
Boraginaceae

Boraginaceae Juss., Gen. Pl.: 128 (1789) ('Borragineae'), nom. cons.

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Annual, biennial or perennial, rarely monocarpic herbs, subshrubs and rarely erect or lianescent shrubs, not aromatic; primary root usually persistent, often developed as strong taproot, rarely primary and secondary roots thickened and spindle-shaped or primary root splitting from above and forming root pleiocorm; stems terete, rarely angular, then often winged from decurrent leaf bases, erect, rarely ascending, sprawling, decumbent or procumbent, prostrate, sometimes forming rhizomes or stolon tubers; indumentum usually present on whole plant, often strongly developed, scabrid to hispid or strigose, sometimes uncinata, very rarely with stiffly deflexed trichomes for climbing or lanate or consisting of stellate trichome complexes or largely absent (trichomes reduced to basal cells), trichomes often scabrid, often mineralized with Si or Ca, often inserted on a multicellular basal tubercle or cystolith cell, rarely unicellular, simple and smooth or uniseriate and gland-tipped. Leaves alternate, rarely opposite, simple, entire, exstipulate, cauline leaves usually sessile to semiamplexicaulous, lamina linear, narrowly ovate to subcircular, usually decurrent on petiole, more rarely base distinctly rounded or cordate and distinctly petiolate, basal leaves usually forming an ephemeral or persistent rosette, sessile or tapering into a petiole. Inflorescences terminal or axillary, frondose, bracteose or ebracteose, paraclades monochasial or dichasial, lax or very dense, usually scorpioid and contracted into boragoids, these paraclades present as simple terminal inflorescence or combined into complex thyrsoids, sometimes with extensive accessory paraclades and metatopia. Inflorescences sometimes congested into terminal "heads" or strongly reduced to axillary or terminal single flowers. Flowers pentamerous, hypogynous, bisexual, often proteran-

drous; perianth biseriate, sepals united at base or nearly to apex, usually radially symmetrical, sometimes slightly or distinctly unequal, calyx tubular to rotate, membranaceous, usually accrescent in fruit, spreading or closing; petals usually united to form distinct tube, rarely united only basally, corolla actinomorphic, rarely zygomorphic or irregular, rotate, hypocrateriform, infundibular, campanulate or tubular, rarely curved or geniculate, corolla tube internally usually appendaged near base with ring-shaped intrusion or 5 or 10 free scales (basal scales = annulus) and near throat with 5 crescent- or scale-shaped intrusions (= faucal scales, fornicies), these closing the tube and/or appressed to anthers and/or protruding to form a ring around opening of tube, erect, recurved or incurved, papillose to pubescent, usually contrastingly coloured (often yellow or white vs. blue or white corolla lobes); corolla lobes reflexed to porrect, narrowly triangular to (usually) subcircular; aestivation usually quincuncial, rarely contorted; stamens epipetalous and antesealous, rarely unequal or some abortive, filaments free from each other, usually short and anthers included in tube or partially or completely exerted, inserted at the same or different heights in tube, filament lengths and/or point of insertion differing between morphs in taxa with stigma height polymorphism or heterostyly; anthers usually free from each other, dorsifixed, dithecal, tetrasporangiate, opening by longitudinal slits, sometimes anthers coherent, connective sometimes appendaged; gynoecium 2-carpellate, syncarpous, usually with basal nectary disc; ovary bicircular, but secondarily subdivided into four chambers by false septa, 4-lobed in flower; style overtopped by the nutlets (gynobasic), usually simple, rarely 2–4 stylodia, included or exerted,

stigmas capitate to oblong; ovules anatropous-epitropous, usually basal or sub-basal, erect to pendulous, unitegmic, tenuinucellate. Fruit a dry schizocarp separating into four 1-seeded, rarely two 2-seeded, indehiscent mericarps, sometimes fewer by abortion or fusion; mericarps (“nutlets”, “eremocarps”) usually equal, rarely heteromorphic (in individual fruit, in fruits on different parts of the plant or in different morphs of a population), nutlet shape and size highly variable, ovoid to subcircular, tetrahedral, lenticellate, bowl-shaped or disc-shaped, often with differentiated, lobed/glochidiate or membranaceous (“winged”) margin, surface smooth and shiny to papillose and dull, pubescent, verrucose or with complex glochidia, sometimes with base strongly modified as ring and/or with basal elaiosome. Mature seeds with scanty endosperm, cotyledons fleshy, embryo usually straight.

The family in the narrow definition here adopted contains ca. 85 genera and 1600–1700 species; cosmopolitan, but largely absent from the wet tropics.

VEGETATIVE MORPHOLOGY. Boraginaceae are predominantly herbaceous, relatively few species are suffruticose or fruticose. Many species are ephemeral, winter/spring flowering annuals with life spans of a few weeks, mostly in temperate, desert and high alpine environments (e.g. some *Myosotis*, *Cryptantha*, *Microcaryum*). Winter annuals are common in warm-temperate and Mediterranean climates (Mediterranean *Cynoglossum*, some *Lithospermum*, many *Amsinckia*, *Cryptantha*, Schaal and Leverich 1982; Parsons and Cuthbertson 2001), but rare in temperate climates (*Omphalodes scorpioides*). Longer-lived, diffusely branched annuals [*Asperugo*, *Bothriospermum*, *Hackelia* p.p. (“*Austrocynoglossum*”)] and biennials (many *Cynoglossum*, *Echium*) are also found. Some of the annuals are likely amongst the smallest angiosperms (*Microcaryum*: ca. 10 mm). Perennials are usually polycarpic, while monocarpic (hapaxanthic) perennials are rare (some *Echium*). Amongst perennial herbs a wide range of growth forms is present, including tiny, high-alpine cushion-forming plants, usually with soft, shaggy pubescence (*Chionocharis*, some *Eritrichium*, *Myosotis*), and prostrate or diffusely decumbent herbs with rooting stems and distichous phyllotaxy (e.g. some *Myosotis*, *Plagio-*

bothrys, *Trigonotis*). Coarse, large-leaved, often stoloniferous taxa, sometimes with gradual transitions to rhizomatous herbs and geophytes, are found in Boragineae (e.g. *Symphytum*, *Moritzia*, *Trachystemon*, *Pulmonaria*), but also Cynoglosseae (*Brachybotrys*, *Cynoglossum*) and Lithospermeae (*Ancistrocarya*). Thick, sympodial rhizomes are rare, but found in *Brachybotrys* (Cynoglosseae) and *Paramoltkia* (Lithospermeae). Distinct stolon tubers are very rare (e.g. *Symphytum tuberosum*, *S. bulbosum*). Pleiocorm herbs (i.e. perennial underground shoots permanently coherent via persistent primary root) are common in the family and are typical for, amongst others, *Mertensia*, *Rindera*, *Trichodesma* and most *Lithospermum*. These pleiocorm herbs usually have large, basal leaf rosettes, but these are absent in some taxa (many *Lithospermum*). Root pleiocorms are sometimes formed by the lengthwise splitting of the primary root from top to bottom in, for example, *Borago pygmaea*, some *Symphytum* and *Mertensia maritima*. Subshrubs, dwarf and small shrubs (<1.5 m) are comparatively frequent in Lithospermeae (e.g. *Lithodora*, *Lobostemon*, some *Lithospermum*) and Echiochileae (*Echiochilon*, some *Antiphytum*). They usually have narrow leaves with revolute margins and are more or less distinctly ericoid. Some shrubby species are strongly stoloniferous, forming large colonies (*Glandora oleifolia*). Larger shrubs are even rarer, but ca. 25 *Echium* species endemic to Macaronesia show clear “insular woodiness”. *Selkirkia berteroi* from the Juan Fernandez Islands is a shrub with leaves crowded at the shoot apices and reaches some 2 m in height. The probably largest species is *Trichodesma scottii*, a shrub up to 4 m high from Socotra. Leaves are generally alternate, sometimes crowded at the shoot apices (*Selkirkia*) or at the base of annual shoots, rarely verticillate (*Brachybotrys*). Opposite leaves are found in *Thaumatocaryon* (*Th. tetraquetrum*), *Antiphytum* and most *Trichodesma* and, at least in the basal part of the axis, are also characteristic of *Pectocarya* p.p. (“*Harpagonella*”), *Suchtelenia* and many *Plagiobothrys*. The leaves lack pulvini and stipules; the lamina is always simple and entire. *Amsinckia* and some *Cryptantha* have deeply bifid cotyledons which are the only divided leaves in the family. Leaves usually have a flat, membranaceous, (widely) ovate lamina, ranging from a few millimetres (some *Myosotis*) to 1.5 m

(*Myosotidium*) in length. Narrow, sometimes even needle-shaped leaves with revolute margins are found in some shrubby species of genera such as *Antiphytum*, *Echiochilon*, *Lithodora* and *Glandora*. Coloured leaf patterning, very rare in the temperate flora, is known only from Boraginaceae—e.g. in *Pulmonaria* (esp. *P. officinalis* group: white and green) and *Symphytum* (e.g. *S. ibericum*: white, purple and green). Leaf venation is mostly brochidodromous or (semi-)craspedodromous, rarely hyphodromous. Scale-like cataphylls are largely restricted to the rhizomes, stolons and stolon tubers of the few taxa with these modifications. Adaptations to periodical exposure to fire exist in several species of *Trichodesma*, *Lithodora*, *Echiostachys* and *Lobostemon*. Loss of the aerial parts through fire leads to vigorous vegetative re-growth from the pleiocorm and subsequent mass flowering and fruiting in *Lobostemon* and *Trichodesma*. Recovery may be very rapid, with reestablishment of the aerial parts in *Lithodora hispidula* taking as little as 4 months (Türkmen and Düzenli 2005).

VEGETATIVE ANATOMY. Vegetative anatomy of Boraginaceae s.str. is poorly understood, with few recent studies available (Solereider 1899; Jodin 1903; Metcalfe and Chalk 1950). The indumentum is usually very well developed and characteristically rough (Fig. 5). A characteristic feature is the presence of usually stalkless cystoliths in the basal cells of the trichomes, sometimes also the sheathing cells. Trichomes are often incrustated with minerals based on x-ray analysis (EDX) silica and calcium are the principal com-

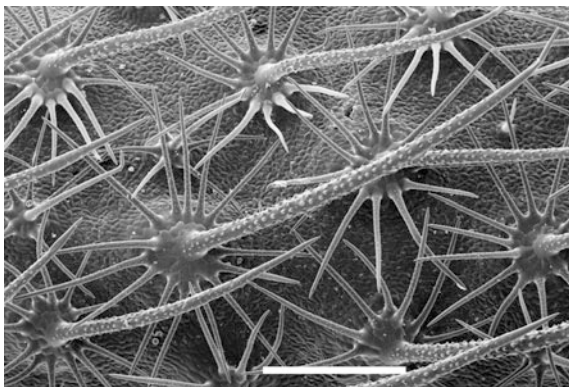


Fig. 5. Boraginaceae. Indumentum of *Onosma echioides*. Bar = 500 μm

ponents; especially the short, stiff trichomes are strongly silicified (Hilger et al. 1993). Some species of *Cerinth*, *Omphalodes* and *Mertensia* have a poorly developed indumentum or are virtually glabrous, leaves are then usually glaucous from epicuticular waxes. Trichome characters have been reported by several researchers and have been used for grouping taxa such as Macaronesian *Echium* species, but the results do not correspond well with DNA phylogenies. Selvi and Bigazzi (2001) investigated the leaf anatomy of more than 50 specific and subspecific taxa belonging to 14 genera of tribe Boragineae. They described seven trichome types, likely covering the majority of trichomes found in Boraginaceae: 1. uniseriate, eglandular, usually erecto-patent, sharply pointed, base surrounded by a conspicuous basal tubercle of 20–30 cells; 2. as 1. but smaller and with only 10–20 basal cells; 3. as 1. but trichome sitting on an inconspicuous ring of 6–8 cells; 4. very short trichome with pointed tip and densely micropapillose surface; 5. hooked (uncinate) trichome without a distinct base; 6. minute trichome tipped with 3-celled glands; 7. long, uniseriate, gland-tipped trichome with elongate head cell. Secretory trichomes functioning as salt glands have been reported from the halophilic *Mertensia maritima*. Straight but stiffly deflexed trichomes are found in subscandent *Hackelia* p.p. (“*Austrocynoglossum*”) and *Asperugo* and possibly elsewhere. Stem anatomy has been studied in only few species (e.g. Park 1982) and shows no striking peculiarities. In the primary stem, open collateral vascular bundles are arranged in a cylinder. Cortical and medullary bundles as well as an internal phloem are absent. Secondary thickening develops from a cambial ring. Cork is usually initiated from a superficial or deep-seated cork cambium. Further studies focussed mainly on the woody Macaronesian *Echium* species (Carlquist 1970; Aldridge 1981) which are pachycaulous with a broad pith. Plants with long-lived shoots have distinct growth-rings, corresponding to annual growth and likely reflecting the seasonality of moisture availability. Xylem rays are present or absent; if present, they are uniseriate or multiseriate with usually erect or isodiametric cells, procumbent ray cells are rare. Axial parenchyma is scanty paratracheal and composed of two to five strands. Vessels are relatively short (between 100 and 300 μm) and narrow

(40–65 μm) in both herbaceous and woody members. Carlquist (1970) found a negative correlation between vessel length and the degree of xeromorphy in Macaronesian *Echium*. Pits are bordered, alternate and circular. Libriform fibres (fibre-tracheids) are short (300–400 μm) and with vestigial borders. Storied wood structure probably is characteristic for all *Echium* species (Carlquist 1970). Oil bodies are absent (Lersten et al. 2006), but Carlquist (1970) observed resin-like compounds in nearly all *Echium* woods. Nodes are unilacunar and the leaf trace is a complex vascular strand leaving a rather wide lacuna (Neubauer 1977). A persistent leaf basal meristem is lacking. Roots are apparently mostly diarch (Jodin 1903) or tetrarch. Periderm develops from the pericycle. Growth rings may be present in the secondary root xylem of *Symphytum officinale* (Dietz and Ullmann 1997) and *Anchusa officinalis* (von Arx and Dietz 2006), thus allowing for a calculation of age on the basis of annual growth rings in the (persistent) primary root. Root hairs on seedling roots of Boraginaceae develop on an epidermis derived from the root cap and the trichoblasts are arranged in a radial pattern (Clowes 2000). The seedling root of *Echium plantagineum* shows a unique pattern with files of long root hairs producing cells separated by one or two files of cells bearing short hairs (Tsai et al. 2003). The leaf anatomy of Boraginaceae is not well studied, but apparently leaves are mostly bifacial with 2–3 layers of palisade parenchyma on the adaxial and spongy parenchyma on the abaxial side, but isobilateral leaves are also common. The mesophyll commonly contains calcium crystals (raphides, druses or solitary-prismatic crystals). Stomata distribution is hypo- to amphistomatic and the stomata are mostly anomocytic or anisocytic, but other types of stomata have also been reported (Dasti et al. 2003). Stomata distribution may vary among leaves of a single shoot (Schitten-gruber 1953). In Boragineae, Selvi and Bigazzi (2001), investigating 14 genera and 49 species, found no correlation of leaf anatomy with taxonomy, but with habitat. Outer cell walls in the adaxial epidermal cells are thicker in more xerophilic or xerotolerant taxa than in mesophilic taxa. Mesophilic taxa have exclusively hypostomatic leaves, while xerophytic (incl. psammophytic) species show increased stomatal density on the adaxial surface. Transfer cells are present in the minor leaf veins in at least 17 genera. They usually have

ingrowths distributed around the periphery (“type A”) of specialized phloem parenchyma (Pate and Gunning 1969). Gunning et al. (1970) also found transfer cells in the shoot axes, associated with the xylem. Boraginaceae have S-type sieve-element plastids (Behnke 1981). Nuclear crystalloids are a common component of sieve elements in the Boraginaceae (Fisher et al. 1989). They are distinct from the P-protein of sieve-element protoplasts. Furthermore, nuclei of phloem parenchyma cells may also occur, but in much fewer species. Fisher et al. (1989) presented a list of species with the distribution of both types of nuclear inclusions, but there is no obvious correlation with the systematic position of the taxa. Chloroplast and nuclear crystalloids differ even within individual genera, only *Amsinckia* apparently shows a unique loose structure of nuclear crystalloids.

INFLORESCENCE STRUCTURE. This paragraph is partly based on Buys and Hilger (2003). Detailed investigations of inflorescence architecture are rare. Boraginaceae have exclusively “closed” (monotelic) inflorescences and paraclades are usually cymose. Schwarzer (2007) found six different synflorescence types investigating only three South American genera (*Cryptantha*, *Pectocarya*, *Plagiobothrys*), including both homoeocladic and heterocladic thyrsoids, anthocladia and creeping special thyrsoids, indicating a high degree of diversification in this character complex. Overall inflorescences are usually frondose, frondose-bracteose, bracteose or ebracteose. Bract morphology often changes abruptly within the inflorescence and the pherophylls of paraclades (mostly frondose) may be morphologically widely different from those subtending dichasial ramifications (mostly bracteose) and these, in turn, may differ widely from the bracts in monochasial portions (distinctly bracteose or absent). Extensive recaulescence may occur with bracts moving far up lateral branches (esp. *Symphytum*). Bracts are usually green, but may be conspicuously coloured and take over the role of pollinator attraction from the obscured corolla in *Cerithe*. The basic unit of Boraginaceae inflorescences is usually a scorpioid (= coiled) cincinnus, the so-called boragoid: the mostly shortly pedicellate and often ebracteose flowers are separated by initially very short internodes and arranged in two alternating rows. Flowers usually

all face in the same direction. Loss of alpha-prophylls and re- and concaulescence of bracts may contribute to the overall architecture of the boragoid (esp. in Boragineae and *Cynoglossum*). Boragoids are often paired and arise from a first dichasial division (from the leaf axils of a pair of opposite bracts preceding an often well-developed terminal flower). These “paired boragoids” or “double boragoids” are a common basic unit of Boraginaceae inflorescences. An individual boragoid or double boragoid may make up the entire terminal inflorescence, in which case the inflorescence can be classified as a mono- or dichasial cymoid. Terminal cymoids may be strongly condensed and few-flowered or even reduced to one-flowered cymoids, with peduncle and internodes overtopped and obscured by foliage leaves, so that there are terminal “heads” (some *Lithodora*) or apparently single, terminal flowers (flowers open sequentially and buds are not immediately visible: cushion-forming *Eritrichium* and *Myosotis*). Commonly, the boragoids and more often the double boragoids are found as paraclades of more or less complex thyrsoids, rarely di- or pleiothyrsoids. Typically, paraclades are well-spaced and have elongated internodes at least basally, immediately revealing the thyrsoidal nature of the inflorescence. However, internodes in the paraclades and between the paraclades may be very short, leading to a basically cylindrical inflorescence resembling a spike (many *Echium*, “miner’s candle” = *Cryptantha* spp.). In some cases the lateral paraclades are additionally reduced to one or two flowers, the overall inflorescence then superficially resembling a spike (*Lobostemon* sect. *Argentei*, Levyns 1934). A superficially capitate inflorescence is formed (some *Cryptantha*, *Plagiobothrys*) when the internodes separating the paraclades are completely reduced. Elongation of internodes, especially during fruit development, is also found in a wide range of taxa. In these cases the bracts are usually frondose. Bract and flower position clearly reveal the monochasial (cincinnal) nature of these inflorescences. These monochasial anthocladia are common in some mostly annual taxa such as *Asperugo*, *Bothriospermum* and some *Anchusa*.

FLOWER MORPHOLOGY AND ANATOMY. Flowers are usually erect, sometimes held horizontally,

nodding (*Pulmonaria*, *Symphytum*) or pendulous (*Onosma*, *Cerinth*). Sepals, petals and stamens originate centripetally as five separate primordia each in quincuncial order and in alternate and aequidistant position, the first sepal arising is median adaxial. Carpel primordia are in a median position. The petal ring fuses (“late sympetaly”, Erbar and Leins 1996) on the abaxial side of the stamen primordia, which are subsequently lifted upwards to form the stamen-corolla tube (Hilger 1985). The calyx is at least basally united and the united portion is very short (<10 % of overall sepal length) or very long with very short free lobes. Calyx lobes are mostly narrowly ovate-acuminate, sometimes linear (e.g. *Rochelia*) or broadly ovate-acuminate with a cordate base (*Trichodesma*). In *Asperugo* the calyx is folded and bilabiate, forming two roughly hemispherical, dentate lobes. Calyx aestivation is apert to valvate. Supernumerary sepals are present in *Plagiobothrys* spp. and *Rochelia* (up to nine in *R. cancellata*). Sepals have a more or less pronounced scabrid to lanate or uncinat indumentum. The corolla is usually conspicuous, the largest flowers of the family are found in American *Lithospermum* p.p. (>90 mm, “*Macromeria*”). Very small flowers with corollas barely reaching 1 mm in length and obscured by the calyx are found in *Cryptantha* and *Microcaryum*. Radially symmetrical, infundibuliform to hypocrateriform corollas with faucal scales protruding from the throat are the most common type in all tribes. (Sub-)Rotate corollas in usually deflexed flowers are found in *Borago*, *Trachystemon*, *Brachybotrys*, *Cystostemon* and *Trichodesma*. More or less campanulate or tubular corollas with porrect or reflexed lobes are characteristic for some groups (*Symphytum*, *Onosma*, *Mertensia*). Distinctly zygomorphic flowers are uncommon, but found scattered in Lithospermeae (slightly curved and widened: *Echium*, *Lobostemon*), Boragineae (strongly geniculate and narrowed: *Lycopsis*) and Echiochileae (*Echiochilon*). Corolla lobes are usually well developed, rectangular, oblong, triangular or suborbicular, spreading, erect or reflexed. The margin of the corolla lobes is usually entire, but fimbriate in *Arnebia fimbriopetala* and incised in *Lithospermum incisum*. Corolla lobes may be connected by smaller additional lobes (*Alkanna*) or trichome tufts (*Arnebia*). Aestivation of the corolla lobes is usually

quincuncial, rarely contort (*Myosotis*). The stamen-corolla tubes rarely persist in fruit (*Anchusa samothracica*). Corollas are commonly blue, purple, pink or white. Orange corollas are largely restricted to Lithospermeae, yellow corollas are common in Lithospermeae and Boragineae but rare elsewhere. Corollas are, apart from the faucal scales, usually uniformly coloured, rarely bicolorous (*Onosma*, *Podonosma*). Colour changes are widespread—e.g. in *Symphytum* and *Pulmonaria* (pink to blue or dark purple)—and often also affect the colour of the faucal scales. Corolla colour polymorphism (usually blue and white) is occasionally found and has been the source of several cultivars. Inner basal scales sometimes cover the nectary disc and/or ovary. They may be annular or scale-shaped, hairy or glabrous; sometimes they are reduced to a barely differentiated fold. The five scales at the filament bases in *Lobostemon* are likely homologous to the basal scales in other genera. In the vast majority of taxa the throat of the corolla tube has characteristic invaginations, the so-called faucal scales or fornications. They often (partially or completely) close the entrance to the corolla tube and are usually well visible from outside by contrasting colours, commonly white or yellow. These scales originate as adaxial folds of the petal, then grow inwards as invaginations. Faucal scales are absent in Trichodesmeae and many Lithospermeae and a few other genera, most of them with tubular flowers. Faucal scales are usually exerted from the tube (hidden in *Alkanna*), but, apart from few exceptions (*Solenanthus albiflorus*, *Czukavina* and Meling 1982), always inserted above the filament bases. Arrangement is commonly in one series (but two series in *Trachystemon*). The scales are variable in shape, ranging from oblong, trapeziform or rectangular to emarginate or bifid and form either a closed ring around the throat (e.g. *Myosotis*) or are distinct and prominent (e.g. *Anchusa*, *Cynoglossum*). In *Symphytum circinnale* the long (8 mm) and narrowly triangular scales sheath the style. In some taxa the faucal scales are reduced to folds or hairy ridges or papillose tufts above or between the anthers.

In most taxa the stamens are inserted near the middle of the tube, in some taxa nearly at the base (e.g. *Neatostema*, *Anchusa* subg. *Buglossoides*, *Melanortocarya*) or at different levels (e.g. *Glandora*). Androecial zygomorphy—e.g. arrange-

ment of anthers at different levels in the tube—occurs in several species of *Alkanna* and *Anchusa* and in taxa with zygomorphic flowers (*Echium*). In zygomorphic flowers the three abaxial stamens are usually inserted at a higher level than the two adaxial stamens. Stamens are usually all fertile except in *Anchusella*, where only two have anthers and three are staminodial. Anthers are usually included, but distinctly exerted from the tube in, for example, *Solenanthus* or *Rindera*. Extreme heteranthery with one very long and exerted stamen occurs in *Nonea* (“*Elizaldia*”) *heterostemon* and *Caccinia monandra*. Anthers are of variable size, often more or less ovoid, rarely sagittate (*Onosma*, *Cerithe*), basifixed to dorsifixed, often connivent to coherent and occasionally appendaged. Appendages may be basal (*Borago*) or apical (*Cystostemon*) and are long and spirally twisted in *Trichodesma*. *Lobostemon* has hairy staminal scales at or below the filament insertion within the tube. The pollen sacs open with longitudinal slits.

The gynoecium is bicarpellate, syncarpous, superior, each carpel giving rise to two uniovulate globular, triangular or erect to curved lobes. The following description is based on Hilger (1985). In flower primordia, the gynoecium bulges out in the centre of the flower. The two carpels are in a median position. After an initially conical growth of the entire ovary, the four ovular lobes begin to overtop the initially terminal stylar primordium, leading to a gynobasic style. Outgrowths—often referred to as “true” – corresponding to carpel boundary and “false” septum – from the ovary roof (apical septa) and from the base (basal septa)—divide and separate the primary two ovarial chambers into four. At maturity, nutlets are attached (apparently) directly to the receptacle or to the more or less conical gynobase. The corresponding scars left after detachment are termed “areole” on the gynobase and “cicatrix” on the nutlet. Deviations from the common pattern of gynoecium structure and merosity are described under “Fruit and Seed”. The style is simple in most species, rarely forked (e.g. *Echium*) to twice forked with four stigmas (*Arnebia*). The style is mostly included in taxa with hypocrateriform corollas, but may be long exerted in tubular corollas. The style usually persists, but plays no role in fruit dispersal. Stigmas are entire or shallowly bilobed, capitate,

conical or cylindrical. Subterminal stigmas are sometimes formed by the extension of a sterile style elongation beyond the stigma (*Buglossoides*, some *Lithospermum*). The stigmatic surface is dry (Heslop-Harrison 1981) and usually has unicellular receptive papillae of various, mostly lageniform (flask-like) shapes.

EMBRYOLOGY. The last comprehensive work on the embryology of the family was published by Wunderlich (1991). Anthers are tetrasporangiate with four-layered walls and development follows the Dicotyledonous type (Khaleel 1977). The cells of the glandular tapetum are either mononucleate or two- to multinucleate (up to 10 in *Pentaglottis sempervirens*, Mascré 1922). There is no differentiation into an inner and an outer tapetum. Pollen formation is simultaneous. Pollen grains are predominantly shed in the three-nucleate stage. Two-nucleate grains have been reported for *Mertensia platyphylla* (Khanna 1964) and *Trichodesma* (Khaleel 1977), but apparently the number of nuclei may vary even within species (*Trichodesma stocksii*, Wunderlich 1991). The ovules are epitropic, unitegmic and tenuinucleate. Their position varies from upright in *Lithospermeae* and *Boragineae* to horizontal or pendant in *Cynoglosseae*. Integuments may consist of up to 20 cell layers (*Cynoglossum denticulatum*). Integumentary rostra serving as obturators are present in *Myosotis* (Svensson 1925), *Lepechinia* p.p. (“*Microparacaryum*”, Briechle and Hilger 1988), *Cynoglossum* and *Trichodesma* (Khanna 1964). An integumentary tapetum is not developed. There is usually one archesporial cell (rarely 2 to 3) developing directly into the megaspore mother cell. Usually, the embryo sac develops according to the *Polygonum* type, the bisporic type was reported for *Anchusa officinalis*. Aposporic embryo sac formation has been reported either from the integument or from the chalaza (*Cynoglossum denticulatum*). The mature embryo sac is usually spherical. The *Boragineae* are apparently unique in the formation of a “diverticle”, i.e. a lateral outgrowth directed towards the funicle (Svensson 1925; Pitot 1937). The synergids are well developed and in some cases larger than the egg cell. Polar nuclei are adjacent to the egg apparatus and usually fuse simultaneously with fertilization. Fertilization is porogamous. The endosperm is either cellular

(reported only from *Myosotis arvensis*), intermediate (sensu Wunderlich 1959, modifications from cellular endosperm) or nuclear (the “*Borago*” type of Svensson 1925). Mature seeds are virtually exendospermous with one or two cell layers of endosperm, the remaining space being taken up by the large embryo. Embryogeny is variable (Souèges 1948; Crété 1963; Briechle and Hilger 1988), corresponding to the first period and megarchetypes II, III, V of Souèges (1948) or the *Aster* and *Chenopodium* type of Johansen (1950). Embryo development may vary in individual genera or even species. The suspensor, if present, is short, usually consisting of only one, rarely two cell layers. The radicle is very short, the cotyledons contain lipids and proteins as storage reserves (McGill et al. 2002). Cotyledons are broadly ovate to nearly subcircular and shortly acuminate cotyledons with fine pubescence appear to be the most common type. In species with glabrous and glaucous adult leaves the cotyledons are also glabrous and glaucous (e.g. *Mertensia*, some *Omphalodes*). A few genera have deeply bifid cotyledons (*Amsinckia*, *Cryptantha* p.p.).

