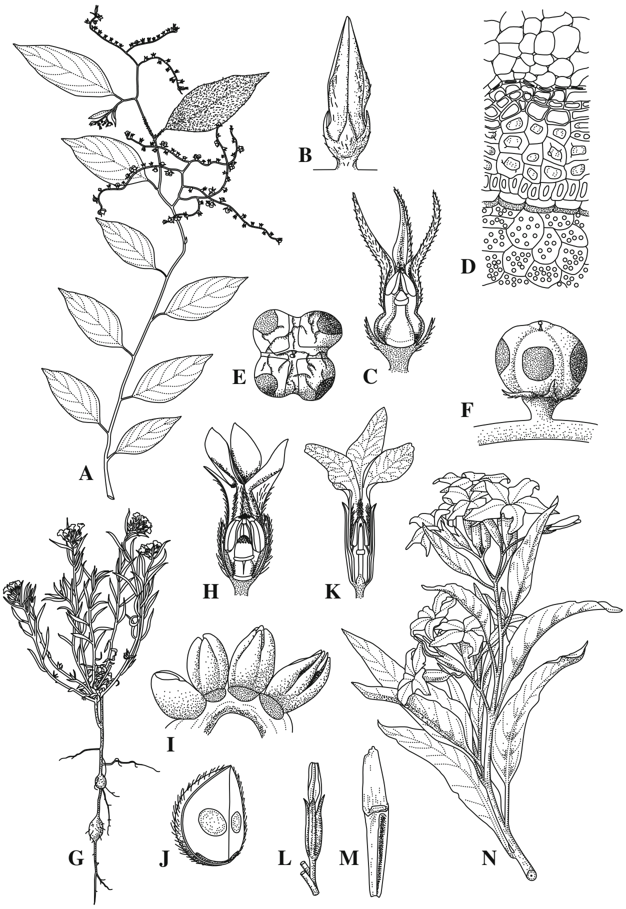

Fig. 39. Heliotropiaceae. **A–F** *Myriopus volubilis*. **A** Habit (after Nowicke 1969). **B** Bud. **C** Dissected flower. **D** Transverse section of endocarp. **E** Fruit in top view. **F** Fruit in lateral view. **G** *Euploca mendocina*. Habit, with root tuber. **H–J** *Euploca procumbens*. **H** Dissected flower. **I** Buds; the three right buds with dissected calyx. **J** Mericarpids with pits. **K–N** *Ixorhea tschudiana* (**L–N** after Di Fulvio 1978). **K** Dissected flower. **L** Bud. **M** Winged mericarpid. **N** Habit. (orig., drawn by Horst Lünser)

