

## 7 Heliotropiaceae Schrad.<sup>8</sup>

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

**General description**—Annual or perennial herbs, subshrubs, shrubs, lianas or small trees, stem often with white pith, bark persistent or exfoliating later. Sometimes with thickened primary root or rhizomes. Indumentum of simple, unicellular, eglandular trichomes, scabrid, or hispid to sericeous, sometimes additionally with glandular cells, rarely exclusively glandular, or glabrous. Leaves alternate, rarely pseudo-opposite or pseudoternate, petiolate or sessile, estipulate; lamina linear to subcircular, margin usually entire; apex mostly acute or acuminate; base cuneate or decurrent; leaf surface flat or bullate; lamina mostly bifacial, rarely equifacial, or succulent. Inflorescences terminal or axillary, once to repeatedly, mostly dichasially branched; partial inflorescences scorpioid cymes, very rarely flowers apparently solitary and axillary; ebracteose, rarely bracteose to frondose. Flowers perfect, actinomorphic, chasmogamous, mostly sessile or shortly pedicellate; perianth heterochlamydeous; calyx tube usually short, mostly campanulate, calyx lobes often unequal, linear to ovate, glabrous to densely hairy; mostly persistent after anthesis, erect, or spreading to reflexed at fruit maturity; aestivation quincuncial; corolla sympetalous, aestivation imbricate cochlear, quincuncial, subvalvate or apert; throat without fornices; sometimes with five intercalary lobules between corolla lobes; corolla lobes ovate to rarely subulate, greenish, white, yellow, rarely orange to purple, sometimes with a nectar guide. Androecium haplostemonous, antesealous and epipetalous, usually included, filaments short, linear; anthers dorsifixed, usually linear, with 4 microsporangia; connective sometimes protracted into acuminate, trichomatose tip and anthers apically coherent; gynoecium superior, syncarpous, bicarpellate, lobed to unlobed, usually 4-loculate with one ovule in each locule; ovule anatropous,

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unitegmic, tenuinucellar; nectary disc at the base of the ovary; style terminal with a conical stigmatic head with a basal stigma and an infertile, sometimes two-lobed apex. Fruit usually 4-seeded, rarely 1--2 seeded, separating into 1--4 mericarpids with 1--2 seeds each, or drupes; embryo minute, straight to curved, embedded in thin endosperm, cotyledons linear to ovoid, never plicate.

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

## 7.1 Heliotropiaceae

**Vegetative Morphology**—The vast majority of taxa are woody plants, and this appears to be the plesiomorphic condition in Heliotropiaceae. Most species of the family are shrubs or subshrubs. Annual or perennial herbs evolved each several times independently from shrubby ancestors in *Euploca* and *Heliotropium*. Conversely, *Tournefortia*, a monophyletic group derived from *Heliotropium*, appears to have shrubby ancestors and contains small trees and lianas. *Myriopus* is largely a liana genus. The leaves of Heliotropiaceae are usually evergreen in perennial taxa. Phyllotaxy is alternate, rarely pseudo-opposite or pseudoternate in some *Tournefortia* species by a shortening of the internodes (Fig. 7-1 A, G, O, Fig. 7-2 A, K).

The primary root always is well developed and persistent, sometimes secondarily thickened into a root tuber in herbaceous taxa from seasonally dry habitats (e.g., *Euploca mendocina*, Fig. 7-1 G). Rhizomes (*H. arguzioides*), and underground stolons (*H. bacciferum*, *H. sibirica*), are occasionally found in *Heliotropium*. Adventitious roots are profusely developed in *Euploca* (*E. hypogaea*).

**Vegetative Anatomy**—The leaves are usually bifacial. Equifacial leaves occur in *Ixorhea*, *Euploca*, and *Heliotropium*. Kranz chlorenchyma organisation is found in *Euploca* (FROHLICH 1978, FÖRTHNER 1998, DIANE *et al.* in press b). Cystoliths of calcium oxalate crystals in the leaves are widespread in all genera (DIANE *et al.* submitted), mostly in the form of druses or sand (*Heliotropium*, *Ixorhea*, *Tournefortia*) or needles (*Myriopus*, *Euploca*).

The indumentum consists of mostly unicellular, eglandular trichomes, rarely interspersed with glandular trichomes with a uniseriate, one- to few-celled stalk. The trichomes are usually straight

and 0.5--8 mm long, often have a slightly bulbous base, sometimes with cystoliths, and vary in shape (METCALFE & CHALK 1950, KUMAR & RAO 1994, FÖRTHNER 1998, DIANE *et al.* in press b). Trichome surface sculpturing varies from smooth to papillose to (rarely) moniliform. Differences in trichome density and structure are often used for distinguishing species, but can be quite variable within taxa depending on ecological conditions. Characteristic trichome types are systematically useful at the generic level, e.g. the trichomes on a pedestal of distinctly enlarged epidermis cells of *Euploca* or the infrageneric level, e.g., the medifixed, two-armed trichomes of two sections of *Heliotropium* (sect. *Coeloma*, sect. *Ruditrothea*, FÖRTHNER 1998, DIANE *et al.* in press b). Absence of trichomes seems to be a derived character. The most aberrant indumentum in Heliotropiaceae is found in *Ixorhea*: Stem and leaves are covered by a strongly aromatic, varnish-like and glutinous resin secreted by 2-celled trichomes with a sessile glandular cell (DIFULVIO 1982).