POLLEN MORPHOLOGY (BY OLIVER MOHR). Studies comparing pollen across floras or the family show that *Boraginaceae* are remarkably eurypalynous (Fig. 6). Differences are found in shape, size, exine sculpturing and number, nature and position of apertures and pseudoapertures, colpus margin differentiation and presence or absence of mesocolpial or apocolpial fields and/or an endocingulum (Fig. 6). The smallest pollen grains of the family (and in Angiosperms) are apparently found in *Cynoglosseae*, namely in *Cryptantha* (ca. $4 \times 2 \mu\text{m}$ in *C. clevelandii*, Hargrove and Simpson 2003), *Myosotis* and *Trigonotis* (ca. $5 \times 2 \mu\text{m}$, Grau and Leins 1968). The largest pollen grains reach up to $55 \times 40 \mu\text{m}$ (*Anchusa*, *Boragineae*, Clarke 1977) and large grains may in general be more typical of *Boragineae* and *Lithospermeae*. Pollen shape is commonly prolate or dumbbell-shaped. Exine sculpturing is variable and ranges from psilate (*Buglossoides*, *Cynoglossum*), perforate-foveolate (*Echium*, *Nonea*), microechinate (*Onosma*, *Cerintho*), microreticulate (*Moltkia*) and verrucate (*Mertensia*, *Symphytum*) to granulate (*Borago*, *Symphytum*—following the terminology of

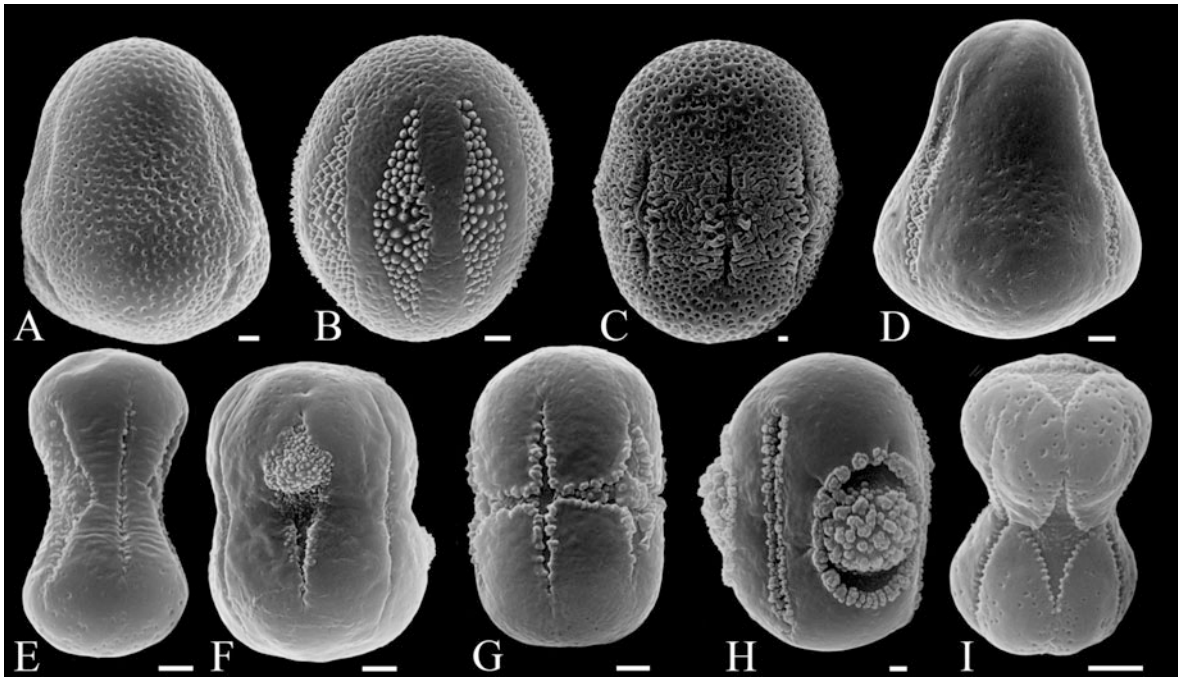


Fig. 6. Boraginaceae pollen grains. A *Echium vulgare*, ovate, 3-colporate. B *Moltkia petraea*, rounded, 8-colporate, echinate ornamentations of apertural surface. C *Nonea vesicaria*, 8-colporate, reticulate, with change of exine ornamentation towards the equatorial level. D *Alkanna hirsutissima*, pear-shaped, 3-colporate. E *Trigonotis rockii*, 6 apertures (simple colpi and colporate apertures alternating), perforate-foveolate exine surface, pores less dense in region of mesocolpium. F *Eritrichium nanum*, 3 colporate alternating with 3 colporate apertures, the pores characteristically

arranged (2 on one, the third on the other sphere of the pollen grain), in the centre of the image colporate aperture with porus on the right side. In the lower left, upper part of porus on the back side, third one hidden. G *Cynoglossum creticum*, 6 apertures (as in *T. rockii*, 3 simple colpi, 3 colporate apertures). H *Solenanthus watieri* (\equiv *Pardoglossum watieri*), typical ("Pardoglossum") apertural peculiarity, 2 types of apertures: simple ones (long, slit-like, parallel sided) and compound apertures (more or less circular, densely granulate). I *Myosotis azorica*, top right the apocolpial field on polar area, apertures compare *T. rockii*. Bars = 1 μ m

Halbritter et al. 2008, examples of genera not necessarily exclusively with one type). Ornamentation can be homogeneous over the entire grain, but it can also be differentiated between apo- and mesocolpia: in *Nonea vesicaria* the apocolpia are perforate-foveolate, mesocolpia are fossulate and reticulate, in *Trigonotis rockii* the density of perforate-foveolate sculpturing decreases towards the equatorial constriction, in some *Lithospermum* the mesocolpium is psilate, but the apocolpium is echinate. Apertures are usually colporate, but porate pollen is also known (some Lithospermeae). The vast majority of taxa has 3–4-aperturate grains. In Echiochileae the pollen is often 2–3-colporate and usually more or less oblong to rectangular in equatorial view (Lönn 1999). Higher aperture numbers are found mainly in Lithospermeae and Boragineae with 6–8 in *Cer-*

inthe (Sahay 1979) and 8-colporate in many (American) *Lithospermum*, 10–12(–15)-colporate (zonoaperturate) in *Borago officinalis*, some *Moltkia* and 15-colporate in *Nonea heterostemon* (Selvi et al. 2006). Apertures are mostly median, but apertures close to one pole are common in Lithospermeae. Some species of *Arnebia* (Lithospermeae) and possibly also some *Lappula* (Cynoglosseae) have dumbbell-shaped grains with bi-aperturate colpi (Khatamsaz 2001). Syncolpate pollen grains with neighbouring colpi anastomosing near the poles (but leaving a small island of exine at the pole itself) are known from, for example, some Lithospermeae (Avetisjan 1956). Syncolpate pollen grains with colpi united across the poles are found in *Heterocaryum* (Cynoglosseae, Avetisjan 1956). The *Lappula* group (Cynoglosseae) shows a very peculiar

aperture position with two pores located closer to one pole and the third one closer to the opposite pole (Avetisjan 1956). Endoapertures are mostly alongate or circular. The ornamentation of the ectoapertural margins ranges from straight and smooth (*Cerithe major*), frayed (*Echium vulgare*), thickened with rounded or elongated ornamentation (*Mertensia ciliata*, *Solenanthus apenninus*) to spinulose (*Anchusella*). The colpus membrane is smooth or granulose with spherical or conical ornamentation (e.g. *Gastrocotyle*). The mean exine thickness ranges from 0.11 μm (*Cryptantha*), 0.5 μm (*Cynoglossum*, *Lappula*) to 3 μm (*Borago*). Heterocolpate pollen is characteristic of the vast majority of Cynoglosseae (but normally tricolporate; e.g. in *Trichodesma*, *Craniospermum*, *Caccinia*, Avetisjan 1956). They usually have 3–4 colporate apertures alternating with 3–4 slit-like pseudocolpi (pseudo-, “simple and compound” apertures) not functional for pollen tube growth. This is not proven by pollen germination studies but corroborated by TEM investigations (Hargrove and Simpson 2003). *Cynoglossum* p.p. (“*Pardoglossum*”) has circular, complex and granular apertures alternating with narrow slit-like pseudocolpi.

Endocingular modifications of the exine along the equator, leading either to a granular reduction of the exine or a slit-like incision forming a belt around the grain are frequent in Boragineae, where they are present as a granular equatorial belt, often diffusely delimited from the remainder of the exine (Bigazzi and Selvi 1998). Conversely, in Cynoglosseae there is often a sharp incision (without or with rugose ornamentation) uniting the colpi and pseudocolpi in the equatorial plain (Avetisjan 1956; Hargrove and Simpson 2003). Both the width of the endocingulum and the ornamentation of its surface show considerable variation. Triangular or circular areas in the apocolpium are known from some species of *Myosotis*, *Trigonotis* and *Cryptantha* (Hargrove and Simpson 2003), but appear not to be present in all species of these genera. In *Myosotis* and *Trigonotis* they are delimited by the margins of the anastomosing colpi, while in *Cryptantha* they are not connected to the colpi and have a distinctly modified margin. Large, rugose, circular apocolpial fields, usually at only one pole, are occasionally found in *Thaumatocaryon* (Boragineae). In

this genus there are always mesocolpial fields of exactly the same shape and sculpture. Rugose, more or less circular mesocolpial fields are found in *Moritzia* and *Thaumatocaryon*, but also in some *Anchusa* s.l. (*Phyllocara aucheri*, Bigazzi and Selvi 1998) and are best considered as derived from the rugose endocingulum that is common in Boragineae. All four subgroups of Boragineae here recognized thus have some unique pollen characters which are typical of a large part of the tribe (e.g. only 2 apertures in Echiochileae, pear-shaped, heteropolar in Lithospermeae, a rugose endocingulum or mesocolpial fields in Boragineae, heterocolporate in Cynoglosseae). However, none of these modifications is present in all representatives of the respective groups. Prolate, 3-colporate pollen grains are found in at least some representatives of all of them. Some smaller subgroups can, however, be clearly delimited by pollen morphology.

KARYOLOGY. The first karyological surveys of Strey (1931), Smith (1932) and Britton (1951) already revealed considerable variation in base and somatic chromosome numbers, ploidy levels and karyotype morphology. Approximately 630 specific and subspecific taxa, representing ca. 35 percent of the Boragineae, have been surveyed at least for chromosome number. The taxonomical and geographical distribution of sampling is highly uneven, with numerous data from Europe and North America and very few data from Asia, Africa and South America. Metaphasic A-chromosomes range from 1–2 to ca. 10 μm (some *Anchusa*); the smallest appear to be more typical of Cynoglosseae (e.g. *Rochelia*, *Lappula*, *Asperugo*), the larger of Lithospermeae and especially Boragineae. Metacentric, submetacentric and subtelocentric chromosomes form the complement of most taxa. Bimodal karyotypes are rare (*Onosma*). Supernumerary B-chromosomes have been observed in only a few genera (see below).

Somatic complements vary between $2n = 8$ (*Amsinckia lunaris*) and $2n = 144$ (*Symphytum tuberosum*). Base numbers do not seem to match the tribal subdivision of the family, although some numbers occur with higher frequency in given taxonomic groups. Echiochileae are karyologically unknown. Boragineae are the most comprehensively studied group. Primary base

numbers are $x = 6, 7, 8, 9$ and 10 , with $x = 8$ being particularly common; of possible secondary origin are $x = 11, 12, 13$ and 15 . In *Anchusa* s.l. (*Anchusa*, *Anchusella*, *Lycopsis*, *Hormuzakia*, *Phyllocara* and some *Gastrocotyle*) diploidy with $2n = 16$ is prevalent, in addition there are some tetraploids ($2n = 4x = 32$ in *Anchusa* spp.) and hexaploids (*Lycopsis arvensis*, $2n = 6x = 48$). *Symphytum* is probably the karyologically most variable genus of the family, showing aneuploidy, dysploidy ($x = 7, 8, 10, 11, 12$ and 15), auto- and allopolyploidy associated with hybridisation (up to dodecaploidy). *Nonea* ($x = 7, 8, 9, 10, 15$, up to decaploid) and *Pulmonaria* ($x = 7, 8, 9, 11, x = 8, 9, 10, 11, 12, 13$ in diploid or polyploid cytotypes) are also karyologically diverse. Supernumerary B-chromosomes have been observed in both *Nonea* and *Pulmonaria*. In those Boragineae investigated, 23% are polyploids, while the rest are exclusively diploid or at least include diploid cytotypes. Lithospermeae have fewer polyploids (16%, with ca. 38% of the species of the tribe surveyed). Primary base numbers are $x = 6, 7, 8, 9, 10$ and (possibly secondarily) $11, 12, 13$ and 15 , with $x = 7$ and 8 being most common and $x = 6$ and 12 rare. The lowest base number, $x = 6$, is known from *Pontechium*, *Huynhia* and *Moltkiopsis* ($2n = 12/24$) and some diploid species of *Onosma* ($2n = 12$). Diploids predominate in *Echium* ($2n = 16$, rarely 10 , some tetraploids with $2n = 32$), *Lobostemon* and *Echiostachys* ($2n = 14$, some tetraploids $2n = 28$), *Arnebia* ($2n = 14, 16, 22, 24$), *Moltkia* ($2n = 14, 16$) and *Cerinthe* ($2n = 16$ or 18). *Onosma*, the largest genus of Boraginaceae (>150 spp.), is karyologically particularly diverse. The most common base numbers are $x = 6$ and 7 , polyploidy is based on $x = 6, 7, 8, 10$ and 11 . Several species show high intra-specific polymorphism and unstable karyotypes. Bimodal karyotypes and other phenomena, such as permanent anorthoploidy, have also been reported. *Lithodora*, *Lithospermum* and *Buglossoides* mostly have the base numbers $x = 7$ and 8 , sometimes $x = 9, 11, 12, 13$; $2n = 20$ seems unique to the Italian endemic *B. calabra*. Polyploidy, mainly based on $x = 7$, is widespread in *Lithospermum* s.l. and in annual species complexes of *Buglossoides*, while the perennial species of *Buglossoides* are mostly diploid. *Lithodora* is rarely diploid ($n = 13, 2n = 16$), more often tetraploid based on $x = 7, 8, 9$ and 10 . An extreme

case of high-level polyploidy is known for the monotypic Balkan genus *Paramoltkia* ($2n = 96, 114$, assuming $x = 8$: 12-ploid or 14-ploid). Cynoglosseae are karyologically relatively homogeneous, with diploids with $2n = 24$ being the most common type. Descending aneuploidy is present in several taxa with $2n = 22$ and $2n = 20$. In *Myosotis* aneuploidy is common ($x = 11, 10, 9, 8, 7$). Polyploidy or aneuploidy are present in over 50% of the species of *Myosotis* studied and may have played an important role in the worldwide diversification of the genus. Polyploidy is less frequent. The karyologically most diverse group in Cynoglosseae appear to be the closely allied genera *Amsinckia* and *Cryptantha*. In *Amsinckia* primary numbers range from $x = 4$ to $x = 8$, plus several odd base numbers of likely secondary origin such as $13, 15, 17$ and 19 . Intra-specific aneuploidy is documented in *A. intermedia* and *A. menziesii*. In *Cryptantha* the base numbers $x = 6, 7, 8, 9$ and 10 have been reported, $2n = 24$ is present in only few species and higher levels of polyploidy are reported from *C. haplostachya* and *C. calycotricha* ($2n = 8x = 64$).

POLLINATION AND REPRODUCTIVE SYSTEM (BY MARKUS ACKERMANN). Zoophilous allogamy is the most common breeding system in Boraginaceae, but selfing is also common across the family and cleistogamy is reported for several genera (see below). Abiotic pollination is unknown. Selfing is typical of small-flowered annual species but also of at least some perennials (e.g. *Anchusa crispera*, Quilichini et al. 2001). In many species fruit set is close to 100% in the complete absence of pollinators. Cleistogamous flowers have been reported from *Cryptantha* (Grau 1983), *Lithospermum* (Lord 1981) and *Neatostema*. Chasmogamous and cleistogamous flowers are generally found on the same plant, with cleistogamous flowers produced near the ground or in the ground in *Cryptantha* p.p. ("Geocarya", Higgins 1971), on the lower, very short branches of the inflorescence (*Lithospermum*) or in poorly developed individuals and towards the end of the growing season (*Neatostema*). Conversely, there are many species which are obligate outcrossers and have developed special mechanisms to avoid selfing: both self-incompatibility and dichogamy are common, protogyny is widespread and proterandry has been reported from, for example,

Trichodesma and *Alkanna*. Herkogamy in the form of a stigma-height dimorphism is frequently observed in *Anchusa* and *Lithodora* (Al-Shehbaz 1991), heterostyly in, for example, *Amsinckia*, *Arnebia*, *Cryptantha*, *Glandora*, *Lithodora* and *Paracaryum*, where it is often associated with pollen heteromorphy (Ganders 1979). True dioecy has not been reported from Boraginaceae, but gynodioecy is known from *Echium* and *Myosotis*. Pollinators are attracted mostly by flower colour and less by scent produced from osmophores (Maurer 1961). Scent is usually not very strong, but may be pronounced especially in some white-flowered species.

Flowers are usually conspicuously coloured, often bicolorous and the corolla limb and faucal scales then show contrasting coloration. White is probably the most common colour in Boraginaceae, followed by blue, purple, yellow and pink. True blue flowers, rare in most other plant families, are particularly common. Yellow corollas are particularly common in Lithospermeae and some Cynoglosseae (*Amsinckia*), red, pink or brownish corollas are found across the family. Colour changes of the corolla during anthesis are relatively common (Weiss 1995). Either the whole corolla, the centre of the flower (androecial parts or faucal scales) or only the nectar guides (e.g. *Amsinckia*, *Huynhia*) change colour. Colour change is probably a visual signal for the pollinators, indicating changes in reward availability. Characteristic UV-reflection and absorption patterns have been documented on the corolla limbs (Rosen and Barthlott 1991). Faucal scales and/or trichome patches largely limit access to the nectar at the base of the tube to animals with sufficiently long and narrow mouth parts and/or foretarsi. In addition, they may serve as pollen exchangers: pollen released by the anthers is trapped by the papillose or pubescent scale surface; pollen is then transferred to the hairy head or body of visiting insects brushing against the scales while trying to reach the nectar at the base of the ovary.

Nectar is the primary floral reward. It is produced by a nectar disc as basal part of the gynoeceum and secreted through modified stomata. Own observations show that within the insect-pollinated taxa nectar production (standing crop) is between 0.03–10.1 μl per flower and

sugar concentrations range from 16 to 59% (Ackermann, Mittelbach, Weigend, unpubl. data, ca. 100 spp.). Nectar is usually rich in glucose, fructose and sucrose; smaller amounts of maltose and arabinose have been found in some taxa (e.g. *Anchusa*, Nepi et al. 2010). Flower visits and pollination follow common patterns. In cultivation in Central Europe the vast majority of Boraginaceae across floral types are visited primarily by long-tongued bumblebees (*Bombus*) and these are also the most important pollinators in some taxa in their natural habitat. However, in nature many species are pollinated by apparently quite specialized, often oligolectic bees, especially *Anthophora* and *Osmia*. A particular case of narrow specialization has been reported for *Cynoglottis barrelieri*, pollinated by *Colletes anchusae* (Apoideae, Müller and Kuhlmann 2003). Species with narrow corolla tubes are primarily pollinated by Diptera such as bee flies and tachinid flies, while butterflies are reported to visit flowers especially with large limbs and long and narrow corolla tubes. Pendulous or deflexed flowers with connivent or coherent anthers of, for example, *Borago*, *Caccinia*, *Cerinth*, *Onosma*, *Symphytum* and *Trichodesma* are buzz-pollinated by various bees (Teppner 2011). Though here pollen is the primary reward, flowers may still be nectariferous (Gilbert et al. 2001). Ornithophily by hummingbirds is known for some North American species of *Lithospermum* with corolla tubes up to 9 cm in length. Red-flowered *Lobostemon* in South Africa is sunbird-pollinated. In Tenerife (Canary Islands), native birds have been observed to visit the red-flowered *Echium wildpretii* and the nectar properties of this species correspond to ornithophily (Dupont et al. 2004). Small lizards (*Gallotia* spp.) have also been observed entering the flowers of *Echium wildpretii* and drinking the dilute nectar, but it has not been verified whether they pollinate the flowers (Olesen and Valido 2004).

FRUIT. The fruits of Boraginaceae provide the single most important set of characters for their classification and taxonomy. During fruit maturation the four parts of the ovary usually develop into four separate, highly characteristic nutlets (= mericarpids, Fig. 7), the calyx is typically accrescent and pedicel and internodes of the

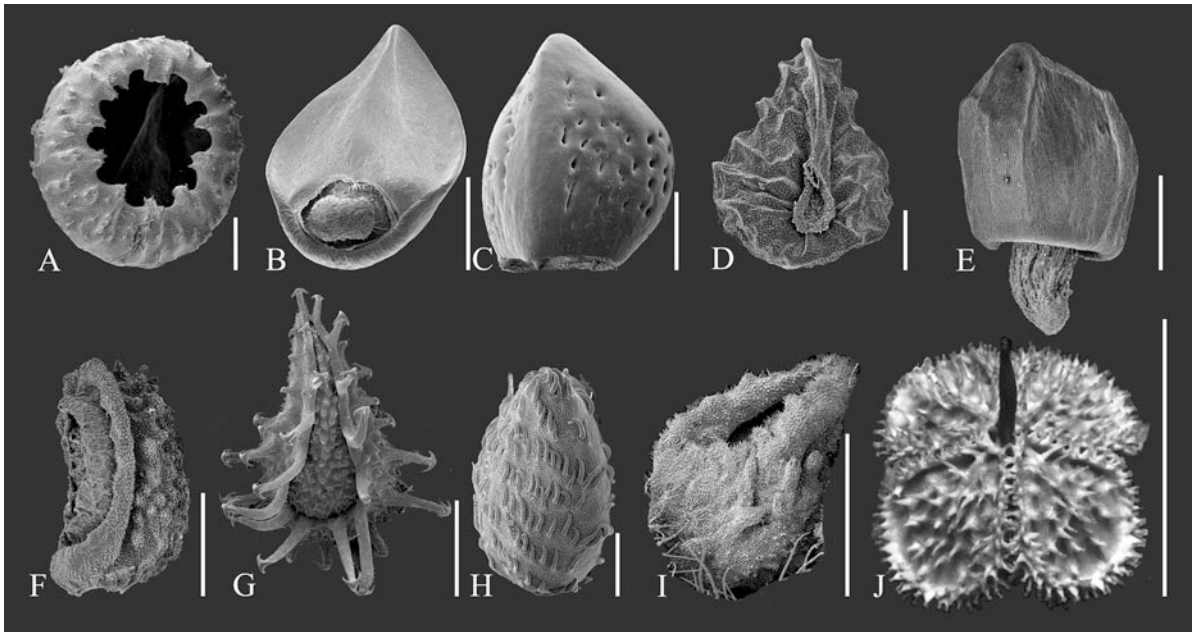


Fig. 7. Nutlets of Boraginaceae. **A** *Omphalodes linifolia*. **B** *Myosotis involucrata* (syn. *Trigonocaryum involocratum*). **C** *Lithospermum cinerascens*. **D** *Plagiobothrys congestus*. **E** *Borago pygmaea*. **F** *Antiotrema dunnianum*. **G** *Lappula squarrosa*. **H** *Lasiocaryum densiflorum*. **I** *Microula pseudotrichocarpa*. **J** *Cynoglossum officinale*, fruit. A, B, D, E, F, G, I bars = 1 mm, C, H bars = 250 μ m, J bar = 1 cm. (G from Hilger 1985, with permission from Borntraeger-Cramer)

inflorescence elongate. There are several exceptions from this basic pattern. Two two-seeded twin-nutlets develop in *Cerinth*. Reduction in the number of nutlets occurs frequently, there are only two nutlets in *Rochelia*, a single nutlet is common in, for example, *Buglossoides*, *Trichodesma*, *Caccinia*, *Moritzia* and *Thaumatocaryon*. Mericarpid multiplication (up to 10) is only known from *Trigonotis* p.p. (“*Zoelleria*”), but its ontogeny has not been investigated. Nutlets are usually dispersed individually and separately from the calyx. Taxa with glochidiate, epizoochorous fruits usually have small and spreading to reflexed sepals (e.g. *Cynoglossum*, *Lappula*, *Hackelia*). In some taxa the calyx is accrescent, but the base becomes wider and the calyx lobes become more or less flaring, providing a wide opening for the nutlets to fall out (e.g. *Symphytum*). In other taxa the mature nutlets remain enclosed in the calyx, with the calyx then usually having uncinat (hooked) trichomes which facilitate epizoochory (some *Myosotis* spp., *Asperugo*, *Pectocarya*, *Moritzia*). In *Moritzia* and *Thaumatocaryon* the single fully developed nutlet does not become detached from the gynobase, but

remains firmly attached to it during dispersal in the closed calyx. In *Asperugo* the calyx folds transversally and closes over the nutlets with two dentate lobes and, in *Pectocarya* p.p. (“*Harpagonella*”), two fused sepals arch over and enclose one of the two nutlets. *Cryptantha circumscissa* has circumscissile calyx dehiscence. In *Suchtelenia*, the broad, wing-like, persistent calyx ensures wind-dispersal. Three basically different types of heterocarpy are found in Cynoglosseae, with fruits differing between individuals, on different parts of a plant (amphicarpy, known only from a few species of *Cryptantha* in Chile) or nutlets differing in the individual fruit (heteromerocarpy). Heteromerocarpy again follows three different patterns and is relatively frequent in widely different groups of the Cynoglosseae. In *Suchtelenia* there is a 2+2 pattern: two nutlets detach and are dispersed separately, the other two nutlets remain firmly attached to the gynobase and the strongly enlarged calyx, but all nutlets are morphologically similar. In *Heterocaryum* a 2+(1+1)-pattern is found: two opposite mericarpids are identical in shape and ornamentation, the other pair differs from the

first pair and the corresponding two nutlets additionally differ from each other. The most widespread form of heteromericarpidy is a 3+1 pattern, with three nutlets becoming detached and a fourth one remaining firmly attached to the gynobase (and sometimes the plant). This is found in several distantly related groups of Cynoglosseae (e.g. *Lappula*, *Lepechiniella*, *Amsinckia*, *Plagiobothrys*, *Cryptantha*). The fourth nutlet is here dispersed either with the calyx or with fragments of the mother plant. The three nutlets which are dispersed separately are usually larger, have a broader rim/wing and/or are distinctly glochidiate, the fourth is smaller and the surface less strongly ornamented and/or unwinged (Hilger et al. 1985). In almost all Boragineae and in some *Lithodora* and *Myosotis*, an often peg-shaped plug of gynobase tissue breaks off with the nutlet. This structure is, at least in Boragineae and *Myosotis*, an elaiosome serving ant dispersal. Nutlet orientation is intimately linked to both the shape of the gynobase and the shape of the nutlet. In Boragineae, Lithospermeae, Echiochileae and some taxa of Cynoglosseae (e.g. *Myosotis*, *Trigonotis*, *Bothriospermum*), the erect nutlets sit on a flat gynobase. The nutlets of *Trichodesma*, *Caccinia* and *Suchtelenia* are sunken into the convex gynobase. Nutlets in Cynoglosseae are mostly elevated on their adaxial side, i.e. sit in an oblique position due to the pyramidal shape of the gynobase. They always have a distinct adaxial and abaxial surface and are often dorsiventrally compressed and differentiated. The “nutlet margin” thus formed may be noticeable as a more or less distinct ridge or may be spectacularly elaborated in the form of a ring-shaped, comb-like or wing-like, sometimes glochidiate, usually simple but sometimes double structure. The ventral side of the nutlet is often convex or more or less sharply keeled, but concave in the mature fruits of *Mertensia*. The dorsal side is usually flat or concave, rarely convex. The nutlets are usually broadest at the base, but sometimes indistinctly (some *Lithospermum*, *Plagiobothrys*, *Alkanna*, *Podonosma*, *Stenosolenium*) or distinctly stipitate (*Thaumatocaryon*, *Echiochilon*). Nutlets, especially in Boragineae and Lithospermeae, are often slightly incurved (e.g. *Borago*, *Echium*) to nearly horizontally incurved (e.g. *Anchusa*, *Alkanna*). Ornamenta-

tion of the nutlet surface is widely variable across the family. Entirely smooth and shiny nutlets occur in relatively few taxa. The common name of *Lithospermum* (“stone seed”, “marble seed”) reflects the white, shiny, porcelain-like appearance of the fruit.

The fruit wall itself has an arrangement of layers characteristic for each tribe (F1 exocarp = outer epidermis, F2 sclerenchyma, F3 parenchyma, F4 endocarp = inner epidermis, Seibert 1978). Boragineae, Lithospermeae and Echiochileae share a common fruit wall type and differ from Cynoglosseae (Seibert 1978; Hilger 1985). The pericarp is also sometimes incrustated with silica and/or calcium carbonate, especially in Lithospermeae, to a lesser degree in Echiochileae. Outer exocarp cell walls often have a distinct secondary sculpturing varying from micropapillose to verrucose and shortly spinulose. Very rarely the nutlet surface is pubescent (*Lasiospermum*, some *Trigonotis*). Commonly the nutlets are ornamented with irregular crests, wrinkles or glochidia (most Cynoglosseae). These glochidia (Figs. 8, 9) are usually complex, multicellular, one- to many-hooked structures, often including subepidermal tissues. Their stiffness depends on the degree of silica incrustation in the cell walls. Nutlet margins are widely variable in Cynoglosseae. In *Cynoglossum* there is often a row of free glochidia along the margin, whereas the bases of these glochidia are more or less united, forming a

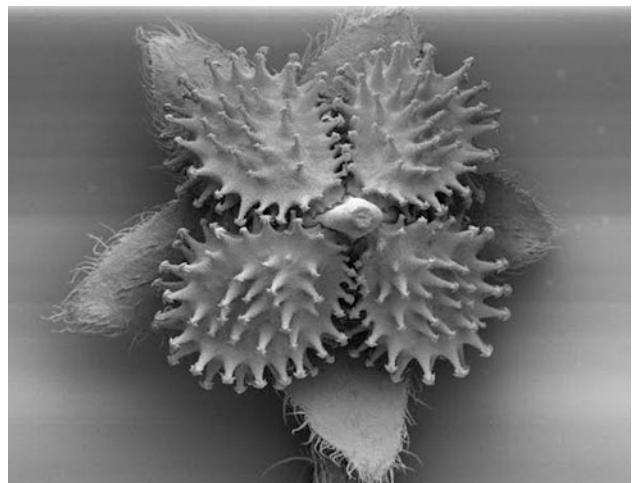


Fig. 8. Boraginaceae. Fruit of *Cynoglossum furcatum* with four densely glochidiate nutlets and the gynobasic style arising from the centre. (phot. H.J. Ensikat)

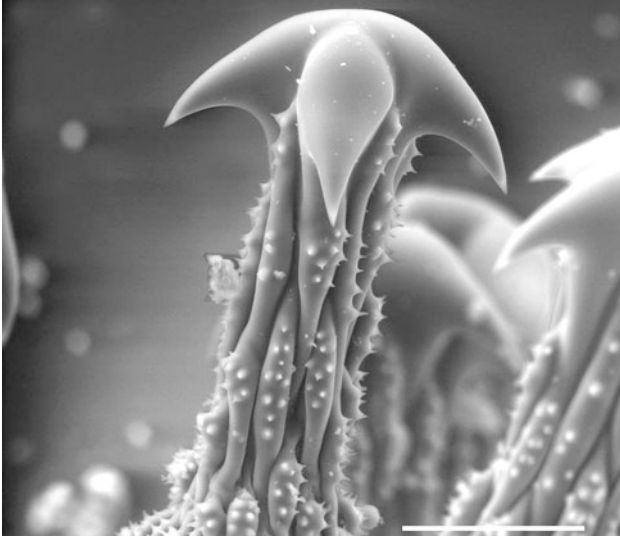


Fig. 9. Boraginaceae. Glochid of *Cynoglossum columnnae*. Bar = 100 μ m

small flat rim or wing along the margin. As a further elaboration these glochidia can fuse completely and lose their glochidiate nature entirely, forming a flat and narrow wing in *Mattiastrum* or a broad one in *Rindera*. In *Omphalodes*, *Lepechiniella* p.p. and *Paracaryum* the wing is thinly membranaceous, incurved and partly closes over the dorsal side of the nutlet, leaving a more or less wide “aperture”. The lateral wing can be displaced into a different position by asymmetrical growth of the nutlet body relative to the margin. In *Bothriospermum* and *Antiotrema* this leads to an inverse morphology with the originally “dorsal” (abaxial) marginal wing facing the style, i.e. displaced into an adaxial position. The “lateral wing” is here turned into an adaxial, umbilicus-like structure (“pseudo-aperture”, often mistaken for a cicatrix).

Seeds, enclosed by a testa consisting only of outer epidermal cells, are exalbuminous. Some taxa show more or less pronounced dormancy. Cold and moist stratification overcomes this dormancy or at least dramatically increases germination rates in many temperate and Mediterranean Boraginaceae such as *Amsinckia*, *Arnebia*, *Buglossoides*, *Pulmonaria*, *Mertensia* and *Lithospermum*. Increased germination after exposure to smoke has been reported for several species of *Cryptantha* (Keeley and Fotheringham 1998) and is likely present in other groups such as *Echium*

and South African *Lobostemon* and *Echiostachys*. Seed longevity is relatively high under dry storage even at relatively high temperatures (several years in some *Lithospermum*, Baskin and Baskin 1991).