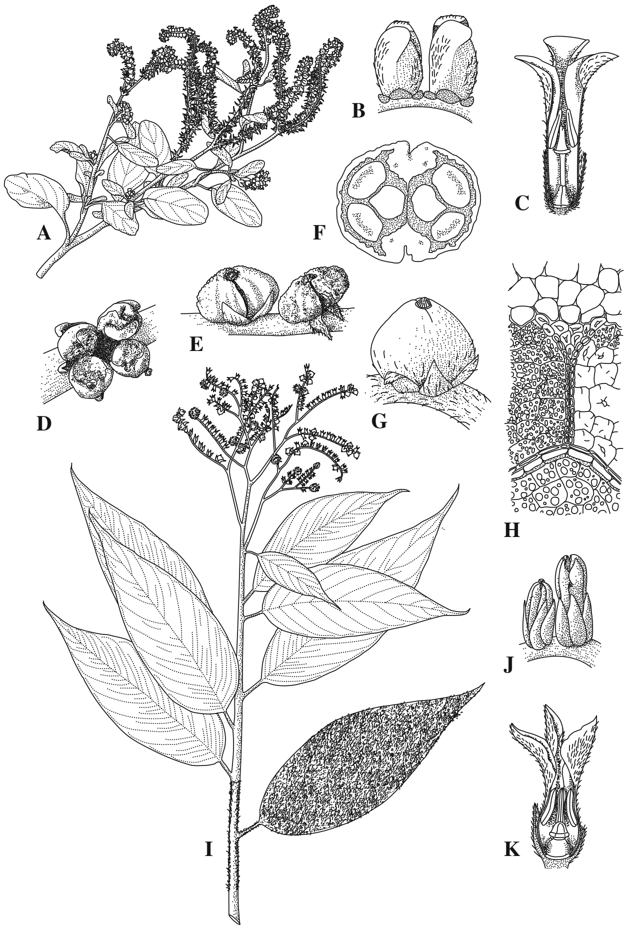

Fig. 40. Heliotropiaceae. **A** *Heliotropium europaeum*. Habit. **B, C** *Heliotropium nelsonii*. **B** Buds with dissected calyx. **C** Dissected flower. **D** *Heliotropium curassavicum*. Fruit. **E** *Heliotropium angiospermum*. Fruits. **F** *Heliotropium nicotianifolium*. Transverse section of fruit. **G** *Heliotropium verdcourtii*. Fruit in lateral view. **H** *Heliotropium angiospermum*. Transverse section of endocarp. **I–K** *Heliotropium verdcourtii*. **I** Habit (after Nowicke 1969). **J** Buds. **K** Dissected flower. (orig., drawn by Horst Lünser)

fuse-porous to semi-ring porous. Vessels are clustered in groups of two or three, and have simple perforation plates. The ground tissue of the wood is composed of tracheids, fibre-tracheids, and libriform fibres. Axial parenchyma is apotracheal diffuse, diffuse-in-aggregates, and paratracheally banded. The rays are one to three cells wide and usually less than twenty cells high, heterogeneous, and composed of square to upright marginal cells. Suberization occurs in the hypodermal layer of *Heliotropium* and *Myriopus*.

Inflorescence Structure. Inflorescences are mostly terminal, rarely axillary thyrsoids with 1–∞ monochasial branches. The monochasial branches are scorpioid cymes, so-called boragoids (Buys and Hilger 2003; Figs. 39A, G, N, 40A, I). Bracts are usually absent, the flowers are well-spaced (especially in *Myriopus*, Fig. 39A), or more or less condensed (most *Heliotropium*, Fig. 40A), but then internodes sometimes elongate postanthetically. In *Euploca* the terminal thyrsoids are usually reduced either to monochasial or dichasial cymoids or to an axillary monochasium with only one flower developing.

FLOWER STRUCTURE. The flowers are mostly sessile to short-pedicellate, rarely long-pedicellate (*Ixorhea*). The calyx is synsepalous, mostly divided nearly to base and shows imbricate quincuncial aestivation. Corolla aestivation varies among genera: *Myriopus* is characterized by subvalvate aestivation with involute corolla lobes (Fig. 39B); *Euploca* by usually apert aestivation (rarely indistinctly cochlear) and involute corolla lobes (Fig. 39I). *Ixorhea* and some *Heliotropium* are characterized by apert-duplicative aestivation sometimes with spirally twisted corolla lobes (Figs. 39L, 40J). *Heliotropium* shows various aestivation types, cochlear aestivation being the most frequent type (Fig. 40B). The anthetic corolla is always sympetalous with usually spreading corolla lobes (Figs. 39C, H, K, 40C, K) which are mostly shorter than the tube, but can be elongated in some taxa (e.g. *H. zeylanicum*). *Myriopus* differs from all other taxa in having long and narrow corolla lobes with involute margins (Fig. 39C). A peculiar character is the presence of compact scales inside the corolla tube (e. g. *H. hirsutissimum*, *H. arbainense*). The androecium is haplostemonous, the stamens are antesepalous, the short and linear filaments insert at different levels on the inside of the corolla tube. The stamens are usually included in the corolla tube (Figs. 39C, H, K, 40C, K). The anthers have 4 pollen sacs and are basifixed, usually linear, rarely ovoidal to cordate, and open with introrse longitudinal slits. Anthers with conspicuously protracted connectives are found in all genera, with the apex smooth in *Ixorhea* (Fig. 39K), papillose in *Myriopus* (Fig. 39C), and pubescent in *Euploca* (Fig. 39H) and some *Heliotropium*. The connectives are apically coherent and close the corolla tube above the style-stigma complex, except in *Ixorhea*, where connectives do not surpass the apex of the stigmatic head. In *Heliotropium* (except section *Heliothamnus*) the anthers are apically free (Fig. 40C, K). The gynoecium is bicarpellate, syncarpous, superior, and usually 4-loculate with one anatropous to hemitropous ovule in each locule. Altogether, four mostly basal septa form chambers which completely surround the ovules and separate them from each other (Hilger 1992). Placentation is axile. Only *Myriopus* has a well-developed placenta consisting of transfer cells (Diane et al. 2002). The style is terminal and terminates in a conical stigmatic head with a basal ring-shaped stigma and a sterile, sometimes two-lobed apex (Khaleel 1978; Figs. 39C, H, L, 40C, K); the sterile apex is usually glabrous, rarely pubescent. Style and stigma morphology are taxonomically useful for differentiation and characterisation of species. The conical stigmatic head with its sterile apex is the key synapomorphy of Heliotropiaceae within the Boraginales.