Wood anatomy has been studied only in a few species of *Tournefortia* and *Heliotropium* (RECORD & HESS 1941, METCALFE & CHALK 1950, PAL 1963, KAMALA *et al.* 1989). Cork arises in the hypodermal layer and is thin-walled. It is well-developed in *Heliotropium*, *Tournefortia*, and *Myriopus*. The primary cortex is composed of chlorenchymatic, collenchymatic, and parenchymatic layers, frequently with isolated strands of sclerenchyma; a continuous ring of sclerenchyma sometimes occurs in *Tournefortia* (e.g. *T. hirsutissima*, *T. microcalyx*). In the cortex and secondary phloem of *Myriopus* large tetrahedral crystals are present, crystal druses are occasionally present in *Heliotropium*, whereas they are absent in *Tournefortia* (HEUBL *et al.* 1990). Growth rings are absent to distinct. The wood is mostly diffuse porous to semi-ring porous. Vessels are clustered in groups of two or three, and have simple perforation plates. Vestured pits in the vessels are only present in *Myriopus*. The ground tissue of the wood is composed of tracheids, fibre-tracheids, and libriform fibres. Axial parenchyma is apotracheal diffuse, diffuse-in-aggregates, and paratracheal banded. The rays are distinct, numerous and one to three cells wide and usually less than twenty cells high, heterogenous, and composed of square to upright marginal cells. Calcium oxalate crystals in the rays of *Tournefortia* and crystal druses in the rays of *Heliotropium* were reported by KAMALA (1989). Own observations indicate that *Myriopus* is characterized by poorly developed white, parenchymatous pith, whereas the pith of *Tournefortia* and *Heliotropium* is well developed and partly lignified at maturity. According to BAMBER & TER WELLE (1994) the wood of *Tournefortia* shows no specific adaptations to lianescent growth. Nothing is known about the wood anatomy of *Euploca* and *Ixorhea*.

**Inflorescence Structure**—Heliotropiaceae are rather conservative in inflorescence architecture. They mostly have terminal, rarely axillary thyrsoids with 1-- $\infty$  monochasial branches, rarely the inflorescence is reduced to a dichasium or monochasium. The monochasial branches are scorpioid cymes, so-called boragoids (SCHUMANN 1889, Fig. 7-1 A, G, O, Fig. 7-2 A, K). Bracts are usually absent, the flowers are well-spaced with long internodes (especially in *Myriopus*, Fig. 7-1 A), or more or less condensed with short internodes (most *Heliotropium*, Fig. 7-2 A), but then internodes sometimes elongate postantheically.

The genus *Euploca* differs from this basic type and two other inflorescence types can be distinguished. Some species have bracteose or frondose cymes, while in other taxa the inflorescences are reduced to a solitary, axillary flower (i.e., an axillary monochasium of which only one flower develops). Inflorescence structure has been used for subdividing *Euploca* into subsections (JOHNSTON 1928, under *Heliotropium* section *Orthostachys*), but molecular data have shown that only subsection *Ebracteata* constitutes a monophylum (DIANE *et al.* 2002a, Hilger & DIANE submitted).

**Flower Structure**—The flowers are mostly sessile to short-pedicellate, rarely long-pedicellate (species of *Euploca* with postfloral elongation of the pedicel, and *Ixorhea*). The calyx is synsepalous, mostly divided nearly to the base and shows imbricate quincuncial aestivation. Corolla aestivation seems to be a conservative character at the genus level: *Myriopus* is characterized by a subvalvate aestivation with involute corolla lobes in bud (Fig. 7-1 B). *Euploca* is characterized by usually apert aestivation (rarely indistinctly cochlear) and pre-anthetically involute corolla lobes (Fig. 7-1 I). *Ixorhea* and *Tournefortia* are characterized by an apert-duplicative aestivation sometimes with spirally twisted corolla lobes (Fig. 7-1 M, Fig. 7-2 M). *Heliotropium* shows various different aestivation types, cochlear aestivation is the most frequent type (Fig. 7-2 B, quincuncial, apert-introflex, apert-duplicative or vicinal-cochlear aestivation are much rarer). *Ixorhea* and some species of *Heliotropium* (*H. supinum*, *H. drepanophyllum*) are characterized by a distinctly urceolate or tubular calyx, which is in the case of mentioned *Heliotropium* species at fruit maturity inflated.

