Wellstediaceae

Wellstediaceae (Pilg.) Novák in S. Prát (ed.), Rostlinopis 9: 530 (1943).
Boraginaceae subfam. Wellstedioideae Pilg., Bot. Jahrb. Syst. 46: 558 (1912).

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Annual herbs, sometimes with basal rosette of large leaves, or more often subperennial to perennial shrublets; branches and leaves often more or less distichous and congested; stems lignified, strong taproot present; indumentum sericeous, of unicellular, densely scabrid trichomes, usually acroscopically appressed. Leaves alternate, exstipulate, shortly petiolate or subsessile, entire, linear to (ob)ovate-elliptical, narrowed at base, apex acute, acuminate or apiculate, indistinctly veined, sometimes primary vein visible below, rarely venation pinnate with ascending secondary veins. Inflorescences bracteose, of dense scorpioid monochasia or dichasia, rarely reduced to single flowers, morphologically terminal but overtopped by and sometimes partly fused with uppermost lateral shoot; when fused, flowers arranged in alternate rows on this shoot. Flowers erect, tetramerous, actinomorphic, bisexual, hypogynous; calyx divided nearly to base, calyx lobes equal, narrowly triangular to narrowly ovate or linear, pubescent or sericeous, slightly enlarging in fruit; corolla pink, white or yellowish, sympetalous, hypocrateriform with very short tube and half-erect to spreading lobes, tube inside with 4 protrusions often fused into a distinct rim, lobes triangular-ovate, margin entire or denticulate to erose; stamens 4, alternating with petal lobes, filaments equal, shorter or longer than anthers, anthers included or exserted; nectary unknown; ovary bicarpellate, style terminal with two very short stigmatic lobes. Fruit a bivalved capsule. Seeds one, rarely two, asymmetrically ovoid in lateral view, strongly laterally compressed, pubescent often with ring of longer hairs near funicular pole, exendospermous.

One genus of six species with a disjunct distribution between the Horn of Africa region (five species in Ethiopia, Somalia to Socotra, Yemen) and western southern Africa (one species in NW South Africa and Namibia).

Vegetative Morphology and Anatomy (Fig. 76). *Wellstedia* is usually described as a dwarf shrub, with rosette leaves rarely present. Branches are decumbent, ascending or rarely erect and usually densely congested. All axes are very hard and likely lignified. The leaves are more or less distinctly distichous. Little is known about the life history of *Wellstedia*, but it likely germinates during the rainy season and continues to grow, flower and fruit as long as sufficient moisture is available. It may thus behave as an annual or ephemeral plant in some places. Branches incurve when the plants dry out completely and spread out again when the plant is wetted (at least in *W. dinteri*). Plants are up to ca. 40 cm tall, but mostly smaller. All parts of the plants, apart from the inside of the flower, are densely sericeous with a dense cover of long, unicellular, usually densely scabrid, rarely smooth trichomes. Cystolithic foot cells are absent. The presence of multicellular peltate glands reported by Hunt (1969) could not be verified by Thulin and Johansson (1996). Shorter, smooth unicellular trichomes are sometimes present. Leaves are narrowly obovate to nearly linear in most taxa, and differ characteristically in size, indumentum and shape between species. Only one species, *W. laciniata*, has distinctly ovate-elliptical leaves with well-visible secondary veins and a distinct petiole. Leaves are amphistomatic.

Inflorescence and Flower (Fig. 76). The inflorescence is extremely congested and consists of terminal mono- or dichasia which soon become overtopped by a branch arising from the axil of the uppermost foliage leaf below inflorescence and is then displaced into a lateral position on

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Fig. 76. Wellstediaceae. *Wellstedia dinteri* subsp. *dinteri*. **A** Habit. **B** Part of lower leaf surface. **C** Branchlets with flowers and fruits. **D** Flower. **E** Flower. **F** Corolla. **G** Same, opened out. **H** Ovary showing placentation and developing seeds, semi-diagrammatic. (From Hunt 1969; artwork by E.M. Stones; with permission from Royal Bot. Gds Kew)

the upper side of the usually more or less plagiotropic or ascending branches. The inflorescence axis itself is then often fused with the overtopping branch, with flowers arising apparently directly from a vegetative branch in two alternating rows. Narrowly ovate to linear bracts are usually present. The flowers are pink, white or yellowish and tetramerous. The calyx is divided nearly to the base with 4 usually more or less triangular, densely sericeous lobes. The corolla tube is very short, cylindrical, and contains 8 vascular bundles. The tube has inside four horizontal protrusions near or below the points of filament insertion. These may be homologous with the faucal scales of Boraginaceae s.str. Corolla lobes are imbricate in bud, (triangular-)ovate, abaxially pubescent and adaxially glabrous, 3-veined and equal. Filaments are inserted near the middle or near the apex of the corolla tube and may be very short (shorter than the anthers) or distinctly longer, far exceeding the anthers. Filaments are usually slightly bent inwards, positioning the anthers in the opening of the corolla tube. Anthers are dorsifixed with introrse dehiscence. The ovary is superior, broadly sessile on the receptacle and widely ovoid at anthesis. It is incompletely bilocular, at least apically densely pubescent, and crowned with a terminal style with a shortly bifid stigma. The two united carpels are partly or largely separated by a thin, hyaline septum. The septum may be present only at the base of the fruit or almost reach the style base. Placentation is subapical with one ovule in each locule or, more commonly, one locule is sterile. Ovules are anatropous and initially pendent and epitropous.

