

Morphology, evolution and taxonomy of *Wachendorfia* (Haemodoraceae)

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Keywords: *Dilatris*, evolution, Haemodoraceae, morphology, phylogeny, taxonomy, *Wachendorfia*

ABSTRACT

Wachendorfia Burm. is a small genus endemic to the Cape Floral Region. Four species are recognised in this study. Two species were originally described by Burman in 1757 and these were followed by numerous other descriptions of what is essentially one very variable species (*W. paniculata* Burm.). This variation is discussed and reasons are given as to why the recognition of formal infraspecific taxa is inappropriate. Formal taxonomic descriptions, distribution maps and a key to the species are provided. Rhizome morphology, leaf anatomy and pollen and seed coat structures were investigated and illustrations are provided. A cladogram was inferred and this is consistent with an ecological speciation model for the genus. The two species with the most restricted distribution (*W. brachyandra* W.F. Barker and *W. parviflora* W.F. Barker) are considered to be the most recently evolved. Features of systematic and ecological interest (e.g. floral enantiomorphy) are discussed.

UITTREKSEL

Wachendorfia Burm. is 'n klein genus endemies aan die Kaapse Floristiese Streek. Vier spesies word in hierdie ondersoek erken. Aanvanklik is twee spesies in 1757 deur Burman beskryf, en hulle is gevolg deur talle ander beskrywings van wat in wese een baie variërende spesie (*W. paniculata* Burm.) is. Hierdie variasie word bespreek en redes word verstrekkend waarom die formele erkenning van infraspesifieke taksons onvanpas is. Formele taksonomiese beskrywings, verspreidingskaarte en 'n sleutel tot die spesies word verskaf. Risoommorfologie, blaaranatomie en stuifmeel- en saadhuidstrukture is ondersoek en word geïllustreer. 'n Kladoogram is afgelei en is in ooreenstemming met 'n ekologiese spesiasiemodel vir die genus. Die twee spesies met die mees beperkte verspreiding (*W. brachyandra* W.F. Barker en *W. parviflora* W.F. Barker) word beskou as dié waarvan die evolusionêre ontwikkeling mees onlangs plaasgevind het. Kenmerke van sistematiese en ekologiese belang (bv. enansiomorfie by die blom) word bespreek.

INTRODUCTION

Wachendorfia Burm. is a small genus (four spp.) of the Haemodoraceae (tribe Haemodoreae), restricted to the Cape Floral Region of southern Africa (*sensu* Bond & Goldblatt 1984).

The Haemodoraceae is divided into two tribes: the Haemodoreae and the Conostyleae (Geerinck 1969; Hutchinson 1973). The southern African Haemodoraceae (*Barberetta* Harv., *Dilatris* Berg. and *Wachendorfia*) are all members of the tribe Haemodoreae, which is defined by the presence of two perianth whorls, a short or absent tube and three or six stamens. The Conostyleae is represented in Australia and North America and is characterised by one perianth whorl, long, often hairy tubes, and six stamens.

The presence of arylphenalenone pigments was hypothesized by Simpson (1990) to be the most reliable synapomorphy defining the Haemodoraceae. These pigments provide the rhizomes, and probably the flowers of *Wachendorfia* and related genera, with their red component. In addition, he suggested that 1, bifurcate cymes; 2, an inferior ovary position; and 3, discoid or ovoid-globose seeds may be further synapomorphies. However, *Barberetta* does not possess a cyme (interpreted as an autapomorphy by Simpson (1990)) and a number of genera including *Wachendorfia* have superior ovaries, a reversal according to Simpson (1990). Almost all of the species (63 out of 78) and the genera (12 out of 17) are found

in South America, southern Africa and Australia. The family may therefore be interpreted as being essentially Gondwanan.

Wachendorfia species have attractive yellow flowers, with a form of enantiomorphy that manifests itself in the production of both 'left' and 'right-handed' floral forms within a population. This form of enantiomorphy is restricted to *Wachendorfia* and *Barberetta* (Ornduff & Dulberger 1978). Floral enantiomorphy has been interpreted as a mechanism to increase intermorph (and thus interplant) pollinations, ensuring effective outcrossing (Wilson 1887; Ornduff & Dulberger 1978), as a means of reducing pollen wastage or of preventing damage to the gynoeceum during pollinator visits. There is, however, still much to be learnt concerning the evolutionary and ecological significance of this trait. The fact that this extremely unusual feature is most common in a small, endemic fynbos genus makes the systematic study of this group potentially fascinating. A sound taxonomic base is essential if one wishes to use the genus for exploring some of the intriguing evolutionary questions posed by the group, yet the taxonomy is at present confused, with the species limits of *W. paniculata* vague, and several possible new species unpublished. In this study we hope to come to an understanding of species delimitation within the genus, and increase our knowledge of the ecology and possible evolutionary history of the species, with a view to highlighting areas of potentially rewarding systematic study.

METHODS

Plant morphology

Gross morphology was determined by field observation and examination of extensive material lodged in BOL,

* Bolus Herbarium, University of Cape Town, Rondebosch 7700. MS. received: 1991-07-09.

NBG, PRE, SAM and STE. These specimens have all been provided with determinavit labels. Rhizome and culm (annual flowering stem) morphology was investigated using fresh plants at different stages of development. Details were observed with a Wild stereo dissecting microscope. Thin sections were hand-cut with a scalpel and then stained with iodine to investigate the presence of starch.