EMBRYOLOGY. Detailed embryological studies are available only for some species of *Heliotropium* (e.g. Khaleel 1978, 1985) and *Ixorhea* (DiFulvio 1978): the ovules are unitegmic and have been described as tenuinucellar with ab initio cellular endosperm and distinctive micropylar and chalazal haustoria. The functional archesporial cell or the nucellar epidermis undergo periclinal divisions forming a parietal layer capping the archaesporial cell which functions as megaspore mother cell. Thus, the ovule appears to be crassinucellate at the beginning of megasporogenesis. Embryo-sac development is of the Polygonum type. The innermost layer of the integument forms an integumentary tapetum. Three types of embryology have been reported so far: *Ixorhea* conforms to the Chenopodiad type, and *Heliotropium* to the Chenopodiad, Solanad or Onagrad type. The anther wall is 4-layered with bi- or multinucleate tapetal cells, and a small amount of microsporogenous tissue. Microsporogenesis is simultaneous, producing tetrahedrally arranged pollen tetrads. The pollen grains are binucleate at anthesis.

POLLEN MORPHOLOGY. Pollen grains are spheroidal to prolate in outline, mostly subprolate with a circular or 6-lobed, very rarely a subtriangular polar shape. The most common pollen type is 6-heterocolporate. The sporoderm is always tectate. The exine is mostly psilate to rugulose, sometimes reticulate along the pseudocolpi. This typical pollen morphology is generally found in *Myriopus*, *Ixorhea* and *Heliotropium*. Various modifications of this pollen type can be found (Nowicke and Skvarla 1974; Perveen et al. 1995; Scheel et al. 1996). The pollen of *Euploca* is always spheroidal to prolate with a circular, rarely a quadrangular polar shape and a psilate to rugulose exine, but showing a vast range of aperture types and numbers (Perveen et al. 1995).

Karyology. Only few chromosome counts are available. Base numbers apparently range from $x = 7$ to $x = 13$, both polyploidy and aneuploidy seem to be common. *Euploca* has base chromosome numbers of $x = 7$ and $x = 8$, and the ploidy levels vary from $2x$ to $8x$. Old World *Heliotropium* has a base number of $x = 8$ and the species are usually di- or tetraploid, rarely hexaploid; exceptions are $2n = 26$ in *H.* (= *Argusia*) *sibiricum* and $2n = 28$ in *H. zeylanicum* and *H. ophioglossum*. In *Heliotropium* sect. *Heliothamnus*, $n = 9$ was reported for *H. arborescens* (Britton 1951). In other New World *Heliotropium*, base numbers are higher and tetraploids exist at least in *Heliotropium veronicifolium* and *H. curassavicum* (DiFulvio 1969). One chromosome count each is available for *Myriopus* ($n = 12$) and *Ixorhea* ($2n = 10$), and no count is available for *Heliotropium* sect. *Cochranea*.

