

The genus *Wellstedia* (Boraginaceae: Wellstedioideae) in southern Africa

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ABSTRACT

This regional taxonomic revision of the genus *Wellstedia* Balf.f., a member of the family Boraginaceae *s.l.* (including Hydrophyllaceae *s.str.*), is part of a series of publications on the Boraginaceae in southern Africa. *Wellstedia* comprises six species, five in Socotra, Somalia and Ethiopia with the remaining one, *W. dinteri* Pilg., occurring in southern Africa. *W. dinteri* Pilg. subsp. *dinteri* occurs in Namibia and the Northern Cape, whereas the newly instated subspecies *W. dinteri* subsp. *gracilior* (D.R.Hunt) Retief & A.E.van Wyk, based on *W. dinteri* Pilg. var. *gracilior* D.R.Hunt, is confined to Namibia only. The disjunct distribution of *Wellstedia* and numerous other plant and animal taxa between the arid regions of northeastern Africa and southern Africa is usually explained by the postulated periodic existence of an arid corridor between the two regions during the arid phases of the Pleistocene and even earlier. *Wellstedia* is treated here in Wellstedioideae, a subfamily of Boraginaceae *s.l.* but is sometimes placed in a family of its own, Wellstediaceae Pilger. Morphologically *Wellstedia* displays strong similarity to genera of the Ehretioideae and also to certain members of the Hydrophyllaceae. The genus is characterized by a perennial, dwarf shrub habit, densely hairy leaves, 4-merous flowers, a terminal, bifid style and a 1- or 2-seeded capsule. A key to the two subspecies, diagnostic characters, a distribution map and illustrations of various macro- and micromorphological features are provided.

INTRODUCTION

Wellstedia was described in 1884 by Balfour after a visit to the island of Socotra. He decided on the name *Wellstedia* in honour of the British Lieutenant J.R. Wellsted, who explored Socotra for the Indian Government in 1834 (Thulin & Johansson 1996). Balfour believed that *W. socotrana* Balf.f., the only species in the genus at the time, had its closest affinity with members of Boraginaceae *s.str.* Besides this species, five more are now recognized on the African continent—four in Somalia and Ethiopia, and one in Namibia and South Africa. Such floristic (and faunistic) disjunctions between the arid regions of northeastern Africa and southern Africa are usually ascribed to the periodic existence of a linking arid corridor between the two regions in the past (Van Wyk & Smith 2001). In 1912 Pilger placed *Wellstedia* in its own subfamily, Wellstedioideae (Boraginaceae). Novák (1943), however, decided on a separate family, Wellstediaceae. Since then, the family classification of *Wellstedia* has been a matter of controversy. Merxmüller (1960), unaware of Novák, also established a new family, Wellstediaceae, thereby creating a later homonym. In 1967 the family was also recognized by Friedrich-Holzhammer in a *Prodromus* on the flora of South West Africa [Namibia], an approach more recently followed by Lebrun & Stork (1997).

Different modern views regarding the delimitation of Boraginaceae exist: splitting Boraginaceae *s.l.* into two separate families, Boraginaceae *s.str.* and Heliotropiaceae with Hydrophyllaceae not included (Diane *et al.* 2002); or recognizing several segregate families, Boraginaceae

s.str., Cordiaceae, Ehretiaceae, Heliotropiaceae, Hydrophyllaceae, Lennoaceae and Wellstediaceae (Lebrun & Stork 1997; Gottschling *et al.* 2001; Gottschling 2003). In the present contribution, *Wellstedia* is regarded as a monotypic genus of the subfamily Wellstedioideae within Boraginaceae *s.l.* (including Hydrophyllaceae *s.str.*, Codonoideae, Ehretioideae, Heliotropioideae and Boraginoideae) (Retief 2003). Ferguson (1999) and the Angiosperm Phylogeny Group II (2003) are followed here in regarding the tribes Phacelieae and Hydrophyllaeae as part of Boraginaceae *s.l.* The capsular fruit of *Wellstedia* is unknown elsewhere in Boraginaceae *s.str.* and has been used to motivate the recognition of a monotypic family Wellstediaceae. However, with members of Hydrophyllaceae, all with capsular fruits, included in a broadly defined Boraginaceae, this argument is no longer of importance. Pollen and other characters such as a terminal style, 4-merous flowers, trichomes with multicellular bases and cymose inflorescences similar to other traditional members of Boraginaceae, support the placement of *Wellstedia* in a subfamily within Boraginaceae *s.l.*