Pollen morphology

Pollen was taken from either herbarium specimens or from live material collected in the field. For both light microscopy (LM) and scanning electron microscopy (SEM), pollen was acetolysed according to the method of Erdtman (1960). Half the acetolysed pollen was mounted in glycerine on a slide and sealed with wax for light microscopy. The other half was mounted on aluminium stubs

TABLE 1.—The characters, character states and coding used in the cladistic analysis. The first state is coded 0, the second, 1 and the third, 2

Gross plant morphology:	
1	Plant height greater than 1 m/less than 1 m
2	*Corm length greater than 30 mm/less than 30 mm
3	Leaf length greater than 500 mm/less than 500 mm
4	Leaf width greater than 50 mm/less than 50 mm
5	Leaves glabrous/with short and dense indumentum
6	Bracts scarious/herbaceous
7	Max. peduncle length greater than 100 mm/less than 100 mm
8	Cilia on the petal margins present/absent
9	Ratio stamen to tepal length: greater than 0.6/less than 0.6
10	Average minimum tepal width greater than or equal to 6 mm/less than 6 mm
11	Max. tepal length greater than 20 mm/less than 20 mm
Leaf anatomical characters:	
12	*Leaf chlorenchyma pallisade two cells wide/one cell wide/absent
13	Sclerenchyma cap on the vascular bundles well developed/poorly developed or absent
14	Mucilage canals along leaf margins/scattered in mesophyll
15	Cuticle thick/thin
16	Lignification of epidermis light/heavy
17	Guard cell with one lip/two lips
18	*Subsidiary cell kidney-shaped/rectangular
19	Cortical cells unlobed/lobed
Pollen characters:	
20	Sulcus to verrucae distance greater than 10 μ m/less than 10 μ m
21	Exine sculpturing verrucate/reticulated
Seed characters:	
22	*Seed shape spherical/ovate/disk-shaped
23	Seed diameter greater than 4 mm/less than 4 mm
24	Epidermal cell shape rectangular/irregular
Chemical characters:	
25	Colour of pressed flowers purple/orange

* cladistically informative characters.

TABLE 2.—Cladistic character codes for each species. Characters arranged according to Table 1, missing data codes as 9

Taxa	Characters				
	5	10	15	20	25
<i>Dilatris</i>	11110	01999	10000	01019	12110
<i>W. thyrsiflora</i>	00000	01000	02111	01000	01001
<i>W. paniculata</i>	10119	00900	01011	01101	00100
<i>W. brachyandra</i>	11110	01110	11011	01101	00100
<i>W. parviflora</i>	11111	19101	11011	11101	00100

and sputter coated with Au/Pd and examined in a Cambridge S200 SEM at 10kV. LM photographs using differential interference contrast and oil immersion were taken on a Zeiss Axioskop photomicroscope using Ilford FP4 film. Pollen measurements were made using engraved stage micrometer units in conjunction with an eyepiece scale.

Pollen sources, vouchers in BOL

- Wachendorfia brachyandra*: Cape Point, Salter 8718.
W. graminifolia: Constantia Nek, Barker 170.
W. paniculata: Hermanus, Burman 936; Mamre, Esterhuysen 5244; Waaihoek Peak, Esterhuysen 8283.
W. parviflora: Clanwilliam, Le Roux 2626.
W. thyrsiflora: Humansdorp, Fourcade 2436.
Dilatis corymbosa: Cape Point, Pillans 4589.
D. pillansii: Cape Point, Salter 7902.

Seed morphology

Seeds were taken from herbarium material or from material collected in the field. Seeds were air dried, mounted on aluminium stubs, and sputter coated with Au/Pd and examined in a Cambridge S200 SEM at 5kV.

Seed sources, vouchers in BOL

- Wachendorfia brachyandra*: Kirstenbosch, NBG s.n.
W. paniculata: Mamre, Esterhuysen 5244; Kommetjie, Helme 7; Boulders beach, Leighton 34; Tulbagh, Leighton 37.
W. parviflora: Kirstenbosch, NBG s.n.
W. thyrsiflora: Kirstenbosch, NBG s.n.
Dilatis ixiooides: Pakhuis Pass, Esterhuysen 3165
D. viscosa: Tulbagh, Leighton 40.

Leaf anatomy

Fresh material used for the anatomical study was collected from plants in the field, and fixed and preserved in Kew Cocktail (16:16:1:1 = distilled water:EtOH:formalin: glycerine). Fresh material was favoured because cellular constitution is more easily observed and is less likely to show distortion than dried and reconstituted material. Sections were sledge microtomed to a thickness of 25 micrometers and stained in Alcian Blue and Safranin (lignin stain and counterstain) for 30 minutes (Tolivia & Tolivia 1987). Sections were then washed in distilled water and dehydrated in an alcohol series before mounting in DPX.

Epidermal leaf scrapes were mounted in Hoyer's solution (Anderson 1954), which results in cleared, permanent mounts. These slides were then used for the examination of leaf surface features such as stomata, cell shape and hair structure.

Cladistic analysis

A cladistic analysis was performed on the four species of *Wachendorfia* and the outgroup, *Dilatis*. Twenty-five characters were investigated for use in the analysis, but only four proved to be cladistically informative (Table 1), because their evolutionary polarity could be determined and they occur in more than one species. A list of character codes is given in Table 2. The most parsimonious cladogram, that is the diagram that requires the least

number of character changes, was determined using Hennig86 (Farris 1988), and PAUP vers. 2.4 (Swofford 1985) was used to calculate the patristic distances for each species and to optimize the characters on the cladogram.

