Hydroleaceae

Hydroleaceae Edwards, Bot. Rev. (Lancaster) 7: Tab. 566 (1821).

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Perennial, rarely annual, herbs or small shrubs, often semi-aquatic, erect, prostrate or decumbent, stems succulent or woody, often with aerenchyma in the primary cortex, glabrous to hispid, glandular trichomes present or not, 1–2 axillary thorns per node, or thorns absent. Leaves alternate, sessile or petiolate, exstipulate, blade linear to ovate, apex acuminate to rounded, base attenuate to cordate, margin entire or serrulate, glabrous to glandular-pubescent. Inflorescence terminal or axillary, cymose or racemose, rarely flowers solitary. Flowers bisexual, actinomorphic or slightly zygomorphic; sepals 5, nearly free to base, usually lanceolate, persistent, glabrous, puberulent or glandular-pubescent; petals 5, imbricate, united at base, blue or white, corolla rotate or campanulate; stamens 5, filaments white or blue, adnate to corolla tube, usually conspicuously dilated at base, anthers sagittate, basifixed; nectary disk absent or present; ovary superior, globose to ellipsoid, oblique to median flower plane, usually 2-locular, ovules very numerous, placentation parietal at the apex, otherwise axillary with enlarged, sometimes bilobed placentas; stylodia 2(−5), free, spreading, persistent, stigma slightly funnelform or capitate, papillose. Capsule with loculicidal, septicidal, or irregular dehiscence, globular to cylindrical. Seeds numerous, ovoid to cylindrical, symmetrical or occasionally asymmetrical, usually with longitudinal ridges. $n = 9, 10, 12$; $2n = 18, 24, 20, 40$.

A single genus with about 11 spp. in tropical or warm-temperate regions, southern U.S.A. to Argentina, Africa, southern Asia to northern Australia.

Vegetative Morphology and Vegetative Anatomy. Typically *Hydrolea* plants are ascendant or erect, but procumbent or dwarf forms are also found, depending on ecological conditions. Plants can be glabrous (rarely, e.g. *H. palustris*) or pubescent or glandular-pubescent; various different trichome types were described for *H. zeylandica*; the glandular trichomes can have a uniseriate or multicellular head (Inamdar and Patel 1973). While in hairs of various genera of Hydrophyllaceae cystolith-like incrustations were found (cf. Solereder 1899), these were not reported for *Hydrolea*. Thorns at the nodes, if present, occur single or in pairs. According to Kainradl (1927), they may have small leaves apically, showing that they are not spines but modified branches. Some species (e.g. *H. quadrivalvis*) may have thorns or not, while other constantly have or lack them. Of the 11 species recognized by Davenport (1988), five never have thorns, two always have them, and four may or may not have them. Leaves are petiolate or sessile, their margin entire or serrulate. Anatomy is poorly studied. The primary cortex has schizogenous air-canals, their neighbouring cells show clustered crystals. Carlquist and Eckhart (1984) included *Hydrolea paraguayensis* (= *H. spinosa* var. *par.*) in a comparative study of the wood anatomy of the Hydrophyllaceae. Growth-rings are basically absent; vessel element perforations are mostly simple and, of the species studied, only *H. spinosa* var. *par.* occasionally also had scalariform perforation plates. Vessel element diameter is 44 μm and length is 458 μm, i.e. notably long. Fibre-tracheids are present and sometimes septate, their walls are gelatinous; diffuse axial parenchyma is absent. Vascular rays with erect cells predominate. Rabaey et al. (2010) reported the presence of vestured pits in the tracheary elements of *Hydrolea*, another difference to Hydrophyllaceae, which lack these. Stomata are present on both leaf surfaces in

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H. spinosa, and druses of calcium oxalate are present in the leaf veins. Patel and Inamdar (1971) described the stomata of *Hydrolea zeylanica* as anomocytic and found a few with a single subsidiary cell situated at right angle to the guard cell. The ontogeny is perigenous.

Inflorescence, Flower Structure and Pollen Morphology (Fig. 42). The flowers are arranged in cymose or racemose, simple or branched inflorescences, sometimes in clusters, corymbose or subcapitate forms (Davenport 1988).