The aim of this paper is to present a taxonomic revision of the genus *Wellstedia* in southern Africa, including Namibia, Botswana, South Africa, Lesotho and Swaziland. Diagnostic characters, an identification key, illustrations and a distribution map are provided. This paper forms part of a revision of the Boraginaceae in southern Africa. The genus description is based on material from southern Africa only.

MATERIALS AND METHODS

Herbarium specimens in BM, BOL, E, GRA, K, NBG, NH, NU, PRE, PRU, SAM and WIND (acronyms as in Holmgren *et al.* 1981) were studied to gather data on morphological characters, phenology and geographical distribution. Pollen and various plant parts were studied with an ISI-SX-25 scanning electron microscope. Measurements of pollen grains were done from aceto-

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lysed grains mounted in glycerine jelly. Acetolysis followed the standard method of Erdtman (1960). Tapetal orbicules were obtained from herbarium specimens and prepared for viewing with a JEOL 6000 F in-lens field emission scanning electron microscope (for procedure followed see Retief *et al.* 2001, 2002).

HISTORICAL OUTLINE

In 1912, Pilger described *W. dinteri* from specimens collected by botanist and botanical explorer Moritz Kurt Dinter (1868–1945) in Namibia. Although Pilger knew the genus only from Balfour's (1884) description and illustration of *W. socotrana*, he was convinced that Dinter had found a *Wellstedtia* in the southwestern part of Africa. He was also of the opinion that *Wellstedtia* belongs to Boraginaceae with affinity to *Coldenia* L. of the Ehretioideae, and not Verbenaceae, a family also mentioned by Balfour (1884) when he described the first species. The capsular fruit with two seeds, however, distinguishes *Wellstedtia* from all other members of Boraginaceae and a new subfamily Wellstedioideae was described by Pilger (1912).

Hunt (1969) divided *W. dinteri* into two varieties. Variety *dinteri* is characterized by flowers and capsules congested on short lateral branches, whereas var. *gracilior* has flowers and capsules on lax branchlets, appearing as if solitary, axillary, rarely close together. When Friedrich-Holzhammer (1967) revised the genus for *Prodromus einer Flora von Südwestafrika*, she did not recognize the two infraspecific taxa proposed by Hunt (1969) and regarded *W. dinteri* as belonging to Wellstediaceae. Thulin & Johansson (1996), in a revision of the genus, also did not maintain the two varieties in *W. dinteri*. They classify the genus in Wellstedioideae and proposed the New World genus *Tiquilia* Pers. (Boraginaceae: Ehretioideae) as a possible sister to it. In the present revision, the status of *W. dinteri* Pilg. var. *gracilior* D.R.Hunt is raised to that of subspecies, a decision based mainly on differences in macromorphology and habitat.

PHYTOGEOGRAPHY

The two subspecies of *Wellstedtia dinteri* in southern Africa (Figure 1) are associated with the Nama-Karoo, Succulent Karoo and Savanna Biomes, according to the biome map in Van Wyk & Smith (2001: 8). *W. dinteri* subsp. *dinteri* is recorded as growing in shale-derived soil mixed with fine gravel (Davidse & Loxton 6339). *W. dinteri* subsp. *gracilior*, however, occurs on dolomite or limestone (Acocks 15641) or on black soil derived from dolomite.