Dilatrix was used as the outgroup because it has many morphological features in common with *Wachendorfia*. The only other possible outgroup is *Barberetta*, but no good material was available of this genus. Ornduff (1979) suggested that, on the basis of chromosome numbers, *Wachendorfia* and *Barberetta* (both with $n=15$) are more closely related to each other than either is to *Dilatrix* ($n = \pm 19-21$). De Vos (1956), however, suggested that *Wachendorfia* and *Dilatrix* are closely related, based on embryological studies, but she unfortunately did not investigate *Barberetta* which possesses an unusual floral structure for the Haemodoraceae, namely, a simple raceme, unlike *Wachendorfia* or *Dilatrix*, which have helicoid cymes. Evidence therefore exists both for and against choosing *Dilatrix* as the outgroup for *Wachendorfia*, although the case for choosing *Barberetta* could be stronger. Simpson (1990) showed that on available information, *Barberetta* is the sister taxon of *Wachendorfia* and that these two together are the sister group of a clade consisting of the New World genera *Schleкия* and *Pyrrothiza*: *Dilatrix* was viewed as more distantly related. However, as the outgroup need not be the sister taxon of the study group (Watrous & Wheeler 1981; Maddison *et al.* 1984), we used *Dilatrix* as the outgroup. It should be borne in mind that this may result in a poorer resolution of the phylogeny than when the sister taxon is used as the outgroup.

TAXONOMY

Historical background

The earliest description of a *Wachendorfia* was by Plukenet in 1700 and he named these specimens from the Cape of Good Hope *Erythrobulbus*. These descriptions were probably based on material collected by Oldenland. Forty years later Breyne (1739) illustrated and described what was clearly a *Wachendorfia* under the name *Asphodelus*. Hendrik Oldenland, the Superintendent of Simon van der Stel's Company Garden in Cape Town during the period 1691–1699, made some of the earliest collections in the vicinity of Cape Town. This collection of notes and plants was neglected for many years, until Johannes Burman published the first post-Linnean descriptions of *Wachendorfia* in his monograph of the genus (Burman 1757). Two species, *W. thyrsoiflora* Burm. and *W. paniculata* Burm., were accurately described. In 1758, Loefler unwittingly applied the name *Wachendorfia* to what is now known as *Callisia* Loefl. (Commelinaceae). The name *Wachendorfia* commemorates E.J. van Wachendorff, who was Professor of Botany and Chemistry at Utrecht during the 18th Century (Jackson 1987).

Thunberg visited the Cape between 1772 and 1775, and made extensive collections, which included specimens of *Wachendorfia*, some of which were described by Linnaeus (filius) as *W. graminifolia* in his *Supplementum plantarum* (1781). Thunberg, in his *Prodromus* (1794) and *Flora capensis* (1811), described *W. graminea*, *W. tenella* and *W. hirsuta*. Salisbury added *W. elata*, *W. humilis*, *W. pallida*

and *W. brevifolia* in 1796, whereas two more names were proposed in the 19th century. Baker (1896) relegated most of these above-mentioned names to the rank of variety or synonym of *W. thyrsoiflora* and *W. paniculata*.

The genus was then virtually ignored for 120 years, until Barker (1949) published two new species, *W. parviflora* W.F. Barker and *W. brachyandra* W.F. Barker. Although these species have a more restricted range and are perhaps less common than the initial two species, it is surprising that such striking plants could go undetected for so long.

***Wachendorfia* Burm.**, in *Wachendorfia*: 2 (1757); Linnaeus: 864 (1759); Bak. 6: 1 (1896); W.F. Barker: 206 (1950); Geerinck: 58 (1969); Dyer: 946 (1976). Type species: *W. thyrsoiflora* Burm.

Wachendorfia Burm.f. (sphalm.) (1768).
Wachendorffia Cothen. (orth. var.) (1790).
Pedilonia Presl (1829).

Pre-Linnean synonyms:

Erythrobulbus Pluk.: v 5 (1700).
Asphodelus Breyne: t. 22 (1739).

Perennial, rhizomatous herbs 0.1–2.5 m tall; leaves usually annual (one species perennial); annual culms develop from a rhizome. *Rhizome* fleshy, bright red, irregular to ovoid, nodes three, opposite, each with an axillary bud, apical bud producing the culm; new rhizome produced annually from an axillary bud, 1–3 old ones remaining attached; roots thin, adventitious, clustered around node between old and new rhizomes; old rhizome leaf bases forming a tunic around rhizome; ramets often formed. *Leaves* erect or spreading, linear, lanceolate, or falcate, firm in texture, always longitudinally plicate, simple and entire, glabrous to hirsute, green to yellow-green, 0.1–0.9 m long; lower leaves sheathing at base of culm; rhizome leaves 3, stem leaves variable in number, lowest two stem leaves amplexicaul and opposite, leaves above spirally arranged and not amplexicaul. *Culm* annual; 0.1–2.5 m tall. *Inflorescence* a lax deltoid to dense cylindrical panicle; peduncles herbaceous, terete to angular, very short to long (up to 0.25 m), near vertical, or spreading; main axis covered in short hairs, pilose at base, glandular nearer apex. *Bracts* erect or recurved, herbaceous or scarious, acute, usually hairy, older scarious bracts often recurved. *Flowers* with tepals 6, borne in 2 whorls, subequal, spreading, oblong; lower 3 free, upper 3 united at base with small dark and light markings near base; two open spur-like nectaries produced from the bases of outer upper tepal and 2 adjacent inner tepals; outer segments hairy on outside, especially central upper tepal; yellow to pale apricot. *Stamens* 3, opposite the inner tepals; filaments free, filiform, declinate, the upper two pendulous, the lowest turning sideways opposite style; anthers ovate-sagittate, two-celled, dehiscing longitudinally, introrse, usually included, 0.2–3.0 × 0.5–1.0 mm; pollen boat-shaped, monosulcate, heteropolar, with a verrucate, two-layered exine. *Ovary* superior, pubescent, 3-locular, 1 ovule per locule, axile placentation; style filiform, bent sideways (left or right in any one plant), in same direction as one of the stamens; stigma minute, capitate. *Fruit* an acutely 3-lobed capsule, dehiscing locu-

licidally, usually glandular, wider than tall, pubescent. *Seeds* 1 per locule, spherical to ovoid, densely hairy.