The corolla is always synsepalous with usually spreading corolla lobes (Fig. 7-1 C, H, L, Fig. 7-2 C, N). The corolla lobes are mostly shorter than the tube, but can be longer and very conspicuous in some taxa (e.g. *H. zeylanicum*). *Myriopus* differs from all other taxa in having long and narrow corolla lobes with involute margins (Fig. 7-1 C). Some species in *Heliotropium* section *Heliotropium* have five alternating intercalary lobules (e.g., *H. myosotoides*). A peculiar

character are compact fornices-like intercalary teeth inside the corolla tube e.g., in *H. hirsutissimum* or *H. arbainense*. They are superficially similar to the hollow fornices of Boraginaceae *s.str.* (subfam. Boraginoideae), but seem to be non-homologous and a derived character within the Heliotropiaceae.

The androecium is haplostemonous, antesealous and epipetalous, with short and linear filaments, inserting at different levels. The stamens are included in the stamen corolla tube (Fig. 7-1 C, H, L, Fig. 7-2 C, N). The anthers with 4 microsporangia are dorsifixed, usually linear, rarely ovoidal to cordate, and open with intrors longitudinal slits. Anthers with conspicuously protracted connectives are found in three genera. Those differentiated connectives are smooth in *Ixorhea* (Fig. 7-1 L), papillose in *Myriopus* (Fig. 7-1 C), pubescent to glandular-pubescent in *Euploca* (Fig. 7-1 H), and are important morphological characters defining these three groups, although pubescent anther apices are also found in *Heliotropium* sect. *Heliothamnus* (but with different flower and fruit morphology). The connectives of the five anthers are apically coherent, or compressed (only *Ixorhea*) and close the corolla tube above the style-stigma complex. In the genera *Heliotropium* (except sect. *Heliothamnus*) and *Tournefortia* the anthers are apically free (Fig. 7-2 C, N). The syncarpous gynoecium is superior, bicarpellate, 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 1987, 1992). The placentation is nearly axile. Rarely, after anthesis only one ovule develops into a fertile seed (*H. supinum*, HILGER 1987). Only in *Myriopus* the placenta is very well developed and consists of transfer cells (DIANE *et al.* 2002b). The style is terminal, and terminates in a conical stigmatic head with a basal ring-shaped stigma and an infertile, sometimes two-lobed apex (GÜRKE 1893, KHALEEL 1978, Fig. 7-1 C, H, L, Fig. 7-2 C, N). Style and stigmatic head vary in size and shape, the sterile apex is sometimes pubescent, but usually glabrous. Style and stigma morphology are systematically useful for the definition of species, but not informative at higher taxonomic levels. The conical style-stigma-complex is the key synapomorphy of Heliotropiaceae.

**Embryology**—Detailed studies on embryology are available only for some species of *Heliotropium* (SVENSSON 1925, PAL 1963, KHALEEL 1978, 1985) and *Ixorhea* (DIFULVIO 1978): the anatropous to hemitropous 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 archesporial cell that 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. The occurrence of a placental obturator has been reported for *Ixorhea* and some species of *Heliotropium*, but is not characteristic for all Heliotropiaceae. Heliotropiaceae are heterogeneous with regard to embryogeny, and three types have been reported so far; *Ixorhea* conforms to the *Chenopodiad* type, and *Heliotropium* to the *Chenopodiad*, *Solanad* or *Onagrad* type with the proembryonal tetrads belonging to the megarchetype III and IV of the C2 and A2 series (SOUÈGES 1943, PAL 1963, DIFULVIO 1978, KHALEEL 1978). All species investigated have a long suspensor. The embryo is straight in *Ixorhea*, *Heliotropium*, and *Tournefortia*, and curved in *Euploca* and *Myriopus*.

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**—Heliotropiaceae have a range of different pollen morphologies. The 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, i.e. there are three colpi alternating with three usually well-developed pseudocolpi. 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 derivatives of this pollen type are found: *Heliotropium bacciferum* has 8-heterocolporate pollen (QURESHI 1985, PERVEEN *et al.* 1995). *Heliotropium indicum* has 3-colporate pollen with a prolate outline and a triangular polar shape, the exine is scabrate to reticulate (QUIROZ-GARCIA 1985, SCHEEL *et al.* 1996). In *Tournefortia* the most common pollen type is also 6-heterocolporate with a circular polar shape. Rarer pollen types include 3-colporate or 6-heterocolporate, subprolate pollen grains with expanded poles and a triangular polar shape and an exine that is psilate at the poles and equatorially verrucose, spheroidal 3-porate pollen grains with a clavate exine or spheroidal to suboblate, and 3--4-colporate pollen grains (with colpi reduced to a narrow slit) with a psilate to finely rugulose exine (NOWICKE & SKVARLA 1974, QUIROZ-GARCIA & PALACIOS-CHÁVEZ 1986, SCHEEL *et al.* 1996). *Euploca* has a range of pollen types. They are always spheroidal to prolate with a circular, rarely a quadrangular polar shape and a psilate to rugulose exine, but show a vast range of aperture types and numbers: apart



from 6-heterocolporate pollen also 4- and 5-colporate or 8--10- and 12-heterocolporate pollen grains occur, with groups of one to three alternating pseudocolpi, and even 7-porate pollen have been described (FROHLICH 1978, QUERESHI 1985, QUIROZ-GARCIA & PALACIOS-CHÁVEZ 1985, PERVEEN *et al.* 1995).