DISPERSAL. Zoochory is likely the most important dispersal mechanism in Boraginaceae, followed by anemochory and hydrochory. Epizoochory is possibly the single most important mechanism. In the majority of Cynoglosseae the nutlets have glochidia permitting the attachment of the fruits to fur and/or feathers (e.g. *Cynoglossum*, *Lindelofia*, *Solenanthus*, *Hackelia*, *Lappula*). Some Cynoglosseae are very widespread, indicating the efficiency of this dispersal mechanism. At least one endemic Malagasy species of *Cynoglossum* has secondarily lost its glochidia for dispersal (*C. tsaratananse*, Miller 2005). In individual taxa throughout the family, the calyx encloses mature nutlets (some or all) and has uncinete trichomes or glochidia for animal dispersal (e.g. *Moritzia*, *Myosotis*, *Amsinckia*). Exozoochorous dispersal is reported for glochidiate nutlets, but even the only “rough” (verrucose) nutlets of *Echium plantagineum* appear to attach readily to fur and are transported in this manner (Parsons and Cuthbertson 2001). In several taxa the fruiting calyx remains firmly attached to the gynobase, and the entire fruit remains firmly attached to the plant, leading to “whole plant dispersal” or to gradual plant disintegration and fruit release. In many species of *Pectocarya* the inflorescence axis disarticulates at fruit maturity and the fruits are dispersed with parts of the inflorescence axis. In one species of *Pectocarya* (“*Harpagonella*”) the mature nutlets are additionally enclosed by two united, accrescent and incurved sepals with glochidia. The enlarged calyx in *Asperugo* also encloses the mature nutlets and is densely covered with uncinete trichomes. However, it remains firmly attached to the plant and the entire plant is covered with uncinete trichomes, so that here large parts of the plant are dispersed on the fur of larger mammals. A similar case may be present in *Rochelia*, where the nutlets remain attached to the gynobase and are additionally enclosed by incurved trichomatose sepals. Granivory, i.e. active collection of fruits for food by animals (and subsequent loss or hoarding), may play a

very important role in the dispersal of a large number of Boraginaceae. The superficially very different fruits of *Lappula*, *Myosotis*, *Cryptantha* and *Lithospermum* are commonly found in rodent faeces and/or middens or around ant mounds. Birds are likely important for the dispersal for the stone-like seeds of Lithospermeae, esp. *Lithospermum* (Best and Smartt 1986), but these are also accidentally consumed by grazing animals and pass into the faeces undigested and viable (e.g. *Echium plantagineum*, Parsons and Cuthbertson 2001). Ants are attracted by the elaiosomes on the nutlet (Bresinsky 1963). Nutlets with large elaiosomes are characteristic for Boragineae, but also *Myosotis* p.p. (incl. "*Trigonocaryum*") and possibly some *Lithodora* (Thomas et al. 2008). Anemochory is largely restricted to Cynoglosseae, namely to taxa with distinctly winged nutlets (*Lepechiniella*, *Mattias-trum*, *Omphalodes*, *Paracaryum*, *Rindera* and *Suchtelenia*), where some nutlets remain attached to the dramatically enlarged calyx. Hydrochory has been reported as dispersal by sea water for the coastal *Mertensia maritima* (Ridley 1930; Skar-paas and Stabbetorp 2001) and *Anchusa crispera* (Quilichini and Debussche 2001). In both species, fruits tolerate exposure to sea water and float for a considerable time (>9 and 1 week respectively). Rain splash dispersal has been reported for *Trigonotis brevipes*: the nutlets are splashed out of the cup-shaped calyces by raindrops (Nakanishi 2002), and it is likely present in a number of *Trigonotis* species with similar fruits. Dispersal by flash-floods has been suggested for *Alkanna orientalis* (Wolff et al. 1997). Whole-plant dispersal by wind or flash-floods is the likely dispersal mechanism for *Lappula* p.p. ("*Sclerocaryopsis*"), where all nutlets remain attached to the mother plant, but the mother plant becomes strongly lignified when fruiting and breaks off near the base.

PHYTOCHEMISTRY (BY DIETRICH OBER). Phytochemistry of Boraginaceae has been studied mostly because of their (former or present) use for medicinal preparations and for dyes. The bulk of the studies concentrated on the most common representatives of Cynoglosseae (*Cynoglossum*), Boragineae (*Anchusa*, *Borago*, *Symphytum*) and Lithospermeae (*Lithospermum*), whereas many species-rich groups remain entirely unstudied.

No reports have been published on tribe Echiochileae. On the basis of the data available, the most characteristic secondary metabolites for Boraginaceae appear to be fructanes, allantoin, γ -linolenic acid as transport and storage compounds and naphthoquinones of the alkannin type and pyrrolizidine alkaloids as typical secondary metabolites. The characteristic storage carbohydrates are fructanes, a group of β -D-fructofuranosides with up to 40 fructose residues attached to a sucrose moiety and belonging to the inulins. They are found predominantly in the underground organs of perennial taxa (up to 5.15% of fresh weight of *Symphytum officinale* roots). They form a demulcent mucilage and several species were used in folk medicine due to this property. Recently, fructo-oligosaccharide cinnamoyl ester derivatives have been identified in *Lindelofia stylosa* with sucrose, 1-kestose and nystose esterified at both ends to caffeic acid derivatives (Choudhary et al. 2006). The cyclit D-bornesitol seems to be widespread within Boraginaceae (Hegnauer 1964), but absent from the other families of the Boraginales (Hegnauer 1997).

The seeds of Boraginaceae have a high oil content, with main component and often also the corresponding tetraenic acid, octadecatetraenoic acid (ODA, = stearidonic acid, C18:4 $\Delta^{6,9,12,15}$, 5–21 %). These two fatty acids are characteristic of Boraginaceae s.str. separating this family from all other Boraginales which lack these compounds (Hegnauer 1989). In humans GLA and ODA act as metabolic precursors of eicosanoids such as prostaglandins and leukotrienes. Due to their ability to lower blood cholesterol levels, oils rich in GLA are of high commercial value for use in dietary supplements (Cook et al. 2002). The oils contain a range of different tocopherols at varying levels (Velasco and Goffman 1999).

Nitrogen storage and transport is mainly mediated by S-Allantoin in Boraginaceae (Hegnauer 1989). This storage compound contains equal amounts of nitrogen and carbon and its nitrogen mobilization is achieved via enzymatic degradation (Kim et al. 2007). Conversely, the nitrogen containing pyrrolizidine alkaloids (PAs) do not serve as storage compounds and show neither turnover nor enzymatic breakdown in the living plant. They are produced by

the plant as chemical defence against herbivores and are poisonous and strong feeding deterrents. They are accumulated in their polar, salt-like *N*-oxide form primarily in young leaves and in the reproductive organs of the plant (reviewed in Hartmann and Ober 2000). Most of the PAs found in species of the Boraginaceae are 1,2-dehydropyrrolizidines that are known to be responsible for acute and chronic poisoning of humans and livestock by causing particularly irreversible liver damage and photosensitivity in cattle and other domestic animals including poultry (Stegelmeier et al. 1999; Authority ANZF 2001; Stewart and Steenkamp 2001). Several species belonging to Boraginaceae are traditionally used as medicinal plants or remedies, but the presence of PAs in many of them spoils their value for medicinal purposes (Roeder 1995, 2000). PAs are esters of a necine base, a bicyclic amino alcohol that is esterified to one or more necic acids. Within the Boraginaceae (as well as in the Heliotropiaceae), PA-structures that belong to the lycopsamine type dominate. These lycopsamine type PAs are characterized by a unique C_7 -necic acid that is synthesized via an intermediate of valine biosynthesis (Hartmann and Witte 1995; Weber et al. 1999). For the biosynthesis of the necine base moiety, homospermidine is the first specific intermediate that is synthesized by homospermidine synthase (HSS) from putrescine and spermidine as substrates (Ober and Hartmann 1999). Based on sequence data of HSS it was shown that this alkaloid-specific enzyme was recruited early in the evolution of the Boraginales by duplication of the gene encoding deoxyhypusine synthase. In spite of this common origin of PA biosynthesis in members of the Boraginales, the site of PA biosynthesis varies significantly between *Symphytum officinale* (biosynthesis in shoots and roots), *Cynoglossum officinale* (exclusively in the roots) and *Heliotropium indicum* (Heliotropiaceae, exclusively in the shoots; Frölich et al. 2007). These observations were supported recently by immunolocalization experiments, showing that in these three species HSS expression is restricted to completely different cell types (Niemüller et al. unpublished).

Naphthoquinones are widespread in Boraginaceae and the liposoluble alkannin and its stereoisomer shikonin are major components of the deep red pigments found especially in the taproot

of many species of the Boraginaceae (esp. Lithospermeae, Hegnauer 1989), but occasionally also in the aerial parts (*Plagiobothrys*, Hegnauer 1997). These red pigments are quite common in Lithospermeae with the two economic sources *Lithospermum erythrorhizon* from E Asia and *Alkanna tinctoria* from W Asia and have also been reported from Cynoglosseae (*Plagiobothrys myosotoides* and *P. arizonicus*). Herbarium sheets of species containing this dye can easily be identified by the intense colouration of the paper. The presence of the red colorant may be species-specific or be present only in individuals or populations of otherwise uncoloured species (e.g. *Buglossoides arvensis*). The use of alkannin, shikonin and their derivatives as pigments for food-colouring and cosmetics and for several medical applications can be traced back many centuries and was reviewed recently (Papageorgiou et al. 1999). These compounds have been shown to possess strong wound healing, antitumor, antimicrobial, anti-inflammatory and antithrombotic properties (Papageorgiou et al. 2006). Alkannin and shikonin are prenylated naphthoquinones that are synthesized from two key precursors, 4-hydroxybenzoate and geranyldiphosphate. With respect to the stereospecificity of many biosynthetic pathways it is remarkable that plants are able to produce both enantiomers simultaneously. Nevertheless, the composition of this mixture varies: 3-alkannin, the *S*-enantiomer, dominates mainly in European plants (for example more than 95% in *Alkanna tinctoria*), while shikonin, the *R*-enantiomer, is the dominant compound (84–93%) in *Lithospermum erythrorhizon* from E Asia (Hegnauer 1997; Papageorgiou et al. 2006).

Rosmarinic acid, an ester of caffeic acid with α -hydroxydihydrocaffeic acid, is found in several plant families, but is most characteristic for members of the Boraginaceae and subfamily Nepetoideae of Lamiaceae (Petersen and Simmonds 2003; Harley et al. 2004). Rosmarinic acid shows various biological activities of which the main activities are adstringent, antioxidative, anti-inflammatory, antimutagen, antibacterial and antiviral (Petersen and Simmonds 2003). Further caffeic acid derivatives that are characteristic for members of the Boraginaceae are lithospermic acid, an ester of three hydroxycinnamic acid moieties and lithospermic acid B, a dimer of rosmarinic acid (Petersen and Simmonds 2003). This

polyphenol is found in *Anchusa*, *Echium*, *Symphytum* and the eponymous *Lithospermum* species (Hegnauer 1989) and was discussed as a plant-derived antifertility agent due to its gonadotropine inhibitory effects (Farnsworth et al. 1975). Other secondary metabolites have only been reported sporadically. Traces of volatile oils (i.a. thymol and carvacrol) have been reported from *Echium* and *Onosma*. Cyanogenic compounds have been found in only very few species (e.g. (2S)-dhurrin from *Borago officinalis*, Van Valen 1979; Hegnauer 1989). Triterpenoids and triterpenoid derivatives such as phytosterols, triterpen alcohols and saponins (glycosides of nonpolar triterpenoids with surface active properties) have been reported from several distantly related species in Boragineae and Cynoglosseae (*Anchusa officinalis*, *Caccinia glauca*, *Trichodesma africanum*, *Symphytum officinale*, Hegnauer 1964, 1989, 1997). The flavonoid glycoside rutin is apparently relatively widespread in the family (Hegnauer 1989). In the dark blue bee pollen of *Echium plantagineum* the anthocyanin petunidin-3-O-rutinoside was identified as the main pigment, while in the violet-blue flowers of *Lobostemon* delphinidin-3,5-diglucoside was identified as the most common pigment (Van Wyk et al. 1997). Cyanidin, delphinidin and malvidin are the dominant chromophores of Boraginaceae flower anthocyanins (Hegnauer 1997). Flavone aglycones were identified in the exudates on the plant surface of *Nonea* species (Wollenweber et al. 2002).

SUBDIVISIONS AND RELATIONSHIPS. Boraginaceae lend their name to the order Boraginales in the Lamiid clade (APG III, Angiosperm Phylogeny Group 2009). Molecular, morphological and phytochemical data clearly indicate that Boraginaceae in their narrow circumscription are monophyletic (Gilg 1907; Nowicke and Miller 1989; Wang and Harley 2004; APG III 2009). *Wellstedia*, traditionally included in Boraginaceae and at one time assigned to a distinct subfamily Wellstedioideae Pilg. (Pilger 1912), is likely the sister group of Boraginaceae and should be treated as Wellstedioideae Novák (Weigend et al. 2014). Traditionally, Boraginaceae have been treated as a family with the four subfamilies Boraginoideae, Heliotropioideae, Cordioideae and Ehretioideae (Gürke 1893). However, capsule-fruited Hydro-

phyllaceae appear to be nested in Boraginaceae in this classical circumscription (Ferguson 1996). The former subfamilies of Boraginaceae can be redefined as Ehretiaceae (incl. Cordiaceae, Lennoaceae and Hoplestigmataceae), Boraginaceae (s.str.) and Heliotropiaceae, all of which are morphologically well-defined. Hydrophyllaceae represent a more complex problem, since they are evidently not monophyletic and their fruit morphology is so different from that of the other groups of Boraginales that none of its subgroups/genera can be readily incorporated into one of the families of the Boraginales without compromising their morphological integrity. A group of genera of Hydrophyllaceae appears to be monophyletic and can be redefined as Hydrophyllaceae s.str., but *Codon* appears to be sister to Boraginaceae s.str. plus Wellstedioideae. Formerly included in Boraginaceae s.str. as subfam. Codonoideae (Retief and van Wyk 2005), it is, however, so different in fruit and flower morphology that we prefer segregation as the monogeneric Codonaceae (Weigend and Hilger 2010; Weigend et al. 2013, 2014). *Hydrolea* has been segregated from Hydrophyllaceae into Solanales as Hydroleaceae.

The infrafamilial classification of Boraginaceae is in urgent need of revision. Up to 13 tribes and eight subtribes have been recognized (Popov 1953), with many monospecific genera and subtribes. Recent attempts at improving this system (Ovczinnikova 2009) caused additional confusion. These and other infrafamilial classifications concentrated on moving individual “aberrant” genera into species-poor tribes or subtribes, but leaving the bulk of genera in the established tribes, leading to an equally complex and confusing infrafamilial classification. The definitions of these small (sub-)tribes are mostly based on evidently apomorphic characters such as twin-nutlets (Cerintheae), zygomorphic flowers (Echieae), increased nutlet number (Zoellerieae), “inverted” nutlets (Bothriosperminae), reduction to two nutlets (Rochelieae) or united sepals curving over the fruit (Harpagonelleae). Some of these tribes become obsolete by the synonymization of their type (and only) genera under larger genera with different tribal placement (*Zoelleria* in *Trigonotis*; *Harpagonella* in *Pectocarya*, *Trigonocaryum* in *Myosotis*).

The most recent listing of tribes was provided by Riedl (1997), recognizing the six tribes

Boragineae, Cynoglosseae DC., Eritrichieae Benth. & Hook., Lithospermeae Dumort., Myosotidae Reichenb. and Trigonotideae Riedl, but molecular studies (e.g. Weigend et al. 2010, 2013) retrieved Eritrichieae, Myosotideae and Trigonotideae as nested within Cynoglosseae sensu lato. Weigend et al. (2013) retrieved a total of four strongly supported lineages, corresponding to the Boragineae, Echiochileae (Riedl) Långström & M.W. Chase, Lithospermeae and Cynoglosseae. Additional tribes (e.g. Eritrichieae, Myosotideae, Trichodesmeae Zak., Craniospermeae DC. ex Meisn., Asperugeae Zak. ex Ovczinnikova) could be recognized, but these are either species-poor or even monospecific, or would have to be extensively redefined. Relationships within three of the major tribes are relatively well understood and have been studied with a combination of molecular and morphological characters: Lithospermeae (Seibert 1978; Thomas et al. 2008; Cecchi and Selvi 2009; Weigend et al. 2009), Boragineae (Guşuleac 1923, 1928, 1931; Hilger et al. 2004; Weigend et al. 2010) and Echiochileae (Lönn 1999; Långström and Chase 2002). These studies led to a consolidated view of generic limits and to the inclusion of several small or monospecific genera into larger genera (e.g. *Elizaldia* into *Nonea*, *Paraskevia* into *Anchusa*, *Lasiarrhenum*, *Onosmodium*, *Macromeria*, *Nomosa* into *Lithospermum*), while also recognizing or confirming some segregate genera which had previously been overlooked or not generally accepted (e.g. *Buglossoides*, *Glandora*, *Melanortocarya*, *Pontechium*). Generic limits and approximate relationships between genera are thus largely resolved for these three tribes.

The largest and taxonomically and morphologically most complex tribe, Cynoglosseae, has been largely resolved by Weigend et al. (2013). It comprises more than half of the species of the family, many of them in several large and/or widespread and/or heterogeneous genera such as *Cryptantha*, *Cynoglossum*, *Microula*, *Lappula*, *Hackelia* and *Omphalodes*. Additionally, numerous small, often monospecific genera have been described, such as *Amblynotus*, *Austrocynoglossum*, *Gyrocaryum*, *Mimophytum*, *Omphalolappula* and *Sinojohnstonia*. These are generally poorly defined and were uncritically segregated from larger genera without a study of the “parent genera” across their range. Comprehensive phy-

logenetic data have so far not been published but preliminary molecular data indicate that, for example, the majority of generic segregates of *Cynoglossum* (*Cynoglossopsis*, *Ivanjohnstonia*, *Lindelofia*, *Paracynoglossum*, *Pardoglossum*) are nested in *Cynoglossum*. Also, *Hackelia*, *Lappula*, *Microula* and *Eritrichium* are paraphyletic in relation to several segregate genera (such as *Amblynotus*, *Austrocynoglossum*, *Omphalolappula*, *Setulocarya*). Weigend et al. (2013) retrieved the following clades: Trichodesmeae (incl. *Lasiocaryum*, *Microcaryum*, *Trichodesma* and *Caccinia*), *Mertensia* group (e.g. *Asperugo*, *Mertensia*), *Omphalodes* group (e.g. *Omphalodes*, *Myosotidium*), *Lappula* group (= Eritrichieae s. str., e.g. *Suchtelenia*, *Heterocaryum*, *Eritrichium*, *Hackelia*, *Rochelia*), *Myosotis* group (= Myosotideae s.str., *Myosotis*, *Decalepidanthus*, *Trigonotis*), and Core-Cynoglosseae (e.g. *Amsinckia*, *Bothriospermum*, *Cryptantha*, *Cynoglossum*, *Microula*). Large-scale generic realignments will be required in Cynoglosseae, with nearly all larger genera polyphyletic and/or paraphyletic (e.g. *Cynoglossum*, *Omphalodes*, *Lappula*, *Eritrichium*, *Hackelia*; Weigend et al. 2013). The present classification and the genera here recognized therefore have to be considered as highly provisional.

In the present treatment we recognize the four well-supported tribes Boragineae, Cynoglosseae, Echiochileae and Lithospermeae. Within Cynoglosseae, genera are further arranged into a total of 10 informal groups, based on morphological and/or molecular data. Genera are recognized when they are well-characterized on the basis of morphological and/or molecular data, but even morphologically distinctive genera are synonymised when they are known to be derived from within other genera (e.g. *Actinocarya* in *Microula*, *Ivanjohnstonia* in *Cynoglossum*). Two genera, while clearly referable to Cynoglosseae, remain unplaced to genus group, because data on their affinities are currently equivocal. Trichodesmeae (composed of the *Trichodesma* and the *Lasiocaryum* groups, sister to each other) are sister to all remaining genera and genus groups of Cynoglosseae. The *Trichodesma* group consists of two genera (*Caccinia*, *Trichodesma*) of robust herbs or shrubs ranging from Africa to Central and South Asia and Australia. They have very short corolla tubes and mostly spreading corolla lobes with long exserted anthers. Unlike Cynoglosseae,

they have tricolporate pollen (versus heterocolpate). The *Lasiocaryum* group consists of three small genera (*Lasiocaryum*, *Microcaryum*, *Chionocharis*) of small, annual to perennial herbs from E Asia. They share the presence of turbinate, mostly pubescent nutlets not found elsewhere in the family. The *Omphalodes* group consists of only three genera, with *Omphalodes* polyphyletic (Weigend et al. 2013) and *Core-Omphalodes* likely paraphyletic to the two other genera of the group, i.e. *Myosotidium* and *Selkirkia*. All three are softly pubescent to glabrescent, annual or perennial herbs or shrublets with nutlets with a distinct but variable dorso-marginal wing and flower generally long-pedicellate. *Omphalodes* is here already widely defined and includes the segregates *Mimophytum* (N America) and *Omphalotrigonotis* and *Sinojohnstonia* (E Asia). The genus is in urgent need of a critical revision across its range and the European species appear to be paraphyletic in relation to the segregate genera proposed. *Myosotidium*, from the Chatham Islands, is morphologically quite aberrant in the family, but molecular data clearly retrieve it as nested in *Omphalodes*. The *Myosotis* group comprises the four genera *Trigonotis*, *Brachybotrys*, *Decalepidanthus* and *Myosotis*, of which all but *Myosotis* are restricted to C and E Asia. They are small-flowered herbs with soft, often appressed pubescence and small, lentil-shaped to dorsally keeled or obliquely tetrahedral, smooth and dark brown to black nutlets. The *Mertensia* group (two closely allied north temperate genera, *Mertensia* and *Anoplocaryum*) consists of perennial, often large-leaved, often more or less glabrous or glabrescent herbs, mostly with large, blue, campanulate corollas. The nutlets of these two genera are differentiated from all other genera by shape: They are irregularly ovoid, sometimes indistinctly winged and are attached to the shortly pyramidal gynobase with a short, submedial stipe arising from the flat or concave adaxial side. Aberrant *Asperugo* is retrieved as sister to these two genera. The *Lappula* group (Eritrichieae s.str.) consists primarily of the three large genera *Eritrichium*, *Hackelia* and *Lappula* (Eurasia and Americas), none of which is monophyletic as currently circumscribed. Central Asian *Heterocaryum* and *Suchtelenia* were retrieved as sister to this clade. Several small genera such as

Austrocynoglossum are here treated as synonyms, but some well-characterized, albeit doubtfully monophyletic genera such as *Rochelia* are maintained as separate. Genera of the *Lappula* group are mainly short-lived, often annual, herbaceous and the flowers have a usually narrowly pyramidal gynobase with glochidiate, often marginally winged nutlets. The *Bothriospermum* group consists of the three E Asian genera *Bothriospermum*, *Antiotrema* and *Thyrocarpus*. The nutlets have a two-layered wing, which is unique in the family. In two of the genera the “wings” are displaced into an adaxial position, which is also unique in the family. The *Cryptantha* group is largely American and consists of small-flowered taxa with dense, much-branched inflorescences and variable nutlet morphology. The nutlets usually have a submedial or medial attachment and a distinct dorsal keel or carina, are mostly small and, apart from *Pectocarya*, unwinged. The subdivision into four genera, followed in floristic treatments, has been shown to be unnatural. Hasenstab-Lehman and Simpson (2012) have found *Cryptantha* to be paraphyletic to *Amsinckia* and *Plagiobothrys*, and *Plagiobothrys* to be polyphyletic in *Cryptantha*. They therefore proposed a subdivision of *Cryptantha* into several segregate genera. The group is very diverse and its largest genus is *Cryptantha* with ca. 190 spp. The relationships between the *Cryptantha* group and the *Cynoglossum* group are unclear and *Microula* probably intercalates between the two. Both genus and species limits are highly controversial. The taxonomically most confusing taxon is *Cynoglossum* s.l., technically characterized by mostly large, glochidiate, sometimes conspicuously winged fruits. It is subcosmopolitan in distribution and highly paraphyletic and polyphyletic (Weigend et al. 2013). The bulk of the monospecific segregates (e.g. *Ivanjohnstonia*, *Cynoglossopsis*) are here treated as synonyms of *Cynoglossum*. Other, often small and always geographically restricted genera have been segregated, such as the Mediterranean/W Asian *Lindelofia*, *Mattiastrum*, *Paracaryum*, *Rindera*, *Trachelanthus* and *Solenanthus*, American *Dasynotus* and African *Afrotysonia*. They are defined by evidently derived types of either fruit (variously winged) or flower (corolla lobes porrect, anthers exerted) morphology. These genera are

here provisionally maintained as separate, but may have to be either synonymised in the future, saved by the segregation of additional entities from *Cynoglossum* or by the transfer of species between genera. All of them are likely to be nested in *Cynoglossum* as currently defined (Weigend et al. 2013).

DISTRIBUTION AND HABITATS. All four tribes have their centre of diversity in Eurasia. Over 70 of the 85 genera here recognized are found in and the majority of them are restricted to Eurasia. The centre of diversity for Boragineae, Lithospermeae and Echiochileae is in W Asia and the Mediterranean basin, with all narrowly endemic genera in Boragineae and Echiochileae and most narrowly endemic genera of Lithospermeae found there. The centre of diversity of Cynoglosseae is E and C Asia. Australia has only representatives of Cynoglosseae and no endemic genera apart from the Chatham Islands (New Zealand) endemic *Myosotidium*. Africa and America have representatives of all four tribes, but Africa has only three endemic genera (*Afrotysonia*, *Echiostachys*, *Lobostemon*) and the Americas seven (*Amsinckia*, *Antiphytum*, *Cryptantha*, *Dasynotus*, *Moritzia*, *Pectocarya*, *Thaumatocaryon*). The only largely American subgroup of Cynoglosseae is the *Cryptantha* group in W North and W South America (*Cryptantha*, *Plagiobothrys*, *Amsinckia*, *Pectocarya*, ca. 300 spp.), but a handful of species of *Plagiobothrys* are found in NW Asia and Australia. The other subgroups are either endemic to E Asia (*Lasiocaryum* group, *Bothriospermum* group, *Craniospermum*) or have their centre of diversity in C and E Asia (*Lappula* group, *Cynoglossum* group, *Myosotis* group, *Trichodesma* group). Several genera are very widespread and present on several continents—e.g. *Trichodesma* (Australia, Asia, Africa), *Lithospermum* and *Lappula* (Eurasia, Africa, S and N America) and *Eritrichium* (Eurasia, North America). *Hackelia*, *Lappula*, *Cynoglossum* and *Myosotis* are present on all continents with a centre of diversity for *Hackelia* in W North America and for *Myosotis* in both the Mediterranean basin and New Zealand. Boraginaceae are a predominantly (warm-) temperate and Mediterranean climate family and in the tropics largely restricted to higher elevations. The *Trichodesma* group, Echiochileae and

Cystostemon (Lithospermeae) are the only groups with a largely (sub-)tropical range and are found in subtropical and tropical semi-desert and desert habitats. Another exception are some species of *Trigonotis* (Cynoglosseae), which are found in SE Asian rainforests and are the only group of Boraginaceae s.str. in this habitat. Boraginaceae grow in nearly all habitats, but the majority prefers open, sunny places. A very large number of species in genera such as *Cryptantha*, *Pectocarya*, *Microcaryum*, *Lasiocaryum*, *Myosotis*, *Cynoglossum*, *Amsinckia* and *Anchusa* grow in open, disturbed ground without closed vegetation cover. There are several coastal species in *Mertensia*, *Lithospermum*, *Anchusa*, *Omphalodes*, numerous species of steppe habitats in *Cynoglossum*, *Lindlofia*, *Myosotis*, *Rindera* and *Lithospermum* and some species of extremely high elevations (>3500 m, *Hackelia* and *Plagiobothrys* in South America, *Eritrichium* in Eurasia, *Chionocharis* in Asia). Mesophytic forest herbs are less numerous, but are common in Boragineae (*Brunnera*, *Symphytum*, *Pulmonaria*, *Trachystemon*) and Cynoglosseae (*Omphalodes*, *Myosotis*, *Mertensia*, *Hackelia*, *Brachybotrys*), but rare in Lithospermeae (*Ancistrocarya*). True hydro- and helophytes are apparently lacking in the family, but some species of *Myosotis* are common in at least seasonally inundated habitats. The majority of taxa appears to prefer neutral or basic soils, often calcareous ground, but there are a few species which prefer distinctly acidic soils in, for example, *Mertensia* and *Decalepidanthus*. Serpentine soils have been colonized by several taxa of Lithospermeae (*Halacsya*, *Paramoltkia*, *Onosma*, Cecchi and Selvi 2009), Boragineae (*Anchusa*) and Cynoglosseae (*Rindera*, *Cryptantha*, *Plagiobothrys*) as true serpentinophytes.

Islands are generally poor in species of Boraginaceae, with the only exception of radiations of *Echium* in Macaronesia (Canary Islands, Madeira, Cape Verde Islands; Böhle et al. 1996) and *Myosotis* in New Zealand (Winkworth et al. 2002). In both cases a dramatic diversification of (esp. vegetative) morphological characters took place. In *Echium* woody ornithophilic taxa arose from herbaceous mainland ancestors, in *Myosotis* a wide range of flower morphologies and colours and growth forms arose from the rather uniform north temperate ancestors. A recent revision of

Cynoglossum in Madagascar and the Comoro Islands recognized six species, five of which are endemic and one of which shows a striking loss of dispersability (glabrous nutlets). Three island endemic (and monotypic) genera of Boraginaceae have been described from the Pacific, namely the shrubby *Selkirkia* (Juan Fernandez Islands, Chile), the spectacular, large-leaved *Myosotidium* (Chatham Islands, New Zealand) and the shrubby *Nesocaryum*, (Isla San Ambrosio, Chile). However, *Nesocaryum* is here included in *Cryptantha* and is probably closely allied to shrubby Chilean species of that genus. Boraginaceae also include some very widespread agricultural weeds; see “Economic Importance”.

PALAEOBOTANY. The fossil record of Boraginaceae is poor and restricted to records of pollen and nutlets. Unambiguous boraginaceous fruits have been found in the Late Miocene (late Clarendonian) Ogallala Series from Texas to South Dakota in North America. Preserved are complete nutlets or parts of them. Extinct genera include *Biorbia* (Elias 1932) and *Prolithospermum* (Elias 1942), *Eliasiana* (Thomasson 1987) and *Prolappula* (Thomasson 1979) with well-preserved glochids. Fossils assigned to extant genera belong to *Cryptantha* (Elias 1932) and *Lithospermum* (Gabel 1987). The anatomy of the F2a pericarp layer in *L. dakotense* is identical to that of extant *Lithospermum* species. Nutlets of *Prolithospermum* have been suggested to resemble those of *Pentaglottis sempervirens* (Thomasson 1979), a clade which has only two early divergent genera (*Moritzia* and *Thaumatocaryon*, Weigend et al. 2010) in the New World. The North American fossils apparently include taxa falling into all three of the four tribes of Boraginaceae here recognized. Fossil pollen supposedly of the *Symphytum* type was found by Van Campo (1976) (cited by Muller 1981) from the upper Miocene of Spain.

ECONOMIC IMPORTANCE. Boraginaceae have little economic importance as food plants due to their content of toxic pyrrolizidine alkaloids and their indumentum. A few species are used as pot herbs, especially *Borago officinalis* and to a lesser extent *Mertensia maritima* are traditionally used for that purpose in Europe. The roots of *Mertensia maritima* are occasionally consumed in Alaska

and native Americans formerly consumed the fruits of several species of *Plagiobothrys*, *Lithospermum* and *Amsinckia* raw and ground and their leaves as a green vegetable (Moerman 1998). The red colour of the roots of several species served to make important dyes in both Eurasia and North America. Mediterranean *Alkanna tinctoria* was used to obtain “alkanna” or “alkanet” since ancient times and was employed (“dyers’ bugloss”) by, for example, women as make-up, hence the German name “Schminkwurz” (make-up plant) for the species. Alkanet is still used to some extent for dying cosmetics and textiles, but is no longer prepared by extraction in camel urine, the method formerly considered to give the best results (Radcliffe 1927). A tincture of *Alkanna* is still used in microscopy for detection of oils and fats. The use of various species of *Arnebia* for dying is still widespread in India (Kaul 1997). *Lithospermum erythrorhizon* is used in Japan to obtain a purple dye and employed in large quantities in, for example, the production of lipstick. Similarly, red roots of various species of *Plagiobothrys* and *Lithospermum* were used by native North American tribes for obtaining a red dye to paint skin and leather (Moerman 1998). Since ancient times species of Boraginaceae were employed for medicinal purposes. One of the oldest records of medicinal use of plants in Europe is for *Lithospermum officinale*. An evidently medicinal preparation of the fruits was found in remains of the Mierzanowice culture (from about 1750–1600 B. C.) in southern Poland (Baczyńska and Lityńska-Zajac 2005). A wide range of species used to be employed in pharmaceutical preparations, but the vast majority of these are obsolete due to the high PA-concentrations and concomitant health hazards. Several medicinal Asian species of *Arnebia* and *Lithospermum* (Duke and Ayensu 1985) have recently been removed from the European market for that reason (Roeder 2000). The European “medicinal” herbs *Anchusa officinalis*, *Alkanna tinctoria*, *Cynoglossum officinale*, *Borago officinalis*, *Lithospermum officinale*, *Myosotis* spp. are no longer used (Roeder 1995). Comfrey (*Symphytum officinale* and *S. x uplandicum*), however, is still used extensively in commercially available ointments for blunt injuries, and a low-PA cultivar has been registered for that purpose.