Key features of the genus

Perennial herbs, three of the four species with annual leaves. Annual flowering stems (culms). *Perennial rhizome* with red sap. *Leaves* lanceolate, linear or falcate, simple, longitudinally plicate, entire. *Inflorescence* a panicle. *Flowers* zygomorphic, yellow, with right- and left-handed forms. *Ovary* 3-locular, locules uni-ovular. Confined to the fynbos biome.

Key to the species

- 1a Perianth segments narrow, 3–6 mm broad; bracts herbaceous, all erect; leaves usually as long or longer than culm; plants usually short (less than 0.25 m tall) 4. *W. parviflora*
- 1b Perianth segments broad, 5–18 mm wide; bracts scarious or submembranous, the upper usually recurved; leaves usually shorter than culm; plants usually tall (greater than 0.25 m tall):
 - 2a Stamens and style about half the length of the tepals, clustered 3. *W. brachyandra*
 - 2b Stamens and style from two-thirds to nearly as long as the tepals, spreading:
 - 3a Plant tall (over 0.6 m); inflorescence dense, cylindrical; leaves broad (greater than 15 mm wide), glabrous, perennial 1. *W. thyriflora*
 - 3b Plant short (usually below 0.6 m); inflorescence variable, lax to very dense panicle; leaves narrow (usually less than 20 mm broad), glabrous to hairy, annual 2. *W. paniculata*

1. ***Wachendorfia thyriflora* Burm.** in *Wachendorfia*: 3 (1757). Thunb.: 306 (1811); Bak. 6: 1 (1896); W.F. Barker: 206 (1950). Type: *Oldenland s.n.* (?G, not seen); iconotype: Burm.: 13, figs 1 & 2 (1757).

W. elata Salisb., Prodr. 45 (1796).

Pre-Linnean synonym:

Asphodelus latifolius Breyne: t. 22 (1739).

Rhizomatous perennial herb; 0.6–2.5 m tall. *Rhizome* up to 150 mm long, irregular, usually cylindrical, sheathed by overlapping leaf bases; rooting from nodes. *Leaves* perennial, erect, lorate to lanceolate, deeply plicate, firm, glabrous, usually shorter than the flowering stem, up to 900 × 80 mm; younger plants with leaves less than 50 mm broad. *Leaf anatomy*: palisade layer not distinct; cuticle with variable lignification; sclerenchyma caps poorly developed; subsidiary cells kidney-shaped; mucilage canals large. *Culm* up to 2.5 m tall, stout (up to 15 mm diameter near base), erect, densely pilose at base (hairs up to 4 mm long) running into short (1 mm long) glandular hairs near apex. *Inflorescence* a dense cylindrical panicle, up to 0.6 × 0.2 m. Peduncles many, short (up to 100 mm), regularly spaced on distal half of axis. Younger plants often more laxly branched; seldom more than 7 pedicels per peduncle; no secondary peduncles. *Bracts* lanceolate, scarious, recurved, persistent, 10–40 mm long. *Tepals* bright yellow, nectar guides on base of upper 3 tepals light to dark; all slightly spatulate; 12–28 × 8–14 mm; outer adaxial tepal narrower and shorter than the rest, slightly recurved; upper 5 tepals overlapping, leaving lower tepals somewhat isolated; tepals sometimes fringed with orange cilia. *Stamens*: filaments $\frac{3}{4}$ tepal length, 15–20 mm long, spreading; anthers 1.2–2.0 × 0.5–1.0 mm. *Gynoecium*: ovary yellowish, 2–3 × 1–2

mm; style 13–18 mm long. *Fruit* a 3-angled capsule, 10 × 7–10 mm. *Seed* large, up to 5 mm long, oval or kidney-shaped; dense microscopic blisters (1.5 μm) on seed hairs. *Chromosome number*: n=15 (Ornduff 1979).

Flowering time: beginning of September to end of November, occasionally to mid-January, with a peak in September and October.

Distinguishing features: large size; marshy habitat; large yellow flowers with long spreading stamens; inflorescence a dense, cylindrical panicle; peduncles short.

Distribution and habitat: *W. thyriflora* is a widespread species, occurring from as far north as the Olifants River valley between Citrusdal and Clanwilliam, south to the Cape Peninsula, inland to the Franschhoek Mountains, and along the south coast and associated mountain ranges as far east as Humansdorp (Figure 1). This species is more of a habitat specialist than any of the other species, and is confined to permanently moist sites, especially along streams and in seepages. The species has a wide altitudinal range, varying from about 5–±1 200 m a.s.l.

Status: locally abundant, often dominant in marshes. Some populations are very small and may be declining due to afforestation or weed infestation. The populations in mountain fynbos are generally stable.

Vouchers: *Leighton 1353* (BOL); *Levyns 3368* (BOL); *Liebenberg 7923* (PRE); *Pillans 8086* (BOL).

2. ***Wachendorfia paniculata* Burm.** in *Wachendorfia*: 11 (1757). Sims: t. 616 (1803); Thunb.: 307 (1811); Bak. 6: 1 (1896); W.F. Barker: 206 (1950). Type: *Oldenland s.n.* (G?, not seen); iconotype: Burm.: 15, fig. 3 (1757).