A detailed study of flower ontogeny and anatomy of *Hydrolea palustris* was undertaken by Erbar et al. (2005). Starting adaxially in the diagonal plane of the flower, sepal primordia appear in a 2/5-sequence, followed by the alternating petal primordia, which appear simultaneously. The corolla development shows late sympetaly resulting in a short basal tube, the aestivation of the lobes is quincuncially imbricate. The stamens are alternipetalous, the filaments broaden abruptly at the base in most species (according to Brand 1913, only slightly so in *H. multiflora* (= *H. elatior*)) and are inserted on the corolla tube. Below the insertion points a low corolla-stamen tube is formed. Anthers are versatile, basifixed and sagittate. The ovary is glabrous or the upper half pubescent, usually 2 carpels are developed, rarely more; carpel number varies within species (in *H. spinosa* 2–4-carpellate ovaries are found). In a bicarpellate ovary in *H. palustris*, the two carpels are not positioned exactly in the median plane but slightly oblique. The gynoecium is synascidiate in its larger part, but symplicate apically, where the septa fuse only postgenitally (*H. palustris*). Placentation either is axile throughout, or the septa in the upper region only protrude deeply into the ovary cavity (*H. spinosa*, pers. obs.). According to Brand (1913), the placentas are entire (sect. *Attaleria*) or bilobed (sect. *Hydrolea*) in cross-section, mostly thick and spongiose (Brand mentions *H. ovata*), rarely membranaceous (no species mentioned by Brand). The U-shaped placenta with numerous ovules almost fills the locules. The stylodia are distinct, the stigma papillose and slightly funnelform or capitate.

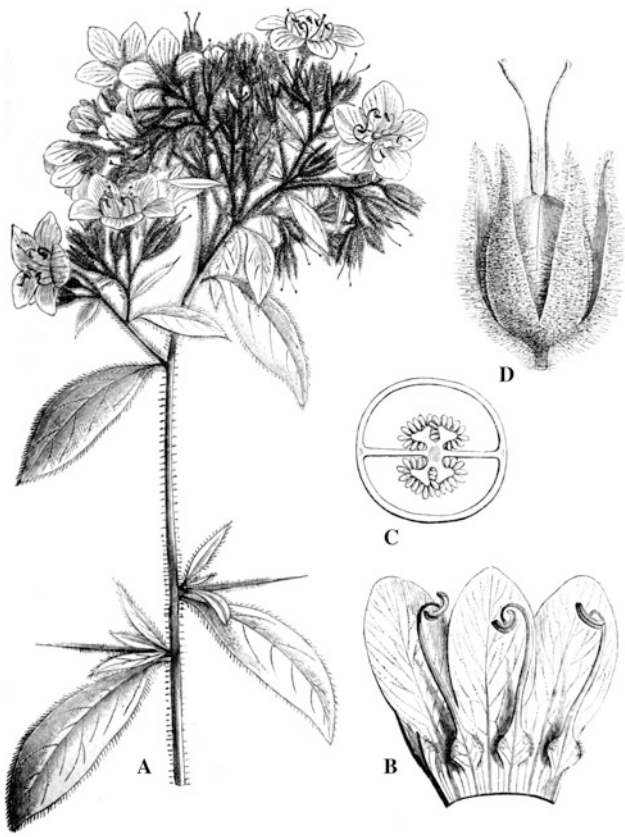

Fig. 42. Hydroleaceae. *Hydrolea spinosa*. **A** Flowering branch. **B** Part of corolla with stamens. **C** Ovary in transversal section. **D** Fruit (closed) with persistent calyx. (From Peter 1897, his Fig. 31)

Although Willis (1894) had described a disk in *Hydrolea spinosa* (sect. *Hydrolea*) producing nectar, Davenport (1988) described flowers of *Hydrolea* as lacking a nectary. Erbar et al. (2005) again reported such a disk with nectary slits and with 5 hump-like swellings alternating with the stamens in *Hydrolea palustris* (sect. *Attaleria*). As the filaments are usually strongly dilated at the base, access to the nectary is only possible for flower visitors at the gaps between the filament bases (Willis 1894; Erbar et al. 2005). Willis (1894) also described the selfing of flowers of *H. spinosa*, cultivated in England.

Pollen is tricolporate with a reticulate tectum without supratectal processes, lumina of various sizes and forms, the larger showing numerous small bacula (Constance and Chuang 1982).

Embryology. Ovules are anatropous, tenuinucellate, unitegmic, the embryo-sac is of the Polygonum-type. No vascular bundles were observed in the ovule, these end at the base of the funicle, and the nucellus disappears early (Kainradl

1927).The polar nuclei degenerate as free nuclei. The mature embryo-sacs in various Hydrophyllaceae studied by Svensson (1925) are rich in starch, in contrast to that of *Hydrolea spinosa*. Svensson (1925) also observed that, in the absence of pollination, the ovary of this species can develop to the size of an immature fruit due to a hypertrophic embryo-sac, but without production of an embryo. Di Fulvio de Basso (1990) also studied *H. spinosa* and reported that endosperm formation is cellular and heteropolar micropylar, while in Hydrophyllaceae it is isopolar. Different from reports by Mitra (1947, for *Hydrolea zeylanica*) and Svensson (1925, for *H. spinosa*), she observed 2 uniseriate pluricellular branched haustoria in *Hydrolea spinosa*. This basically confirms the observations of Kainradl (1927) for the same species, who also reported two strongly developed polar branched haustoria growing mycelia-like into the integument. Kainradl (1927), however, regarded these haustoria as unicellular with one nucleus each. Di Fulvio de Basso (1990) also reported that in Hydrophyllaceae s.str. haustoria are either absent or inconspicuous and unbranched (Phacelieae) or unicellular (Hydrophylleae). According to Mitra (1947), embryo development of *H. zeylanica* is of the solanaceous type.