Also, homoeopathic preparations of *Lithospermum* p.p. (“*Onosmodium*” *virginianum*) are widely marketed. The most important current market for Boraginaceae products are seed oils of Boraginaceae, which are very rich in highly unsaturated fatty acids and tocopherols and very low in PAs. Until recently mainly Borage oil was on the market (*Borago officinalis*), but there is now also a considerable market for Comfrey oil (*Symphytum officinale* and *S. x uplandicum*) and *Echium* oil (*E. plantagineum*, *E. vulgare*). The latter is the best dietary source of stearidonic acid known so far. A number of species of Boraginaceae are commonly grown as ornamentals, with biennial cultivars of *Myosotis* (mainly of *M. alpestris* and *M. latifolia*) probably commercially the most important and most widely used. Additionally, some annual species of *Anchusa* (*A. capensis*), *Echium* (*E. plantagineum*) and a range of perennial herbs such as *Omphalodes verna* and *O. cappadocica*, *Brunnera macrophylla*, several species of *Symphytum*, *Pulmonaria*, *Lithodora* are also widely grown in the temperate zone. The economic importance of Boraginaceae is possibly highest in its negative aspects. Weedy species of, for example, *Echium*, *Cynoglossum*, *Buglossoides* and *Amsinckia* cause enormous economic damage due to the invasion of native vegetation, degradation of pastures, as agricultural weeds and by livestock poisoning especially in Australia and North America (e.g. Parsons and Cuthbertson 2001).

CONSPECTUS OF BORAGINACEAE

- I. Tribe Echiochileae (Riedl) Långström & M. W. Chase (2002)
Genera 1–4
- II. Tribe Lithospermeae Dumort. (1827)
Genera 5–28
- III. Tribe Boragineae Bercht. & J. Presl (1820)
Genera 29–45
- IV. Tribe Cynoglosseae Bercht. & J. Presl (1823)
 1. *Trichodesma* group
Genera 46–47
 2. *Lasiocaryum* group
Genera 48–50
 3. *Omphalodes* group
Genera 51–53
 4. *Myosotis* group
Genera 54–57

5. *Mertensia* group
Genera 58–60
6. *Lappula* group
Genera 61–66
7. *Bothriospermum* group
Genera 67–69
8. *Cryptantha* group
Genera 70–74
9. *Cynoglossum* group
Genera 75–84
10. unplaced
Genus 85

KEY TO THE GENERA OF BORAGINACEAE

1. Gynobase flat; nutlets erect or incurved, round in transverse section or laterally compressed (rarely dorsiventrally compressed, then smooth, black or dark brown, < 5 mm, lentil-shaped or oblique tetrahedral, usually ventrally keeled, sometimes also dorsally, neither winged nor pubescent nor glochidiate); cicatrix basal or suprabasal, usually subcircular 2
 - Gynobase shortly pyramidal to subulate; rarely flat (then nutlets distinctly winged and/or pubescent and/or with narrowly triangular cicatrix); nutlets straight, not or dorsiventrally compressed, sometimes triangular in cross-section, marginally keeled or winged and/or pubescent and/or glochidiate; cicatrix usually suprabasal to apical, rarely subcircular, usually triangular to narrowly triangular (*Cynoglosseae* excl. *Myosotis* group) 51
2. Shrublets, rarely annuals; leaves opposite throughout or only below, basal leaves rarely present (then calyx > corolla, corolla < 3 mm long; *Ogastemma*); corolla small (<10 mm), zygomorphic or radially symmetrical, tube narrow, curved in zygomorphic taxa, faucal scales absent but throat with ciliate or papillate appendages; nutlets slightly laterally compressed, smooth, rugose or verrucose, never pubescent, glochidiate or dark and shiny, ventrally keeled and often also dorsally keeled; cicatrix in proximal half of nutlet, at lower end of ventral keel or terminating in a downward-projecting stipitate prolongation (*Echiochileae*) 3
 - Perennials, sometimes annuals or shrubs, leaves alternate throughout (if opposite, then large rosette leaves present; *Thaumatocaryon*), basal leaves usually present; corolla often larger (>10 mm long), radially symmetrical, rarely zygomorphic with wide tube, faucal scales usually present in taxa with hypocrateriform flowers; nutlets variable, sometimes dorsiventrally compressed, broadly sessile or with narrowed base, rarely smooth, rugose or verrucose, sometimes winged or angular, ventrally keeled or grooved; cicatrix subapical to basal, nutlets rarely with basal stipitate prolongation 6
3. Annual to 25 cm high; calyx longer than corolla; stigma terminal 3. *Ogastemma*

- Perennials or shrublets, rarely annuals, then much larger; corolla always longer than calyx; stigma subterminal and overtopped by sterile tip, rarely terminal 4
- 4. Corolla hypocrateriform, radially symmetrical, tube cylindrical and limb spreading, with 5 invaginations at throat 1. *Antiphytum*
- Corolla, infundibuliform, zygomorphic or not, tube conical or cylindrical, limb half erect, without invaginations at throat but densely pubescent 5
- 5. Nutlets ovoid with cordate base, adaxially with longitudinal narrow sulcus, cicatrix basal to subbasal, subcircular to triangular or boomerang-shaped with downcurved ends; corolla mostly zygomorphic, tube conical, often constricted 2. *Echiochilon*
- Nutlets erect, ovoid, smooth and shiny or ornamented, adaxially indistinctly keeled, shortly stipitate with basal subcircular cicatrix; corolla radially symmetrical, tube short, cylindrical 4. *Sericostoma*
- 6. Nutlets small, 1–3(5) mm, obliquely tetrahedral, lentil-shaped or with flat abaxial side and ventrally keeled, dark brown to black (*Cynoglosseae* – *Myosotis* group) 7
- Nutlets mostly larger (>5 mm), variously shaped and coloured, but never tetrahedral or lentil-shaped (*Lithospermeae* & *Boragineae*) 10
- 7. Rhizomatous perennial (rhizome ca. 1 cm thick) with large leaves crowded near end of stem; inflorescence a terminal boragoid of nodding flowers; corolla widely campanulate with porrect limb, violet-blue; anthers coherent around style (NE Asia) 57. *Brachybotrys*
- Leaves (at least initially) in basal rosette, often with above-ground runners or below-ground stolons, sometimes with creeping shoots and erect inflorescences, inflorescences variable; flowers never widely campanulate with porrect limb; anthers never coherent around style 8
- 8. Perennials with underground stolons, leaves in dense rosettes, narrowed at base but epetiolate; inflorescences mono- or dichasial, with 1–3 (rarely more) leaves, elevated above rosette, flowers campanulate, infundibuliform to hypocrateriform, usually blue or pink (Himalayas) 56. *Decalepidanthus*
- Annuals or perennials, often with creeping shoots, rarely cushion-forming, without underground stolons, basal leaf rosette usually absent in perennial taxa, if present then leaves long petiolate; inflorescence shoots usually repeatedly branched, rarely dichasial, then flowers small, rotate to hypocrateriform, white, or densely cushion-forming herb with flowers apparently single directly from rosette 9
- 9. Corolla with contort aestivation; nutlets lentil-shaped, never stipitate, but sometimes with elaiosome 54. *Myosotis*
- Corolla with valvate aestivation; nutlets (obliquely) tetrahedral, often stipitate, never with elaiosome 55. *Trigonotis*
- 10. Nutlets without well-developed, plug-shaped elaiosome at base (if present evergreen shrubs), pericarp mineralized, hard, white, grey, rarely brown, smooth and shiny or perforate to verrucose; annuals or perennials, subshrubs or shrubs, sometimes ericoid (*Lithospermeae*) 11
- Nutlets with well-developed, plug-shaped elaiosome and ± thickened basal ring around cicatrix, rarely single nutlet firmly enclosed in calyx, then elaiosome absent; pericarp not calcified, dark brown or black, tessellate, verrucose and/or papillose; plants mostly hispid, coarse-leaved perennials with basal leaf rosettes, annuals or perennials, never shrubs or subshrubs, never ericoid (*Boragineae*) 35
- 11. Anthers coherent, connective protracted into long terminal appendage 12
- Anthers not coherent, connectives not protracted into conspicuous terminal appendages 14
- 12. Corolla with lobes as long as or longer than corolla tube, spreading or reflexed (Africa, SW Asia) 13. *Cystostemon*
- Corolla tubular, infundibuliform or hypocrateriform; corolla lobes much shorter than tube, erect, spreading or reflexed 13
- 13. Corolla cylindrical, calyx lobes narrow, elongate, more or less parallel, separated by a very narrow, usually closed sinus (Europe, Asia) 11. *Onosma*
- Corolla subspherical, calyx lobes more or less triangular, separated by an open triangular sinus (E Asia) 12. *Maharanga*
- 14. Nutlets narrow (>7 x as long as wide), with hook-shaped tip, smooth and white; inflorescence ebracteose above (E Asia) 28. *Ancistrocarya*
- Nutlets wider (<3 x as long as wide), apex rounded or acute, but never protracted into hook, smooth or rough, grey, brown, mottled or white; inflorescence usually bracteose or frondose-bracteose 15
- 15. Leaves subglabrous and glaucous; nutlets united in pairs with each nutlet 2-locular and 2-seeded 10. *Cerinth*
- Leaves hispid or pubescent, never glaucous; 4 separate nutlets present or 2–3 by abortion (i.e. nutlets unilocular and not united in pairs) 16
- 16. Nutlets shortly stipitate at base, densely tuberculate; annual herb; corolla mauve 9. *Stenosolenium*
- Nutlets broadly sessile at base, smooth to densely tuberculate; annual or perennial herbs or subshrubs, corolla rarely pink, usually yellow orange, white or blue 17
- 17. Nutlet body strongly incurved (90–130°, when slightly incurved compare *Echium* and *Halacsya*); plants sometimes glandular above 18
- Nutlets straight (or rarely slightly bent in *Echium* and *Halacsya*); plants eglandular 19
- 18. Corolla infundibuliform, lobes rounded, half-spreading to spreading; throat usually glandular,

- faucal appendages borne low in the corolla throat, deeply included; stamens inserted at different levels **5. *Alkanna***
- Corolla tubular with lobes porrect or reflexed, not spreading; throat glabrous (eglandular) and lacking faucal appendages; all stamens inserted at one level **20**
19. Corolla tubular with very short, triangular, reflexed corolla lobes, bicolorous (pink/blue tube with yellow/orange apex); anther apices exerted **6. *Podonosma***
- Corolla tubular with usually long, triangular, porrect corolla lobes, uniformly coloured, mostly blue, rarely yellow, anthers included or long exerted **20. *Moltkia***
20. Thick sympodial rhizome present; leaves all cauline (basal leaves absent); lobes of fruiting calyx disarticulating at base and falling off individually; corolla lobes adaxially finely papillose (Balkans) **21. *Paramoltkia***
- Rhizome absent; basal and cauline leaves present (though often not simultaneously); lobes of fruiting calyx not disarticulating at base and not falling off individually; corolla lobes adaxially not papillose **21**
21. Corolla usually zygomorphic and/or with five conspicuous and densely pubescent scales borne below filament attachment **22**
- Corolla radially symmetrical, rarely slightly zygomorphic (then long and greenish-yellow on shrubs with ovate, coarsely veined leaves); annulus absent or present, if present not situated at filament base but near base of tube **26**
22. Corolla bright yellow, deeply lobed (ca. 1/2 of length), annulus absent; inflorescences on long, annual shoots with only 1–3 elongating monochasia; thecae with apiculate hairs along margins (Balkans) **18. *Halacsya***
- Corolla white, pink, red or blue, less deeply lobed (<1/3 of length), annulus present; inflorescences terminal, dense, often complex, dense terminal thyrsoids or monochasia reduced and few-flowered; thecae without hairs **23**
23. Annulus 1 mm or less from base of corolla tube, composed of minute collar or ring of 5–10 minute, sparingly hairy lobules **24**
- Annulus 1.5–6 mm from base of corolla tube; five conspicuous densely pubescent bulges or scales borne below filament attachment (S Africa) **25**
24. Stigma apically bifid **14. *Echium***
- Stigma entire **15. *Pontechium***
25. Perennials with basal leaf rosette; annulus present as five conspicuous, densely pubescent bulges at point of filament attachment **17. *Echiostachys***
- Subshrubs or shrubs without basal leaf rosette; annulus present as five pubescent scales at point of filament attachment **16. *Lobostemon***
26. Style deeply 2- or 4-divided, each branch terminating in a single stigma, corolla predominantly yellow to orange-red with tube at least 2.5 times longer than limb **7. *Arnebia***
- Style undivided, stigma single, rarely shallowly bilobed or apparently two (*Glandora*), then corolla blue or purple (never yellow) with tube less than 2.5 times longer than limb **27**
27. Corolla tube abaxially glabrous, corolla throat without glandular hairs **28**
- Corolla tube abaxially pubescent and/or corolla throat glandular **29**
28. Annual; corolla tubular with very short lobes, < 7 mm long, annulus present as villose ring; calyx at anthesis united for 1/3 of its length, basal part elongating postflorally, then united for ca. 1/2 to 2/3 of its length (NW Africa and Canary Islands) **19. *Mairetis***
- Subshrubs or dwarf shrubs; corolla hypocrateriform, > 10 mm long, annulus absent; calyx free nearly to base (W and SE Europe, N Africa and SW Asia) **24. *Lithodora***
29. Annual, filaments inserted nearly at base of corolla tube; corolla yellow, small (<7 mm), with lobes ad- and abaxially glandular **23. *Neatostema***
- Annuals, perennial herbs or subshrubs, filaments inserted higher up in corolla tube and/or corolla distinctly larger (>11 mm), corolla lobes eglandular or glandular only abaxially at base **30**
30. Filaments attached to the corolla tube at distinctly different levels **31**
- Filaments attached at the same level (or rarely at different levels in *Glandora prostrata*, but then corolla blue to purple and calyx not circumscissile) **32**
31. Perennial; corolla sulphur-yellow with spreading limb and blackish spots at sinuses, 18–25 mm across, tube without basal annulus; calyx not circumscissile at base; nutlets symmetrical with straight ventral keel (Caucasus) **8. *Huynhia***
- Small shrub; corolla blue or purple, subtubular, 4–5 mm across; calyx circumscissile; tube with hairy annulus; nutlets slightly asymmetrical with oblique ventral keel **22. *Moltkiopsis***
32. Receptacle with areoles cupulate, rarely oblique with ventral depression; nutlets with distinct peg-like appendage, rarely appendage minute; annulus and corolla invaginations absent **27. *Glandora***
- Receptacle with areoles flat to slightly concave; nutlet appendage absent or minute; corolla with annulus and/or faucal scales or vertical pleats **33**
33. Corolla blue or purple, 15–20 mm long, throat and tube with 5 distinct vertical, pubescent and/or glandular pleats and 5 congregations of glandular hairs beneath filament attachment **25. *Buglossoides* (sect. *Margarospermum*)**
- Corolla yellow or orange, whitish or, when blue or purple, corolla much shorter (<10 mm) or corolla invaginations absent; faucal scales absent or present or when weakly developed vertical invaginations present, then plants annual to biennial, corolla at most 10 mm long and congregations of glandular hairs directly beneath the attachment of the filaments absent **34**

34. Annuals; corolla with 5 vertical lines of simple or glandular hairs inside; nutlets tuberculate and tumulose
 25. *Buglossoides* (sect. *Buglossoides*)
- Perennials, rarely subshrubs, shrubs, biennials or annuals; corolla usually with faucal scales; nutlets usually smooth, white and shiny, sometimes with scattered perforations, rarely brown, tuberculate, rugose or tumulose
 26. *Lithospermum*
- Boragineae (from 10*)**
35. Fruit with a single nutlet remaining firmly enclosed in accrescent and closed calyx at maturity, distinctly stalked, elaiosome absent (S & C America) 36
- Usually more than one nutlet developing, calyx accrescent, but with spreading lobes at maturity and nutlets dispersed separately from calyx, elaiosome present (Old World) 37
36. Calyx externally with uncinata trichomes
 29. *Moritzia*
- Calyx externally without uncinata trichomes
 30. *Thaumatocaryon*
37. Corolla distinctly zygomorphic with oblique, half-spreading limb 38
- Corolla actinomorphic with regular and spreading limb 39
38. Inflorescence simple; corolla tube slightly curved; fertile stamens 2, 3 staminodial 32. *Anchusella*
- Inflorescence branched; corolla tube sharply incurved at middle; all 5 stamens fertile 35. *Lycopsis*
39. Corolla lobes revolute and rolled outwards, abaxially pubescent; faucal scales in two series; filaments pubescent 45. *Trachystemon*
- Corolla lobes neither revolute nor rolled, abaxially glabrous; faucal scales in one series; filaments glabrous 40
40. Flowers on long pedicels (up to 30 mm); corolla tube very short or nearly absent; faucal scales glabrous; filaments with acute or rounded appendage at base
 38. *Borago*
- Flowers sessile or on short pedicels (10 mm); corolla tube always present and well-developed; faucal scales pubescent or papillose at least along margins; filaments without basal appendage 41
41. Corolla narrowly clavate to subcylindrical; style exerted; scales narrowly triangular to lanceolate, papillose along margins 44. *Symphytum*
- Corolla hypocrateriform, infundibuliform or rotate; style included; scales never triangular-lanceolate, \pm rounded and shorter, pubescent or ciliate-papillose on entire surface 42
42. Nutlets with an excentric, stalked attachment at base
 43. *Pentaglottis*
- Nutlets without excentric stalked attachment at base 43
43. Corolla rotate to subrotate, with short tube (ca. 2 mm) and \pm flat limb; scales shortly ciliate-papillose 44
- Corolla hypocrateriform or infundibuliform with longer tube (5 mm); scales \pm densely hairy or penicillate 46
44. Plants rhizomatous; cymes ebracteate 39. *Brunnera*
- Plants not rhizomatous; cymes bracteate 45
45. Perennials; corolla 6–8 mm in diam., well exceeding calyx; nutlets erect-oblong, without lateral beak
 33. *Cynoglottis*
- Annuals; corolla 3–4.5 mm in diam., not or hardly exceeding calyx; nutlets transversely ovoid with lateral beak
 34. *Gastrocotyle*
46. Nutlets erect-ovoid, with smooth and \pm pubescent surface, constricted at base above distinct collar-like ring 47
- Nutlets transversely ovoid with a lateral beak or oblong-erect and parallel-sided, with a ribbed, tuberculate or variously sculptured surface, usually glabrous or glabrescent, with \pm thickened basal annulus but not constricted at base 48
47. Annual; corolla hypocrateriform with 5 hairy scales prolonged downward into the tube along veins; stamens inserted near base of tube
 40. *Melanortocarya*
- Perennials; corolla infundibuliform with a ring of hairs at throat; stamens inserted at or above middle of tube
 42. *Pulmonaria*
48. Inflorescence usually subcapitate and with sessile flowers, bracts frondose, erecto-patent, much longer than flowers 49
- Inflorescence with ovate-triangular bracts not much longer than flowers, \pm lax at least in fruit; flowers with distinct pedicels 50
49. Corolla hypocrateriform, blue; scales densely white-hairy; nutlets subhemispherical, helmet-shaped, with a lateral cleft and a plicate-dentate basal ring
 36. *Hormuzakia*
- Corolla infundibuliform, pinkish to purple; scales shortly hairy-papillose, yellowish; nutlets transversely reniform, with a thin basal ring
 37. *Phyllocara*
50. Plants usually without glandular hairs; corolla usually blue, rarely white or yellow, faucal scales triangular-oblong to linear, at least as long as wide, hairy or penicillate; fruiting calyx not or slightly accrescent and mostly cylindrical to urceolate 31. *Anchusa*
- Plants usually with glandular hairs; corolla usually not blue, white, yellow or orange-pink, purple to dark purple, dark brown, rarely dark-violet, scales replaced by tufts of hairs, shorter than wide or absent; fruiting calyx strongly accrescent and spherical-sacciiform 41. *Nonea*

Cynoglosseae (from 1*)

51. Calyx strongly two-lipped in fruit, completely enclosing the nutlets; nutlets dorsiventrally flattened with cicatrix asymmetrically placed to one side of flat adaxial side of nutlet
60. *Asperugo*
- Calyx not strongly two-lipped; nutlets variable, but cicatrix always symmetrically in centre of adaxial side 52
52. Anthers exerted from corolla tube, either all equal and with connective appendages spirally twisted into a cone or very unequal with at least one anther much longer than the rest 53
- Anthers included or exerted, but always equal and never with appendages twisted into cone 54
53. Glauous, coarsely hispid herbs with obovate leaves; anthers very unequal with at least one much longer than the rest
47. *Caccinia*
- Densely pubescent, often sericeous herbs or shrubs with oblong to narrowly ovate, acuminate leaves; anthers, all equal and with connective appendages spirally twisted into a cone 46. *Trichodesma*
54. Nutlets turbinate to ovate, not winged, adaxially with ovate suprabasal cicatrix (reaching to middle of nutlet), appressedly pubescent; dwarf annuals or perennials 55
- Nutlets not turbinate (usually dorsiventrally compressed, sometimes acuminate from ovoid base), cicatrix variable, often triangular, nutlets smooth, glochidiate or verrucose, very rarely pubescent, then distinctly winged and pubescence spreading or erect; often perennials 56
55. Dense, cushion-forming perennial; flowers arising directly from leaf rosettes; leaves fan-shaped from linear base
50. *Chionocharis*
- Annuals with basal rosette, not cushion-forming; inflorescences with distinct peduncle; leaves ovate to elliptical
48. *Lasiocaryum*
56. Corolla throat without faucal scales; stamens exerted; nutlets with cupular emergence abaxially
85. *Craniospermum*
- Corolla throat with faucal scales; stamens included, rarely exerted; nutlets variable, sometimes with cupular emergence abaxially or adaxially 57
57. Nutlets with double, cupular or incurved wing (pseudo-cicatrix) ventrally or apically (only E Asia) (Cynoglosseae – *Bothriospermum* group) 58
- Nutlets unwinged or with simple, usually dorsomarginal, rarely dorsal wing, sometimes wing flat, cupular or incurved 60

Cynoglosseae – *Bothriospermum* group

58. Anthers exerted from corolla; biennials or perennials
68. *Antiotrema*
- Anthers included in corolla; annuals or biennials 59

59. Nutlets with apical, cupular and incurved double-wing, the outer dentate/laciniate, the inner entire

69. *Thyrocarpus*

- Nutlets with adaxial, cupular and incurved double-wing, both wings entire 67. *Bothriospermum*
60. Nutlets slightly dorsiventrally compressed, rugose or verrucose, never glochidiate or pubescent, sometimes with flattened margin, cicatrix in proximal half of nutlet, stalked on flat or concave adaxial side of nutlet (Cynoglosseae – *Mertensia* group) 61
- Nutlets dorsiventrally compressed or not, smooth, rugose, verrucose, glochidiate and/or pubescent, sometimes with flattened margin and/or membranaceous wing; cicatrix variable, if stalked then adaxial side convex and attachment suprabasal or basal 62

***Mertensia* group**

61. Perennials, mostly robust; inflorescence bracteose to ebracteose; corolla with long cylindrical, rarely conical tube and then abruptly widened, lobes porrect to half-spreading, faucal scales absent or, if present, not visible from the side
58. *Mertensia*
- Small annuals, erect to ascending; inflorescence frondose; corolla hypocrateriform with cylindrical tube and spreading lobes, conspicuous yellow faucal scales exposed (E & C Asia)
59. *Anoplocaryum*
62. Ovary two-parted, 1–2 nutlets in ripe fruit, these acuminate, oblique-ovoid in lateral view, overtopped by the incurved linear (rarely cordate-acuminate) calyx lobes
64. *Rochelia*
- Ovary four-parted, typically four nutlets in ripe fruit, these often dorsiventrally compressed, circular to ovoid in dorsal view, often with marginal wing, never overtopped by linear incurved calyx lobes 63
63. Rhizomatous perennials with large leaves (>30 cm long), adaxially glabrous or subglabrous (but not glaucous) 64
- Plants not rhizomatous or not perennial, leaves usually smaller, if glabrous then glaucous and plants annual 65
64. Leaves glabrous, dark green and glossy adaxially, abaxially sericeous, nutlets with coriaceous spreading wing, glabrous; flower hypocrateriform (Chatham Islands)
52. *Myosotidium*
- Leaves not glossy adaxially, subglabrous on both sides, nutlets not winged, only with slightly elevated rim abaxially, densely glochidiate; corolla cylindrical with erect to slightly spreading limb (Asia)
84. *Trachelanthus*
65. Shrub to 2 m tall, with leaves only at the end of branches; flowers in widely and diffusely branched pleiothyrses (Juan Fernandez Islands, Chile)
53. *Selkirkia*
- Plants herbaceous or suffruticose, much smaller; inflorescences variable, but often compact or sparsely branched 66

66. Annuals, glabrous and glaucous; fruits always winged, wing often incurved
 51. *Omphalodes* (Mediterranean, annual group)
 - Annuals, perennials or subshrubs, usually pubescent to hispid, if glabrous then fruits dorsally distinctly convex and not winged 67
67. Calyx spreading and enlarged in fruit, saucer-shaped; nutlets dorsally convex, 1-4, if 3-4 then 1-2 much larger and firmly attached to gynobase and partly sunken in it, remainder small, abortive, easily detached; annuals, pubescent or glabrous and glaucous (C Asia) 62. *Suchtelenia*
 - Calyx not spreading and enlarged in fruit, rarely enlarged, but then fruits dorsally concave; fruits all equal in size; annuals or perennials and subshrubs, never glabrous and glaucous 68
68. All four nutlets firmly attached to gynobase at maturity; gynobase columnar or pyramidal and fruits accordingly parallel or basally divergent 69
 - At least 1-2 nutlets detached from gynobase at maturity; not parallel, not differentiated into two opposite pairs and/or not attached to the gynobase along their entire adaxial surface 70
69. Gynobase pyramidal to narrowly pyramidal, nutlets at least basally divergent; nutlets triangular-ovate, all four equal, rarely one differing from the other three, surface glochidiate, tuberculate or with horn-shaped processes 63. *Lappula*
 - Gynobase columnar and nutlets parallel, attached to the columnar gynobase along their entire adaxial surface; nutlets narrowly ovate to oblong, glochidiate, differentiated into two opposite pairs, nutlets of one pair distinctly wider than those of the other 61. *Heterocaryum*
70. Nutlets 2, one enclosed by upper calyx lobes, the second free; calyx irregular, 2 upper lobes fused, accrescent and incurved over nutlets, at maturity with 5-10 strong basal processes, 3 lower calyx lobes free nearly to base
 73. *Pectocarya* p.p. (*Harpagonella*)
 - Nutlets 4, rarely fewer; calyx regular, with 5 lobes 71
71. Nutlets erect and more or less parallel on flat to narrowly pyramidal gynobase, triangular-ovate (rarely turbinate or flattened), not winged, at most laterally slightly differentiated into a flattened ridge, sometimes with ovate to subcircular depression dorsally (depression usually much narrower than nutlet) or apically, then nutlets less than 3(5) mm in diam. 72
 - Nutlets basally divergent on widely pyramidal gynobase, subcircular, ovate or oblong in dorsal view; distinctly winged laterally or dorsally, wing membranaceous, incurved to spreading or with clearly differentiated margin differentiated from nutlet body, sometimes consisting of connected bases of flattened glochidia, nutlets > 5 mm in diam. 77
72. Diminutive annual (<5 cm), leaves very closely spaced; inflorescence superficially umbellate with individual flowers long pedicellate, pedicels longer than leaves; nutlets < 1 mm 49. *Microcaryum*
 - Plants larger, pedicels shorter than leaves and inflorescences, usually with elongated, scorpioid cymes at least in fruit, never umbellate; nutlets mostly > 1 mm 73
73. Length of deflexed pedicel much exceeding fruit diameter; nutlets long glochidiate (glochidia about as long as or longer than nutlet diameter); dorsomarginal wing absent or poorly differentiated, then consisting of the indistinctly confluent flattened bases of the glochidia 66. *Hackelia*
 - Fruits shortly pedicellate (pedicel < fruit diameter); nutlets not glochidiate or glochidia shorter than nutlet diameter; dorsomarginal wing present or absent 74
74. Gynobase shortly pyramidal to nearly flat; nutlets with narrowly triangular cicatrix along their entire adaxial side, usually dorsally with oblong to subcircular depression, rarely dorsally keeled or cicatrix basal and stipitate, then nutlet flattened and spinose or glochidiate 74. *Microula*
 - Gynobase pyramidal to subulate; nutlets with short cicatrix submedially or suprabasally, not stipitate, without dorsal depression 75
75. Corolla without faucal scales, throat open, orange or yellow; (winter) annuals 71. *Amsinckia*
 - Corolla with faucal scales, throat closed, corolla usually white with yellow faucal scales, rarely yellow, then plants perennial 76
76. Nutlets ventrally keeled, keel with longitudinal groove; leaves always alternate; ephemeral to perennial herbs, sometimes shrublets (Americas) 70. *Cryptantha*
 - Nutlets ventrally keeled, keel not grooved; leaves opposite or alternate; ephemeral to perennial herbs, never shrublets (SW USA and SW South America, Australia, NE Asia (Kamchatka)) 72. *Plagiobothrys*
77. Nutlets oblong with concave back, spreading to recurved and attached with small cicatrix near apex (and nutlet body extending outside the calyx), arranged in two opposite pairs in form of a St. Andrews cross (one angle < 90°, the other angle > 90°); margin coarsely dentate from half-spreading to spreading flattened glochidia; ephemeral herbs with linear leaves, flowers minute, very shortly pedicellate 73. *Pectocarya*
 - Nutlets variable, broadly attached or attached in the middle or near the base, rarely attached near apex, but always arranged regularly (same angle between all nutlets); nutlet margin, flower and habit variable 78
78. Corolla hypocrateriform, tube 1-1.5 cm long, white; nutlets without glochidia, widely turbinate from hemispherical base, cicatrix small, situated centrally on adaxial side, sides, base and dorsomarginal rim smooth and shiny, pale brown, concave dorsal depression roughly pubescent (NW USA) 77. *Dasynotus*

- Corolla cylindrical or infundibuliform to hypocrateriform, tube shorter than 1 cm and/or differently coloured; nutlets often glochidiate, with concave or convex back, but never turbinate from hemispherical base, cicatrix usually larger; dorsomarginal rim usually glochidiate or protracted into membranaceous wing 79
- 79. Nutlets at apex free from gynobase, overtopping apex of gynobase, nutlets usually < 6 mm and/or lacking glochidia; nutlets always with differentiated dorsomarginal rim or wing 80
 - Nutlets attached to apex of gynobase or along their entire length, not overtopping apex of gynobase, nutlets usually > 6 mm and/or densely glochidiate; nutlets with or without differentiated dorsomarginal rim or wing; rarely nutlets attached only in the middle of the adaxial side, then nutlets depressedly globose and glochidiate (*Cynoglosseae* s.str.) 82
- 80. Nutlets spreading on nearly flat gynobase, strongly compressed, dorsolateral margins all in one plane; leaves obovate to cordate-acuminate, basal rosette usually present, if absent then leaves long petiolate with rounded to cordate base, plants pilose or pubescent, but never densely so (not canescent, sericeous or hispid) 51. *Omphalodes* (perennial species, American species)
 - Nutlets spreading to oblique on widely pyramidal to subulate gynobase, dorsolateral margins not in one plane; leaves linear, oblong, ovate or obovate, base narrowed or decurrent, never distinctly petiolate, plants pubescent, sometimes canescent, hispid or sericeous 81
- 81. Gynobase widely pyramidal, nutlets attached in the middle of the adaxial side; perennials, often cushion-forming and vegetative rosettes present when in flower, often canescent 65. *Eritrichium*
 - Gynobase narrowly pyramidal, nutlets attached nearly along their entire length, rarely attached only below apex; mostly annuals or biennials, never cushion-forming and vegetative rosettes absent when in flower, not canescent 63. *Lappula*
- Nutlets not winged, sometimes with indistinct, flattened, wing-like margin, with glochidia on entire surface 86
- 84. Corolla tubular, with small acute or obtuse teeth and weakly developed faucal scales 82. *Rindera*
 - Corolla funnel-shaped to hypocrateriform, with well-developed limb and faucal scales 85
- 85. Marginal wing of nutlet spreading 80. *Mattiastrum*
 - Marginal wing of nutlet incurved 81. *Paracaryum*
- 86. Corolla cylindrical to narrowly funnel-shaped, corolla lobes narrow (oblong to narrowly obovate), porrect or half-spreading; faucal scales small, not closing the corolla throat 87
 - Corolla hypocrateriform, corolla lobes widely ovate to subcircular; faucal scales large, more or less closing the corolla throat 88
- 87. Plants densely pubescent to sericeous, inflorescence compact, internodes shorter than individual boragoids in flower 83. *Solenanthus*
 - Plants subglabrous, inflorescence lax, internodes longer than individual boragoids in flower 84. *Trachelanthus*
- 88. Corolla limb spreading, with faucal scales elevated and protracted at mouth of tube forming an extension, filaments and anthers long exerted; pedicels much longer than flowers 78. *Afrotysonia*
 - Corolla limb spreading to half erect, faucal scales not elevated and not protracted at mouth of tube, filaments always included in tube, but anthers sometimes half-exserted; pedicels roughly as long as flowers or shorter 89
- 89. Anthers (but not filaments) half-exserted from corolla tube; corolla tube longer than limb 79. *Lindelofia*
 - Anthers included in corolla tube, corolla tube shorter or equal to limb 76. *Cynoglossum*

GENERA OF BORAGINACEAE

I. TRIBE ECHIOCHILEAE (Riedl) Långström & M.W. Chase (2002).

Lithospermeae Dumort. subtr. Echiochilinae Riedl (1967).