W. graminifolia L.f.: 101 (1781). *W. graminea* Thunb.: 309 (1811) nom. illeg. Type: near river at Drakenstein. *Thunberg 1242* (UPS, lecto. –BOL, microfiche!).

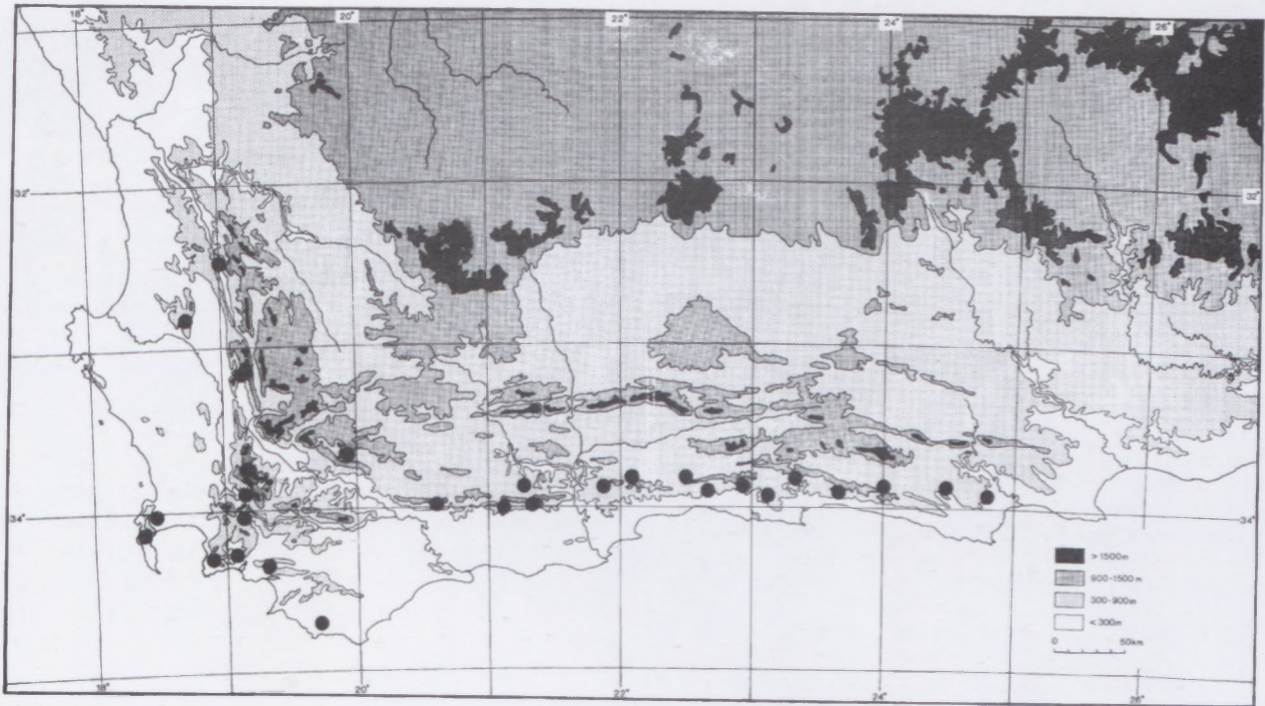
W. hirsuta Thunb.: 308 (1811); Sims: t. 614 (1803). Type: sand fields between Swartland and Saldanha Bay. *Thunberg 1243* (UPS, holo. –BOL, microfiche!).

W. tenella Thunb.: 308 (1811). Type: between Langevelei and Heerenlogement. *Thunberg 1246* (UPS, holo. –BOL, microfiche!).

W. brevifolia Solander ex Ker-Gawl. (1809). Type: in the Banksian Herbarium (BM).

W. herbertii Sweet: 400 (1826), based on *W. paniculata* var. β Herbert (1826). Specimen from the Cape of Good Hope, flowering at Spofforth in July. Iconotype: *Botanical Magazine 53*: t. 2610 (1826), here designated.

Rhizomatous perennial herb; 0.1–0.9 m tall. *Rhizome* ovoid, up to 50 mm in diameter, appearing tunicate when dry. *Leaves* annual; narrowly lanceolate or linear to broadly falcate, erect or spreading, dull green to yellow-green, glabrescent to hairy, 3-nerved; 0.1–0.7 × 5–(20)–35 mm. *Leaf anatomy*: palisade layer one cell thick; cuticle with intermediate lignification; sclerenchyma cap development variable; subsidiary cells rectangular; mucilage canals small. *Culm* occasionally up to 1 m tall, slender to robust (3–15 mm diameter), erect, covered with short, dense simple hairs. *Inflorescence* a lax to dense racemose panicle, composed of 5–20 scorpioid cymes, each cyme bearing 1–7 flowers. Peduncles variable in number and length, longer at the base (may be branched again to form a secondary peduncle), up to 0.4 m long, slender to robust; pedicels short (less than 100 mm). *Bracts*

FIGURE 1.—Distribution of *W. thyrsiflora*.

scarious (often submembranous when fresh), often recurved, especially when old, 5–50 mm long, veined, long-acuminate, pilose, partly sheathing. *Tepals* apricot, yellow, or orange; slightly scented; 13.0–(21.0)–31.0 × 4.0–(10.0)–16.0 mm; inner abaxial tepal often slightly broader than the rest; outer adaxial tepal shorter, narrower, recurved; margins sometimes fringed with short cilia. *Stamens* from two-thirds to three-quarters the tepal length, spreading; anthers 2–3 × 0.8–1.0 mm. *Gynoecium*: style 15–22 mm long, as long as shortest tepal. *Fruit* an acutely three-lobed capsule; 10 × 5 mm. *Seed* spherical, coarsely pilose, brown, 2 mm in diameter. *Chromosome number*: $n=15$ (Ornduff 1979). Figure 2.