Arid regions of the African continent are phytogeographically linked by a large number of taxa with disjunct distributions. This pattern is particularly well developed between arid regions in southern Africa and northeastern Africa (Horn of Africa and adjacent Arabian Peninsula). *Wellstedtia* is a typical example of a taxon with a disjunct distribution between the arid areas of northeastern Africa and southern Africa: *W. din-*

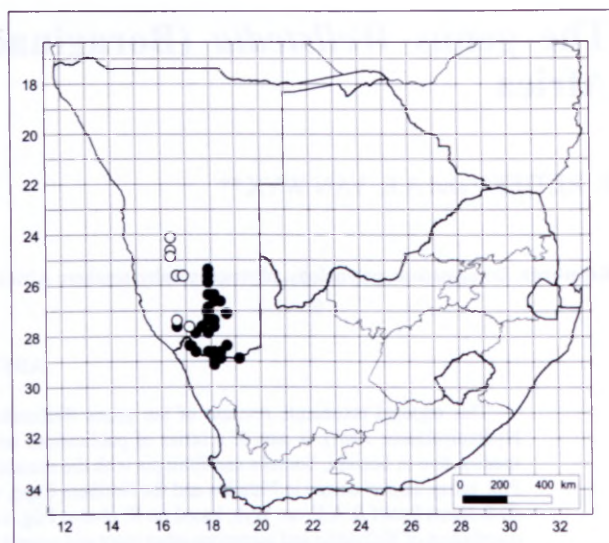


FIGURE 1.—Known distribution of *Wellstedtia dinteri* subsp. *dinteri*, ●; and *W. dinteri* subsp. *gracilior*, ○.

teri occurring in Namibia and Northern Cape (Figure 1), whereas *W. filtuensis* Hunt & Lebrun is endemic to Ethiopia, with *W. somalensis* Thulin & A.Johanss, *W. robusta* Thulin and *W. laciniata* Thulin & A.Johanss. confined to Somalia. The disjunct pattern is usually explained by the postulation of an arid corridor (or corridors) linking these regions during arid phases of the Pleistocene and even earlier (Verdcourt 1969; Goldblatt 1978; Van Wyk & Smith 2001). Various other authors, for example, De Winter (1971), Thulin (1994) and Thulin & Johansson (1996) also commented on the recurring pattern of disjunct distributions. *Gaillonia* A.Rich. ex DC. (Rubiaceae), as circumscribed by Thulin (1998), is another example of a genus with a disjunct distribution comparable to that of *Wellstedtia* (Thulin 1994).

Disjunct distributions in Africa and the New World are rather unusual, but for southern Africa, as many as seven families and many more genera are involved (Goldblatt 1978). *Codon* L., an exclusively southern African genus, has its nearest relatives, members of Hydrophyllaceae *s.str.*, in North America. However, *Wellstedtia* also shows similarities in pollen and habit characters with some of the genera of Hydrophyllaceae *s.str.* A possible explanation for this disjunct distribution pattern is the existence of a Tertiary North Atlantic land bridge (Tiffney 1985), whereas over-water dispersal seems unlikely, except during the early stages of continental separation.

CHARACTERS OF TAXONOMIC SIGNIFICANCE

Habit

Members of the Boraginaceae are mainly herbaceous, but shrubs and trees do occur. *Wellstedtia* is characterized by a woody, dwarf shrub habit, a growth form also displayed by *Tiquilia*, of the subfamily Ehretioideae—suggested as a potential sister group of *Wellstedtia* (Thulin & Johansson 1996). The woody habit and other morphological similarities with the Ehretioideae support the classification of *Wellstedtia* as a member of the Boraginaceae *s.l.* instead of placing it in a family of its own.

Leaves

The narrowly obovate to ovate leaves of the southern African species with its two subspecies are densely pubescent (Figure 2A, B). The trichome complement consists of

rigid setae with multicellular bases, usually 3-layered, scattered on the blade (Figure 2C) and fine setae with undeveloped bases. Leaves of *Wellstedia dinteri* subsp. *gracilior* are smaller in size and different in colour, greyish white compared to yellowish green in *W. dinteri* subsp. *dinteri*.