Pollination. The frequent occurrence of yellow nectar guides in the flowers, UV-patterns (Frohlich 1976), the secretion of nectar, and an often intense floral scent in *Euploca* and *Heliotropium* suggest insect pollination (Knuth 1899, 1905). Our own observations document that the flowers of *Heliotropium* sect. *Heliothamnus* and sect. *Cochranea* are visited by insects, especially Lepidoptera. The anthers are positioned above the stigma and self-fertilization is thus very likely when the plants are self-compatible.

Fruit and Seed. The fruits are usually 4-seeded, rarely 1–2-seeded, falling apart into 1- or 2-seeded mericarpids (Figs. 39E, F, J, M, 40D, E, G). Dry mericarpids with a dry, brown, glabrous exocarp and a thin and dry mesocarp are the most common type. Fleshy fruits seem to have evolved several times independently within Heliotropiaceae. Typical drupes have a white to bright orange exocarp and a juicy mesocarp (all species of *Myriopus* and some *Heliotropium*, Figs. 39E, F, 40G). Some taxa have a brown to black exocarp and a more or less dry to spongiose mesocarp (some species of *Euploca* and some *Heliotropium*). The endocarp is homogenous, and sclerified with ligneous, strongly thickened cell walls filling the cell lumina (Fig. 40H). Sometimes one or more empty cells are found next to the locules in some species-groups of *Heliotropium* (Johnston 1928; Fig. 40F). Calcium oxalate crystals (mostly druses and crystal sand) are usually embedded in the cell walls of the endocarp. All Heliotropiaceae except *Myriopus* have a clear, longitudinal dehiscence line in the endocarp (Fig. 40H). The testa consists of an epidermis of transfer cells with protuberances of the inner tangential and radial cell walls (Diane et al. 2002) and a few inner layers of thin-walled cells, persisting or not. *Myriopus* has a 4-layered endocarp (Fig. 39D). All species investigated have a long suspensor. The embryo is straight in *Ixorhea* and *Heliotropium*, and curved in *Euploca* and *Myriopus*.

Dispersal. The dry or drupaceous fruits seem to reflect alternative mechanisms of dispersal, though only anecdotal evidence is available. Endozoochory can be assumed for drupaceous fruits present in *Myriopus* and *Heliotropium*. Air-filled empty chambers in mericarpids (several species of *Heliotropium*), a spongiose mesocarp (e.g. *H. foertheri*, *H. gnaphalodes*) or inflated calyces (*H. supinum*, *H. drepanophyllum*) suggest adaptations to hydrochory. In some species of *Euploca*, elaiosomes are found in two pits on the adaxial side of each mericarpid (Fig. 39J) and myrmecochory has been inferred (Craven 1996). *Euploca serpylloides* shows postfloral elongation of the pedicel, and *E. hypogaea* is geocarpic. The long-winged mericarpids of *Ixorhea* (Fig. 39M) and some *Heliotropium* species such as *H. pterocarpum* are probably anemochorous.

Phytochemistry. Pyrrolizidine alkaloids (PAs) are present in Heliotropiaceae (Culvenor 1978; Boppré 2011). The PAs are composed of necines (aminoalcohols) and necic acid and are also occasionally found in the form of nitrogen oxides. All hepatotoxic PAs consist of unsaturated necines (with a 1,2 double bond) and show esterification of the CH_2OH groups in the side chains. The most frequently found compounds are mono- and diester PAs. Flavonoids and aromatic geranyl derivatives have been reported to be present in the resinous exudates of some species of *Heliotropium* sect. *Cochranea* (Urzúa et al. 2000).