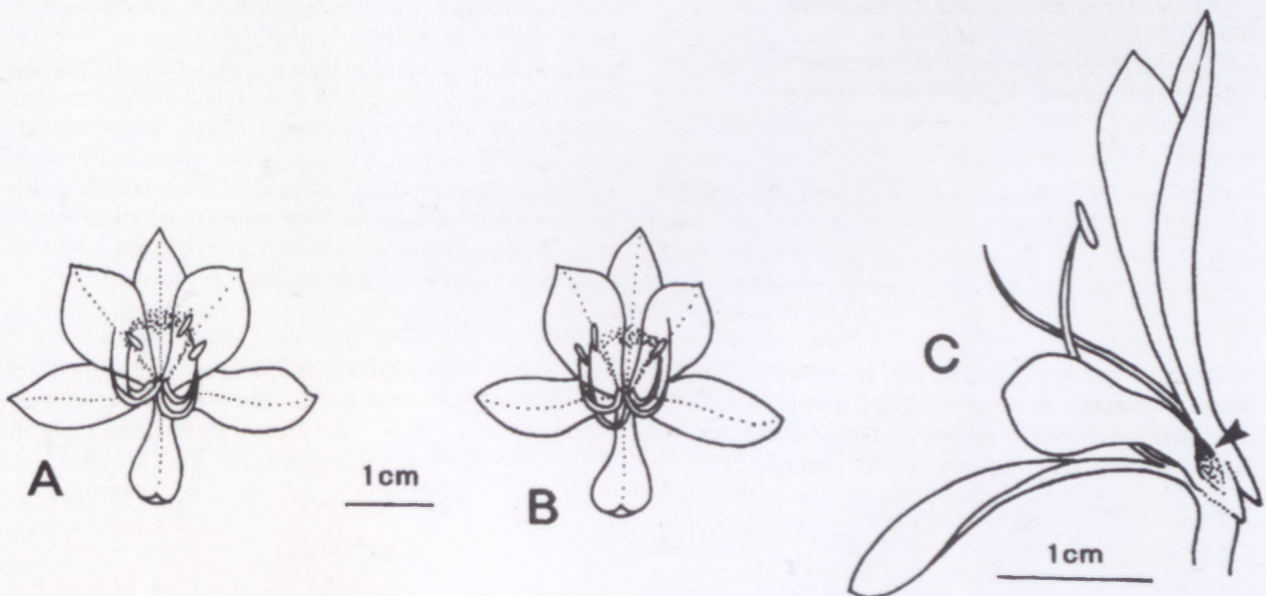
Flowering time: August to December, very rarely to early February (high altitude), with most records from September to November.

Common name: rooikanol or spinnekopblom.

Distinguishing features: plants from 0.15–0.80 m tall; bracts scarious when mature; stamens and style spreading, from two-thirds to three-quarters the length of the tepals; tepals broad; leaves usually shorter than the flowering stem.

Nomenclatural notes: according to Savage (1945) there is a specimen of *Wachendorfia* in the herbarium of the Linnean Society, annotated by Burman as '*Wachendorfia paniculata*'. As the Burman herbarium is generally thought to be in the Delessert Herbarium at Geneva (Stafleu & Cowan 1976) further investigation would be required to determine where the type of the name is housed.

The types of Linnaeus the Younger are mostly housed in the herbarium of the Linnean Society. However, there

FIGURE 2.—*W. paniculata* flower structure. A, left-handed flower (stigma deflected to left); B, right-handed flower (stigma deflected to right); C, side view showing large perianth-aperture (arrowed).