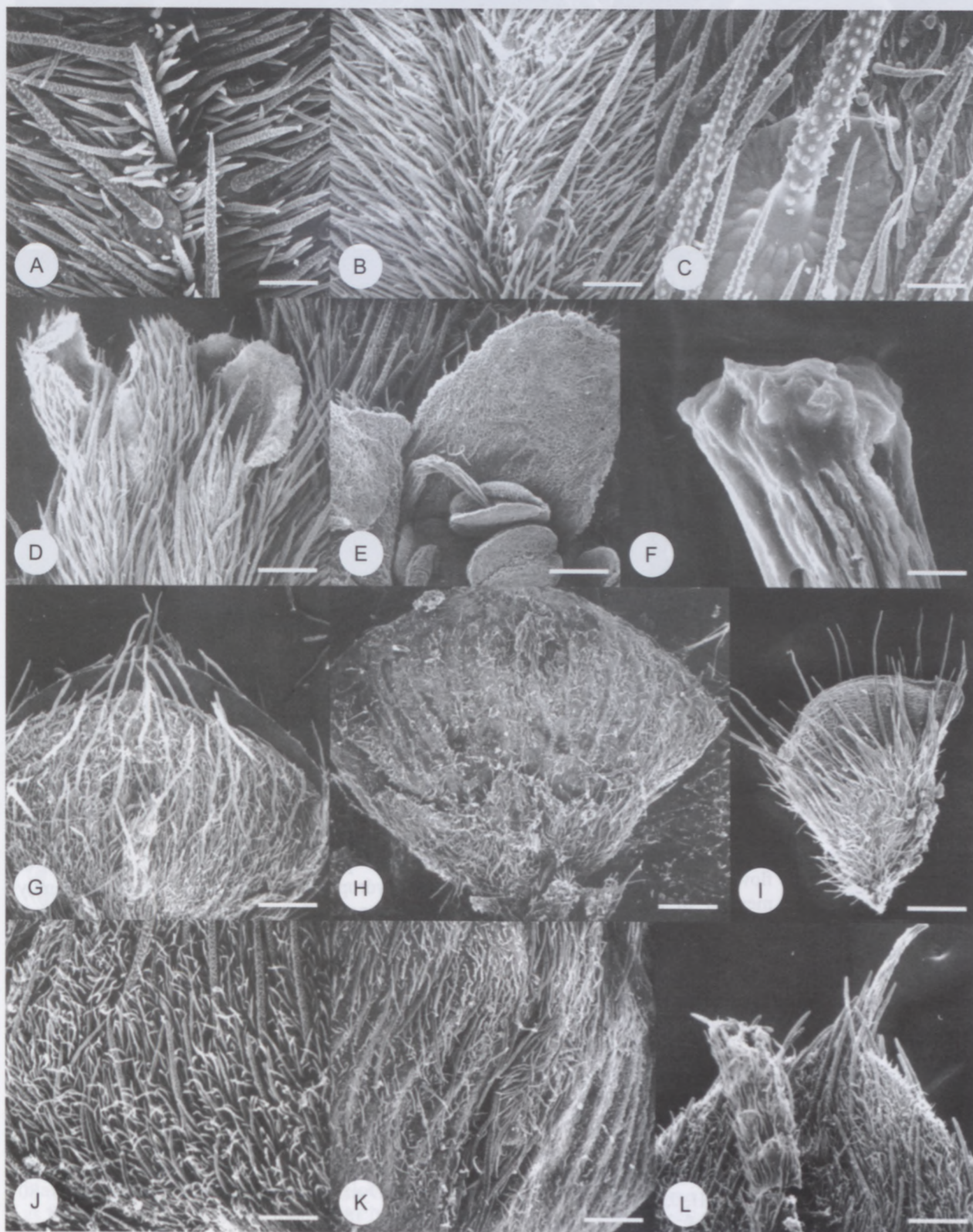


FIGURE 2.—Morphology of *Wellstedia*. A–C, leaf: A, *W. dinteri* subsp. *dinteri*, Acocks 15615, upper leaf surface; B, *W. dinteri* subsp. *gracilior*, Müller 1329, upper leaf surface; C, *W. dinteri* subsp. *dinteri*, Liebenberg 5179, multicellular base of a seta. D–F, flower: D, *W. dinteri* subsp. *gracilior*, Müller 1329, calyx and corolla; E, *W. dinteri* subsp. *dinteri*, Leistner 2589, anthers; F, *W. dinteri* subsp. *dinteri*, Oliver & Müller 6397, stigma and style. G–K, fruit: *W. dinteri* subsp. *dinteri*, Oliver & Müller 6397: G, capsule splitting open; I, seed; J, indumentum of capsule. *W. dinteri* subsp. *gracilior*, Müller 1329: H, capsule; K, indumentum of capsule. L, *W. dinteri* subsp. *dinteri*, Oliver & Müller 6397, part of capsule and calyx lobe. Scale bars: A, 75 µm; B, 259 µm; C, 89 µm; D, 365 µm; E, 24 µm; F, 16 µm; G, 460 µm; H, 431 µm; I, 314 µm; J, 259 µm; K, 254 µm; L, 509 µm.