Erect shrublets, rarely herbs, mostly perennial, sometimes annual, old branches with exfoliating bark; well-developed persistent primary root present. Leaves opposite basally or throughout, small, narrowly ovate or obovate or linear, sessile to subsessile, indumentum dense, often sericeous and appressed, sometimes hispid and/or glandular. Inflorescences mostly with long, straight monochasia, rarely much and shortly branched.

Cynoglosseae s.str.

- 82. Nutlets with concave back, 2–4 mm long; annuals with narrowly obovate leaves and without basal leaf rosette at flowering; nutlets more or less parallel on narrowly pyramidal gynobase (C and W Asia, NE Africa) 75. *Lepechiniella*
 - Nutlets > 5 mm long and/or with convex back; biennials or perennials, rarely subshrubs, with ovate or obovate leaves, rarely robust annuals with basal leaf rosette at flowering; nutlets divergent on pyramidal gynobase 83
- 83. Nutlets distinctly winged, wing clearly demarcated from disc, without glochidia on adaxial side 84

Flowers subsessile to shortly pedicellate; calyx divided nearly to base, sometimes asymmetrical and tetramerous, lobes usually unequal; corolla radially symmetrical or zygomorphic, tube narrow and curved in zygomorphic taxa, faucal scales absent but throat with ciliate or papillate appendages or indistinct invaginations; pollen bi- or sometimes tricolporate; gynobase flat or shortly pyramidal, style with sterile tip and two subterminal stigmas, rarely with terminal stigma (*Ogastemma*). Nutlets smooth, rugose or verrucose, not or laterally compressed, often with narrowed base, ventrally and sometimes dorsally keeled, cicatrix at lower end of ventral keel or terminating a downward-projecting stipitate prolongation at base, erect or incurved.

Four genera, three in W Eurasia, one in the Americas. The group consists of predominantly shrubby species, mostly with small flowers and narrow leaves with a sericeous, only rarely hispid indument, the corollas always lack typical faucal scales.

1. *Antiphytum* DC. ex Meisn.

Antiphytum DC. ex Meisn., Pl. Vasc. Gen. I: 280, II: 188 (1840); Johnston, Contr. Gray Herb. 68: 48–52 (1923), rev.

Perennial herbs or shrublets; branched from base, erect to procumbent; plants densely pubescent with appressed, scabrid trichomes, often glandular above. Leaves cauline, bases often shortly connate and sheathing, sometimes basal leaf rosette present at flowering time. Inflorescences straight, frondose cymoids, sometimes strongly branched (annual taxa) or reduced. Corolla infundibuliform, limb spreading to half-erect, with indistinct invaginations at throat, white or blue; stamens included; style filiform, forked. Nutlets erect, ovoid, nearly smooth to ornamented, ventral side distinctly keeled, keel terminating in short stipe with basal subcircular cicatrix.

10 to 15 species, disjunct between Mexico/SW USA and SW South America.

2. *Echiochilon* Desf.

Echiochilon Desf., Fl. Atlant. 1: 166, t. 47 (1798); Johnston, J. Arnold Arbor. 38: 255–294 (1957), rev.; Lönn, Bot. J. Linn. Soc. 130: 185–259 (1999), rev., morph., phylog.; Långström & Chase, Pl. Syst. Evol. 234: 137–153 (2002), phylog.

Perennial (rarely annual) herbs or shrublets; branched from base, procumbent to erect; subglabrous to densely pubescent with erect, hooked and/or appressed, scabrid trichomes, sometimes with glandular trichomes. Leaves cauline, narrowly ovate to narrowly oblong. Inflorescence terminal, straight, frondose-bracteose cymoids. Flowers erect but corolla often curved (arcuate) to spreading corolla narrowly infundibuliform, actinomorphic to zygomorphic, then bilabiate with 2-lobed upper and 3-lobed lower lip, tube longer than calyx, faucal scales absent but throat densely pubescent; stamens included to exerted, filaments often inserted at different levels in tube; style filiform with 2 subterminal stigmas. Nutlets ovoid with cordate base, smooth to verrucose, adaxially with narrow longitudinal sulcus, cicatrix basal to subbasal, subcircular to triangular or boomerang-shaped with down-curved ends.

14 species, N Africa to SW Asia, Macaronesia.

3. *Ogastemma* Brummitt

Ogastemma Brummitt, Kew Bull. 36: 679 (1982); Lönn, Bot. J. Linn. Soc. 130: 185–259 (1999), rev.

Megastoma (Benth. & Hook. f.) Coss. & Durieu ex Bonnet & Barratte (1895), nom. illeg.

Annual herb; branched from base, stems erect. Inflorescences terminal, straight, frondose-bracteose cymoids. Flowers erect, subsessile; calyx lobed to base, lobes unequal, elongating and closing over the fruit; corolla narrowly infundibuliform, short (equalling longest calyx lobes), tube long (>> lobes), white, faucal scales absent but throat densely pubescent; stamens included; style filiform, short with 2 subterminal stigmas. Nutlets erect, ovoid, apex conical to rostrate, verrucose, ventral side with narrow sulcus; cicatrix submedian, narrowly triangular.

One species, *O. pusillum* (Coss. & Durieu ex Bonnet & Barratte) Brummitt, Macaronesia, N Africa, to Arabian Peninsula.

4. *Sericostoma* Stocks

Sericostoma Stocks in Wight, Icon. Pl. Ind. Orient. (Wight) 4: 14, t. 1377 (1848); Lönn, Bot. J. Linn. Soc. 130: 185–259 (1999), rev.

Perennial shrublet; branched from base, branches erect to procumbent, densely pubescent with

erect and/or appressed, scabrid trichomes. Inflorescences frondose to frondose-bracteose, dense, little branched thyrsoids, clearly delimited from vegetative shoots by 1–3 bracts per flower. Calyx lobed to base, lobes equal, slightly accrescent in fruit; corolla infundibuliform, tube short, limb half-erect, white, faucal scales absent but throat villous; stamens exerted; style filiform, stigmas 2, subterminal, horizontal. Nutlets erect, ovoid, smooth and shiny or ornamented, indistinctly keeled, shortly stipitate with basal subcircular cicatrix.

One species, *S. pauciflorum* Stocks, Pakistan and W India.

II. TRIBE LITHOSPERMEAE Dumort. (1827).

Tribe Cerintheae Dumort. (1829).

Tribe Echieae Dumort. (1829).

Annual to perennial herbs, subshrubs or shrubs, sometimes rhizomatous or stoloniferous; well-developed, sometimes massive and red-staining primary root present, rarely absent (rhizomatous and stoloniferous taxa). Leaves alternate throughout, small to very large, linear to widely ovate or elliptical, sessile to shortly petiolate, indumentum usually dense, often hispid, rarely sericeous and appressed or glandular, glabrous in *Cerinthe*. Inflorescences with typical boragoids, rarely reduced and few-flowered, often in complex thyrsoids. Flower subsessile to pedicellate; calyx divided nearly to base to largely united with only free teeth, lobes usually equal; corolla radially symmetrical or zygomorphic, then tube wide, faucal scales often present and well-developed, but sometimes missing and replaced by pubescent or glandular patches; pollen with three or (mostly) more apertures and (sometimes) pseudoapertures; gynobase flat, style with or without sterile tip and two, rarely four terminal or subterminal stigmata. Nutlets hard and walls incrustated with calcium carbonate, often smooth and shiny, sometimes perforate, foveate, rugose or verrucose, often white or beige, rarely brownish or mottled, sometimes incurved or laterally compressed, often with narrowed base, ventrally and sometimes dorsally keeled, widely ovoid to subspherical.

23 genera, 21 in Eurasia, especially W Asia and the Mediterranean, two endemic to Africa, only one genus also in the Americas (*Lithosper-*

mum). Lithospermeae are characterized by a flat gynobase in combination with ovoid or incurved, smooth or rugose, always very hard (mineralized) nutlets, which are typically keeled both ventrally and dorsally.

5. *Alkanna* Tausch

Alkanna Tausch, Flora 7: 234 (1824), nom. cons., non Adans. (1763); Rechinger, Ann. Naturhist. Mus. Wien 68: 191–220 (1965), reg. rev.

Perennial, rarely annual herbs or subshrubs, indumentum often glandular; thick, sometimes woody taproot present, often dark red. Leaves cauline, usually also basal, oblong to obovate, sessile. Inflorescences frondose-bracteose cymoids or thyrsoids. Flowers subsessile, erect to pendulous; calyx lobed almost to base, often basally accrescent; corolla infundibuliform, regular, rarely slightly zygomorphic, faucal scales inconspicuous, inserted at constricted tube below throat, sometimes three inserted higher; basal scales usually annular; stamens included, filaments mostly inserted at different levels in the tube; style included, stigma capitate to nearly bilobed. Nutlets 1–2(4), obliquely horizontal, more or less incurved, adaxially keeled, usually rugose to verrucose, base distinctly stipitate. $2n = 14, 20, 22, 28, 30, 37$.

Ca. 40 species, Mediterranean and SW Asia.

6. *Podonosma* Boiss.

Podonosma Boiss., Diagn. Pl. Orient. II, 11: 113 (1849); Johnston, J. Arnold Arbor. 35: 1–81 (1954), rev.; Riedl, Anzeiger Österr. Akad. Wiss. Math.-Nat. Kl. (Wien) 101: 354–362 (1964), rev.

Perennial herbs; indumentum hispid and often glandular. Leaves ovate to oblong, sessile, sometimes semiamplexicaulous. Inflorescences frondose-bracteose. Flowers pendulous, pedicellate; calyx lobed almost to base, accrescent in fruit; corolla cylindrical with lobes triangular, reflexed, blue to pink with yellow to orange apex, faucal scales absent, annulus 10-lobed, pubescent; stamens partially exerted, connective protracted into an acute apical appendage; style exerted, stigma minutely bilobed. Nutlets strongly incurved with apical beak, ventrally keeled, base shortly stipitate.

Three species, NE Africa, E Mediterranean and SW Asia.

7. *Arnebia* Forssk.

Arnebia Forssk., Fl. Aegypt.-Arab. 62 (1775); Johnston, J. Arnold Arbor. 35: 1–81 & 158–166 (1954), rev.; Riedl, Österr. Bot. Z. 109: 45–80 (1962), part. rev.; Riedl, Österr. Bot. Z. 111: 149–153 (1964), part. rev.; Riedl, Ann. Naturhist. Mus. Wien 75: 209–222 (1971), part. rev.; Sadat, Mitt. Bot. Staatss. München 28: 1–210 (1989), reg. rev.

Annual or perennial herbs, sometimes with well-developed pleiocorm; thick, sometimes woody taproot present, often dark red. Leaves all cauline or basal and cauline, narrowly oblong, lanceolate or elliptic. Inflorescences (often dense) frondose-bracteose cymoids (perennials) or thyrsoids (annuals). Flowers erect to pendulous, sessile or shortly pedicellate, distylous; calyx lobed almost to base, accrescent, often hardening and tightly enclosing nutlets in fruit; corolla narrowly infundibuliform or hypocrateriform, regular or obscurely zygomorphic, yellow or cream, rarely blue or purplish, corolla lobes ovate or subcircular, sometimes erose or lacerate, faucal scales or folds absent, annulus absent (perennials) or present (annuals), then usually pubescent; stamens inserted at one level in tube, included or sometimes partially exerted (depending on stylar morph); style included or slightly exerted (depending on stylar morph), usually shortly once or twice forked, each branch ending in stigma. Nutlets 1–4, straight or slightly incurved at the apex, ovoid or subglobose, ventrally keeled or ventral keel obscure, dorsally rounded, sometimes keeled in the distal part, ornamented or rarely almost smooth. $2n = 14, 16, 22, 24$.

About 30 species, mainly SW and C Asia, Himalaya, also NE Africa and SE Europe.

8. *Huynhia* Greuter

Huynhia Greuter, Willdenowia 11: 37 (1981).

Perennial herb from stout pleiocorm; indumentum densely patent-pilose. Leaves basal and cauline, basal ones oblong, cauline ones narrowly ovate. Inflorescence a dense, bracteose cymoid. Flowers distylous; calyx divided nearly to base with lobes obtuse, not hardening and without thickened nerves or angular projections in fruit; corolla hypocrateriform, tube narrow, puberulent

outside, without faucal scales or annulus, limb spreading; stamens inserted at two different levels below the throat (3+2); stigma capitate-bilobed. Nutlets erect, ovoid-subglobose, apically acute and shortly beaked, ventrally keeled, finely tuberculate-scrubulate.

One species, *H. pulchra* (Willd. ex Roemer & Schultes) Greuter & Burdet, E Anatolia, Caucasus and NW Iran.

9. *Stenosolenium* Turcz.

Stenosolenium Turcz., Bull. Soc. Imp. Naturalistes Moscou 13: 253 (1840); Johnston, J. Arnold Arbor. 35: 1–81 & 158–166 (1954), rev.

Annual herbs with erect to ascending stems; indumentum hispid; thin, purplish-brown taproot present. Leaves basal and cauline, obovate to linear. Inflorescences frondose-bracteose cymoids. Flowers erect, shortly pedicellate; calyx lobed to base, accrescent in fruit; corolla narrowly infundibuliform, tube yellowish, limb usually purple, faucal scales absent, annulus hairy; stamens included, filaments inserted spirally; style short, included, forked shortly below the apex, with two terminal stigmas. Nutlets straight, oblique ovoid, ventrally keeled, tuberculate, cicatrix on a short, stout, basal-ventral stipe.

One species, *S. saxatile* (Pall.) Turcz., NE Asia. Doubtfully distinct from *Arnebia*.

10. *Cerithe* L.

Fig. 10

Cerithe L., Sp. Pl. 136 (1753); Johnston, J. Arnold Arbor. 35: 1–81 & 158–166 (1954), rev.; Selvi, Cecchi & Coppi, Taxon 58: 1307–1325 (2009), rev., morph., phylog.

(Winter-)Annual, biennial or perennial herbs, glabrous and glaucous. Leaves often irregularly blotched, trichomes reduced to tubercles; leaves basal and cauline or all cauline, obovate to oblong, cauline leaves sessile to amplexicaulous. Inflorescences frondose to frondose-bracteose cymoids of 1–2 scorpioid monochasia. Flowers pendulous; calyx lobed to middle or nearly to the base, lobes very unequal, narrowly ovate or oblong, accrescent in fruit; corolla cylindrical with short lobes, yellow, often tinged with violet, red or blue, faucal scales absent, annulus a glabrous ring or collar; stamens included or partially exerted, anthers appendaged apically and basally, apically

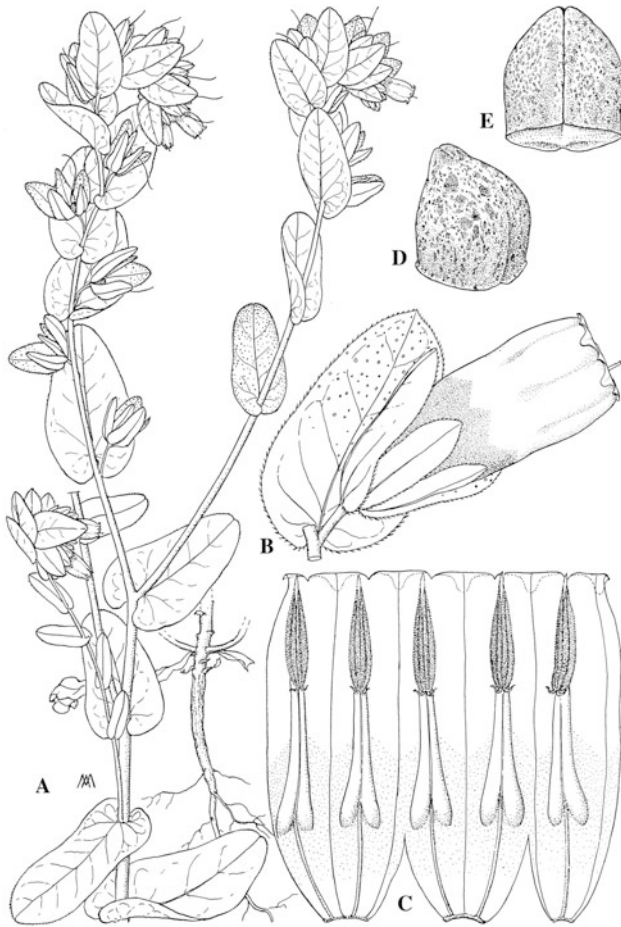


Fig. 10. Boraginaceae. Tribe Lithospermeae: *Cerinthe major* subsp. *major*. A Habit. B Flower with bract. C Corolla, longitudinal section. D, E Nutlets. (Selvi et al. 2009, drawn by A. Maury)

coherent; style long, exserted, stigmas 1 or 2. Nutlets pair-wise united into 2 two-seeded carpids; erect, broadly ovoid to subglobose, smooth. $2n = 16, 18, 24, 36$.

Seven to ten species from Europe and NW Africa to W Asia.

11. *Onosma* L.

Onosma L., Sp. Pl. ed. 2: 196 (1762); Johnston, J. Arnold Arbor. 32: 201–225 (1951), reg. rev. *Choriantha* Riedl (1961).

Biennial or perennial herbs, dwarf shrubs or subshrubs; indumentum dense and hispid, often with stellate trichome complexes, rarely sericeous; strong taproot usually present, sometimes with

well-differentiated pleiocorm or rhizomatous. Leaves basal and cauline, narrowly obovate to linear. Inflorescences bracteose or frondose-bracteose cymoids. Flowers pendulous at anthesis, rarely erect, pedicellate with pedicel elongating in fruit; calyx lobed nearly to base, often accrescent and connivent in fruit; corolla tubular to narrowly infundibuliform, lobes short, yellow, whitish or cream-coloured, rarely blue, often changing colour during anthesis, faucal scales absent, annulus present, often irregularly lobed; stamens included or partially to completely exserted, anthers connivent, forming a tube, connective conspicuously protracted into a short to elongate, attenuate to oblong appendage; style long, usually exserted, stigmas 1 or 2. Nutlets erect, ovoid, usually smooth, ventrally keeled, dorsally usually convex. $2n = 12, 14, 16, 18, 20, 21, 22, 24, 26, 27, 28, 30, 32, 38, 44, 50, 51$.

Circa 150 species, NW Africa, Europe and Asia.

12. *Maharanga* DC.

Maharanga DC., Prodr. (DC.) 10: 71 (1846); Johnston, J. Arnold Arbor. 35: 1–81 (1954), rev.

Biennial or perennial herbs or subshrubs; indumentum hispid, often with stellate trichome complexes; strong taproot usually present, sometimes with well-differentiated pleiocorm. Leaves basal and cauline, narrowly (ob-)ovate. Inflorescences cymoids, frondose-bracteose. Flowers pendulous to erect, pedicellate, pedicels elongating in fruit; calyx lobed to the middle or slightly below, weakly accrescent and incurved in fruit; corolla urceolate to subspherical, contracted at both ends, usually widest near the middle, usually with inflexed longitudinal folds below the sinuses of the lobes and below the lobes inflated with lamellae protruding between the calyx lobes, corolla lobes recurved, much shorter than the tube, faucal scales absent, annulus of 5 basal scales, hairy; stamens included or apex slightly exserted; style long, included or slightly exserted, stigmas 1 or 2. Nutlets slightly incurved, ovoid, ventrally keeled, dorsally rounded, ornamented. $2n = 14$.

Nine species in C & E Asia. Closely related to *Onosma* and sometimes synonymised with it.

13. *Cystostemon* Balf. f.

Cystostemon Balf. f., Proc. Roy. Soc. Edinb. 12: 82 (1883); Miller & Riedl, Roy. Bot. Gard. Edinb. 40: 11–21 (1982), rev.

Vaupelia Brand (1914).

Perennial herbs, subshrubs or shrubs, branched from base; strong lignescent taproot present, usually crowned with lignescent pleiocorm; leaves all cauline, sessile to shortly petiolate, lamina narrowly ovate to elliptical. Inflorescences frondose-bracteose, simple to many-branched thyrsoids, bracteoles sometimes present. Flowers long pedicellate; calyx lobed nearly to base, sometimes accrescent in fruit; corolla hypocrateriform with tube \ll limb, limb spreading, faucal scales absent; stamens long exserted, filaments very short and flattened, sometimes inflated or with adaxial triangular to oblong, basal appendage, anthers oblong to narrowly oblong, connective conspicuously protracted into linear appendage, all connective appendages together forming a narrow, straight cone above anthers; style exserted, stigma capitate. Nutlets oblique ovoid with acuminate apex, more or less angular, keeled at least ventrally, densely rugose.

About 15 species in SW Arabia, tropical Africa.

14. *Echium* L.

Echium L., Sp. Pl. 139 (1753); Bramwell, Lagasalia 2: 37–115 (1972), reg. rev.

Megacaryon Boiss. (1875).

Annual, biennial or poly- or monocarpic perennial herbs, rarely shrubs with many erect, ascending or decumbent stems (Macaronesian species); indumentum dense and hispid, sometimes sericeous. Leaves basal and cauline or cauline only (shrubs), usually narrowly obovate to broadly ovate. Inflorescence mostly bracteose, densely branched thyrsoids with many short boragoids as branches. Flowers usually erect to horizontal, shortly pedicellate; calyx divided almost to base, often accrescent in fruit; corolla zygomorphic, narrowly to broadly infundibuliform, mostly blue, rarely pink, red, yellow or white, faucal scales absent, annulus of 5–10 lobes or swellings present; stamens with long filaments, usually at least 2 exserted; style long, exserted, stigmas 2.

Nutlets 4 or 1–2 by abortion, straight to slightly incurved, more or less tuberculate and rugose. $2n = 8, 10, 12, 14, 16, 24, 28, 32, 64$.

About 60 species, primarily in Mediterranean Europe and Macaronesia, N Africa, C Europe and W Asia. A few species introduced to the Americas and Australia. *Echium plantagineum* L. is considered a noxious weed.

15. *Pontechium* U.-R. Böhle & Hilger

Pontechium U.-R. Böhle & Hilger, Taxon 49: 743 (2000).

Biennial herb, stems erect, simple; indumentum densely hispid; taproots present. Leaves basal and cauline, narrowly obovate or narrowly elliptical, sessile. Inflorescences bracteose thyrsoids. Flowers horizontal to erect, dark red, shortly pedicellate; calyx lobed almost to base, lobes linear, weakly accrescent in fruit; corolla narrowly infundibuliform, zygomorphic, red, abaxially pubescent, adaxially glabrous, lobes ovate to subsemiorbicular, ascending, faucal scales absent, annulus of 5–10 lobes or united as ring, glabrous; stamens long exserted, anthers versatile; style long, exserted, pubescent, stigma bicapitate. Nutlets slightly incurved, ovoid, ventrally keeled, dorsally rounded, keeled in the distal part, tuberculate. $2n = 24$.

One species, *P. maculatum* (L.) U.-R. Böhle & Hilger, E Europe to W Asia.

16. *Lobostemon* Lehm.

Lobostemon Lehm., Linnaea 5: 378, t. 5. (1830); Levyns, Bot. J. Linn. Soc. 49: 393–451 (1934), rev.; Buys, S. Afr. J. Bot. 72: 383–390 (2006), morphol.

Shrubs, dwarf shrubs, rarely subshrubs; indumentum densely hispid. Leaves all cauline, linear or narrowly ovate, rarely oblong or narrowly obovate, sessile. Inflorescences frondose-bracteose thyrsoids, paraclades sometimes reduced to 1–2 flowers. Flowers erect to pendulous, sessile or shortly pedicellate; calyx lobed almost to base, often zygomorphic, slightly accrescent in fruit; corolla infundibuliform to campanulate, usually zygomorphic, blue, pink, white or red, lobes ascending to horizontally spreading, faucal scales and annulus absent but pubescent staminal scales present; stamens exserted or some or all included; style included or exserted, stigma bilobed. Nutlets

usually 1–2, straight or slightly incurved, ovoid, ventrally keeled, dorsally convex but often keeled distally, usually ornamented. $2n = 14, 28, 42$.

About 30 species, endemic to South Africa.

17. *Echiostachys* Levyns

Echiostachys Levyns, J. Linn. Soc., Bot. 49: 445 (1934).

Perennial herbs from persistent pleiocorm; indumentum spreading or tomentose. Leaves basal and cauline, linear, narrowly obovate or narrowly elliptic. Inflorescences very dense, spike-like bracteose thyrsoids. Flowers horizontal to erect, shortly pedicellate; calyx lobed almost to base, lobes linear, accrescent in fruit; corolla narrowly infundibuliform, slightly zygomorphic, white, blue or pink, lobes ovate, porrect to half-spreading, faucal scales and annulus absent but with tufts of trichomes at point of filament insertion or with trichomes along the filaments and sometimes on the tube below; stamens exerted, filaments pubescent at base; style often long, exerted, usually pubescent, minutely forked at apex, stigmas 2. Nutlets 4 or 1–2 by abortion, straight, ovoid, ventrally keeled, dorsally convex but apically keeled, almost smooth or sculptured with minute white trichomes. $2n = 14, 28$.

Three species, endemic to South Africa.

18. *Halacsya* Dörfl.

Halacsya Dörfl., Herb. Norm. Sched. Cent. 44: 103 (1902); Johnston, J. Arnold Arbor. 35: 158–166 (1954); Cecchi & Selvi, Taxon 58: 700–714 (2009), phylog.

Subshrub with erect or ascending stems from stout rhizome; indumentum of appressed scabrid trichomes. Leaves basal and cauline, basal ones narrowly obovate with narrowed base, cauline narrowly oblong or narrowly ovate, sessile. Inflorescences cymoids of 1–2 frondose-bracteose, scorioid monochasia. Flowers suberect, shortly pedicellate; calyx lobed almost to base, lobes linear, accrescent in fruit; corolla infundibuliform, slightly zygomorphic, glabrous, lobes ascending, widely ovate, yellow, faucal scales and annulus absent; stamens included or partially exerted, connivent, connective protracted into a short, acute appendage; style exerted, stigma entire or obscurely bilobed. Nutlets usually 1–2, slightly

incurved in upper half, ovoid, ornamented, ventrally keeled. $2n = 22$.

One species, *H. sendtneri* (Boiss.) Dörfl., Balkans (C Serbia, N Albania and NW Greece), ser-pentinophyte.

19. *Mairetis* I.M. Johnst.

Mairetis I.M. Johnst., J. Arnold Arbor. 34: 4 (1953).

Annual herb with ascending to erect branches; primary root present. Leaves all cauline, sessile, narrowly obovate to narrowly oblong. Inflorescences cymoids of 1–2 bracteose, scorioid monochasia. Flowers erect to pendulous, subsessile; calyx divided to middle, strongly accrescent in fruit; corolla cylindrical, tube yellow, throat and lobes blue, glabrous, faucal scales absent, annulus present as ring of trichomes; stamens included; style short, included, stigma capitate. Nutlets 4, slightly incurved, pyriform, verrucose, ventrally keeled.

One species, *M. microsperma* (Boiss.) I.M. Johnst., NW Africa (W Morocco and Canary Islands).

20. *Moltkia* Lehm.

Moltkia Lehm., Neue Schriften Naturf. Ges. Halle 3(2): 3 (1817).

Subshrubs or perennial herbs from pleiocorm, indumentum of appressed scabrid trichomes, sometimes hispid; massive taproot present. Leaves basal and cauline or all cauline, basal leaves narrowly obovate or linear, sometimes shortly petiolate, cauline leaves linear to narrowly obovate, sessile. Inflorescences frondose-bracteose or bracteose cymoids of 1–2 monochasia or with additional paraclades distally. Flowers deflexed, pendulous or ascending, shortly pedicellate; calyx lobed almost to base, lobes linear, weakly accrescent in fruit; corolla narrowly infundibuliform, lobes porrect, ovate, blue or rarely yellow, faucal scales and annulus absent; stamens exerted, rarely included; style exerted, stigma entire or emarginate. Nutlets usually 1–2, incurved, ovoid, smooth or ornamented, ventrally keeled, dorsally convex. $2n = 16, 18, 108, 112$.

Six species in S Europe and SW Asia.

21. *Paramoltkia* Greuter

Paramoltkia Greuter, Willdenowia 11: 38 (1981); Cecchi & Selvi, Taxon 58: 700–714 (2009), phylog.

Perennial herb from thick, sympodial rhizome, indumentum sparse, shortly but roughly pubescent. Leaves all cauline, sessile, narrowly ovate-acuminate, median cauline larger than the basal ones. Inflorescences frondose-bracteose cymoids with 1–2 scorpioid monochasia. Flowers pendulous to erect, subsessile or shortly pedicellate; calyx lobed almost to base, lobes linear, accrescent in fruit; corolla narrowly infundibuliform, glabrous, lobes broadly ovate to subsemicircular, porrect, violet-purple, faucal scales and annulus absent; stamens included, filaments shorter than anthers; style long, exerted, stigma entire or obscurely bilobed. Nutlets 1–2, ovoid, slightly incurved in upper half, ventrally keeled, dorsally convex, smooth. $2n = 108, 112$.

One species, *P. doerfleri* (Wettst.) Greuter & Burdet, endemic to the SW Balkan peninsula (NE Albania and Kosovo/SW Serbia), serpentine-phyte.

22. *Moltkiopsis* I.M. Johnst.

Moltkiopsis I.M. Johnst., J. Arnold Arbor. 34: 2 (1953).

Subshrub, old bark white; indumentum densely ciliate-hispid. Leaves cauline, ovate-acuminate, sessile. Inflorescences frondose-bracteose cymoids of 1–2 scorpioid monochasia. Flowers erect, sessile or subsessile, calyx lobed almost to base, corolla subtubular, abaxially pubescent, lobes blue to purple, faucal scales absent but with 5 patches of trichomes in throat, annulus indistinctly 10-lobed, often pubescent; stamens included, attached at distinctly different heights, with 3 filaments longer; style usually included, stigma 1, terminal; calyx circumscissile above the base at maturity. Nutlets usually 2–3, almost straight, ovoid, slightly asymmetric, smooth or with few tubercles, ventrally keeled. $2n = 12, 24$.

One species, *M. ciliata* (Forssk.) I.M. Johnst., NE Africa, SW Asia.

23. *Neatostema* I.M. Johnst.

Neatostema I.M. Johnst., J. Arnold Arbor. 34: 5 (1953).

Erect annual herb. Leaves basal and cauline, narrowly obovate to linear. Inflorescences frondose-bracteose thyrsoids or reduced to cymoids. Flowers erect, subsessile, cleistogamous flowers sometimes present; calyx lobed almost to base, lobes linear to narrowly triangular, accrescent and connivent in fruit; corolla narrowly infundibuliform, lobes orange-yellow, pubescent, partly glandular, faucal scales absent but throat with 5 patches or a ring of trichomes, annulus 10-lobed, pubescent; stamens included; style very short, included, stigma capitate to obscurely 2-lobed. Nutlets ovoid, incurved, verrucose, ventrally keeled, dorsally convex, with weakly prominent keel in distal part. $2n = 28$.

One species, *N. apulum* (L.) I.M. Johnst., Mediterranean and Macaronesia.

24. *Lithodora* Griseb.

Lithodora Griseb., Spicil. Fl. Rumel. 2: 85 (1844); Browicz, Ann. Mus. Goulandris 7: 39–48 (1986); reg. rev.; Thomas et al., Taxon 57: 79–97 (2008), phylog., genus delimitation.

Dwarf shrubs or shrubs, with sericeous or hispid pubescence; strong, lignescent taproot present. Leaves cauline, sessile, narrowly oblong. Inflorescences frondose-bracteose to bracteose cymoids of 1–2 monochasia, sometimes subcapitate, rarely reduced to single flower. Flowers deflexed to erect, (sub-)sessile, with stigma-height dimorphism; calyx lobed almost to base, lobes linear or narrowly triangular, accrescent in fruit; corolla narrowly infundibuliform, generally glabrous, lobes ovate to subsemicircular, blue, purple, rarely white, faucal scales and annulus absent; stamens included or partially exerted (depending on stylar morphs); style long or short and included (depending on stylar morph), stigmas 2, terminal, juxtaposed. Nutlets 1–2, straight to strongly incurved, ovoid, ornamented, ventrally keeled, dorsal side convex, cicatrix basally with a pyramidal to asymmetrical appendage (elaiosome?), areoles deeply cupulate. $2n = 26, 28, 35, 38, 40$.