Fruit and Seed. The fruit is wedge-shaped, rhomboidal or obcordate in lateral view and laterally strongly compressed. It contains mostly one, rarely two seeds (*W. dinteri*). The style may be overtopped by the lateral parts of the growing capsule. Depending on the extent of the septum, the ovule will shift from a pendulous to an erect position at maturity. Dehiscence is loculicidal, with the sharp edge of the capsule opening from apex to base. At least in *W. dinteri* fruits are hygrochasious and open only when wetted, releasing the seeds after rare rains. The seeds are laterally strongly compressed, (obliquely) ovoid in lateral view and densely pubescent. Trichomes are short at the chalazal pole and gradually longer towards the funicular pole, ending in a distinct ring of long trichomes near the funicular pole. The slightly curved funicular pole itself is glabrous. The short funicle remains attached to the mature seed. The seed is completely filled by the large embryo and is exalbuminous. The embryo has accumbent cotyledons and a superior radicle. Germination is only known for *W. dinteri*, where it is phanerocotylar with widely ovate, densely pubescent cotyledons.

Pollen Morphology. Pollen grains are isopolar, oblate to subprolate and 12–25 × 8–15 μm in size. Grains are tricolporate, with colpi 11–14 μm long and 1–3 μm wide, and have a granular colpus membrane. Pseudocolpi are sometimes present. The tectum is perforate to reticulate, usually coarsely so at the centre of the mesocolpia with lumina smaller towards apocolpia and colpus margin (Thulin and Johansson 1996; Retief and van Wyk 2008).

Dispersal. Plants apparently die after fruiting, remaining in the soil with incurved twigs. After wetting the congested and incurved twigs spread out and the capsules open and release the seeds. The characteristic pubescent seeds may also be dispersed by wind after release. Fruiting plants are also said to form tumbleweeds by breaking off at the base and rolling over the ground.

Affinities. Morphologically, *Wellstedia* is quite isolated in Boraginales with its peculiar vegetative morphology, tetramerous flowers, bilaterally compressed, capsular, 1–2-seeded fruit and unique seed morphology. Balfour (1888) placed it as a "genus anomalum" at the end of the Gamopetalae, and both Gürke (1893) and Pilger (1912) assigned it to Boraginaceae s.l. as subfam. Wellstedioideae. Family rank was first suggested by Novák (1943) and has been followed by, for example, Friedrich-Holzhammer (1967). Because of its ecology and habit, an affinity to Ehretiaceae (*Tiquilia* and *Coldenia*, the latter also with tetramerous flowers) was then assumed. However, all Ehretiaceae have fruits separating into mericarpids. Pollen morphology has been used to argue for an affinity with Hydrophyllaceae (Constance and Chuang 1982; Thulin and Johansson 1996) and with *Codon* (Retief et al. 2001), here treated as a separate family Codonaceae. However, pollen

morphology itself is not particularly distinct, with the subprolate, reticulate, tricolporate pollen representing one of the most common pollen types in Eudicots. Regarding its specific characters in capsule, flower, seed or vegetative morphology, *Wellstedia* is quite dissimilar from both Codonaceae and Hydrophyllaceae. Recent molecular studies based on four chloroplast markers (Weigend et al. 2013, 2014) could finally clarify the correct placement for Wellstediaceae as sister to Boraginaceae s.str., a clade which is in turn sister to Codonaceae and represents one of the two major clades of Boraginales. The relationship to Hydrophyllaceae and Ehretiaceae is quite remote. The peculiar flowers and capsular fruit for Wellstediaceae clearly warrant separation from Boraginaceae (with four nutlets) and recognition as a distinct, monogeneric family.

Distribution and Habitats. *Wellstedia* is disjunct between NE Africa and Socotra (5 spp.) and Namibia and the extreme north of the Cape Province of South Africa (1 sp.), a distribution pattern shared by many arid zone taxa. Plants grow in arid habitats with open vegetation. *W. socotrana* is listed as threatened on the IUCN Red List.

One genus:

Wellstedia Balf. f. Fig. 76

Wellstedia Balf. f., Proc. Roy. Soc. Edinb. 12: 407 (1884); Friedrich-Holzhammer, Prodromus einer Flora von Südwestafrika, Lieferung 13 (1967); Retief & van Wyk, Bothalia 38: 57–63 (2008); Thulin, Flora of Somalia 3: 31–60 (2006).

Characters as for family.

Species are well circumscribed (Thulin and Johansson 1996; Thulin 2006). Thulin and Johansson (1996) assume a basal position of the southwest African *W. dinteri* based on morphology, but molecular data are not yet available.

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