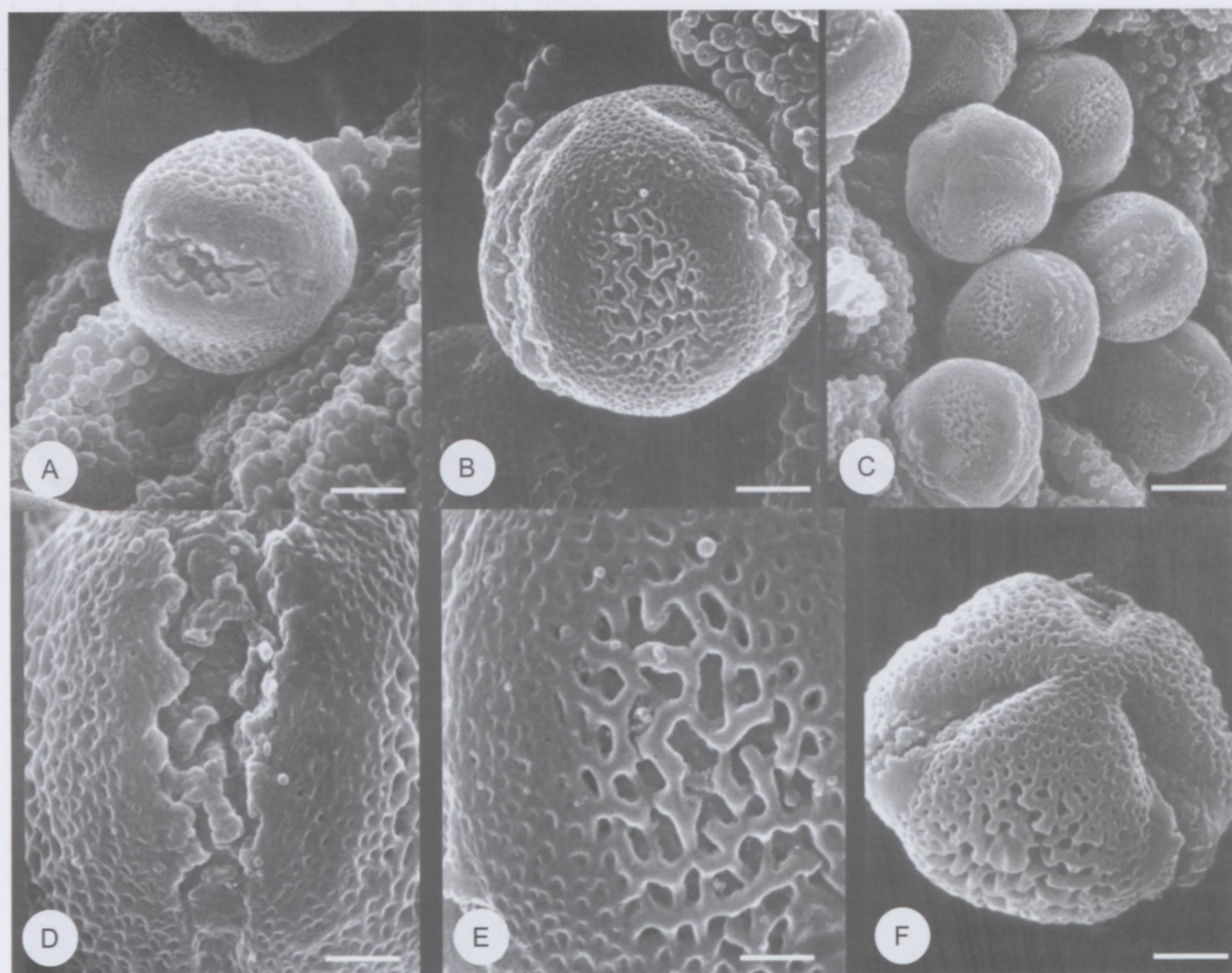


FIGURE 3.—Pollen morphology of *Wellstedia dinteri* subsp. *dinteri*. A–E, *Leistner 2589*: A, pollen grain in equatorial view, tapetum clothed with orbicules; B, grain showing mesocolpial concavity; C, grains in different views; D, compound aperture; E, mesocolpial concavity, tectum reticulate. F, *Oliver & Müller 6397*, grain \pm in polar view. Scale bars: A, 4 μ m; B, 2.9 μ m; C, 23 μ m; D, 2.1 μ m; E, 1.2 μ m; F, 2.5 μ m.

Flowers

Flowers of *Wellstedia* are 4-merous (Figure 2D), a state which is rare in Boraginaceae *s.l.* It is often used to support the recognition of a separate family, Wellstediaceae. However, the flowers of *Coldenia*, a monotypic genus and also a member of the Ehretioideae, is similarly 4-merous. This is another link between *Wellstedia* and a member of Boraginaceae *s.l.* The calyx is deeply lobed and accrescent in fruit (Figure 2L). The outer surface of the corolla is densely pubescent (Figure 2D), but the inner surface is glabrous (Figure 2E). A terminal style is present (Figure 2F), persistent (Figure 2L) and slightly bifid with capitate stigmas, the latter covered with exudate when receptive (Figure 2F).

Fruit and seed