**Karyology**—Chromosome counts are available for less than 20% of all species of Heliotropiaceae and most karyological data are from *Euploca* and *Heliotropium*. Chromosome counts for 16 species of *Euploca* are available. *Euploca* seems to have a base chromosome number of  $x = 7$  (rarely 8). The ploidy levels range from  $2x$ ,  $3x$ ,  $4x$ ,  $6x$  to  $8x$ . For few species varying chromosome base numbers and ploidy levels have been reported (FARQUI 1961, DIFULVIO 1969, FROHLICH & FERRONE 1984). In *Heliotropium* three karyological groups can be distinguished, *Tournefortia* falls into one of them: in New World *Heliotropium* and *Tournefortia* the base chromosome numbers are  $x = 7, 10, 11, 12, 13$  or  $14$  and most taxa are diploid. In *Heliotropium veronicifolium* and *H. curassavicum* tetraploids also exist (BRITTON 1951, DIFULVIO 1969, FROHLICH & COLBURN 1980). *Heliotropium schreiteri* is pentaploid (DIFULVIO 1969). *Heliotropium* section *Heliothamnus* is diploid with  $x = 9$  as base number (LUQUE 1996). Old World *Heliotropium* usually has a base number of  $x = 8$  and the species are usually di- or tetraploid, rarely hexaploid (exceptions are  $x = 13$  in *H. sibirica*;  $x = 14$  in *H. zeylanicum* and *H. ophioglossum*, ploidy level each  $2x$ ). A few species have cytological races (*H. europaeum* and *H. suaveolens*,  $x = 8$ , ploidy levels  $2x, 3x, 6x, 8x$ ; LUQUE 1996, FEDEROV 1969, FARQUI 1961).

One chromosome count each is available for *Myriopus* and *Ixorhea*, and the data should be interpreted with caution. The counts are  $n = 12$  for *Tournefortia* (= *Myriopus*) *paniculata* var. *austrina* (DIFULVIO 1967),  $2n = 10$  for *Ixorhea tschudiana* (DIFULVIO 1978). In all groups of Heliotropiaceae polyploidization and aneuploid changes thus seem to have been fairly common events.

**Pollination**—Little is known about the pollination of Heliotropiaceae. The occurrence of often yellow nectar guides in the flowers, UV-patterns (FROHLICH 1976), the secretion of nectar, and an often intense floral scent in *Euploca*, *Heliotropium*, and *Tournefortia* indicate potential pollination by insects such as butterflies, bumble bees, bees and thrips (KNUTH 1899, 1905). Our own observations document that the flowers especially of *Heliotropium* sect. *Heliothamnus* are visited by insects, with butterflies as the most frequent visitors. The anthers more or less close the narrow corolla tube in some taxa, rendering the stigma nearly inaccessible for insects, and are positioned above the stigma, which facilitates self-pollination (*Euploca*; many

*Heliotropium* species; *Myriopus*, NOWICKE & SKVARLA 1974; *Ixorhea*, DIFULVIO 1980) so that autogamy is very likely. *Myriopus* lacks nectar. Further evidence for at least facultative self-pollination comes from the good seed set many of the species show in the complete absence of pollinators (FÖRTHNER 1998).

**Fruit and Seed**—The fruits are usually 4-seeded, rarely 1--2-seeded, separating into 1- or 2-seeded mericarpids or drupes (Fig. 7-1 E, F, K, N, Fig. 7-2 D, E, G, I). Dry mericarpids with a dry, brown, glabrous or rarely pubescent exocarp and a thin and dry mesocarp are the most frequently found fruit type in Heliotropiaceae. Exclusively in *Heliotropium supinum* and *H. drepanophyllum* the fruits are enclosed in the persistent and inflated clayx. Drupes have evolved several times independently within Heliotropiaceae. They either have a white to bright orange exocarp and a juicy mesocarp (all species of *Myriopus* and *Tournefortia*, Fig. 7-1 E, F, Fig. 7-2 I), or a brown to black exocarp and a more or less dry to spongy mesocarp (some species of *Euploca* and *Heliotropium*, Fig. 7-2 G). The endocarp is homogenous, and sclerified with ligneous, strongly thickened cell walls filling the cell lumina (Fig. 7-2 H). Sometimes one or more empty (air filled at maturity) chambers of varying shape are found next to the locules in some species of *Heliotropium* (e.g. *H. messerschmidoides*, *H. indicum*, *H. nicotianaefolium*, Fig. 7-2 F) and the most species of *Tournefortia* (Fig. 7-2 L). Calcium oxalate crystals (mostly druses and crystal sand) are usually embedded in the cell walls of the endocarp. In *Myriopus* the endocarp is 4-layered: the innermost layer lacks crystals, the next layer has embedded tetrahedral crystals of calcium oxalate in the cell walls and lumina, followed by some layers of suberized tissue, while the outermost layer consists of narrow cells with tetrahedral crystals in the cell lumina (Fig. 7-1 D). All Heliotropiaceae except *Myriopus* have a clear, longitudinal dehiscence line (free of crystals and cells with small lumina) in the endocarp (Fig. 7-2 H). The testa epidermis consists of transfer cells with protuberances of the inner tangential and radial cell walls (DIANE *et al.* 2002b). The minute embryo is straight to curved and embedded in the thin endosperm.