Subdivision and Affinities. Generic limits have been drawn very differently in the past (De Candolle 1845; Gürke 1893; Johnston 1935; Förther 1998; Hilger and Diane 2003). Förther (1998) recognized ca. 450 species in eight genera, i.e. *Argusia*, *Ceballosia*, *Heliotropium*, *Hilgeria*, *Ixorhea*, *Nogalia*, *Schleidenia* and *Tournefortia*. Most species were placed in the two large genera *Heliotropium* and *Tournefortia*, while the other genera mostly had only one to three species. Molecular studies (Hilger and Diane 2003; Luebert and Wen 2008; Luebert et al. 2011) indicate that Heliotropiaceae consist of two large clades with the position of *Ixorhea* still uncertain. The first clade is composed of *Myriopus* (=*Tournefortia* sect. *Cyphocyema*) and *Euploca* (incl. *Hilgeria*, *Schleidenia*, *Heliotropium* sect. *Orthostachys*), and is morphologically characterized by curved embryos and involute corolla aestivation. *Ixorhea* seems to be sister to these two genera (Weigend et al. 2014), but its position still needs to be confirmed. The remaining groups of the family constitute the second large clade, treated here as the genus *Heliotropium*, which in turn consists of four well-supported subclades: (i) *Heliotropium* sect. *Heliothamnus*, (ii) Old World *Heliotropium* (incl. *Argusia*, *Ceballosia*, *Nogalia*), (iii) *Heliotropium* sect. *Cochranea* and (iv) all remaining New World sections of *Heliotropium* plus *Tournefortia* sect. *Tournefortia*. The inclusion of *Tournefortia* sect. *Tournefortia*, as well as the genera *Argusia*, *Ceballosia* and *Nogalia*, in *Heliotropium* (Craven 2005) is in accordance with molecular phylogenetic evidence (Hilger and Diane 2003; Luebert and Wen 2008; Luebert et al. 2011) and is supported by morphology (Hilger and Diane 2003; Diane et al. 2003). Heliotropiaceae have mostly been treated as a subfamily of Boraginaceae s.l. (together with the subfamilies Cordioideae, Ehretioideae and Boraginoideae). Molecular phylogenetic analyses show that this Boraginaceae s.l. is paraphyletic in relation to Hydrophyllaceae and Lennoaceae, and contains clear subclades (Ferguson 1999; Gottschling et al. 2001). Gottschling et al. (2001), based on ITS sequences, and our own unpublished results based on plastid sequence data suggest that Heliotropiaceae are sister to the family Ehretiaceae (incl. Cordioideae and Lennoaceae), but other studies based only on the plastid gene *ndhF* (e.g. Ferguson 1999; Luebert and Wen 2008) fail to resolve clear sister relationships.

Distribution and Habitats. Heliotropiaceae are distributed worldwide, mainly in tropical and subtropical zones. *Heliotropium* is most diverse in temperate and subtropical zones such as the Mediterranean, the Irano-Turanian region and southern South America, frequently dominating the vegetation of dry, disturbed areas, but the genus is also diverse in montane and alpine environments of the Neotropics. *Euploca* has centres of diversity in Africa, Australia, and the tropical and subtropical regions of the Americas where it is most abundant and diverse in semiarid habitats. *Myriopus* is essentially restricted to dry forest in the Caribbean and Central America south to central Peru and northern Argentina. *Ixorhea* is a xerophyte endemic to north-western Argentina.

Palaeobotany. Heliotropiaceae fossils are poorly documented, and only pollen grains of *Heliotropium* have been reported (as *Tournefortia*). Pollen ascribed to the *Tournefortia bicolor* type (Muller 1981 = pollen type III of Nowicke and Skvarla 1974) has been recorded by Graham and Jarzen (1969) from the Oligocene of Puerto Rico and by Graham (1976) and Graham and Dilcher (1998) from the middle Pliocene of Mexico.