All members of *Wellstedia* are characterized by hairy, mussel-like capsules (Figure 2G, H, J, K), but differ in dissepiment morphology (Thulin & Johansson 1996). The seeds (Figure 2I) are truncate, and pitted above with a circle of long, rigid trichomes in the upper part.

Pollen

Pollen grains (Figure 3A–F) of *Wellstedia* are tricolporate, isopolar and with mesocolpial concavities (some-

times regarded as ‘pseudocolpi’) and a reticulate tectum, showing strong similarity with genera of the subfamily Ehretioideae (Retief & Van Wyk 2001). *Wellstedia* and members of Ehretioideae furthermore show similarity in their pollen morphology with members of the tribes Hydrophyllae and Phacelieae of the family Hydrophyllaceae, here regarded as part of Boraginaceae *s.l.* Doughnut-shaped tapetal orbicules (Retief *et al.* 2001: fig. 2), occur in both *Wellstedia* and *Codon*, confirming the close relationship of these genera.

TAXONOMIC TREATMENT

***Wellstedia* Balf.f.** in Proceedings of the Royal Society of Edinburgh 12: 402 (1884); Gürke: 131 (1897); Pilg.: 558 (1912); E.Phillips: 633 (1951); Friedr.-Holzh.: 121 (1967) as Wellstediaceae; D.R.Hunt: t. 3665, 3666 (1969); R.A.Dyer: 514 (1975); Thulin & Johansson: 80 (1996); Retief: 183 (2000). Type: *W. socotrana* Balf.f.