Three to five species in W and SE Europe, N Africa and SW Asia.

25. *Buglossoides* Moench¹

Buglossoides Moench, Meth. 418 (1794); Clermont et al., Feddes Repert. 114: 58–70 (2003), reg. rev., morph.; Johnston, J. Arnold Arbor. 35: 1–81 & 158–166 (1954), genus delimitation.

Aegonychon Gray (1821).

Margarospermum (Rchb.) Opiz (1839).

Annual or perennial herbs or subshrubs, with erect, ascending or decumbent stems, some with arching stems rooting at the apex; indumentum of appressed or spreading trichomes. Inflorescences many-flowered, frondose-bracteose cymoids. Flowers erect, (sub-)sessile; calyx lobed nearly to base, accrescent in fruit, sometimes becoming oblique or asymmetric through asymmetrical swelling of pedicel; corolla narrowly infundibuliform, lobes subcircular to oblong, half-spreading, metallic blue to pink or white, sometimes with elevated, white, central crease, faucal scales absent but with 5 distinct trichome bands on faucal invaginations; annulus ring-shaped or 10-lobed, sometimes missing; stamens included; style short, included, stigmas 2, subterminal or terminal. Nutlets 1(2) (perennials) or 4 (annuals), erect to slightly incurved, ovoid, white and smooth (perennials) or brown and verrucose (annuals), dorsally convex. $2n = 14, 16, 20, 24, 28, 36, 42$.

About 10 species, Mediterranean and SW Asia, a single species, *B. zollingeri* (A. DC.) I.M. Johnston., in E Asia., the genus may not be monophyletic and falls into two very distinct groups, sect. *Buglossoides* with annual, small- and mostly pale-flowered species with verrucose nutlets and sect. *Margarospermum* (Rchb.) I.M. Johnston. with perennial, large- and metallic blue-flowered species with smooth nutlets. *B. arvensis* (L.) I.M. Johnston. is a cosmopolitan weed.

26. *Lithospermum* L.

Lithospermum L., Sp. Pl. 1: 132 (1753); Johnston, J. Arn. Arbor. 35: 1–81 (1952), rev. of *Lithospermum*; Johnston, J. Arn. Arbor. 35: 1–81 (1954a), rev. Lithospermeae; John-

ston, J. Arn. Arbor. 35: 158–166 (1954b), rev. Lithospermeae; Turner, Phytologia 77: 38–44 (1994), rev. *Lasiarrhenum*; Turner, Phytologia 78: 39–60 (1995a), rev. *Onosmodium*; Turner, Phytologia 77: 393–407 (1995b), rev. *Macromeria*; Weigend et al., Molec. Phylog. Evol. 52: 755–768 (2009), genus delimitation; Cohen & Davis, Brittonia 61: 101–111 (2009), genus delimitation. *Lasiarrhenum* I.M. Johnston. (1924).

Macromeria D. Don (1832).

Nomosa I.M. Johnston. (1954).

Onosmodium Michx. (1808).

Perittostema I.M. Johnston. (1954).

Psilolaemus I.M. Johnston. (1954).

Ulugbekia Zakirov (1961).

Perennial, rarely annual herbs, subshrubs or shrublets, indumentum hispid or sericeous, strong primary root always developed, sometimes red to purple. Leaves cauline and sometimes some basal, subsessile, narrowly to widely ovate or obovate, rarely elliptical or nearly linear, base rounded or attenuate, rarely decurrent. Inflorescences frondose-bracteose to bracteose, monochasial or dichasial cymoids, rarely thyrsoids. Flowers mostly erect, rarely pendulous or deflexed, shortly pedicellate, chasmogamous, rarely cleistogamous, sometimes distylous; calyx divided nearly to base, slightly accrescent in fruit; corolla usually symmetrical, tubular, infundibuliform or hypocrateriform, rarely slightly zygomorphic, often papillose and/or glandular in throat, lobes reflexed to porrect, sometimes with erose to ciliate margin, white, yellow or orange, faucal scales and basal scales present or absent; stamens included to long exerted; style filiform, included, sometimes exerted, stigma small, two-lobed, surpassed by sterile, two-lobed tip. Nutlets erect, rarely slightly incurved, ovoid to pyriform, sometimes slightly dorsiventrally compressed or ventrally keeled, dorsally convex, fruit wall smooth to irregularly grooved, rarely verrucose. $2n = 14, 24, 28$.

About 80 species in Eurasia, Africa and both Americas, centre of diversity in North America. *Ulugbekia* and the American segregate genera have recently been synonymised with *Lithospermum* based on molecular and morphological data (Cohen and Davis 2009; Weigend et al. 2009).

¹ Cecchi et al. (2014) transferred two additional species to *Glandora* and segregated the perennial taxa of *Buglossoides* (sect. *Margarospermum*) into the re-instated genus *Aegonychon* Gray.

27. *Glandora* D.C. Thomas, Weigend & Hilger¹

Glandora D.C. Thomas, Weigend & Hilger, *Taxon* 57: 92 (2008).

Much-branched dwarf shrubs, often with lignescent underground stolons, sometimes mat-forming; indumentum mostly sericeous. Leaves cauline, sessile, narrowly oblong, narrowly elliptic or narrowly obovate. Inflorescences frondose-bracteose cymoids of 1–2 weakly scorpioid monochasia. Flowers erect, (sub-)sessile to shortly pedicellate; distylous; calyx lobed almost to base, lobes linear or narrowly triangular, accrescent in fruit; corolla infundibuliform, abaxially pubescent, adaxially usually with glandular trichomes in the throat, otherwise glabrous or with 5 pubescent patches on base of lobes or in the tube, lobes half-spreading, blue, purple or rarely white, faucal scales and annulus absent; stamens included or partially exerted (depending on stylar morph); style long or short and included (depending on stylar morph), stigmas 2, juxtaposed at the minutely forked or notched style apex. Nutlets 1–3, straight or rarely distally slightly incurved, ovoid, smooth, rarely ornamented, ventrally keeled, dorsally convex, cicatrix often with a peg-like appendage (elaiosome?), areoles cupulate. $2n = 16, 26, 28, 32, 40, 50$.

Eight species in S and SW Europe and N Africa.

28. *Ancistrocarya* Maxim.

Ancistrocarya Maxim., *Bull. Acad. Imp. Sci. Saint-Petersbourg III*, 17: 443 (1872); Johnston, J. *Arnold Arbor.* 35: 1–81 & 158–166 (1954), genus delimitation.

Perennial herb with erect simple stems; thick, shortly branched rhizome present; indumentum of appressed scabrid trichomes. Leaves cauline, crowded in upper third of shoot, sessile, obovate-acuminate with long cuneate base. Inflorescences loose thyrsoids with up to 6 monochasia, more often reduced to a cymoid, with 1–2 bracts at the base of each monochasium, otherwise ebracteose. Flowers erect to half-spreading, shortly pedicellate; calyx lobed almost to base, lobes linear to narrowly ovate, slightly accrescent in fruit; corolla narrowly infundibuliform, lobes ascending to spreading, pale blue or white, faucal scales absent, annulus of 10 tufts of trichomes; stamens

included; style short, included, stigmas 2, terminally juxtaposed. Nutlets 1–2, narrowly ovoid with apex tapering and uncinata, smooth, ventrally keeled, dorsally convex.

One species, *A. japonica* Maxim., in C and S Japan, Korea. An easily recognizable taxon, but possibly nested in *Lithospermum*.

III. TRIBE BORAGINEAE Rchb. (1831).

Anchuseae W.D.J. Koch (1837).

Symphyteae D. Don (1832).

Perennial, rarely annual herbs, sometimes rhizomatous or sometimes with stolon tubers; plants hispid, rarely sericeous, erect, rarely ascending or appressed, uncinata trichomes sometimes present. Leaves often cauline and basal (basal leaf rosette usually present), mostly large and widely ovate-acuminate, more rarely narrowly ovate or obovate, oblong or cordate, distinctly petiolate or with decurrent leaf bases. Inflorescence thyrsoids or cymoids, frondose or frondose-bracteose, rarely bracteose. Calyx united for most of its length or deeply divided, mostly tubular-cylindrical at anthesis, often accrescent in fruit; corolla radially symmetrical or zygomorphic, infundibular to hypocrateriform, rarely rotate, faucal scales large, conspicuous, often exerted from throat, in one or rarely two series, pubescent or papillose, rarely glabrous (*Borago*); stamens 5 (rarely 2 by abortion, *Anchusella*), pollen mostly isocolpate, mostly 4-colpate (rarely up to 15 zonocolpate), often with mesocolpial fields; gynobase flat, style with truncate or capitate stigma, rarely bilobed or shallowly bifid, with flask-shaped papillae, these with or without apical plate-like cap. Nutlets erect or incurved, more or less laterally compressed, usually tessellate and papillose, ventrally keeled, base narrowed into thin stalk (*Pentaglottis*, *Thaumatocaryon*, *Moritzia*) or more commonly widened into broad, collar-like ring and with large, white elaiosome (from gynobase tissue), areola basal. Nutlets dispersed individually or only one nutlet present and firmly enclosed in accrescent calyx (only *Moritzia*, *Thaumatocaryon*).

17 genera, 15 in W Eurasia and N Africa, two in South America. Boragineae are mostly mesophilic herbs, often with large leaves and a dense, hispid indumentum. The nutlets are typically

keeled both ventrally and dorsally and have a papillose surface. With the exception of *Moritzia* and *Thaumatocaryon*, the fruits are provided with an elaiosome.

29. *Moritzia* DC. ex Meisn.

Moritzia DC. ex Meisn., Pl. Vasc. Gen. [Meisner] 280 (1840); Johnston, Contr. Gray Herb. Harvard Univ. 78: 1–118 (1927), rev.; Fernandes-Soares, Iheringia 17: 28–33 (1973), rev.; Weigend et al., Syst. Bot. 35: 409–419 (2010), phylog., morph.

Perennial herbs, with several erect flowering stems from short, erect rhizome and with arching, frondose runners, rooting at apex; indumentum sericeous to hispid, sometimes reduced. Leaves (ob-)ovate, in dense basal rosette and some much smaller cauline leaves. Inflorescences ebracteate thyrsoids with narrowly spaced paraclades, these with peduncles much shorter than monochasia, initially very dense and nearly capitate, then elongating. Flowers erect, (sub)sessile; calyx divided about 1/2 of its length, abaxially with very short scabrid and much longer uncinatate trichomes, basally asymmetrically accrescent and enclosing the nutlet; corolla hypocrateriform, tube short, lobes erect to spreading, white or blue, faucal scales widely subcircular to ovate; stamens included or rarely exerted; style filiform, stigma capitate. Nutlet 1 by abortion, erect, straight, oblique-ovoid, laterally compressed with distinct dorsal and ventral keel, base shortly stipitate ending in small, circular cicatrix.

Three species in NW and SW South America. Allied to *Thaumatocaryon*, but clearly distinct.

30. *Thaumatocaryon* Baill.

Thaumatocaryon Baill., Bull. Soc. Linn. Paris, 2: 839 (1890); Johnston, Contr. Gray Herb. Harvard Univ. 78: 1–118 (1927), rev.; Fernandes-Soares, Iheringia 17: 28–33 (1973), rev.; Weigend et al., Syst. Bot. 35: 409–419 (2010), phylog., morph.

Perennial herbs, with several erect flowering stems from short, erect rhizome and arching, frondose or scale-leaved runners, rooting at apex. Leaves in loose basal rosette and some much smaller cauline leaves alternate or opposite, basal ones sometimes attenuate into long petiole. Inflorescences bracteate thyrsoids with widely spaced paraclades (peduncles equalling mono-

chasia), ascending, initially dense, later with elongating internodes. Flowers erect, (sub-)sessile; calyx lobed to middle, lobes triangular-ovate, abaxially with very short scabrid trichomes; corolla hypocrateriform, tube short, lobes subcircular to oblong, erect to spreading, white or blue, faucal scales subcircular, not clearly delimited, densely papillose to pubescent; stamens included; style filiform, long, stigma capitate. Nutlet 1 by abortion, erect, straight, oblique-ovoid, laterally compressed with distinct dorsal and ventral keel, base shortly stipitate ending in small, circular cicatrix.

Three species in SW South America. Allied to *Moritzia*, but clearly distinct.

31. *Anchusa* L.

Anchusa L., Sp. Pl.: 133 (1753); Guşuleac, Bul. Fac. Şti. Cernauti 1: 73–123 & 235–325 (1927), reg. rev.; Hilger et al., Ann. Bot. 94: 201–212 (2004), phylog.; Selvi & Bigazzi, Bot. J. Linn. Soc. 142: 431–454 (2003), reg. rev.

Annual, biennial or perennial herbs; indumentum hispid-setose to coarsely tuberculate-strigose. Leaves basal and cauline, linear, lanceolate, ovate or oblanceolate, entire or crispate-undulate. Inflorescences bracteate thyrsoids, ± lax and elongating in fruit. Calyx divided to 1/3 or to base, often slightly accrescent in fruit; corolla hypocrateriform to broadly infundibuliform, tube long, rarely limb reduced, faucal scales triangular-oblong, pubescent or penicillate; filaments inserted near or above middle of tube, stamens mostly included; style included to slightly exerted (stylar polymorphism in some species), stigma capitate-ovoid, bilobed. Nutlets ovoid, horizontally inflexed, adaxially shortly beaked or oblong-erect and rounded at apex, rugose-tuberculate; cicatrix with ± incrassate basal ring. $2n = 16, 22, 32$.

About 35 species in Europe, Africa and W Asia, centre of diversity in the Mediterranean region.

32. *Anchusella* Bigazzi, Nardi & Selvi Fig. 11

Anchusella Bigazzi, Nardi & Selvi, Pl. Syst. Evol. 205: 253 (1997).

Annual herbs; indumentum hispid-strigose. Leaves basal and cauline, sessile, narrowly ovate,

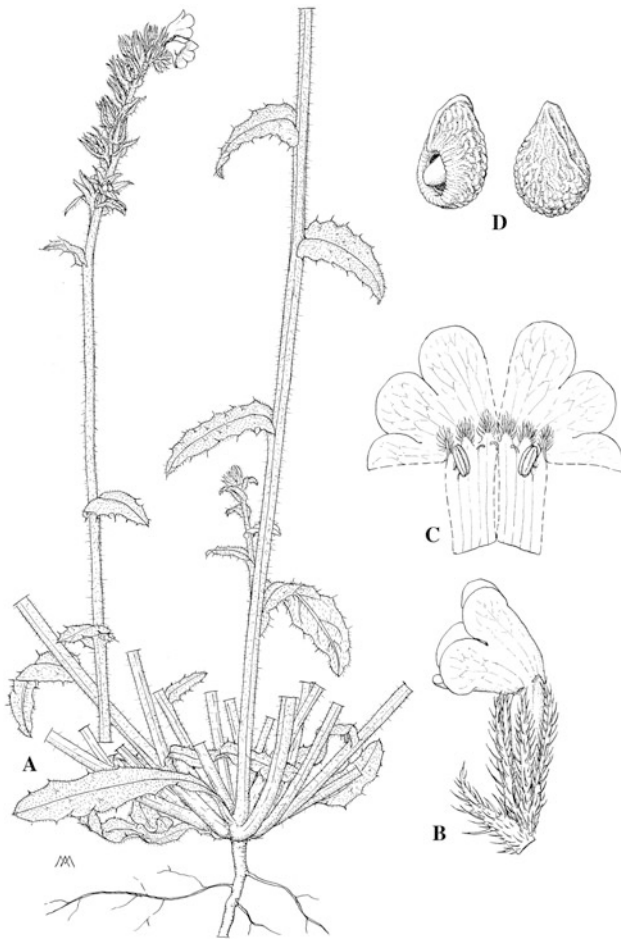


Fig. 11. Boraginaceae. Tribe Boragineae: *Anchusella cretica*. A Habit. B Flower. C Open corolla. D Nutlets. (Bigazzi et al. 1997, original drawn by A. Maury)

margins repand-dentate. Inflorescences monochasial, bracteose cymoids. Calyx lobes acute, spreading in fruit; corolla obliquely infundibuliform, zygomorphic, tube slightly curved, limb oblique, lobes unequal, rounded, blue with white lines or white with dark-purple spots. Filaments inserted in upper part of tube, two stamens functional, three staminodial; style included, weakly curved, stigma shallowly bifid with corniculate lobes. Nutlets widely ovoid to orbicular, horizontally inflexed (long axis parallel to hypanthium), nearly smooth to ornamented, cicatrix with scarcely thickened ring. $2n = 16$.

Two species in the central to E Mediterranean.

33. *Cynoglottis* (Guşul.) Vural & K. Tan

Cynoglottis (Guşul.) Vural & K. Tan, Notes Roy. Bot. Gard. Edinb. 41: 71 (1983); Selvi & Bigazzi, Pl. Biosystems 132: 113–142 (1998), rev. reg.; Bigazzi & Selvi, Bot. J. Linn. Soc. 136: 365–378 (2001), cytogeography; Selvi et al., Pl. Syst. Evol. 246: 195–209 (2004), phylog.

Perennial herbs; indumentum shortly hispid-setose. Leaves oblong-spathulate to almost linear, margins entire or slightly undulate-crenate. Inflorescences bracteose thyrsoids. Flowers shortly pedicellate; corolla subrotate, tube very short (equalling or shorter than calyx), lobes ovate-orbicular, spreading, blue, faucal scales finely papillose; filaments inserted slightly below scales; style short, included, stigma truncate, slightly bilobed. Nutlets erect, oblong-ovoid, ornamented; cicatrix with thin ring. $2n = 18, 36$.

Two species, one in Europe and one in Asia Minor.

34. *Gastrocotyle* Bunge

Gastrocotyle Bunge, Ann. Sci. Nat., Bot. 3, 12: 363 (1949); Bigazzi, Selvi, Fiorini, Edinb. J. Bot. 56: 239–251 (1999), genus delimitation; Guşuleac, Bul. Fac. Şti. Cernauti 2: 394–461 (1928), genus delimitation.

Annual herbs; indumentum coarsely setose-hispid. Leaves narrowly obovate with entire or obscurely erose-dentate margins. Inflorescences dichotomously branched frondose cymoids (= flowers apparently axillary); corolla infundibuliform, subrotate to subcampanulate, pink or blue, tube short, equalling calyx or slightly longer, faucal scales widely oblong, emarginate, papillose; stamens included; style included, stigma cylindrical with spherical and trichoid papillae. Nutlets widely ovoid, horizontally inflexed (long axis parallel to hypanthium), adaxially shortly beaked, ornamented, cicatrix with thickened ring. $2n = 16, 18, 20$.

Two species, one in the Saharo-Sindic region and one in the southern Balkans.

35. *Lycopsis* L.

Lycopsis L., Sp. Pl.: 139 (1753); Bigazzi et al., Giorn. Bot. Ital. 129: 121 (1995), morph.; Guşuleac, Bul. Fac. Şti. Cernauti 1: 73–123, 235–325 (1927), rev.; Selvi & Bigazzi, Pl. Biosystems 132: 113–142 (1998), rev. reg.

Annual herbs; indumentum hispid-strigose. Inflorescences initially dense bracteose cymoids. Flowers subsessile; calyx accrescent or spreading in fruit; corolla zygomorphic, blue; tube sharply bent at middle, equalling calyx, lobes unequal, subcircular to oblong, faucal scales white-papillose; filaments inserted in the middle of tube, stamens included; style included, stigma bilobed, capitate-ovoid. Nutlets widely ovoid, horizontally inflexed (long axis parallel to hypanthium), adaxially shortly beaked, ornamented, cicatrix with thickened basal ring. $2n = 16, 48$.

Two species in Europe and W Asia.

36. *Hormuzakia* Guşul.

Hormuzakia Guşul., Publ. Soc. Nat. Bucur. 6: 83 (1923); Bigazzi et al., Edinb. J. Bot. 56: 239–251 (1999), genus delimitation; Guşuleac, Bul. Fac. Şti. Cernauti 2: 394–461 (1928), genus delimitation; Selvi & Bigazzi, Biosystems 132: 113–142 (1998), reg. rev.

Annual or perennial herbs; indumentum white, coarsely hispid; massive, succulent primary root present. Leaves cauline and basal, basal ones linear to narrowly obovate, margins obscurely erose-dentate; cauline leaves linear, sessile. Inflorescences frondose, compact cymoids with densely aggregated, sessile flowers, rarely internodes elongating; calyx divided to base, accrescent and spherical in fruit; corolla hypocrateriform, tube slightly longer than calyx, lobes acute, blue, faucal scales prominent, oblong-erect, densely white-pilose; annulus present as pubescent ring; filaments inserted below or at the same level as faucal scales; style included, stigma capitate. Nutlets 2–4, hemispherical and helmet-shaped with a lateral cleft, papillose; cicatrix with a plicate-dentate ring. $2n = 16$.

Two species in the SE Mediterranean.

37. *Phyllocara* Guşul.

Phyllocara Guşul., Bul. Fac. Şti. Cernauti 1: 119 (1927); Bigazzi et al., Edinb. J. Bot. 56: 239–251 (1999), genus delimitation.

Annual herb with decumbent to ascending shoots, these simple or dichotomously branched above; indumentum hispid-strigose. Inflorescences frondose, dense and compact cymoids. Flowers subsessile; calyx slightly accrescent and deflexed in fruit; corolla pinkish to purple, nar-

rowly infundibuliform, tube longer than calyx, lobes half-spreading; faucal scales oblong, erect, yellowish, papillose to shortly pubescent; stamens included; style included, stigma capitate-bilobed. Nutlets reniform, horizontally inflexed (long axis parallel to hypanthium), finely rugose-tuberculate; cicatrix with thin basal ring. $2n = 16$.

One species, *P. aucheri* (DC.) Guşul., Irano-Turanian region.

38. *Borago* L.

Borago L., Sp. Pl. 137 (1753); Guşuleac, M. Bul. Fac. Şti. Cernauti 2: 394–461 (1928), rev.; Selvi et al., Ann. Bot. 98: 857–868 (2006), phylog.

Annual or perennial herbs; indumentum hispid. Leaves basal and cauline or cauline only, basal leaves ovate to oblong-obovate, petiolate, cauline leaves sessile or semiamplexicaulous. Inflorescences lax, bracteose cymoids. Flowers long pedicellate, pedicels deflexed in fruit; calyx divided to base, accrescent in fruit; corolla subrotate with very short tube and (half-)spreading to reflexed, ovate-acuminate lobes (subg. *Borago*) or narrowly campanulate with suberect lobes (subg. *Buglossites*), blue or whitish; faucal scales glabrous, trapezoid; filaments inserted near base of tube, with an acute or rounded appendage at base, anthers exerted or included, connivent, mucronate; style included; stigma capitate. Nutlets oblong-ovoid, erect, cicatrix with a thin basal ring. $2n = 12, 16, 18, 30, 32, 48$.

Five species, mainly W Mediterranean, one species (*B. officinalis* L.) widely cultivated as culinary herb and often naturalized.

39. *Brunnera* Steven

Brunnera Steven, Bull. Soc. Imp. Naturalistes Moscou 24 (1): 582 (1851); Bigazzi & Selvi, Bot. J. Linn. Soc. 136: 365–378 (2001), cytogeogr.; Guşuleac, M. Bul. Fac. Şti. Cernauti 2: 394–461 (1928), rev.; Selvi et al., Pl. Syst. Evol. 246: 195–209 (2004), phylog.

Perennial herbs, shortly bristly-setose; rhizomes present, robust; stems erect, usually branched only above. Basal leaves long petiolate, ovate-cordate or ovate-lanceolate. Inflorescence of ebracteose lax cymes. Flowers short pedicellate, pedicels elongate in fruit; calyx divided to 3/4, slightly accrescent in fruit; corolla blue, subrotate with short tube, lobes oblong; faucal scales

trapezoid, ciliate, closing throat, white; stamens inserted near top of tube, included; style included, stigma capitate, gynobase flat. Nutlets obliquely oblong-ovoid, sculptured, cicatrix surrounded by slightly thickened basal ring. $2n = 12, 14, 24, 36, 72$.

Three species in W Asia and SE Mediterranean.

40. *Melanortocarya* Selvi, Bigazzi, Hilger & Papini

Melanortocarya Selvi, Bigazzi, Hilger & Papini, Taxon 55: 915 (2006).

Annual herb; indumentum hispid. Leaves basal and cauline, ovate-acuminate. Inflorescences often simple frondose cymoids with few subsessile flowers, pedicels deflexed in fruit; calyx divided to base, accrescent; corolla hypocrateriform, tube slightly longer than calyx, lobes spreading, trapezoid; corolla sky blue, faucal scales shaggy pubescent, pubescence extending downward into tube; filaments inserted near base of tube, stamens included; style very short; stigma bilobed. Nutlets erect, oblong-ovoid, black, smooth and glossy, but minutely puberulent. $2n = 20$.

Only *M. obtusifolia* (Willd.) Selvi, Bigazzi, Hilger & Papini, SE Mediterranean.

41. *Nonea* Medik.

Fig. 12

Nonea Medik., Philos. Bot. 1: 31 (1789); Sadat, Mitt. Bot. Staatss. München 28: 1–210 (1989), reg. rev.; Selvi et al., Taxon 51: 719–730 (2001), morphol.; Selvi et al., Taxon 55: 907–918 (2006), phylog. *Elizaldia* Willk. (1852).

Annual or perennial herbs; indumentum hispid and usually glandular. Inflorescences frondose to frondose-bracteose cymoids, \pm elongated in fruit. Flowers shortly pedicellate; calyx accrescent, spherical-sacciform and deflexed in fruit; corolla radially symmetrical or weakly zygomorphic, narrowly or broadly infundibuliform, white, yellow, blue or purple to almost black, faucal scales absent but throat with 5 tufts or a ring of trichomes, rarely glabrous; filaments inserted near middle of tube or in distal half, anthers included or partially exerted at corolla mouth, rarely one stamen completely exerted (*N. heterostemon*); style included, stigma capitate-bilobed. Nutlets broadly ovoid to reniform, horizontally inflexed (long axis parallel to hypanthium), incurved or



Fig. 12. Boraginaceae. Tribe Boragineae: *Nonea persica*. A Habit. B Flower. C Corolla tube. D Open corolla. E Nutlet. (Selvi and Bigazzi 2001, drawn by A. Maury)

erect, reticulate, cicatrix with incrassate, rarely dentate ring. $2n = 14, 16, 18, 20, 22, 28, 30, 32, 40, 44, 59, 60$.

About 35 species in Europe, N Africa and W Asia.

42. *Pulmonaria* L.

Pulmonaria L., Sp. Pl. 135 (1753); Bolliger, Phaner. Monogr. 8: 1–215 (1982), reg. rev.; Kerner, Monographia Pulmonarum, Oeniponte: 1–52, tab. I–XIII (1878), rev.; Selvi et al., Taxon 55: 907–918 (2006), phylog. *Paraskevia* W. Sauer & G. Sauer (1980).

Perennial herbs with short rhizomes; indumentum pubescent and usually glandular. Leaves basal and cauline, basal rosette with large, ovate leaves, usually developing after flowering, rarely before (*P. cesatiana*), cauline leaves smaller,

semiamplexicaulous. Inflorescences bracteose cymoids, rarely weakly branched thyrsoids. Flowers shortly pedicellate, usually distylous (except *P. cesatiana*); calyx divided to 1/3, cylindrical at anthesis, calyx lobes porrect, triangular-ovate, calyx ventricose-campanulate in fruit; corolla infundibuliform, purple, pink or blue, faucal scales absent but throat with a ring of trichomes; filaments inserted at or below throat; style included or slightly exerted (depending on stylar morph), filiform, stigma capitate-bilobed. Nutlets erect, ovoid, smooth to pubescent, constricted at base above a distinct collar-like ring. $2n = 14, 16, 22, 18, 20, 21, 22, 26, 28, 30$, commonly 14 or 28.

About 17 species, Europe, one species extending to E Asia.

43. *Pentaglottis* Tausch

Pentaglottis Tausch, Flora 12: 643 (1829).
Caryolopha Fisch. & Trautv. (1837).

Perennial herb with thick rhizome; indumentum hispid. Leaves basal and cauline, basal leaves large, ovate-acuminate, long petiolate, cauline leaves much smaller, sessile. Inflorescences bracteose-frondose thyrsoids. Flowers shortly pedicellate; calyx divided to base, accrescent in fruit; corolla hypocrateriform, bright blue, tube about as long as calyx, lobes spreading, oblong to trapezoid, faucal scales shortly trapezoid, white, shortly pubescent; filaments inserted in distal half of tube, included; style included, stigma capitate. Nutlets small, excentrically stalked, obliquely ovoid, beaked, surface finely scabrid, cicatrix with a slightly thickened annulus. $2n = 22$.

One species, *P. sempervirens* (L.) Tausch ex L. H. Bailey, SW Europe.

44. *Symphytum* L.

Symphytum L., Sp. Pl. 136 (1753); Kurtto, Acta Bot. Fenn. 19: 177–192 (1982), rev.; Sandbrink et al., Proc. Kon. Ned. Akad. v. Wetensch. 93: 295–334 (1990), phylog. *Procopiana* Guşul. (1928).

Perennial herbs with persistent, later splitting primary root (root-pleiocorm) or stoloniferous with stolon tubers or rhizomatous; indumentum hispid. Leaves basal and cauline, widely ovate-acuminate with cuneate, rounded to subcordate base, basal leaves long petiolate, cauline leaves

subsessile or decurrent. Inflorescences bracteose thyrsoids. Flowers long pedicellate (pedicel to 8 mm); calyx cylindrical to campanulate, divided to 1/3 or nearly to base, accrescent in fruit, calyx lobes narrowly triangular-ovate; corolla cylindrical to campanulate, sometimes hypocrateriform with spreading to reflexed lobes and very short tube ("*Procopiana*"), faucal scales linear or subulate, papillose along margins; stamens included, rarely exerted, connectives sometimes with apical appendages; style filiform, exerted, stigma small, entire. Nutlets ovoid, erect or oblique, verruculose and often rugose, obliquely keeled, cicatrix surrounded by collar-like thickened toothed ring, teeth clasping receptacle. $2n = 18, 20, 22, 24, 28, 30, 32, 34, 36, 40, 42, 44, 48, 56, 60, 64, 72, 84, 96, 104, 120, 128, 144$.

About 35 species in Europe and W Asia, apparently including several interspecific hybrids.

45. *Trachystemon* D. Don

Trachystemon D. Don, Edinburgh New Philos. J. 13: 239 (1832).

Perennial herb from thick, branched rhizome; indumentum shortly hispid. Leaves cauline and basal, basal leaves large, ovate-acuminate from cordate base, long petiolate, developing at flowering time, cauline leaves much smaller, sessile. Inflorescences bracteose thyrsoids. Flowers long pedicellate, deflexed; calyx cup-shaped, lobes ovate, accrescent in fruit; corolla with short, conical tube and very long lobes (> tube), lobes nearly linear, reflexed and spirally twisted, violet-blue, faucal scales in two series of 5, white, the lower villous, the upper thick and papillose, protruding from throat; filaments inserted in distal half of tube, pink, pubescent at base, anthers long-exserted and connivent; style long-exserted, violet-purple, stigma punctiform. Nutlets ovoid, horizontally inflexed (long axis parallel to hypanthium), adaxially shortly beaked, beak keeled, papillose-tuberculate, cicatrix with thin ring. $2n = 56$.

One species, *T. orientalis* (L.) D. Don, Black Sea region.

IV. TRIBE CYNOGLOSSEAE W.D.J. Koch (1837).

Asperugeae Zakirov ex Ovczinnikova (2007).
Cryptanthae Brand (1925), nom. illegit.

Eritrichieae Gürke (1893).
 Myosotideae Rchb.f. (1858).
 Trigonocaryeae Kerimov (2005).