Economic Importance. Reviews of the economic use of Heliotropiaceae have been provided by Al-Shehbaz (1991) and Förther (1998). Extracts from some species show significant antitumor activity. The resin of some species of *Heliotropium* sect. *Cochranea* have compounds with antioxidant, antibacterial and antiviral properties. Various species of Heliotropiaceae are cultivated as ornamentals (e.g. *Heliotropium arborescens*, *H. amplexicaule*). *Heliotropium arborescens* is also used in the perfume industry. *Heliotropium* species which contain unsaturated pyrrolizidine alkaloids are noxious weeds poisonous to livestock if they contaminate hay and are also dangerous to humans if food grain is contaminated with their fruits (Boppré 2011).

Key to the Genera

1. Shrubs with glandular trichomes only, covered with strongly scented resin, especially after drying; flowers long-pedicellate; corolla limb broader than 2 cm in diameter; fruit with 4 apically winged mericarpids; endemic to north-western Argentina **1. *Ixorhea***

– Annuals to trees or lianas with numerous eglandular and with or without glandular trichomes, usually without strong scent after drying; flowers sessile or sub-sessile; corolla limb not broader than 1.5 cm in diameter; fruit with 1–4 wingless or laterally winged mericarpids 2

2. Anthers apically glabrous, connectives not protracted **4. *Heliotropium***

– Anthers with pubescent or papillose apex, connectives protracted 3

3. Corolla lobes subulate; anthers apically papillose; fruit with fleshy mesocarp; lianas or subscandant shrubs **2. *Myriopus***

– Corolla lobes rounded; anthers with pubescent apex; fruit dry, without fleshy mesocarp; annuals, perennial herbs or erect shrubs 4

4. Stigmatic apex pubescent; anthers apically coherent; calyx lobed to 1/3–1/2; embryo curved **3. *Euploca***

– Stigmatic apex glabrous; anthers rarely coherent apically; calyx lobed nearly to base; embryo straight **4. *Heliotropium***

GENERA OF HELIOTROPIACEAE

1. ***Ixorhea*** Fenzl Fig. 39K–N

Ixorhea Fenzl, Verh. K. K. Zoolog.-Bot. Ges. Wien 36: 287 (1886).
Oxyosmyles Speg. (1901).

Shrub; entire plant, except corolla limb, densely glandular, covered with an aromatic, varnish-like, glutinous resin. Leaves alternate to pseudo-opposite, lanceolate, margin entire. Inflorescences branched, ebracteose, few-flowered. Calyx tubular, lobed to 1/3 to 1/4; corolla whitish to violet-rose, lobes triangular; aestivation apert-duplicative; anthers long protracted, connectives not surpassing the apex of the stigmatic head; style long, stigmatic head long protracted. Fruit dry, separating into one-seeded, apically winged mericarpids. Embryo straight. $2n = 10$.

One species, *Ixorhea tschudiana* Fenzl, endemic to north-western Argentina (provinces Salta and Tucumán).

2. ***Myriopus*** Small Fig. 39A–F

Myriopus Small, Manual Southeast. Fl. 1131 (1933); Johnston, Contr. Gray Herb. 92: 66–89 (1930), reg. rev. as *Tournefortia* sect. *Cyphocyema*; Johnston, J. Arnold Arbor. 16: 46–56 (1935), reg. rev. as *Tournefortia* sect. *Cyphocyema*; Macbride, Fl. Peru 5(2): 540–553 (1960), reg. rev.; Miller, Ann Missouri Bot. Gard. 75 456–521 (1988), reg. rev. as *Tournefortia* sect. *Cyphocyema*; Feuillet, J. Bot. Res. Inst. Texas 2(1): 263–265 (2008), reg. rev. *Tournefortia* L. sect. *Cyphocyema* I.M. Johnst. (1930).

Lianas, rarely subscandant shrubs. Leaves alternate to pseudo-opposite, lanceolate to ovate, margin entire, glabrous to sericeous. Inflorescence 1–∞-branched, ebracteose. Calyx lobed to 1/2 or nearly to base; corolla orange, yellow, greenish, lobes subulate, margins involute, base of corolla tube inflated; anthers long protracted with papillose apex, apically coherent, closing the corolla tube; style long, stigmatic head truncate-cylindrical. Fruit fleshy, deeply 4-lobed, white or bright orange, with four one-seeded mericarpids. Embryo curved. $2n = 24$.