**Dispersal**—The dry or drupaceous fruits of Heliotropiaceae seem to reflect alternative mechanisms of fruit dispersal. However, little is known beyond anecdotal evidence. At present there is limited evidence for hydrochory, anemochory, myrmecochory, and endozoochory. Endozoochory can probably be assumed for all drupaceous fruits with juicy mesocarp (*Tournefortia*, *Myriopus*). The drupes of neotropical *Tournefortia* species with juicy mesocarp are reported to be dispersed by unspecialized frugivorous birds (SNOW 1981). Air-filled empty



chambers in mericarpids (e.g. *Heliotropium messerschmidoides*, *H. indicum*, *H. nicotianaefolium*, the most species of *Tournefortia*), a spongy mesocarp (e.g. *H. foertheri* [= *T. argentea*], *H. gnaphalodes*) or inflated calyces as floating organs (*H. supinum*, *H. drepanophyllum*) suggest adaptation to hydrochory. Dispersal on drift logs and pumice, has also been suggested for the coastal *H. foertheri* and *H. curassavicum* (RIDLEY 1930, LESKO & WALKER 1969). *Heliotropium foertheri* was among the first species colonizing the island of Krakatau after the volcanic eruption (DOCTERS VAN LEEUWEN 1936). Birds such as ducks, quails or pigeons reportedly occasionally eat the dry mericarpids of other species and may play a role in endozoochorous dispersal (RIDLEY 1930, BARKER & VESTJENS 1989, 1990). In some species of *Euploca* elaiosomes are found in two pits on the adaxial side of each mericarpid (Fig. 7-1 K) and myrmecochory has been inferred (CRAVEN 1996). *Euploca serpylloides* shows postfloral elongation of the pedicel, and *Euploca hypogaea* is clearly geocarpic. The long-winged mericarpids of *Ixorhea* (Fig. 7-1 N) and some *Heliotropium* species such as *H. pterocarpum* are probably anemochorous. In spite of the wide range of dispersal mechanisms that have been suggested, there is little doubt that the majority of taxa in *Heliotropium* and *Euploca* are autochorous and reach new habitats only by chance dispersal.

**Phytochemistry**—Characteristic chemical markers of Heliotropiaceae are the pyrrolizidine ester alkaloids which are also found in many genera of Boraginaceae *s.l.* and Asteraceae. Alkaloid content seems to peak at the beginning of anthesis (CATAFALMO *et al.* 1982) and the highest concentrations are found in roots and inflorescences. Pyrrolizidine alkaloids (PA) are esters of hydroxylated 1-methylpyrrolizidines. The PAs are composed of necines (aminoalcohols) and necic acid. The PAs are also occasionally found in the form of nitrogen oxides. Both the aminoalcohol part and the characteristic necic acids of these ester alkaloids are biosynthetically derived from amino acids. The hepatotoxic activity of pyrrolizidine compounds depends on structural features. All hepatotoxic PAs consist of unsaturated necines (with a 1,2 double bond) and show esterification of the CH<sub>2</sub>OH groups in the side chains. The toxicity increases from pyrrolizidine aminoalcohols with a 1,2-double bond to monoesters to non-cyclic diesters and culminates in macrocyclic diesters, which are the most toxic. All these types have been reported from Heliotropiaceae (CULVENOR 1978). The most frequently found compounds are mono- and diester PAs. Unsaturated pyrrolizidine esters are poisonous to humans and animals, mainly due to their alkylating capacity. The compounds are mainly hepatotoxic, but there are also reports for carcinogenic, mutagenic, antimitotic, hemolytic, and pulmotoxic effects, a repellent effect on insect pests, and the protection against fungal infections. While most Heliotropiaceae are thus

poisonous, those species that lack unsaturated PAs are harmless (CULVENOR 1973, FROHLICH 1980, LAKSHMANAN & SHANMUGASUNDARAM 1995). PAs play a major role in insect-plant coevolution. Some butterflies and moths feed on the foliage of alkaloid-containing plants, or sequester the compounds from the nectar. These sequestered compounds then render the insects themselves noxious to their predators (ROBINS 1985, BOPPRÉ 1986, 1995, 1999), and/or they are converted into male pheromones (ROBINS 1986).