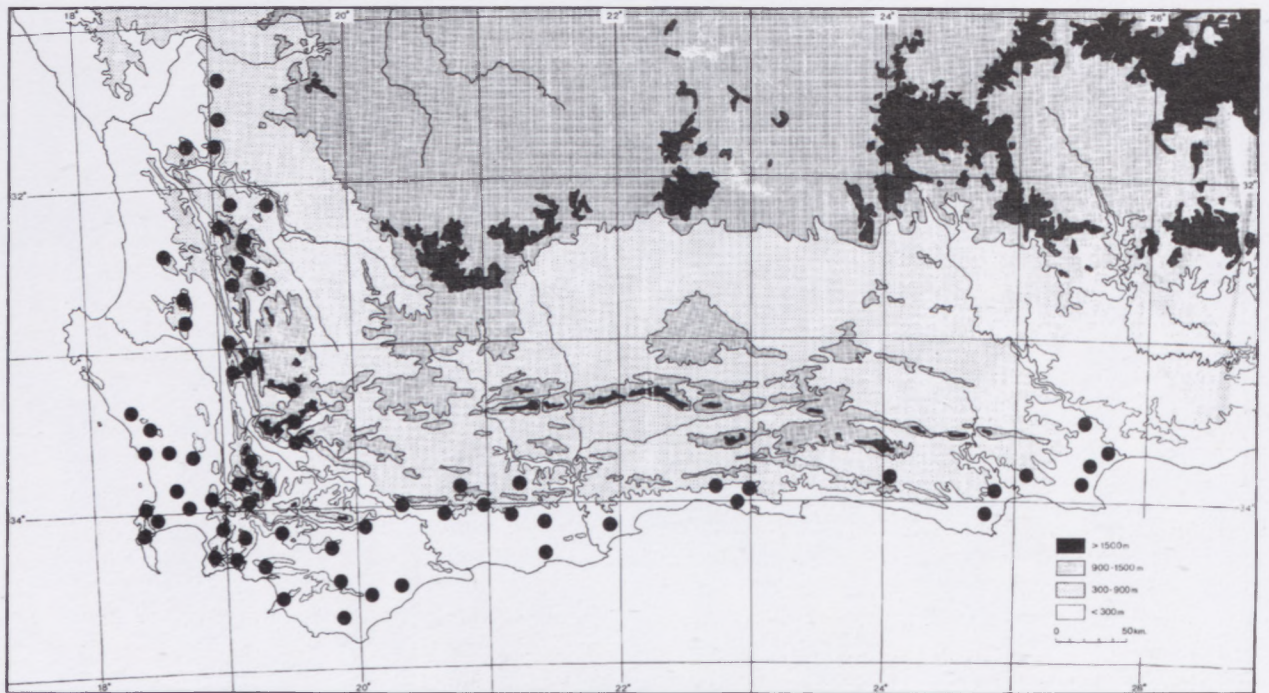


FIGURE 3. —Distribution of *W. paniculata*.

is no material of *W. graminifolia* (Savage 1945), whereas there is a specimen annotated as such by Thunberg at Uppsala. This may well be the type material, but can in the absence of further information only be designated as a lectotype.

Distribution and habitat: this is the most widespread species, ranging from Nieuwoudtville to Port Elizabeth (Figure 3). It is ubiquitous in the fynbos biome, and is found mainly on soils derived from Table Mountain Sandstone, although it has also been recorded from areas with granitic soils, alluvial sands, and clayey soils derived from Malmesbury shales. The species is found from sea level to about 1 700 m.

W. paniculata grows in mesic and dry mountain fynbos, lowland fynbos on acid or alkaline soils, renosterveld, and strandveld. It is most common in younger vegetation (less than 10 years since last fire), probably because it favours less dense vegetation. The species does not require permanent moisture and can be found in areas ranging from seasonally dry sands to permanently moist shales. This wide ecological tolerance is certain to be one of the major reasons for the success of the species.

Status: locally abundant, but usually varies from sparse to common. This species is unlikely to become endangered in the near future due to its wide distribution, varied habitats, and ability to thrive in disturbed (even ploughed) sites.

Variation within the species: *W. paniculata* is exceptionally variable with respect to plant size, leaf hairiness and shape, and flower size and structure. This has resulted in the large number of synonyms for this species.

Barker (1950) resurrected *W. graminifolia* L.f. as a segregate of *W. paniculata*. However, there is a continuum of variation in all traits mentioned by Barker as reliable discriminators, for example, perianth length, plant robustness, leaf hairiness and width. In addition, specimens show combinations of characters which make the separation of

two species, based on these characters, futile, e.g. a plant may be robust and have tepals 25–30 mm long (both *W. graminifolia* characteristics), as well as narrow, hairy leaves (both *W. paniculata* characteristics). The various combinations are endless. For these reasons we do not think that *W. graminifolia* can be separated from *W. paniculata*.

An extensive review of all available herbarium specimens showed that there is neither temporal nor geographical separation between the 'varieties'. In addition, the chromosome number is constant for specimens from a wide geographical range, and exhibiting a wide range of morphological variation (Ornduff 1979). This evidence supports the idea that *W. paniculata* and all plants closely resembling it represent a single species. This variation in *W. paniculata* should somehow be recognised. However, the variation is too continuous to recognize formal taxa, and Rosendahl's (1949) comment probably applies here: 'some authors when dealing with highly polymorphous groups seem to feel that it is necessary to take account of all variants that can be distinguished and fit them into a formal scheme. The trouble with this procedure is that in attempts to set up a series of units of descending rank, a point of diminishing returns is soon reached, beyond which confusion rather than clarification results. Such schemes may have something to commend them in theory but not in practice'. The alternative is to recognize informal forms.

Stuessy (1990) defines 'form' as 'specimens with small genetic variations, not geographically correlated, and often growing with more 'typical' plants'. Subspecies and varieties apply only to allopatric taxa, and the variation within *W. paniculata* should thus be described as forms.

Form 1: this form has been recorded from Kleinmond in the east, north to Mamre, and south to the Cape Peninsula, and is characterised by large tepals fringed with dark cilia. There is continuous variation for this and other characters in the plants, and the distinctness of the morph as a whole is doubted.

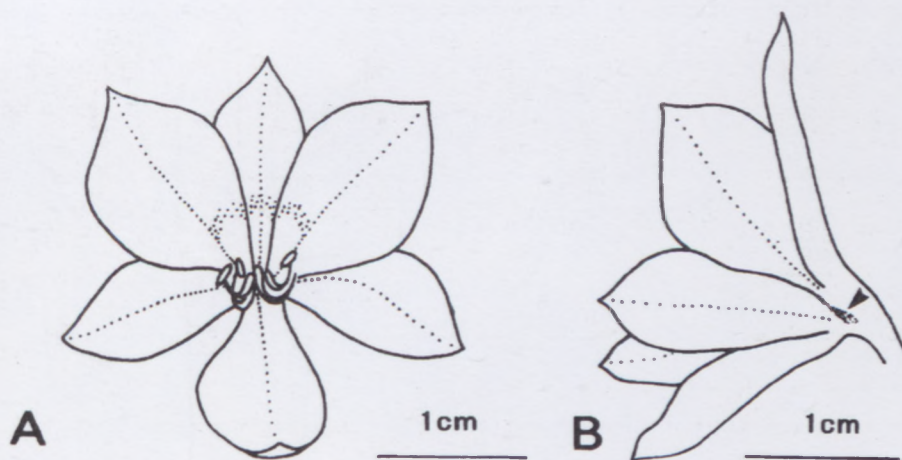


FIGURE 4.—*W. brachyandra* flower structure. A, right-handed flower illustrating clustered stamens and style characteristic of species; B, side view showing small perianth aperture (arrowed).