About 25 spp. in the Caribbean, Central and South America.

3. ***Euploca*** Nutt. Fig. 39G–J

Euploca Nutt., Trans. Amer. Phil. Soc. II, 5: 189 (1836); Johnston, Contr. Gray Herb. 81: 3–83 (1928), reg. rev. as *Heliotropium* sect. *Orthostachys*; Verdcourt, Fl. Trop. E. Africa, Boraginaceae: 51–77 (1991), reg. rev. as *Heliotropium* sect. *Orthostachys*; Craven, Aust. Syst. Bot. 9: 521–657 (1996), reg. rev. as *Heliotropium* sect. *Orthostachys*; Förther, Sendtnera 5: 35–241 (1998), rev. as *Heliotropium* sect. *Orthostachys*, *Hilgeria* and *Schleidenia*.
Heliotropium L. sect. *Orthostachys* (R. Br.) G. Don (1831).
Preslaea Mart. (1827) nom. illeg. non *Preslia* Opiz (1824).
Schleidenia Endl. (1839).
Hilgeria Förther (1998).

Annual or perennial herbs or small shrubs. Leaves alternate, rarely pseudo-opposite, linear to (ob)ovate. Indumentum variable, rarely glabrous. Inflorescences unbranched or 1–4-branched, ebracteose, bracteose, frondose, or reduced to solitary, axillary flowers. Calyx lobed 1/3 to 1/2 of length; corolla white to yellow, lobes subcircular to ovate-acuminate, lobes involute in bud; anthers long protracted with pubescent apex, apically coherent, closing the corolla tube. Fruit dry, separating into one-seeded mericarpids each with two pits on the abaxial side, rarely dry drupes. Embryo curved. $2n = 14, 24, 28, 32, 42, 48$.

About 100 species, cosmopolitan with centres of diversity in Africa, Australia, and tropical America.

The name *Preslaea* Mart. (1827) is older than *Euploca* Nutt. (1836). However, there is established practice in considering *Preslaea* Mart. and the earlier name *Preslia* Opiz (1824, Lamiaceae) as homonyms, which makes *Preslaea* Mart. illegitimate. This practice dates back to Endlicher (1839: 646), who noticed the homonymy and created the replacement name *Schleidenia*. This has been followed in treatments by *Heliotropium* specialists (Johnston 1928: 46; Förther 1998: 133), in general works (Meissner 1839: 187; De Candolle 1845: 557; Post and Kuntze 1904: 459) as well as in the treatment of the Brazilian Heliotropiaceae (Fresenius [in Martius] 1857: 33), from where the type species (*Preslaea paradoxa* Mart. ≡ *Euploca paradoxa* (Mart.) J.I.M. Melo & Semir ≡ *Schleidenia paradoxa* (Mart.) DC.) comes. *Preslaea* Mart. has not been accepted or even used in any other recent work.

4. ***Heliotropium*** L. Fig. 40A–K

Heliotropium L., Sp. Pl. 1: 130 (1753); Johnston, Contr. Gray Herb. 81: 3–83 (1928), reg. rev.; Johnston, Contr. Gray Herb. 92: 66–89 (1930), reg. rev. as *Tournefortia* sect. *Eutournefortia*; Johnston, J. Arnold Arbor. 16: 46–56 (1935), reg. rev. as *Tournefortia* sect. *Eutournefortia*; Macbride, Fl. Peru 5(2): 540–568 (1960), reg. rev.; Johnston in Lundell et al., Fl. Texas 1: 138–160 (1964), reg. rev.; Gibson, Fieldiana, Bot. 24: 138–149, 157–167 (1970), reg. rev.; Brummit, Fl. Eur. 3: 84–86 (1972), reg. rev.; Popov, Fl. URSS 19: 86–113 (1974), reg. rev.; Miller, Ann Missouri Bot. Gard. 75: 456–521 (1988), reg. rev.; Nowicke and Miller, Revis. Handb. Fl. Ceylon 7: 18–20, 29–33 (1991), reg. rev.; Verdcourt, Fl. Trop. E. Africa, Boraginaceae: 48–77 (1991), reg. rev; Akhani and Förther, Sendtnera 2: 187–276 (1994), reg. rev.; Ge-ling et al., Fl. China 16: 329–427 (1995), reg. rev.; Craven, Aust. Syst. Bot. 9:521–657 (1996), reg. rev.; Förther, Sendtnera 5: 35–241 (1998), rev.