***Distribution and Habitats***—Heliotropiaceae are distributed worldwide mainly in the tropical and subtropical region. Some species of Heliotropiaceae are halophilous and grow mostly along the coast (*Heliotropium foertheri* [= *Tournefortia argentea*], *H. curassavicum*, *H. gnaphalodes*). *Heliotropium* is most diverse in temperate and subtropical areas such as the Mediterranean, the Irano-Turanian region, and southern South America, frequently dominating the vegetation of dry, disturbed areas. *Euploca* has centres of diversity in Africa, Australia, and the tropical and subtropical regions of the Americas where it is most abundant in semi-arid habitats with seasonal or erratical dry periods. *Tournefortia* is most diverse in the Neotropics, with only 13 species in the Paleotropics. *Myriopus* is restricted to seasonally dry regions of the Caribbean and Central America with a few species in innerandean valleys of South America. *Ixorhea* is a xerophytic endemic of northwestern Argentina.

***Subdivision***—In Heliotropiaceae (Boraginaceae subfam. Heliotropioideae according to classical systems) generic limits have fluctuated dramatically. The problems in classifying Heliotropiaceae were, at least partly, caused by the fact that starting from LINNÉ (1753) generic definitions have been largely to exclusively based on fruit morphology. The two large core-genera have always been maintained, namely *Heliotropium* and *Tournefortia*, but the various segregates have been controversially discussed (DECANDOLLE 1845, GÜRKE 1893, JOHNSTON 1935). FÖRTHNER (1998) in his most recent revision of the Heliotropiaceae recognized a total of ca. 450 species in the genera *Argusia* Böhm., *Ceballosia* (L.f.) Kunkel, *Heliotropium* L., *Hilgeria* Förther, *Ixorhea* Fenzl, *Nogalia* Verdc., *Schleidenia* Endl. and *Tournefortia* L. The small segregate genera differ mainly in aberrant fruit morphology (mostly dry vs. drupaceous) and habit from the two large genera, which otherwise comprise an enormous range of morphological characters.

Molecular studies (DIANE *et al.* 2002a, Hilger & DIANE submitted) and detailed data on fruit morphology and anatomy reveal that traditional generic limits need to be re-adjusted. At this stage we propose recognizing a total of 5 genera. It can be demonstrated that the evolution of

drupaceous fruits from dry fruits took place several times independently. This obliterates the major distinction between *Heliotropium* and *Tournefortia*. Our redefinition creates two genera (*Euploca*, *Heliotropium*) which include species with both dry and drupaceous fruits. Molecular data indicate that Heliotropiaceae fall in two large clades. The first clade includes *Ixorhea* from Argentina in a basal position. The neotropical liana genus *Myriopus* (formerly *Tournefortia* sect. *Cyphocyema*) is in sister group relationship to *Euploca* (formerly *Heliotropium* sect. *Orthostachys*, *Hilgeria*, *Schleidenia*). Their relationship is also well supported by morphological synapomorphies. *Ixorhea* is the morphologically most aberrant taxon in Heliotropiaceae and is characterized by unique characters such as a dense cover of resin glands and mericarpids with long apical wings (FENZL 1886, SPEGAZZINI 1901, HAUMAN 1922, DIFULVIO 1978). *Myriopus* and *Euploca* are characterized by, e.g., curved embryos and involute corolla lobes in bud.

The remainder of the sections of *Heliotropium*, the type section of *Tournefortia* and three small segregate genera (Asian *Argusia*, Macaronesian *Ceballosia*, and African *Nogalia*) constitute the second large clade. *Argusia*, *Ceballosia*, and *Nogalia* cluster with species of *Heliotropium* and are reduced to synonymy under this genus. *Heliotropium* under this definition is still paraphyletic with regards to *Tournefortia* because Old World *Heliotropium* and the Andean woody *Heliotropium* sect. *Heliothamnus* are more distantly related to the other groups of New World *Heliotropium* than is *Tournefortia* sect. *Tournefortia*. However, since our data currently can not satisfactorily resolve this polytomy, we propose to maintain the technically easily defined *Tournefortia*.

**Affinities**—The Heliotropiaceae have mostly been treated as a subfamily of Boraginaceae *s.l.* Molecular data have now shown that Boraginaceae *s.l.* are paraphyletic and include Hydrophyllaceae R. Br. ex Edwards and Lennoaceae Solms-Laubach. Cladistic analyses show that the Boraginales fall into clear subclades, which deserve recognition at family rank (BÖHLE & HILGER 1997, FERGUSON 1999, GOTTSCHLING *et al.* 2001), and the Heliotropiaceae are one of these. Heliotropiaceae have at least one very clear morphological synapomorphy, the conical style-stigma complex which is unique in the Boraginales. According to molecular data a clade of Cordiaceae R.Br., Ehretiaceae Mart. ex Lindl., and probably Lennoaceae constitutes the sister group of Heliotropiaceae (GOTTSCHLING *et al.* 2001), also supported by the exclusively presence of a hard endocarp together with transfer cells in the testa (DIANE *et al.* 2002b).