Annual or perennial herbs, sometimes minute and ephemeral, rarely subshrubs or shrubs, sometimes rhizomatous or stoloniferous, basal leaf rosette usually present (at least initially), leaves (ob-)ovate-acuminate, (ob-)ovate, elliptical or linear, usually with cuneate or decurrent base, rarely cordate and/or distinctly petiolate; plants hispid, sericeous, pubescent or villous, trichomes erect, rarely ascending or appressed, uncinete trichomes sometimes present. Inflorescence frondose to ebracteose thyrsoids or cymoids. Calyx variously united, often only in lower third, rotate to campanulate, sometimes accrescent in fruit; corolla radially symmetrical, mostly hypocrateriform or infundibuliform, faucal scales large, conspicuous, often exerted from throat, pubescent or papillose, rarely glabrous or absent; stamens equal or rarely unequal (*Caccinia*), anthers sometimes with long connective appendages; pollen eurypalynous, but mostly heterocolporate with 3–4 apertures and 3–4 pseudoapertures, rarely tricolporate (*Caccinia*, *Trichodesma*); gynobase widely to narrowly pyramidal to subulate, rarely almost flat, style with truncate or capitate stigma, rarely bilobed. Nutlets 1–4(10), straight or spreading, rarely recurved (never incurved), often oblique with apex close to style base and nutlet base widely divergent, dorsiventrally compressed, sometimes ventrally keeled, rarely ovoid to subcylindrical or lenticellate, then usually with ventral keel, variously papillose or glochidiate, rarely smooth, often with distinct dorsomarginal wing, wing spreading or erect to incurved, nutlets usually with ovate to triangular cicatrix, often in median or subapical position, rarely basal, elaiosome usually absent (present in some *Myosotis*). Nutlets dispersed singly or remaining enclosed in accrescent calyx or attached to the calyx or the plant.

Subcosmopolitan, 40 genera, centre of diversity in E Asia. Cynoglosseae, as the largest subgroup of Boraginaceae, are highly heterogeneous in both generative and vegetative characters, but the presence of dorsiventrally flattened, often marginally keeled or winged fruits is common to the majority of representatives. The gynobase is usually pyramidal to subulate and nutlet attachment then ventral rather than basal.

IV.1 TRICHODESMA GROUP

Robust perennial or biennial herbs, often (sometimes tall) shrubs; plants hispid to sericeous, sometimes leaves additionally glaucous. Leaves elliptical to obovate, subsessile. Calyx divided to base or to the middle; corolla radially symmetrical or slightly zygomorphic; pollen tricolporate. Nutlets often 1 or up to 4, oblique to horizontal, dorsiventrally compressed and usually winged.

Two genera, Africa, Asia, Australia.

46. *Trichodesma* R. Br.

Fig. 13

Trichodesma R. Br., Prodr.: 496 (1810), nom. cons.; Brummitt, Kew Bull. 37: 429–450 (1982), reg. rev.; Sadat, Mitt. Bot. Staatss. München 28: 167–191 (1989), reg. rev.

Robust annual herbs or shrubs to small trees, often with lignescent to ligneous pleiocorm; indumentum hispid to sericeous, rarely subglabrous. Leaves all cauline, mostly sessile and elliptical, alternate or frequently opposite almost throughout; inflorescence bracteose to frondose cymoids or few-branched thyrsoids. Flowers long pedicellate, deflexed; calyx divided almost to base, sepals ribbed or cordate-winged near base, accrescent in fruit; corolla campanulate to hypocrateriform, tube shorter than calyx; faucal scales absent, rarely trapezoid and deeply lobed and apparently 10; stamens 5–6, with short filaments and long anthers, these usually widely exerted, connective with a long terminal appendage, all appendages together forming a narrow, spirally twisted cone above anthers; style filiform, stigma capitate, gynobase shortly pyramidal. Nutlets large, 1–4, oblique or horizontal, ovoid to subcircular in outline, often with a narrow, erect or spreading, dentate wing margin, smooth or rugose to glochidiate; cicatrix large, medial to subapical. $2n = 14, 22, 24, 44$.

A genus of about 40 to 50 species from S Africa to S and SE Asia and Australia.

47. *Caccinia* Savi

Caccinia Savi, Cose Botaniche 1, 7, t. 1 (1832); Papava, Not. Syst. Geogr. Inst. Bot. Tbiliss. 12: 39–45 (1944), reg. rev.

Heliocarya Bunge (1871).

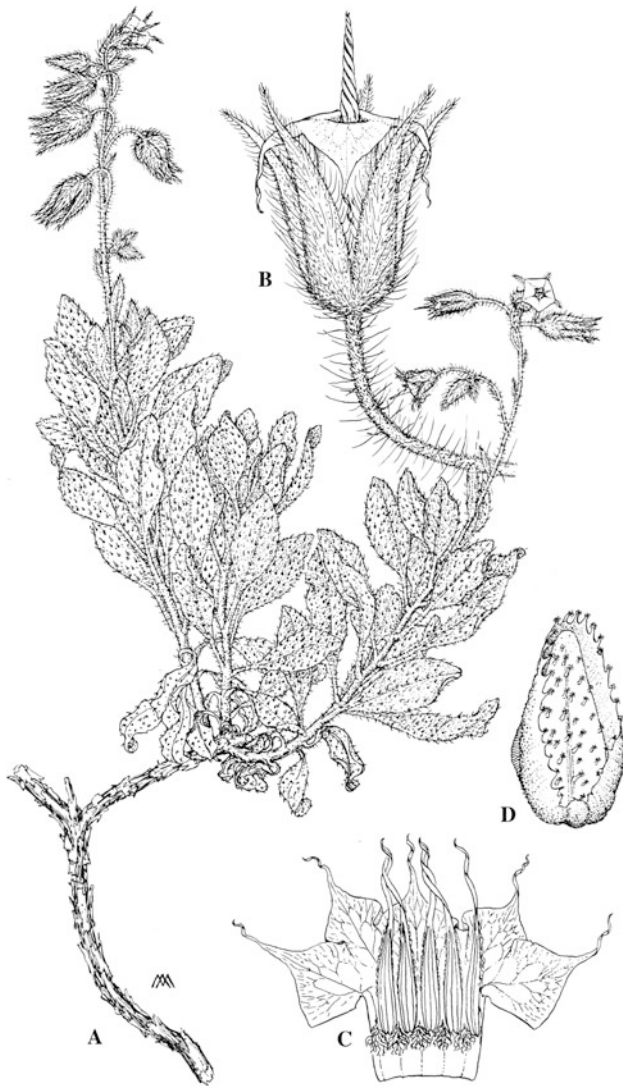


Fig. 13. Boraginaceae. Tribe Cynoglosseae, *Trichodesma* group: *Trichodesma cinereum*. A Habit. B Flower. C Open corolla. D Nutlet. (Mosti and Selvi 2007, original drawn by A. Maury)

Robust biennial or perennial herbs, sometimes extensively rhizomatous; indumentum sparsely hispid, leaves often glaucous. Shoots ascending or erect. Leaves all cauline or some basal, obovate to narrowly oblong, ciliate from hispid trichomes. Inflorescences many-branched thyrsoids, bracteose-frondose to bracteose. Flowers spreading, pedicellate; calyx lobed for 1/2 to 3/4, strongly accrescent in fruit; corolla hypocrateriform, narrow tube much longer than calyx, lobes asymmetrically spreading, narrowly ovate-triangular;

faucal scales oblong to rectangular; stamens inserted near apex of tube, filaments very unequal, at least one very long exerted, others short or reduced; gynobase shortly pyramidal, style filiform, stigma capitate. Nutlets 1(2), large, horizontal, straight, ovoid to subspherical, completely covering the receptacle, dorsally often keeled, rugose and with glochidiate wing; cicatrix large, subapical. $2n = 24$.

About six species from Iran to southern C Asia.

IV.2 LASIOCARYUM GROUP

Small to minute herbs. Indumentum sericeous to villous. Leaves obovate to spatulate, subsessile. Calyx divided to base; corolla radially symmetrical, hypocrateriform. Nutlets 4, erect, ovoid to subcylindrical, pubescent at least dorsally or rugose, cicatrix triangular, triangular-ovate to elliptical, suprabasal on adaxial side.

Three genera, essentially Himalayan, sister to *Trichodesma* + *Caccinia* (Weigend et al. 2013).

48. *Lasiocaryum* I.M. Johnst.

Lasiocaryum I.M. Johnst., Contr. Gray Herb. 75: 45 (1925); Banerjee & Bhattacharjee, Bull. Bot. Soc. Bengal 39: 33–39 (1985), reg. rev.

Oreogenia I.M. Johnst. (1924) non *Orogenia* Watson (1871).

Setulocarya R.R. Mill & D.G. Long (1996)

Small annual herbs from basal rosette. Indumentum pubescent to villous. Leaves basal and cauline, obovate to elliptic. Inflorescences bracteate cymoids, initially dense, later elongated; corolla hypocrateriform, blue or whitish, tube equalling calyx; faucal scales small, broadly rectangular, basal scales present; filaments inserted at middle of tube, anthers included; style short, stigma capitate, included; gynobase columnar. Nutlets erect, turbinate with longitudinal keel on abaxial side, pubescent on abaxial side; cicatrix broadly elliptic, reaching from base to upper half of nutlet.

Four species from N India to China.

49. *Microcaryum* I.M. Johnst.

Microcaryum I.M. Johnst., Contr. Gray Herb. 73: 63 (1924); Banerjee & Bhattacharjee, Bull. Bot. Soc. Bengal 39: 33–39 (1985), reg. rev.

Minute (<5 cm) ephemeral herb, stiffly erect, unbranched or sparsely branched; indumentum scabrid to villous. Leaves sessile, narrowly obovate. Inflorescences bracteose cymoids, all pedicels long and overtopping main axis, appearing umbellate. Pedicels strongly elongated in fruit; calyx divided nearly to base, lobes acute; corolla equalling calyx, blue to white, faucal scales ovate to crescent-shaped, basal scales five; stamens included; style included. Nutlets oblong-ovoid, 1 mm long, rugose, glabrous, adaxially with basal triangular attachment scar continuing into a broad, raised sulcus, abaxially rounded to slightly keeled.

One species, *M. pygmaeum* (C.B. Clarke) I.M. Johnst., from NE India to China. Clearly allied to and distinct from *Lasiocaryum*.

50. *Chionocharis* I.M. Johnst.

Chionocharis I.M. Johnst., Contr. Gray Herb. 73: 65–66 (1924).

Small cushion-forming perennial herb, simple or dichotomously branched, individual stems clavate in outline by crowded, densely overlapping leaves. Leaves all cauline and crowded towards the shoot apex, flabellate, basally sparsely pubescent, distally long and densely villous with soft, silky trichomes. Flowers apparently solitary, scarcely protruding from cushions; calyx villous; corolla hypocrateriform, tube short (< lobes), faucal scales broadly rectangular, white or yellow; filament insertion unknown, anthers included; style short, stigma capitate, included; gynobase shortly subulate. Nutlets erect, ovate to cylindrical, black, basally appressed pubescent, apically long pubescent; cicatrix elliptic, reaching from base to upper half of nutlet.

One species, *C. hookeri* (C.B. Clarke) I.M. Johnst., high alpine (3500–5800 m), NE India to China.

IV.3 OMPHALODES GROUP

Medium-sized to large annual or perennial herbs, often rhizomatous. Indumentum pubes-

cent or leaves at least adaxially glabrous. Leaves ovate to oblong, lower leaves (if present) petiolate. Corolla hypocrateriform; stamens included; gynobase widely pyramidal, style linear, short, stigma capitate, included. Nutlets 4, rarely 1, oblique or horizontal on gynobase, ovoid to subcircular, glabrous or pubescent, sometimes sparsely glochidiate, dorso-marginally differentiated, cicatrix in median position, ovate to elliptical.

Three genera, one widespread but local in northern hemisphere, one only on Juan Fernandez Islands, one only on Chatham Islands.

51. *Omphalodes* Mill.²

Omphalodes Mill., Gard. Dict. Abr. ed. 4. (1754); Nesom, Sida 13: 25–30 (1988), reg. rev.

Gyrocaryum Valdés (1983).

Mimophytum Greenm. (1905).

Omphalotrigonotis W.T. Wang (1984).

Sinojohnstonia Hu (1936).

(Winter-)Annual, biennial or perennial herbs, often rhizomatous or stoloniferous, aerial stems stiffly erect or diffuse; indumentum soft pubescent, often appressed, sometimes glabrous and glaucous. Leaves initially basal and cauline, basal ones (long-) petiolate, sometimes later absent, lamina broadly ovate-acuminate from cordate base or ovate to oblong, cauline leaves sometimes amplexicaulous. Inflorescences cymoids, rarely thyrsoids, ebracteose or frondose below and ebracteose above, rarely frondose-bracteose, sometimes rooting near apex and forming a new leaf rosette. Flowers erect, pedicellate, pedicels sometimes elongating and curved in fruit; calyx lobed nearly to base, rotate, rarely campanulate, not or strongly accrescent in fruit; corolla hypocrateriform, rarely infundibuliform, white or bright blue; lobes > tube, faucal scales present, broadly rectangular, often emarginate. Nutlets oblique-obconical in lateral view, ovoid to circular in dorsal view, glabrous, rarely pubescent, dorsomarginal wing spreading, erect or incurved, membranaceous or coriaceous, entire or serrate, sometimes glochidiate. $2n = 19, 20, 22, 24, 28, 36, 42, 48$.

² Two lineages of *Omphalodes* recognized as not belonging to the core-group of the genus have been removed to the novel genera *Memoremea* A. Otero, Jim.-Mejías, Valcárcel & P. Vargas and *Nihon* A. Otero, Jim.-Mejías, Valcárcel & P. Vargas. *Memoremea* is the first-branching lineage of the *Mertensia*-group and *Nihon* falls into the *Bothriospermum*-group (Weigend et al. 2013; Otero et al. 2014).

About 20–30 species, Eurasia and N America. A widespread and highly heterogeneous taxon. The segregate genera proposed may be monophyletic, but the remainder of the genus is then likely to be paraphyletic. *Omphalodes* is therefore here defined broadly until a critical study of the genus across its range is undertaken. Poorly known *Gyrocarium* from Spain is provisionally included here. Both *Myosotidium* and *Selkirkia* are probably nested in *Omphalodes* (Weigend et al. 2013).

52. *Myosotidium* Hook.

Myosotidium Hook. Bot. Mag. 85: t. 5137 (1859).

Robust rosulate perennial herb from thick rhizome; indumentum sparse, soft sericeous on abaxial leaf surface, glabrous and dark green on adaxial leaf surface. Leaves coriaceous when dry, basal ones petiolate, up to 1.5 m long, broadly ovate to reniform, cauline leaves cordate to elliptical. Inflorescence a much-branched thyrsoid. Flowers pedicellate; calyx divided to base with oblong, marginally ciliate lobes; corolla hypocra-teriform, blue or white; tube shorter than lobes, lobes subcircular, faucal scales depressedly rectangular, carnos. Nutlets large (10–15 mm), flat, with a spreading, unevenly serrated wing, black. $2n = 40, 42$.

A single species, *M. hortensia* (Decne.) Baill., endemic to Chatham Islands (New Zealand), probably nested in *Omphalodes*.

53. *Selkirkia* Hemsl.³

Selkirkia Hemsl., Bot. Challenger III, 1: 47 (1884).

Sparsely branched shrub; indumentum sparse, appressed, leaves adaxially glabrous. Leaves crowded at branch apices, petiolate, lamina ovate to elliptical, apex abruptly acuminate, chartaceous. Inflorescences widely branched (“corymbose”) ebracteose thyrsoids. Flowers pedicellate; calyx slightly accrescent in fruit; corolla white, hypocra-teriform, tube short and wide, lobes widely subcircular, half erect to spreading, usually pubescent at least abaxially, faucal scales present, semicircular,

annulus present; gynobase shortly pyramidal, much shorter than nutlets in fruit. Nutlets (1–)4, erect, straight, triangular-ovoid in dorsal view, densely glochidiate but with thick glochidia lacking reflexed tips, ventrally keeled, indistinctly winged; cicatrix large, medial, subcircular.

A single species, *S. berteri* Hemsl., Juan Fernandez Islands (Chile). A close affinity to *Hackelia* has been suggested, but *Selkirkia* is probably nested in *Omphalodes*.

IV.4 MYOSOTIS GROUP

Tiny to medium-sized annual or perennial herbs, sometimes ephemeral, often rhizomatous or stoloniferous. Indumentum pubescent or puberulent, rarely sericeous or villous. Leaves elliptical, (ob-)ovate-acuminate or oblong, lower leaves (if present) petiolate. Gynobase nearly flat to shallowly pyramidal; style filiform, stigma sub-capitate, sometimes obscurely bilobed. Nutlets 4, rarely fewer or up to 10, small (< calyx), erect, lenticellate to tetrahedral, usually with lateral, often also with ventral keels, dark brown to black, rarely triangular, glabrous, smooth or papillose, cicatrix circular to elliptical, supraba-sal, rarely cicatrix distinctly stalked.

Four genera, three in E Asia, one subcosmopolitan (*Myosotis*).

54. *Myosotis* L.

Myosotis L., Sp. Pl.: 131 (1753); Grau & Leins, Ber. Deutsch. Bot. Ges. 81: 107–115 (1968), palyn., infragen.; Schuster, Feddes Repert. 74: 39–98 (1967), partial rev.; Winkworth et al., Mol. Phyl. Evol. 24: 180–193 (2002), phylog.

Exarrhena (A. DC.) O.D. Nikiforova (2000).

Gymnomyosotis (A. DC.) O.D. Nikiforova (2000).

Strophostoma Turcz. (1840).

Trigonocaryum Trautv. (1875).

Annual, biennial or perennial herbs, rarely decumbent or stoloniferous or cushion-forming; indumentum pubescent, rarely glabrescent or villous, uncinuate trichomes often present. Leaves basal (at least initially) and cauline. Inflorescences cymoids, often monochasial, ebracteose at least above.

³ New molecular data retrieve *Selkirkia* and *Myosotidium* (the “Pacific *Omphalodes*”) together, deeply nested in *Ompalodes*, in a clade together with native South American *Cynglossum*. Generic realignments are in progress in order to accommodate these results.

Flowers pedicellate, pedicel often elongating and curved in fruit; calyx lobed 1/3 to 1/2, often with uncinat trichomes and accrescent in fruit, enclosing nutlets; corolla hypocrateriform to infundibuliform, tube short (= lobes), blue to pink, white or yellow, throat yellow or white, lobes oblong to subcircular, contort in bud; faucal scales semicircular to narrowly rectangular and largely reduced; anthers included, rarely exerted; style included, rarely exerted. Nutlets (1-)4, erect, usually ovoid, dorsiventrally compressed with more or less distinct marginal keel and ventrally keeled, usually smooth and shiny, black; cicatrix basal, subcircular, sometimes with extruding white elaiosome ("*Strophostoma*", "*Trigonocaryum*"). $2n = 12, 14, 16, 18, 20, 22, 24, 28, 30, 32, 36, 40, 44, 46, 48, 52, 54, 64, 66, 72, 84, 86, 88$.

About 80–100 species, subcosmopolitan with centres of diversity in the Mediterranean and New Zealand.

55. *Trigonotis* Steven

Trigonotis Steven, Bull. Soc. Imp. Naturalistes Moscou 24 (1): 603 (1851); Starchenko, Izv. Sib. Otd. Akad. Nauk SSSR, Ser. Biol, Nauk 36–44 (1979), reg. rev. *Zoelleria* Warb. (1892).

Annual, biennial or perennial herbs, rosette-forming and rhizomatous or with decumbent, rooting shoots with distichous phyllotaxy; indumentum densely pubescent to subglabrous. Leaves cauline, sometimes also basal, basal leaves long petiolate, cauline leaves sessile, ovate-acuminate to elliptical-acuminate. Inflorescences cymoids, often elongated scorpioid monochasia or boragoids, ebracteose at least above. Flowers subsessile to long pedicellate; calyx divided 1/3 to 1/2, lobes triangular-ovate, often spreading in fruit; corolla hypocrateriform, white or rarely blue, tube short (< calyx), lobes subcircular, imbricate in bud; faucal scales small, semicircular to depressedly rectangular, often emarginate, white to yellow or orange-red; stamens inserted in middle of corolla tube, anthers included; style usually included. Nutlets (1-)4(10), erect to half-erect, usually tetrahedral, sessile or stipitate, adaxially keeled, usually smooth, glabrous or minutely pubescent to tuberculate, rarely narrowly winged ("*Stephanocaryum*"), cicatrix very small, at basal end of adaxial keel. $2n = 36, 48$.

About 60 species, mainly E & SE Asia, west to SE Russia.

56. *Decalepidanthus* Riedl

Decalepidanthus Riedl, Österr. Bot. Z. 110: 608–612 (1963); Dickoré & Hilger, Phytotaxa 226: 131–143 (2015). *Oreocharis* (Decne.) Lindl. (1846), nom. rej. non Benth. (1876). *Pseudomertensia* Riedl (1967). *Scapicephalus* Ovcz. & Czukav. (1974).

Perennial herbs with dense, basal leaf rosettes, rhizomatous and stoloniferous; indumentum pubescent to sericeous. Leaves mostly basal, long petiolate, lamina ovate-acuminate to obovate. Inflorescences initially dense, postflorally elongate ebracteose cymoids or weakly developed thyrsoids. Flowers pendulous or spreading, shortly pedicellate; calyx divided 1/2 to nearly to base, shorter than corolla tube; corolla campanulate, infundibuliform to hypocrateriform, blue or pink, lobes often short, porrect to spreading, faucal scales triangular to narrowly oblong, rarely absent, annulus of 10 basal scales; stamens included to long exerted; style filiform, included or exerted. Nutlets erect, straight, ovoid, dorsiventrally compressed, adaxially sharply keeled, smooth.

About 10 species, Himalayas.

57. *Brachybotrys* Maxim. ex Oliv.

Brachybotrys Maxim. ex Oliv., Hooker's Icon. Pl. 13: 43, t. 1254 (1878).

Perennial herb from slender, branched rhizomes, aerial stems unbranched, erect, basally with scale leaves, foliage leaves crowded in upper half; indumentum sparsely tomentose pubescent to appressed pubescent above, subglabrous below. Inflorescences ebracteose, dichasial cymoids. Flowers pendulous, long pedicellate; calyx divided to base, lobes linear, slightly accrescent in fruit and apparently enclosing the fruit; corolla campanulate, purple, tube short (< lobes), lobes porrect, triangular-ovate, faucal scales triangular to depressedly rectangular. Anthers exerted from tube; style filiform, long-exserted. Nutlets tetrahedral, smooth to pubescent, black. $2n = 24$.

A single species, *B. paridiformis* Maxim. ex Oliv., NE Asia (Russia, China, Korea).

IV.5 MERTENSIA GROUP²

Small to large perennial herbs, often with pleiocorm; indumentum sparse, pubescent or puberulent, often glabrous and glaucous. Leaves elliptical or ovate-acuminate, lower leaves (if present) petiolate. Gynobase shallowly pyramidal; style exerted or included, stigma capitate. Nutlets 4, oblique on pyramidal gynobase, ovoid to subcircular in dorsal view, weakly dorsiventrally flattened, dorsally more or less convex, ventrally flat or concave, brown to black, smooth or irregularly verrucose or rugose, sometimes very indistinctly winged along margins, cicatrix medial, on short \pm distinctive stalk.

Two genera, one Asia, one widespread in the northern hemisphere (*Mertensia*).

58. *Mertensia* Roth

Mertensia Roth, Catal. Bot. 1: 34 (1797), nom. cons.; Williams, Ann. Missouri Bot. Gard. 24: 17–159 (1937), reg. rev.; Popov, Bot. Mater. Notul. Syst. 15: 248–266 (1953), reg. rev.; Matthews, Proc. Utah Acad. Sci. Arts Lett. 45: 590–602 (1968), reg. rev.; Starchenko, Bot. Zhurn. 64: 1666–1669 (1979), reg. rev.

Perennial herbs with pleiocorm or root-pleiocorm; indumentum puberulent to pubescent, often subglabrous to glabrous and glaucous; massive taproot usually present, sometimes also root tuber. Leaves basal and cauline, basal leaves long petiolate or with decurrent margins, lamina ovate to elliptical, rarely flabellate, membranaceous to thinly succulent. Inflorescences cymoids or thyrsoids, monochasia ebracteose, but each subtended by one large bract. Flowers long pedicellate, usually pendulous; calyx divided 1/2 to nearly to base, short (< corolla tube), not or slightly accrescent in fruit; corolla narrowly infundibuliform to campanulate, blue or pink to white, lobes ovate to semicircular, obtuse; faucal scales usually small, triangular; filaments inserted between faucal scales or slightly below. Nutlets oblique, with flat, rounded, rarely inflated back, margin sometimes narrowly winged, apex sometimes distinctly acuminate, smooth or rugulose to verrucose, ventrally sharply keeled above and more or less convex below; cicatrix submedial, small, triangular-ovate, elevated onto small stipe. $2n = 24, 48, 72$.

About 40 species in E Asia, N America, one reaching NW Europe.

59. *Anoplocaryum* Ledeb.

Anoplocaryum Ledeb., Fl. Ross. 3: 154 (1847).

Perennial herbs with stems branching from base, decumbent to ascending; indumentum pubescent; persistent taproot present. Leaves obovate to oblong. Inflorescence short bracteose cymoids, strongly elongating in fruit. Flowers pedicellate; calyx divided nearly to base, spreading in fruit; corolla hypocrateriform, blue, tube equalling limb; faucal scales depressedly rectangular, papillose, white to yellow; anthers included. Nutlets small, ventrally keeled above and more or less convex below; cicatrix submedial, small, triangular-ovate, elevated onto small stipe; black, finely tuberculate; cicatrix submedial, small, narrowly triangular.

Five species in C Asia.

60. *Asperugo* L.

Asperugo L., Sp. Pl. 1: 138 (1753).

Lax to scrambling annual herb; indumentum on stem retrorsely uncinata, otherwise scabrid. Leaves basal and cauline, distinctive rosette absent, ovate to elliptical, lower leaves opposite to pseudovercillate, long petiolate, upper leaves sessile, alternate. Inflorescences frondose cymoids (mostly monochasial), later very lax. Flowers subsessile, pedicels elongating and recurved in fruit; calyx bilobed almost to base, strongly accrescent, 2-lipped in fruit with two broadly triangular lobes, one lip 7-, the other 8-dentate, enclosing the nutlets; corolla infundibuliform to hypocrateriform, very small, blue to white, faucal scales small, crescent-shaped; stamens included; style included, stigma capitate, gynobase subulate. Nutlets laterally flattened, finely tuberculate, cicatrix suprabaasal and asymmetrically placed to one side of flattened nutlet. $2n = 24$.

A single species, *A. procumbens* L., in Europe and Asia. Morphologically highly divergent, but retrieved with *Mertensia* (Weigend et al. 2013).

IV.6 LAPPULA GROUP

Small to medium-sized annual or perennial herbs, sometimes ephemeral or cushion-forming. Indumentum mostly hispid, sometimes pubescent, sericeous or villous. Leaves elliptical, (ob-)

ovate-acuminate or oblong, rarely linear, lower leaves (if present) sessile or petiolate. Calyx usually divided nearly to base; corolla hypocrateriform to infundibuliform; anthers included; gynobase (narrowly) pyramidal to subulate, rarely widely pyramidal; style filiform, included, stigma capitate. Nutlets 1–4, oblique on pyramidal gynobase or parallel to subulate gynobase (perpendicular to receptacle), ovate to subcircular in dorsal view, glochidiate, rarely only verrucose or nearly smooth, cicatrix triangular or triangular-ovate, medial.

Eight genera recognized here, but generic limits highly problematical, essentially an Old World group with centre of diversity in C Asia. *Heterocaryum* and *Suchtelenia* are apparently more closely allied to each other and sister to genera 61–64. *Selkirkia*, albeit morphologically superficially similar to *Hackelia*, may indeed be closer to Chilean *Cynoglossum*.

61. *Heterocaryum* A. DC.

Heterocaryum A. DC., Prodr. (DC.) 10: 144 (1846).

Annual herbs; taproot present. Leaves all cauline (in flower), linear, sessile. Inflorescences bracteose cymoids, elongating in fruit. Flowers shortly pedicellate, pedicels usually elongating in fruit; calyx accrescent in fruit; corolla cylindrical to narrowly infundibuliform, tube short (< calyx), faucal scales minute, depressedly rectangular; gynobase columnar, subulate in fruit, winged between areoles, nutlets oblong, heteromorphic (3+1 or 2+2), either with dentate-glochidiate wing or not winged, permanently attached to gynobase along entire adaxial surface. $2n = 24, 48$.

About six species in W Asia. Closely related to and sometimes included in *Lappula*.

62. *Suchtelenia* Karel. ex Meisn.

Suchtelenia Karel. ex Meisn., Pl. Vasc. Gen. [Meisner] 1: 279 (1840); Kerimov & Askerova, Bot. Zh. 90: 264–267 (2005), syst.

Annual herb; indumentum hispid, more often subglabrous and glaucous. Leaves subopposite

below, alternate above, slightly succulent. Inflorescences few-flowered, ebracteose cymoids. Flowers pedicellate; calyx divided 1/2 to 3/4, strongly accrescent and patelliform in fruit; corolla minute, infundibuliform, blue, faucal scales depressedly rectangular; gynobase widely pyramidal, ultimately hollow. Nutlets (1–)4, ovoid with convex back, smooth or spinulose, adaxial side sunken in gynobase, heteromorphic, either persisting or leaving cavities or frames when abscising.

A single species, *S. calycina* (C.A. Mey.) A. DC., in C Asia, infraspecific taxa are variously recognized or not.

63. *Lappula* Moench⁴

Lappula Moench, Meth. (Moench): 416 (1794); Goloskov, Fl. Rast. Res. Kaz. 1975: 69–80 (1975), reg. rev.; Ovczinnikova, Pjak & Ebel, Turczaninowia 7: 5–13 (2004), reg. rev.; Voytenko & Oparina, Bot. Zhurn. 70: 865–875 (1985), morph.; Sadat, Mitt. Bot. Staats. München 28: 18–51 (1989), reg. rev.; Zhu et al., Flora of China 16: 403–413 (1995), reg. rev. *Omphalolappula* Brand (1931). *Sclerocaryopsis* Brand (1931).

Annual or rarely biennial or perennial herbs, stems stiffly erect or decumbent, rarely trailing; indumentum hispid or pubescent, rarely uncinata; well-developed taproot usually present. Leaves basal and cauline, narrowly (ob-)ovate to linear, sessile or shortly petiolate. Inflorescences erect, frondose, frondose-bracteose, bracteose, distally sometimes ebracteose thyrroids, rarely cymoids, elongating in fruit. Flowers (sub-)sessile to pedicellate, pedicel sometimes elongating and recurved in fruit; calyx accrescent in fruit; corolla cylindrical or infundibuliform, sometimes hypocrateriform, blue to whitish, faucal scales present, often saccate; gynobase pyramidal to subulate. Nutlets oblique to perpendicular to receptacle, often heterocarpic or heteromericarpic, nutlets triangular-ovate to ovoid in dorsal view, dorsally concave, rarely convex, usually with dorsomarginal wing of either confluent bases of glochidia or distinctly membranaceous, often hyaline, wing spreading to incurved, sometimes dentate, rarely nutlets glabrous and firmly attached to gynobase

⁴ Synonymy and placement are highly tentative: these three genera are very poorly understood and – depending on generic type species – *Lepechiniella* may turn out to be a member of the *Lappula*-group, and possibly synonymous with *Lappula*, while *Microparacaryum* undoubtedly belongs here.

(“*Sclerocaryopsis*”), cicatrix triangular to circular, medial. $2n = 22, 24, 46, 48$.

A difficult, probably paraphyletic genus of about 50–60 species in Eurasia, Australia, N Africa, W North America; some species introduced worldwide, centre of diversity in E Asia (>40 species in China). The Australian segregate *Omphalolappula* represents a specialized lineage within *Lappula* and is not recognized at generic rank here. Delimitation from the other genera of the group here recognized (esp. *Heterocaryum*) is also doubtful, as are the limits between *Eritrichium* and *Lappula*.

64. *Rochelia* Rchb.

Rochelia Rchb., Flora 7(1): 243 (1824), nom. cons.

Annual herbs; indumentum hispid, rarely pubescent. Leaves linear, 1-veined. Inflorescences bracteose cymoids. Flowers pedicellate; calyx lobes linear to lanceolate, rarely widely ovate, accrescent and mostly incurved in fruit; corolla minute, infundibuliform, light blue; tube straight or slightly curved; faucal scales sometimes present; gynobase subulate, columnar in fruit, ovary 2-locular. Nutlets 1–2, obliquely subpyriform, laterally compressed, glochidiate or smooth, permanently attached to the gynobase. $2n = 20$.

About 15 species, W Europe to C, SC & SW Asia. Nested in *Lappula* according to Weigend et al. (2013).

65. *Eritrichium* Schrad. ex Gaudin

Eritrichium Schrad. ex Gaudin, Fl. Helvetica, 2: 4, 57 (1828); Sadat, Mitt. Bot. Staatss. München 28: 11–17 (1989), reg. rev.; Zhu et al., Flora of China 16: 378–390 (1995), reg. rev.

Amblynotus I.M. Johnst. (1924).