Dwarf shrubs, densely pubescent with trichomes appressed; trichome complement consists of rigid setae with prominent multicellular bases or fine setae with undeveloped bases. Branches decumbent or ascending. Leaves spirally arranged; blade narrowly obovate to spatulate, decurrent, often upper part (‘blade’) forms an



FIGURE 4.—*Wellstedtia dinteri* subsp. *dinteri* (= *W. dinteri* var. *dinteri*), Acocks 18101. A, habit, $\times 1$; B, part of lower leaf surface, $\times 6$; C, branchlets with flowers and fruits, $\times 3$; D, flower, $\times 8$; E, flower, $\times 12$; F, corolla, $\times 12$; G, corolla opened out, $\times 12$; H, placentation and developing seeds (semi-diagrammatic), $\times 24$. Artist: E.M. Stones, with kind permission; taken from Hunt (1969).

abscission, with lower part ('petiole) persistent, becoming spine-like. *Flowers* small, regular, in dense, scorpioid cymes or solitary, well separated on lax branches. *Calyx* deeply 4-lobed. *Corolla* pink or white, with a short, campanulate tube, slightly constricted at throat, membranous with 4 ovate lobes \pm as long as tube or shorter. *Stamens* 4, borne on corolla throat, shorter than corolla lobes; filaments linear, exserted; anthers subglobose, \pm as long as filaments, 2-locular, dehiscing introrsely. *Disc* absent. *Ovary* bilocular, compressed, densely hairy, with a single ovule in each loculus; style terminal, bifid at apex; stigmas small, capitate. *Fruit* a capsule, variously pubescent, loculicidally dehiscent. *Seeds* \pm triangular, truncate and pitted above with a circle of long, rigid trichomes in upper part below pitted area, acute and shortly pubescent below.

Key to subspecies

- Flowers and capsules congested on short, lateral branchlets; leaves yellowish green, $10\text{--}50 \times 3.5\text{--}6.0$ mm; leaf blade surface with multicellular-based setae prominent and an under layer of fine setae with undeveloped bases 1. *W. dinteri* subsp. *dinteri*
- Flowers and capsules well spaced on lax branchlets; leaves greyish white, $7\text{--}15 \times 2.0\text{--}4.5$ mm; leaf blade surface densely pubescent, with fine setae with undeveloped bases and scattered setae with multicellular bases 2. *W. dinteri* subsp. *gracilior*

1. *Wellstedtia dinteri* Pilg. subsp. *dinteri* in Botanische Jahrbücher 46: 559 (1912); Friedr.-Holzh.: 1 (1967) pro parte; D.R.Hunt: 4 (1969). Syntypes: Namibia, Karasberge, Sandverhaar, *Dinter* 1193 (B⁺); Namib, *Dinter* 1379 (B⁺); Auchab, *Range* 691 (B⁺; SAM!); Karibis, *Dinter* 1250 (B⁺; SAM!, lectotype, designated here).



FIGURE 5.—*Wellstedtia dinteri* subsp. *gracilior* (= *W. dinteri* var. *gracilior*), Strey 2140. A, habit, $\times 1$; B, branchlet with flowers and fruit, $\times 3$; C, older branchlet with fruit, $\times 3$; D, flower, $\times 10$; E, corolla, $\times 10$; F, corolla opened out, $\times 10$. Artist: E.M. Stones, with kind permission; taken from Hunt (1969).

Illustration: Hunt: t. 3666 (1969). Figure 4.

Dwarf shrub, up to 300 mm high, with pseudodistichous branching. Stems procumbent, decumbent or ascending. Leaves yellowish green, $10\text{--}50 \times 3.5\text{--}6.0$ mm; leaf blade with multicellular-based setae, distinctly spaced, and an under layer of fine trichomes prominent. Corolla pink, white or pale rose in centre, white along margins; tube ± 1 mm long. Flowering time: April to May, August to October.

Distinguishing characters: dwarf shrub; leaves $10\text{--}50 \times 3.5\text{--}6.0$ mm; flowers and capsules mostly congested on short, lateral branchlets; leaf blade with multicellular-based setae, setae distinctly spaced, and an under layer of fine trichomes prominent.