**Palaeobotany**—Heliotropiaceae fossils are poorly documented. Fossil pollen grains of *Tournefortia* described as the *Tournefortia bicolor* type (MULLER 1981) have been recorded by

GRAHAM & JARZEN (1969) from the Oligocene of Puerto Rico and by GRAHAM (1976) from the upper Miocene of Mexico. This pollen type is equivalent to pollen type III (spheroidal 3-porate pollen grains with a clavate exine) of NOWICKE & SKVARLA (1974).

**Economic Importance**—A review of the economic importance of Heliotropiaceae has been provided by ALSHEBAZ (1991) and FÖRTHNER (1998). Uses in folk medicine, mostly without major economic importance, have been reported for various species of *Heliotropium* (HARTWELL 1968, UPHOF 1968, PERRY 1980, AYENSU 1981, BURKILL 1985, DUKE & AYENSU 1985). Extracts from some species have shown significant antitumour activity against certain types of leukaemia and melanoma (HARTWELL 1968, DUKE & AYENSU 1985). *Heliotropium foertheri* (= *T. argentea*) and *H. gnaphalodes* are planted to stabilize beaches and coastal dunes (CRAIG 1978). *Heliotropium foertheri* is also cultivated as a tobacco substitute by the natives of the Seychelles and other regions of tropical Asia (UPHOF 1968, LEWIS & ELVIN-LEWIS 1977), and its wood is used in the fabrication of shoe-lasts in Guam (BURKILL 1966). Various species of Heliotropiaceae are also cultivated as ornamentals, either locally (*H. gnaphalodes* in Florida; CRAIG 1978) or worldwide (*Heliotropium arborescens*, *H. amplexicaule*, and *H. curassavicum*; BRUMMIT 1972, RIEDL 1978). *Heliotropium arborescens* is also extensively grown for the extraction of its volatile oil, which is used in the perfumery industry (GRAF 1978). *Heliotropium* species which contain unsaturated pyrrolizidine alkaloids are noxious weeds poisonous to livestock if they contaminate hay and are also dangerous to humans if grain is contaminated with fruits of *Heliotropium* (BULL *et al.* 1968, BIRECKA *et al.* 1980, FÖRTHNER 1998, PRAKASH *et al.* 1999). New investigations aim at identifying natural enemies of poisonous *Heliotropium* species, e.g. the biological control of *Heliotropium amplexicaule* in Australia with the help of leaf-beetles (BRIESE & ZAPATER 2001).

## 7.2 Key to the genera

- 1** Plants strongly scented, resinous, without eglandular trichomes;  
4 apically winged mericarpids; endemic to northwestern Argentina **1. *Ixorhea***
- Plants not resinous and/or with numerous eglandular trichomes;  
mericarpids smaller and wing(s) lateral, if present **2**
- 2** Corolla lobes subulate with involute margins; fruits drupaceous  
white or bright orange, sometimes with up to 4 dark spots on surface,  
mature fruit distinctly 4-lobed; lianas or subscandant shrubs **2. *Myriopus***
- Corolla lobes not with involute margins; fruits mostly dry,  
if drupaceous then never orange or with dark spots on surface  
and never 4-lobed; herbs, subshrubs, shrubs, small trees,  
very rarely lianas **3**
- 3** Fruits 4 one-seeded mericarpids each with two pits on the inner side  
or rarely brownish dry drupes with 4 one-seeded endocarpids;  
inflorescences sometimes bracteose, frondose, or reduced to a solitary  
flower; corolla with involute lobes in bud; anthers long protracted with  
pubescent apex, coherent apically; herbs and subshrubs **3. *Euploca***
- Fruits 4 one- or 2 two-seeded mericarpids or drupes; inflorescences  
always ebracteose and many-flowered; corolla without involute lobes  
in bud; anthers usually glabrous at apex (if pubescent then the  
mericarpids without pits) **4**
- 4** Fruit dry, separating into one- or two-seeded mericarpids when ripe  
(only in few cases dry drupes); corolla aestivation imbricate;  
mostly herbs or small shrubs, rarely shrubs, never lianas **4. *Heliotropium***
- Fruit drupaceous with juicy exo- and mesocarp; corolla aestivation  
apert-duplicative; shrubs and small trees, occasionally lianas **5. *Tournefortia***

### 7.3 The genera of Heliotropiaceae

#### 1. *Ixorhea* Fenzl (Fig. 7-1 L to O)

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

= *Oxyosmyles* Speg. (1901).

Shrub; leaves alternate to pseudo-opposite, lanceolate, margin entire, entire plant (except corolla limb) densely glandular, covered with an aromatic, varnish-like, glutinous resin. Inflorescences branched, ebracteose, few-flowered. Calyx tubulose, lobed to 1/3<sup>rd</sup> to 1/4<sup>th</sup>; corolla whitish to violet-rose, lobes triangular; aestivation apert-duplicative. Anthers long protracted, compressed apically, closing the corolla tube. Style long, stigmatic head long protracted. Fruit dry, separating into one-seeded, apical winged, mericarpids. Embryo straight. One species, *Ixorhea tschudiana* Fenzl. Endemic to northwestern Argentina (provinces Salta and Tucumán).