Argusia Böhm. (1760).

Ceballosia Kunkel ex Förther (1994).

Messerschmidia L. ex Hebenstr. (1763).

Nogalia Verdc. (1987).

Pittonia Mill. (1754).

Tiaridium Lehm. (1818).

Tournefortia L. (1753), nom. cons.

Annual or perennial herbs, subshrubs, shrubs or small trees, rarely scandent or lianescent. Leaves alternate to pseudo-opposite, rarely pseudoternate, linear to broadly ovate or obovate, margin entire to repand, rarely crenate, dentate, or pinnatisect, sometimes revolute, membranous to chartaceous, rarely succulent; indumentum variable, rarely glabrous. Inflorescence 1–∞-branched, ebracteose, many-flowered. Calyx lobed to 1/2 or nearly to base; corolla mostly white, green, rarely yellow, orange or purple; lobes subcircular, oblong to lanceolate; anthers sometimes protracted, apex usually glabrous, rarely pubescent; style short to long, sometimes not visible; stigmatic head obtuse to long protracted. Fruit dry or fleshy; dry fruits separating into one- or two-seeded mericarpids, rarely dry drupes, fleshy fruits unlobed, white, composed of usually two 2-seeded mericarpids, often with empty chambers. Embryo straight. $2n = 14, 16, 18, 22, 24, 26, 28, 32, 44, 48, 50, 52, 64$.

About 300 species. Cosmopolitan, with centres of diversity in the Irano-Turanian region and in the Neotropics.

The genus, as defined here, is monophyletic. *Heliotropium* sect. *Heliothamnus* I.M. Johnst. forms a well-supported monophylum sister to all other sections. The Old World sections of *Heliotropium* (*Heliotropium* sects. *Heliotropium*, *Chamaetropium* Griseb., *Monimantha* M.A. Franch., *Odontotropium* Griseb., *Pleurolasia* Bunge, *Pseudocoeloma* Förther, *Pterotropium* (DC.) Bunge, *Rutidotheca* (A.DC.) Verdc. and *Zeylanica* Förther) together with the synonymized genera *Argusia* and *Ceballosia* form another monophyletic group (Hilger and Diane 2003); relationships among these sections and their delimitation have been discussed in detail by Förther (1998) but still need to be clarified through more detailed phylogenetic studies. *Heliotropium* sect. *Cochranea* (Miers) Kuntze, endemic to the Atacama Desert, is also monophyletic (Luebert and Wen 2008), and is sister to a large clade comprising *Tournefortia* sect. *Tournefortia* and the remaining New World sections of *Heliotropium* (*Heliotropium* sects. *Coeloma* (DC.) I.M. Johnst., *Heliotrophytum* G. Don, *Hypsogenia* I.M. Johnst., *Plagiomeris* I.M. Johnst., *Platygyne* Benth., *Schobera* (Scop.) I.M. Johnst. and *Tiaridium* (Lehm.) Griseb., Johnston 1928; Förther 1998; Luebert et al. 2011). Several nomenclatural changes are still needed to transfer all *Tournefortia* to *Heliotropium* but should be preceded by a critical taxonomic revision of the former. The taxonomy of *Tournefortia* is chaotic due to plasticity, widespread variable species and weak character differentiation.

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