Distribution and habitat: *Wellstedtia dinteri* subsp. *dinteri* is found in Namibia and Northern Cape (Figure 1). It occurs on arid, gravelly hillocks, in shallow soil between rocks and stones.

2. *Wellstedtia dinteri* subsp. *gracilior* (D.R.Hunt) Retief & A.E.van Wyk, comb. et stat. nov.

W. dinteri Pilg. var. *gracilior* D.R.Hunt in Hooker's *Icones Plantarum* 37: t. 3667 (1969). Type: Namibia, Buellspoor, Strey 2140 (K!, holo.; BOL!, PRE!, WIND!).

Illustration: Hunt: t. 3667 (1969).

Procumbent, dwarf shrub with branches radiating from centre, $\pm 100\text{--}150$ mm high, $300\text{--}400$ mm diam. Leaves greyish white, $7\text{--}15 \times 2\text{--}4.5$ mm; leaf blade surface densely pubescent with fine setae, bases unde-

veloped, and scattered setae with multicellular bases. Corolla white; tube \pm 1.5 mm long. Flowering time: August to February. Figure 5.

Distinguishing characters: procumbent, dwarf shrub; leaves 7–15 \times 2.0–4.5 mm; flowers and capsules mostly solitary on lax branchlets; leaf blade surface densely pubescent, with fine setae, bases undeveloped, and scattered setae with multicellular bases.

Distribution and habitat: *Wellstedtia dinteri* subsp. *gracilior* is found in Namibia (Figure 1). It occurs on rocky hillsides, black rocks and broken veld on dolomite.

SPECIMENS EXAMINED

The numbers in brackets signify the identity of the specimens: (1) *W. dinteri* subsp. *dinteri*; (2) *W. dinteri* subsp. *gracilior*.

Acocks 15615 (1) PRE; 15641 (2) PRE; 18101 (1) K, PRE, WIND.

Bean, Vlok & Viviers 1817 (1) BOL.

Craven 2532, 2597 (1) WIND.

Davidse 6339 (1) PRE. De Winter 3270 (1) K, PRE, WIND. Dinter 1250 (1) SAM; 4845 (1) BOL, K, PRE, SAM.

Galpin 14163 (1) E, PRE. Giess 14521 (1) WIND. Giess & Müller 12165 (1) PRE, WIND; 14324 (1) WIND. Giess, Volk & Bleissner 5324 (2) K, PRE, WIND; 6829, 6978 (1) PRE, WIND; 8763 (1) PRE. Goldblatt & Manning 8856 (1) PRE, WIND; 8763 (1) PRE. Günster 9366 (2) WIND.

Kubirske & Coetzee 98 (1) WIND.

Jürgens 22412 (1) PRU; 22710 (1) PRE.

Leistner 2589 (1) PRE, WIND. Liebenberg 5179 (1) K, PRE, WIND; 5179 A (1) PRE.

Merxmüller & Giess 3444 (2) K, PRE, WIND; 3642 (1) K, PRE, WIND. Müller 265 (1) PRE, PRU, WIND; 1329 (2) PRE, WIND; WIND26709 (1) WIND.

Oliver & Müller 6397 (2) K, PRE. Oliver, Muller & Steenkamp 6322 (1) K, PRE.

Pearson 4669 (1) BOL, GRA, SAM; 8576 (1) K, BOL, PRE.

Range 691 (1) SAM. Rodin 2843 (1) BOL, K, PRE.

Schlieben 9084 (1) BM, K, NBG, PRE. Strey 2140 (2) K, PRE, WIND. Strohbach, Kubirske & Sheuyange 3011 (1) WIND. Smook 7562 (2) PRE. Strohbach & Chivell 3474 (1) WIND.

Thompson & Le Roux 206 (1) NBG.

Van Jaarsveld, Forester & Jacobs 8428 (2) NBG. Van Wyk 8709 (1) PRE, PRU, WIND. Volk 12277 (1) WIND.

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