#### 2. *Myriopus* Small (Figs. 7-1 A to F, and 1-12, 1-16 of the introduction)

*Myriopus* Small, Manual Southeast. Fl. 1131 (1933).

= *Tournefortia* L. sect. *Cyphocyema* I.M. Johnst. (1930).

= *Messerschmidia* [R. & Sch. (non Linn.)] Miers (1868) *nomen confusum*

Lianas, rarely subscandant shrubs; leaves alternate to pseudo-opposite, lanceolate to ovate, margin entire, glabrous to sericeous. Inflorescence 1--∞ branched, ebracteose, many-flowered. Calyx lobed to 1/2 or nearly to base; corolla orange, yellow, greenish, lobes subulate, margins involute, base of the corolla tube inflated; aestivation subvalvate with involute margins. Anthers long protracted with papillose apex, coherent apically, closing the corolla tube. Style long, stigmatic head truncate-cylindrical. Fruit drupaceous, juicy, deeply 4-lobed, white or bright orange, sometimes with up to 4 dark spots, one-seeded endocarpids. Embryo strongly curved. Five--12 spp., centres of diversity in the West Indies, Central and South America.



**3. *Euploca* Nutt.** (Figs. 7-1 H to K, and 1-6, 1-17 of the introduction)

*Euploca* Nutt., Trans. Amer. Phil. Soc., n.s. 5: 189 (1837).

= *Schleidenia* Endl. (1839).

= *Heliotropium* L. sect. *Orthostachys* R. Br. subsect. *Axillaria* I.M. Johnst (1928).

= *Hilgeria* Förther, Sendtnera 5: 132 (1998).

Herbs, small shrubs, often at least basally decumbent; leaves alternate, rarely pseudo-opposite, lanceolate to ovate, sometimes tiny, scale-like, margin often revolute, indumentum variable, rarely glabrous. Inflorescences unbranched or 1--4 branched, ebracteose, bracteose, frondose, or reduced to a solitary flower. Calyx lobed to 1/3<sup>rd</sup> to 1/2; corolla white to yellow, lobes subcircular to ovate-acuminate; aestivation mostly apert, always with involute corolla lobes in bud. Anthers long protracted with pubescent apex, coherent apically, closing the corolla tube. Style short to long, stigmatic head obtuse to long protracted. Fruit dry, separating into one-seeded mericarpids each with two pits on the abaxial side, rarely dry drupes with 4 one-seeded endocarpids. Embryo curved. Circa 100 spp., cosmopolitan with centres of diversity in Africa, Australia, and tropical America.

**4. *Heliotropium* L.** (Figs. 7-2 A to H, and 1-2, 4, 5, 7, 9 to 11, 13 to 15 of the introduction)

Most recent revision: FÖRTHNER (1998).

*Heliotropium* L., Sp. pl. 1: 130 (1753).

= *Nogalia* Verdc. (1987).

= *Ceballosia* Kunkel (1980).

= *Argusia* Böhm. (1760).

Herbs, subshrubs, shrubs, prostrate to erect; leaves alternate to pseudo-opposite, linear to ovate, margin entire to repand, rarely crenate or dentate, sometimes revolute, leaves rarely succulent, indumentum variable, rarely glabrous. Inflorescence 1--∞ branched, ebracteose, many-flowered. Calyx lobed to 1/2 or nearly to base; corolla mostly white, rarely yellow, orange, purple, lobes subcircular to lanceolate; aestivation mostly imbricate. Anthers sometimes protracted, apically pubescent and coherent only in section *Heliothamnus*. Style short to long, stigmatic head obtuse to long protracted. Fruit dry, separating into one- or two-seeded mericarpids, rarely dry drupes,

sometimes empty chambers present. Embryo straight. Circa 200 spp., cosmopolitan, semiarid to rarely tropical. The Irano-Turanian region and South America are centres of diversity.

**5. *Tournefortia* L.** (Figs. 7-2 L to N, and 1-3, 1-8, 1-18 of the introduction)

*Tournefortia* L., Sp. pl. 1: 140 (1753).

= *Pittonia* Mill. (1754).

= *Tournefortia* section *Pittonia* (H.B.K.) G. Don (1838).

= *Tournefortia* section *Eutournefortia* I.M. Johnst. (1930) *nomen illigittimum*.

Small trees, scandent, erect shrubs; leaves alternate to pseudo-opposite, rare pseudoternate, lanceolate to obovate, margin entire, pubescent, rarely glabrous. Inflorescence 1-- $\infty$  branched, ebracteose, many-flowered. Calyx lobed to 1/2 or nearly to base; corolla green, white, pale yellow, lobes subcircular to triangular-ovate ; aestivation apert-duplicative. Anthers apically not compressed or coherent. Style short to long, stigmatic head obtuse to long protracted. Fruit drupaceous, mostly juicy, unlobed, white, usually two-seeded endocarpids, often empty chambers present. Embryo straight. Circa 100 spp., pantropical (13 spp. in the Old World) with centres of diversity in Central America and tropical South America.