Fruit, Seeds and Dispersal. Fruits are 2(3–5)-locular dry capsules, dehiscing septicidally, loculicidally or irregularly; regular and irregular deshiscence can occur in the same species. The capsules are glabrous or puberulent or glandular-pubescent in the upper half, and contain numerous seeds. The seeds are small and typically have longitudinal, more rarely transversal ridges, and a surface with prominent reticulations (Davenport 1988). The ridges are formed by enlarged epidermis cells; the other thick epidermis cells contain oil (Netolitzky 1926). The integument is 6–7 cell layers thick. According to Kainradl (1927), several narrow conical structures grow from the inner periclinal wall into the lumen of the epidermal cells. Below the epidermis a 4–5 cell-layered pigmented middle-layer is present; this is mostly absorbed during embryo development. The innermost layer forms an endothelium. The embryo is small and straight. The endosperm contains oil and aleuron and is completely absorbed in the ripe seed (Kainradl 1927 for *H. spinosa*). Hydrochory was suggested as seeds can float for several says and may germinate when still floating, as observed in *H. spinosa* (Kainradl 1927).

Karyology. Chromosome counts for section *Hydrolea* ($2n = 20, 40$) indicate a base number of 10, with *H. spinosa* apparently being diploid or tetraploid (Davenport 1988). The counts reported for *H. zeylanica* (sect. *Attaleria*) are ambiguous with $n = 9$, $2n = 18$ and 24. The data suggest, however, that the base number is different from that in sect. *Hydrolea*.

Affinities. Robert Brown (1818, p. 32) was the first to suggest to move *Hydrolea* into an own family together with the genus *Nama*. As he probably considered *Nama* in the sense of Linnaeus (1759) and thus as a genus of Hydrophyllaceae s.s., he did not completely separate *Hydrolea* from that family. Following Brown (1818), Hydroleaceae subsequently normally included *Nama* and perhaps other related genera. Choisy (1846) and Brand (1913), who included *Hydrolea* in an own tribe (Hydroleae) of Hydrophyllaceae, and Constance (1963) emphasized the distinctiveness of *Hydrolea* with its completely bilocular capsule, axile placentation, and differences in the texture of the placentas: fleshy or cartilaginous in the Hydrophyllaceae s.str. and spongiose (rarely membranaceous) in *Hydrolea*. Also the aerenchyma in the primary cortex (Solereder 1899), the presence of vestured pits in the tracheary elements (Rabaey et al. 2010), and the heteropolar endosperm formation with pluricellular haustoria (Di Fulvio de Basso 1990) are characteristic for *Hydrolea* but unknown from Hydrophyllaceae. Di Fulvio de Basso (1990) therefore proposed to exclude *Hydrolea* from Hydrophyllaceae and put it into a monogeneric family of its own. Probably most taxonomists preferred to keep *Hydrolea* included in the Hydrophyllaceae (or Boraginaceae s.l.) because of its similarity with *Nama*, until phylogenetic analyses based on DNA sequences (Cosner et al. 1994; Ferguson 1998) definitely showed that the genus had to be excluded from the Boraginales. The monogeneric Hydroleaceae belong to the Solanales as sister-group to Sphenocleaceae (Cosner et al. 1994; Soltis et al. 2011). Different from the late sympetaly of most Solanales incl. *Hydrolea*, however,

Sphenoclea shows early sympetaly (Erbar et al. 2005).

Distribution and Habitats. The species of section *Hydrolea* occur in the Americas while those of sect. *Attaleria* occur in Africa, Australia and Asia. The most common habitats are swamps, lakes and margins of waterways, but various species are also encountered in other moist but non-inundated habitats.

Economic Importance. *Hydrolea spinosa* is invasive. A few species are of minor horticultural importance.

Only one genus:

Hydrolea L. Fig. 42

Hydrolea L., Sp. Pl. ed. 2: 328 (1762), nom. cons.; Davenport, Rhodora 90: 169–208 (1988), rev.
Nama L. (1753) nom. rej. non *Nama* L. (1759), nom. cons.

Characters as for family.

Brand (1913) recognized 2 sections, sect. *Hydrolea* (as sect. *Sagonea* (Aubl.) Brand) and sect. *Attaleria* (Poir.) Brand, both also accepted by Davenport (1988). The species of sect. *Hydrolea* occur in the Americas and their placentas are divided into 2 lobes, thorns are present or absent. Those of sect. *Attaleria* occur in Africa, Asia and Australia, and have entire placentas; thorns are always absent.

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