Sauria M.S. Bajtenov (1996).

Tianschaniella B. Fedtsch. (1951).

Annual, biennial or perennial herbs, often cushion-forming, caespitose; indumentum sericeous, strigose or villous. Leaves basal and cauline, basal ones petiolate, cauline ones sessile, oblanceolate to spatulate. Inflorescences frondose-bracteose cymoids or ebracteose distally. Flowers pedicellate; calyx often rotate in fruit; corolla hypocrateriform, rarely infundibuliform, blue or white, tube equaling calyx, faucal scales depressedly rectangular; filaments inserted on middle of corolla tube; gyno-

base shortly pyramidal. Nutlets 4, turbinate to ovoid, mostly dorsiventrally compressed, abaxial side usually flat or very slightly concave, with narrow wing and triangular marginal teeth or glochidiate appendages forming an ultimately incurving wing-like margin; cicatrix supramedial. $2n = 20, 22, 24, 28, 36, 46, 48$.

Some 50 species, Asia to Europe and N America. The alpine cushion-forming species from Eurasia and North America apparently are monophyletic, but the remainder may represent several unrelated lineages, some of them close to *Lappula*. *Sauria*, a very imperfectly known genus, is only tentatively included here.

66. *Hackelia* Opiz

Hackelia Opiz in Bercht. & Opiz, Ökon.-techn. Fl. Böhmens 2(2): 146 (1839); Gentry & Carr, Mem. New York Bot. Gard. 26: 121–227 (1976), reg. rev.

Austrocynoglossum Popov ex R.R. Mill (1989).

Embadium J.M. Black (1931).

Perennial, rarely annual herbs, often with pleiocorm or rhizomatous; indumentum hispid, pubescent or sericeous; well-developed taproot often present. Leaves basal and cauline, ovate-acuminate to oblong, basal ones long petiolate, cauline ones shortly petiolate to sessile. Inflorescences ebracteose or basally bracteose thyrsoids, rarely cymoids. Flowers pedicellate, pedicel elongating and reflexed in fruit; corolla hypocrateriform, tube short (< lobes), faucal scales semicircular to triangular; gynobase shortly pyramidal. Nutlets oblique to nearly perpendicular to receptacle, triangular-ovoid in dorsal view, usually glochidiate on disc, margin winged with crest of separate or basally confluent glochidia, sometimes incurved, ventrally keeled; cicatrix medial or submedial, rarely subapical, ovate. $2n = 24, 48$.

About 45 species, mostly W North America, S America, Asia, Australia, Europe.

IV.7 BOTHRIOSPERMUM GROUP²

Small to medium-sized annual or perennial herbs, lax and trailing or compact with distinct basal leaf rosette. Indumentum pubescent, sometimes hispid or villous. Leaves basal and cauline, obovate-acuminate or oblong from cuneate base. Calyx divided nearly to base; corolla hypocrateriform to infundibuliform; gynobase flat, widely pyramidal; style filiform, included, stigma usually

capitate. Nutlets typically 4, erect or incurved on pyramidal gynobase, ovate to circular in dorsal view, usually glochidiate, rarely only verrucose, “dorso-”marginal wing often double, erect or incurved, often much smaller than nutlet diameter (“pseudocicatrix”), displaced into a dorsal-apical or even ventral position, cicatrix triangular or triangular-ovate, medial.

Three genera, all E Asia, evidently closely related and sharing the unique character of a distinct “double wing”. Apparently sister to the *Cynoglossum* group s.str. (excl. American species) and *Lepechiniella*.

67. *Bothriospermum* Bunge

Bothriospermum Bunge, Enum. Pl. Chin. Bor. 47 (1833); Zhu et al., Flora of China 16: 418–420 (1995), reg. rev.

Annual or biennial herbs, sometimes trailing; indumentum densely scabrid to hispid; roots fibrous. Leaves alternate, all cauline or some in basal rosette, (ob-)ovate-acuminate, base cuneate to decurrent. Inflorescences frondose to frondose-bracteose cymoids, sometimes anthocladal. Flowers erect, pedicellate, pedicels often elongating in fruit and incurved; calyx deeply lobed, lobes narrowly ovate-acuminate, slightly accrescent in fruit; corolla hypocrateriform to infundibuliform, tube short, lobes subcircular to oblong, blue or white, faucal scales semicircular to depressedly rectangular; gynobase flat or very shallowly pyramidal, style filiform, included, stigma capitate. Nutlets erect or slightly incurved, ovoid, back densely tuberculate, convex, ventral (style facing) side concave, with a “pseudoaperture” formed by 2 concentric structures, outer one a thickened, elevated margin, inner one a membranaceous, incurved, sometimes dentate wing; cicatrix usually basal, triangular-ovate to subcircular. $2n = 24$.

Five species in C & E Asia.

68. *Antiotrema* Hand.-Mazz.

Antiotrema Hand.-Mazz., Anz. Akad. Wiss. Wien. Math.-Nat. Kl. 57: 239 (1920).

Perennial herb with perennial basal rosette; indumentum dense, scabrid to hispid. Leaves basal and cauline, narrowly (ob-)ovate. Inflorescences on long, erect scapes, sparsely branched above, ebracteose, sometimes frondose-bracteose at base. Flowers pendulous, shortly pedicellate, pedicels elongating and recurved in fruit; corolla infundibuliform, tube short, lobes subcircular, blue or purple, faucal scales oblong, papillose, white; stamens exserted; stigma terete. Nutlets erect, ovoid, ventrally (adaxially) with double, incurved cupular wing, outer wing dentate, inner wing membranaceous.

One species, *A. dunnianum* (Diels) Hand. Mazz., W China.

69. *Thyrocarpus* Hance

Thyrocarpus Hance, Ann. Sci. Nat. Bot. IV, 18: 225 (1862); Zhu et al., Flora of China 16: 430–431 (1995), reg. rev.

Annual herbs, with 1(3) stems, these stiffly erect and branched only above, densely pubescent with scabrid and hispid trichomes. Leaves cauline and (at least initially) basal, (ob-)ovate-acuminate to elliptical, margin entire or indistinctly serrate. Inflorescences lax, frondose to frondose-bracteose cymoids. Flowers erect, pedicellate, pedicel elongating in fruit; calyx with narrowly ovate-acuminate lobes, slightly accrescent in fruit; corolla lobes subcircular to oblong, blue or white, faucal scales oblong to nearly linear, sometimes emarginate, white; stamens included; stigma terete. Nutlets held horizontally, slightly incurved, ovoid to subcircular, abaxially tuberculate, “ventral” (upper) side parallel to receptacle with a “pseudoaperture” with 2 concentric wings, outer one often erect, dentate, inner one more or less involute and, hiding abaxial nutlet surface, cicatrix apical, ovate to subcircular. $2n = 24$.

Three species, China, Vietnam.

IV.8 CRYPTANTHA GROUP⁵

Small to medium-sized, ephemeral, annual or perennial herbs, usually compact with distinct basal leaf rosette, rarely shrublets (some

⁵ *Dasynotus* is now firmly placed at the base of the New World *Cryptantha*-group, together with several North American species of *Cynoglossum* (Weigend et al. 2013). Resolution in this clade is very poor and the description of two additional genera, *Adelinia* and *Andersonglossum*, to accommodate the representatives of *Cynoglossum* in this group, appears premature. *Oncaglossum* from Mexico likely also belongs here (Cohen 2015).

Cryptantha) or creeping and rooting at nodes (some *Plagiobothrys*); indumentum pubescent, sometimes hispid, villous or sericeous, very rarely glaucous and hispid. Leaves basal and cauline, rarely cauline only, linear to narrowly oblong or elliptical, more rarely obovate-acuminate, sessile with narrowed base. Corolla hypocrateriform to infundibuliform; gynobase widely or narrowly pyramidal to subulate. Style filiform, included or exerted, stigma capitate. Nutlets typically 4, erect, spreading or recurved, ovate-acuminate to oblong in dorsal view, verrucose, rugulose or glochidiate, dorsomarginal wing usually absent or present as distinct glochidiate teeth with united bases (only *Pectocarya*) or as indistinct, flattened nutlet margin (some *Cryptantha*), nutlets ventrally sharply keeled, keel sometimes with distinct groove, cicatrix triangular or triangular-ovate, suprabaasal, rarely apical (*Pectocarya*).

Five genera, American, *Plagiobothrys* also Australia and NE Asia, *Microula* Asian. A further subdivision of *Cryptantha* into several genera based on molecular data has been proposed by Hasenstab-Lehman and Simpson (2012), but the genus is here adopted in its traditional circumscription. This group is retrieved with several species of *Cynoglossum* nested in it (Weigend et al. 2013) and generic realignments will be required.

70. *Cryptantha* Lehm. ex G. Don

Cryptantha Lehm. ex G. Don, Gen. Hist. 4(1): 373 (1837); Grau, Mitt. Bot. München 18: 379–400 (1982), reg. rev.; Higgins, Brigham Young Univ. Sci. Bull., Biol. Series 13: 1–63 (1971), part. rev.; Johnston, Contr. Gray Herb. 74: 1–114 (1925), reg. rev.; Pérez-Moreau, Darwiniana 20: 155–188. (1976), reg. rev.
Nesocaryum I.M. Johnst. (1927).

Annual, biennial or perennial herbs, rarely shrublets, stems stiffly erect, one main stem from the base or with several long basal branches, sometimes cushion-forming; indumentum densely scabrid to uncinata, rarely sericeous or villous. Leaves basal (at least initially) and cauline, lamina narrowly obovate to linear. Inflorescences ebracteose or basally bracteose complex thyrsoids, rarely reduced to cymoids, sometimes very dense and subcapitate. Flowers erect, subsessile, sometimes distylous, geoflorous and cleistogamous flowers sometimes present; calyx deeply lobed,

sometimes circumscissile in fruit; corolla narrowly infundibuliform or salverform, shorter or longer than calyx, usually white with yellow throat, rarely yellow, faucal scales usually absent, rarely present, basal scales 5–10 (conspicuous in perennials); stamens included or exerted (depending on floral morph); style included or exerted (depending on floral morph). Nutlets straight, triangular-ovoid, dorsally convex, smooth to ornamented, rarely indistinctly winged, ventrally keeled and keel with groove, keel often forked towards base with small, triangular to triangular-ovate cicatrix; nutlets often heteromericarpous (3+1), those in geocarpic flowers often widely differing. $2n = 12, 14, 20, 24, 36, 62, 64, 120, 124$.

About 160 species, SW North America and W South America. Several groups have been recognized at genus level in the past, including the Isla San Ambrosio (Chile) endemic *Nesocaryum*. We here treat the genus in a wide sense. It is clearly closely allied to both *Plagiobothrys* and *Amsinckia* and generic limits as currently defined are almost certainly artificial.

71. *Amsinckia* Lehm.

Amsinckia Lehm., Sem. Hort. Bot. Hamburg 1831: 7 (1831), nom. cons.; Macbride, Contr. Gray Herb. 49: 1–16 (1917), reg. rev.; Ray & Chisaki, Amer. J. Bot. 44: 529–536 (1957), reg. rev., morph.

(Winter-)annual, stiffly erect herbs; indumentum densely hispid, scabrid to uncinata, rarely setose and glaucous. Leaves initially in dense basal rosette, cauline leaves (sub-)sessile, narrowly obovate to linear. Inflorescences ebracteose or basally bracteose cymoids or thyrsoids. Flowers erect, subsessile, sometimes distylous; calyx lobes equal or unequal; corolla narrowly infundibuliform or hypocrateriform, orange to orange-yellow, often with 5 darker spots on lobes, faucal scales usually absent; stamens included or exerted (depending on stylar morph); style included or exerted (depending on stylar morph). Nutlets (1–)4, usually heteromericarpous (3+1), erect, straight, triangular-ovoid, dorsally convex or keeled, smooth or ornamented, ventrally sharply keeled, cicatrix basal at lower end of keel, small, triangular to triangular-ovate; cotyledons deeply bifid. $2n = 8, 10, 12, 14, 24, 26, 30, 32, 34, 38$.

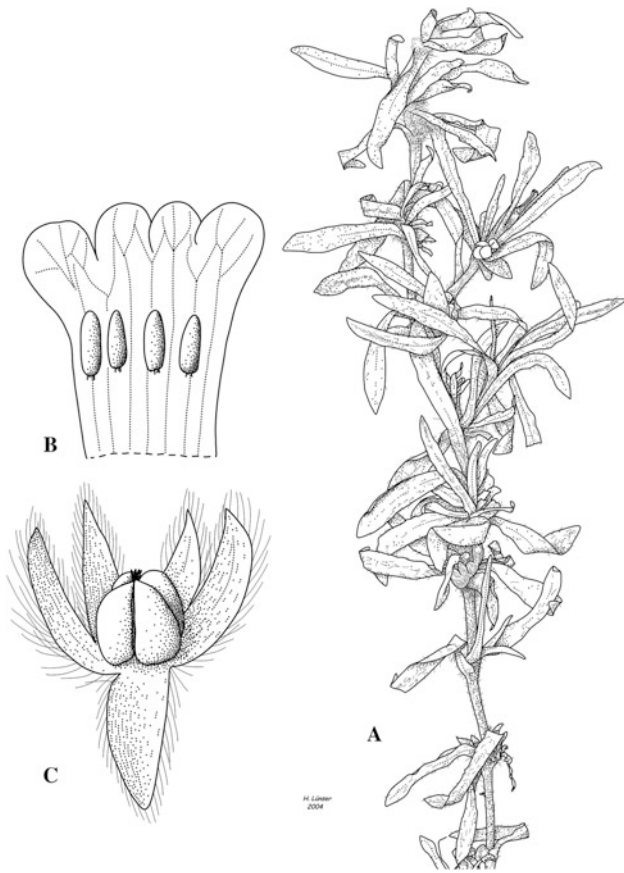


Fig. 14. Boraginaceae. Tribe Cynoglosseae, *Cryptantha* group: *Plagiobothrys humilis*. A Habit. B Open corolla. C Fruit. (orig., drawn by H. Lünser)

About 15 species, SW North America and SW South America, two species widely naturalized nearly worldwide.

72. *Plagiobothrys* Fisch. & C.A. Mey. Fig. 14

Plagiobothrys Fisch. & C.A. Mey., Index Sem. Hort. Bot. Petrop. 2: 46 (1836); Johnston, Contr. Gray Herb. 68: 57–80 (1923), synopsis; Johnston, J. Arnold Arbor. 3: 3–82 (1932), reg. rev.
Allocarya Greene (1887).

Annual to perennial herbs, stiffly erect or with creeping, rooting shoots; indumentum sparse and pubescent or scabrid to uncinat. Leaves (at least initially) basal and cauline, some or most opposite, (sub-)sessile, (ob-)ovate, oblong or linear. Inflorescence ebracteose or irregularly bracteose cymoids, rarely thyrsoids, sometimes strongly congested into capitula. Flowers erect, subsessile

to shortly pedicellate; corolla infundibuliform, white, lobes erect to spreading, usually pubescent at least abaxially, faucal scales present, usually yellow, annulus present, indistinct; stamens included; style included. Nutlets (1–)4, erect, straight, (triangular-)ovoid, dorsally convex, more or less ornamented, ventrally sharply keeled, keel not grooved; cicatrix basal to medial, at lower end of the strong ventral keel or rarely terminating on a stipitate prolongation. $2n = 24, 34, 36, 48, 58, 72$.

A difficult, possibly paraphyletic genus of ca. 70 species, most in SW North America and Andean South America, five species in Australia, one in NE Asia (Kamchatka).

73. *Pectocarya* DC. ex Meisn.

Pectocarya DC. ex Meisn., Pl. Vasc. Gen. [Meisner] 1: 279; 2: 188 (1840).
Harpagonella A. Gray (1876).

Ephemeral herbs with horizontally spreading branches; indumentum scabrid to hispid. Leaves initially basal, later only cauline. Inflorescences frondose to frondose-bracteose, irregularly branched thyrsoids or cymoids. Flowers erect, (sub-)sessile; calyx spreading at maturity or highly asymmetrical ("*Harpagonella*": 2 upper lobes fused, strongly accrescent in fruit, at maturity with 5–10 large basal processes with uncinat trichomes, 3 lower lobes free nearly to base); corolla narrowly infundibuliform, white, throat often yellow, faucal scales present, minute, semi-circular, yellow, annulus indistinct; stamens included; gynobase very shortly pyramidal, style very short, included. Nutlets 4, horizontally spreading to reflexed, narrowly obovate, with more or less distinct marginal wing of basally confluent glochidia or rarely half-erect, obovoid, pubescent, one enclosed by upper calyx lobes, the second free, pedicel reflexed in fruit, axis disarticulating ("*Harpagonella*"). $2n = 24, 72$.

15 species, mainly SW North America and SW South America. A highly distinctive genus, apart from aberrant monotypic *Harpagonella*, which is here included following Veno (1979).

74. *Microula* Benth.

Microula Benth. in Benth. & Hook., Gen. Pl. 2: 853 (1876); Banerjee & Banerjee, Bull. Bot. Surv. India 15: 71–75

(1973), reg. rev.; Wang, *Acta Phytotaxon. Sin.* 18: 266–283 (1980), rev.; Zhu et al., *Flora of China* 16: 391–401 (1995).
Actinocarya Benth. (1876).
Glochidocaryum W.T. Wang (1957).
Metaeritrichium W.T. Wang (1980).
Schistocaryum Franch. (1891).
Tretocarya Maxim. (1881).

Annual, biennial or perennial herbs, acaulescent or with erect, ascending or prostrate stem; indumentum sparse and setose, pubescent, villous or sericeous. Leaves usually basal and cauline, sessile to petiolate, elliptical, oblong or obovate. Inflorescences initially dense, frondose-bracteose cymoids, later elongating and spike-like. Flowers pedicellate, pedicels often elongating in fruit. Calyx divided nearly to base; corolla infundibuliform to hypocrateriform, blue or whitish, faucal scales crescent-shaped; stamens included; style included, stigma subglobose; gynobase nearly flat. Nutlets erect to spreading, ovoid, sometimes strongly flattened (“*Setulocarya*”, “*Actinocarya*”), rarely turbinate, usually tuberculate, shortly pubescent, rarely glochidiate or setose, usually with an abaxial triangular to elliptic rimmed pseudoaperture/foveola and adaxial keels, cicatrix basal, small, circular to elongate. $2n = 24$.

A genus of 30 species from N India to China, centre of diversity is China with 29 species. Close to the *Cryptantha* group, but likely an early derived group, sister to an African clade of *Cynoglossum* (Weigend et al. 2013). Proposed generic segregates are clearly linked to the core of the genus via morphological intermediates.

IV.9 CYNOGLOSSUM GROUP

Medium-sized to mostly robust perennial, rarely annual or ephemeral herbs, often with distinct basal leaf rosette; indumentum pubescent, sometimes hispid, villous or sericeous. Leaves basal and cauline, rarely cauline only, narrowly oblong or elliptical to widely ovate, usually with cuneate, sometimes with cordate base. Calyx divided nearly to base, erect to spreading; corolla hypocrateriform to infundibuliform, rarely cylindrical; gynobase widely pyramidal; style filiform, included or exerted, stigma capitate. Nutlets typically 4, large, oblique on gynobase, ovate-acuminate to subcircular in dorsal view, usually glochidiate all around, rarely glabrous, dorso-

marginal rim often differentiated and delimitating a convex back or differentiated into a distinct, flat or incurved wing, cicatrix triangular or triangular-ovate, subapical, rarely central.

Nine genera, subcosmopolitan. Genus limits extremely doubtful and *Cynoglossum* in its current circumscription apparently paraphyletic in relation to the remaining genera (Weigend et al. 2013).

75. *Lepechiniella* Popov⁴

Lepechiniella Popov, *Fl. USSR* 19: 713 (1953); Shmida, *Pl. Syst. Evol.* 129: 323–326 (1978), reg. rev.
Brandella R.R. Mill (1986).
Microparacaryum (Popov ex Riedl) Hilger & Podlech (1985).

Annual herbs with slender taproot and stems branched from base. Leaves basal (rosette) and cauline or only cauline, linear-lanceolate. Inflorescence cymoids of scorpioid monochasia, ebracteose. Flowers small, sessile or short-pedicellate, pedicels sometimes elongating and recurved in fruit; calyx divided to base, spreading in fruit; corolla infundibuliform, tube equalling lobes, faucal scales present. Nutlets with spreading or incurved wing, wing usually deeply dentate, teeth often with glochidiate apices, often heterocarpous with individuals differing in nutlet morphology or heteromerocarpous, then often 1 of the 4 nutlets unwinged and firmly attached to gynobase; cicatrix large, ovate.

About six species in NE Africa to SW Asia. Systematics and affinities of this genus are unclear, but it appears to be closer to the *Cynoglossum* group than to the *Lappula* group, in spite of the superficial similarity to the latter (small, annual plants with small nutlets).

76. *Cynoglossum* L.

Figs. 8, 9, 15

Cynoglossum L., *Sp. Pl.*: 134 (1753); Brand in Engl., *Pflanzenreich*, IV, 252 (Heft 78): 115–153 (1921), rev.; Mill & Miller, *Notes Roy. Bot. Gard. Edinb.* 41: 473–482. 1984), reg. rev.; Miller, *Adansonia* III, 27: 113–127 (2005), reg. rev.

Adelocaryum Brand (1915).
Cynoglossopsis Brand (1931).
Ivanjohnstonia Kazmi (1975).
Oncaglossum Sutorý (2010).⁵
Paracaryopsis (Riedl) R.R. Mill (1991).
Paracynoglossum Popov (1953).
Pardoglossum Barbier & Mathez (1973).



Fig. 15. Boraginaceae. Tribe Cynoglosseae, *Cynoglossum* group: *Cynoglossum columnae*. A, B Habit. C Open corolla. D Fruit. E Glochidium from nutlet surface. (orig., drawn by A. Maury)

Robust, biennial, perennial, rarely annual herbs; massive primary root and sometimes pleiocorm present. Leaves basal and cauline, basal ones often long petiolate. Inflorescences ebracteose, rarely basally bracteose thyrsoids, considerably elongating in fruit. Flowers pedicellate; calyx accrescent in fruit; corolla blue, dark purplish red, purple or yellow-green, rarely white, hypocrateriform, campanulate, rarely cylindrical or infundibuliform, tube usually short (< calyx), lobes subcircular, faucal scales depressedly rectangular, oblong or crescent-shaped; stamens included. Nutlets usually large, ovate to subcircular in outline, glochidiate, back convex or shallowly concave with distinct, glochidiate margin, cicatrix large, apical to central, nutlets often awned. $2n = 24, 48$.

A difficult and undoubtedly para- and polyphyletic taxon with 80–100 species, subcosmopolitan. Several segregate genera have been proposed, but no comprehensive study of the genus has been carried out yet. Recent data indicate that the genus is both polyphyletic and paraphyletic (Weigend et al. 2013). Even recently segregates have been proposed without any study of infrageneric phylogeny. Some species (*C. officinale* L., *C. amabile* Stapf & J.R. Drumm., *C. glochidiatum* Wall. ex Benth.) are widely introduced weeds.

77. *Dasynotus* I.M. Johnst.⁵

Dasynotus I.M. Johnst., J. Arnold Arbor. 29: 233 (1948).

Perennial, rhizomatous herb; indumentum pubescent to scabrid. Leaves basal and cauline, basal ones long petiolate. Inflorescences ebracteose or with a few frondose bracts at base, cymoids or thyrsoids. Flowers erect, long pedicellate, pedicels recurved in fruit; calyx spreading in fruit; corolla large, hypocrateriform, white, tube short; lobes subcircular; faucal scales large, narrowly oblong, ciliate to papillose, apex bifid and recurved, usually yellow, annulus distinct; stamens included (rarely exerted); style included. Nutlets (1–)4, large, shortly cylindrical, subcircular in dorsal view, adaxially keeled, dorsally with low, cup-shaped rim, initially dorsally setose, later shiny glabrescent; cicatrix central or supramedial, subcircular.

One species, *D. daubenmirei* I.M. Johnst., endemic to NW N America (Idaho). Closely allied to American species of *Cynoglossum* and the *Cryptantha* group.

78. *Afrotysonia* Rauschert

Afrotysonia Rauschert, Taxon 31: 558 (1982); Mill, Notes Roy. Bot. Gard. Edinb. 43: 467–475 (1986), rev.

Tysonia Bolus (1890), nom. illegit. non Fontaine (1889) nec F. Muell. (1896).

Tall, perennial herbs; pleiocorm with persistent leaf bases present. Leaves basal and cauline, basal ones long petiolate, ovate to lanceolate; indumentum pubescent to scabrid. Inflorescence bracteose-frondose to bracteose thyrsoids, multiply branched and corymbose. Flowers pendulous or deflexed, pedicels elongating in fruit; calyx

accrescent in fruit; corolla campanulate or shortly hypocrateriform, pink, white to dull yellow, faucal scales depressedly rectangular to crescent-shaped, annulus of 10 emarginate scales; anthers widely exerted; style exerted. Nutlets large, either dorsiventrally or laterally compressed, densely glochidiate or largely glabrous, winged with undulate, cartilaginous wing or unwinged, cicatrix apical, triangular to lanceolate.

Three species in southern and E Africa. Doubtfully monophyletic and doubtfully distinct from *Cynoglossum*.

79. *Lindelofia* Lehm.

Lindelofia Lehm., Neue Allg. Deutsche Garten-Blumenzeitung 6: 351 (1850); Sadat, Mitt. Bot. Staatss. München 28: 100–117 (1989), reg. rev.

Perennial herbs from massive pleiocorm; indumentum pubescent to scabrid. Leaves basal and cauline, basal leaves long petiolate, ovate-acuminate to elliptical. Inflorescences ebracteose or basally bracteose cymoids or thyrsoids. Flowers nodding to pendulous; calyx slightly accrescent and spreading in fruit; corolla infundibuliform, blue, tube usually longer than calyx; lobes orbicular-obtuse, faucal scales oblong, rarely reduced; anthers exerted; style widely exerted, thickened and persistent in fruit. Nutlets ovate, with distinct disc, back flattened to concave, with multiseriate glochidia along margin, glochidia often fused into narrow wing; ventral part of nutlet spinulose or tuberculate; cicatrix central, extending to apex, large, triangular-ovate, nutlets awned. $2n = 24$.

About 10–20 species, Asia. Nested in an Asian clade of *Cynoglossum* (Weigend et al. 2013) and with unclear species limits.

80. *Mattiastrum* (Boiss.) Brand

Mattiastrum (Boiss.) Brand, Repert. Spec. Nov. Regni Veg. 14: 150 (1915); Sadat, Mitt. Bot. Staatss. München 28: 60–99 (1989), reg. rev.

Biennial or perennial herbs often from well-developed pleiocorm; indumentum hispid, scabrid or villous. Leaves basal and cauline, narrowly (ob-)lanceolate. Inflorescences ebracteose or basally bracteose thyrsoids or cymoids. Flowers pedicellate, pedicels often reflexed in fruit; calyx reflexed in fruit; corolla infundibuliform to sub-

campanulate, blue to brownish-purple, rarely yellow, faucal scales linear to depressedly rectangular; anthers included or only tips exerted; style included. Nutlets subcircular to ovate or narrowly ovate in outline, often dorsally keeled and glochidiate, with a broad, flat wing; cicatrix central, extending to apex, large, ovate, nutlet awned. $2n = 24$.

About 50 species, Asia. An imperfectly known genus, often included in *Paracaryum*, nested in *Cynoglossum* s.str. (Weigend et al. 2013)

81. *Paracaryum* Boiss.

Paracaryum Boiss., Diagn. Pl. Orient. I, 11: 128 (1849); Hilger et al., Pl. Syst. Evol. 148: 291–312 (1985), genus delimitation.

Biennial or perennial herbs often from well-developed pleiocorm; indumentum hispid, scabrid or villous. Leaves basal and cauline, narrowly (ob-)lanceolate. Inflorescences ebracteose or basally bracteose thyrsoids or cymoids. Flowers small, pedicellate, pedicels often reflexed in fruit; calyx spreading to reflexed in fruit; corolla infundibuliform to subcampanulate, blue to brownish-purple, faucal scales crescent-shaped; anthers included or only tips exerted; style included. Nutlets ovate in outline, tuberculate or nearly smooth, surrounded by a scarios, strongly inflexed, mostly denticulate-glochidiate wing, leaving only a small aperture, often dorsally keeled and glochidiate, with a broad, flat wing; cicatrix central extending to apex, large, ovate, nutlet awned. $2n = 24$.

About 10–15 species, SW Asia, mainly in the Irano-Turanian region, nested in *Cynoglossum* s.str. (Weigend et al. 2013).

82. *Rindera* Pall.

Rindera Pall., Reise Russ. Reich 1: 486 (1771). *Bilegnum* Brand (1915).

Perennial herbs with well-developed pleiocorm; indumentum sericeous or villous. Flowers in ebracteose cymoids, these often corymbose or paniculate in outline. Flowers long pedicellate; calyx reflexed in fruit; corolla tubular-campanulate, usually purple, faucal scales crescent-shaped to ligulate, rarely absent, sometimes a second whorl of appendages near middle or base of

tube; anthers exerted or reaching mouth of corolla tube; style usually exerted. Nutlets large, circular to ovate in outline, dorsally concave, glabrous, with wide, flat, spreading wings, ventrally keeled, with very few glochidia or surface tuberculate or even smooth and shiny; glochidia rarely along margins or 1 row of large, flat glochidia along keel; cicatrix central, extending to apex, large, ovate, nutlet awned. $2n = 22$.

About 20–25 species, E Europe to C Asia. Close to and doubtfully distinct from *Paracaryum* and *Mattiastrum*, nested in *Cynoglossum* s.str. (Weigend et al. 2013).

83. *Solananthus* Ledeb.

Solananthus Ledeb., Ic. Fl. Ross. 8, t. 26 (1829); Fl. Alt. 1: 193 (1829).

Biennial or perennial herbs with well-developed pleiocorm; indumentum densely appressed pubescent. Leaves basal and cauline, basal leaves large, long petiolate. Inflorescence mostly large, many-branched, ebracteose thyrsoids, paraclades dense, often coiled in bud, becoming open thyrsoidal and elongated in fruit; calyx usually enlarging in fruit; corolla tubular-infundibuliform to subcampanulate, mostly reddish-purple, faucal scales inserted near middle of corolla tube; anthers exerted; style exerted. Nutlets ovate to subcircular in outline, glochidiate, sometimes with distinctly elevated margin, cicatrix central, extending to apex, large, ovate, nutlet awned. $2n = 24, 48$.

About 10 species, S Europe to Asia, doubtfully monophyletic and nested in *Cynoglossum* s.str. (Weigend et al. 2013).

84. *Trachelanthus* Kunze

Trachelanthus Kunze, Bot. Zeitung (Berlin) 8: 665 (1850).

Perennial herbs with well-developed pleiocorm; indumentum sparse, pubescent to glabrescent. Leaves basal and cauline, basal leaves very large, long petiolate. Inflorescences lax thyrsoids. Flowers pedicellate, erect or nodding; corolla cylindrical, lobes erect, subequalling tube, yellow, faucal scales crescent-shaped, sometimes small; anthers included but nearly equalling lobes; style exerted. Nutlets large, widely ovate in outline, ventrally densely spiny, glochidiate or disc

smooth, not winged, cicatrix central, extending to apex, large, ovate, nutlet awned.

Four species, W Asia. Nested in *Cynoglossum* s.str. (Weigend et al. 2013).

IV.10 CRANIOSPERMUM GROUP

85. *Craniospermum* Lehm.

Craniospermum Lehm., Pl. Asperif. Nucif. 3: 336 (1818); Ovczinnikova, Bot. Zhurn. 85: 77–87 (2000), rev.

Biennial or perennial herbs, often with pleiocorm; indumentum hirsute to floccose. Leaves basal and cauline, narrowly ovate. Inflorescences ebracteose or basally bracteose cymoids or thyrsoids. Flowers erect, sessile or short pedicellate; calyx lobes narrowly ovate to linear, elongating in and enclosing the fruit; corolla cylindrical, lobes erect to half-spreading, (triangular-)ovate, faucal scales absent, sometimes scale-like emergences between corolla lobes present; stamens inserted at middle of corolla tube, anthers long exerted; gynobase shortly pyramidal, style exerted, persistent, stigma depressedly capitate to discoid. Nutlets erect, ovoid, transversely rugose, dorsally or dorso-apically with pseudoaperture with narrow, coriaceous, unequally dentate wing almost closing over dorsal disc, cicatrix basal.

Four or five species in C and E Asia. The genus represents an isolated lineage firmly placed in Cynoglosseae.

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