Form 2: specimens from the mountains between Ceres and Pakhuis Pass are frequently very tall, with extremely lax panicles and long, thin leaves. This form does have a degree of environmental and geographical correlation, which suggests that it might be viewed as a subspecies (allopatric, genetically similar). However, the form is not strictly allopatric as the typical form of *W. paniculata* is known to occur in the area and for this reason we would not recommend the use of a formal subspecific rank for this taxon.

Form 3: dwarf specimens with very narrow, hairy leaves can often be found growing together with more 'typical' forms, for example in the hills above Glencairn and Simonstown.

Vouchers: *Barker 169, 1097* (NBG); *Lewis in BOL 22263* (BOL); *Pillans 9138* (BOL); *Stokoe 818* (BOL); *Wolley Dod 526* (BOL).

3. *Wachendorfia brachyandra* W.F. Barker in *Journal of South African Botany* 15: 41 (1949); W.F. Barker: 207 (1950). Type: Cape Peninsula, Kirstenbosch, *Barker 1096* (NBG, holo.!).

Rhizomatous perennial herb, 0.10–0.65 m tall. *Rhizome* small, globose to ovate-oblong, 5–20 mm diameter. *Leaves* annual, erect or spreading, linear to lanceolate, often falcate, glabrous, dark green to yellow green, up to 700 × 35 mm. *Leaf anatomy*: palisade layer poorly defined, consisting of one or two cells; cuticle lightly lignified; sclerenchyma cap development variable; subsidiary cells rectangular; mucilage canals small. *Culm* about 3 mm in diameter, covered in short glandular hairs, seldom branched to form secondary peduncles; usually less than 0.4 m long. *Inflorescence* a lax panicle with 6–17 flowers per peduncle; peduncles and pedicels slender; peduncles short near tip of axis, a few much longer at the bottom (up to 0.2 m long). *Bracts* mostly scarious, oblong ovate acuminate, almost sheathing, not recurved lower down, up to 80 mm long; densely pilose. *Tepals* light apricot yellow, the markings dark; 12–20 × 4–14 mm; outer adaxial tepal smaller than the others, only slightly recurved; cilia seldom present on tepal edges. *Stamens* clustered, not spreading, half as long as tepals, 6–14 mm long; anthers 2.0–2.5 × 0.5–1.0 mm. *Style*: short, not much curved sideways, 7–12 mm long. *Fruit* a 3-lobed, dry capsule broader than long, 5 × 8–10 mm, carpels obtuse. *Seeds* spherical, coarsely hairy, 2 mm diameter. Figure 4.

Flowering time: late August to early December, with a peak in September and October.

Distinguishing features: stamens and style short, half the length of the tepals, clustered; inflorescence lax; tepals pale yellow-apricot.

Distribution and habitat: this species has the most restricted range of all the species, and is confined to the extreme southwestern Cape (Figure 5). It is undoubtedly undercollected, and is known from altitudes ranging from 50–±600 m on either sandstone or granite derived soils. The species seems to favour damp sites, often growing in partial shade in forest margins, or in seeps and drainage lines in fynbos. It is also commonly found in recently burnt fynbos areas, and will persist for many years in a fairly open habitat (e.g. herbaceous margins of forests).

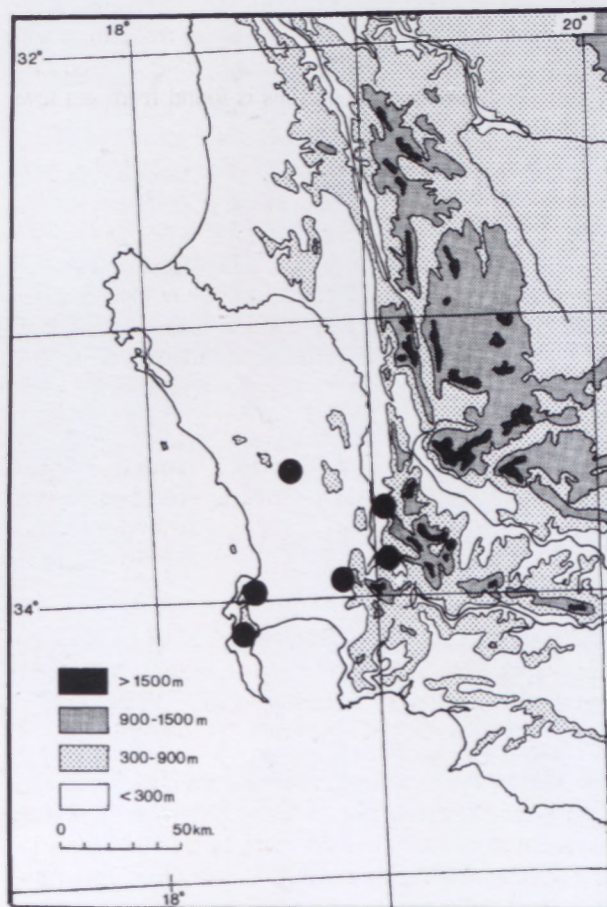


FIGURE 5.—Distribution of *W. brachyandra*.

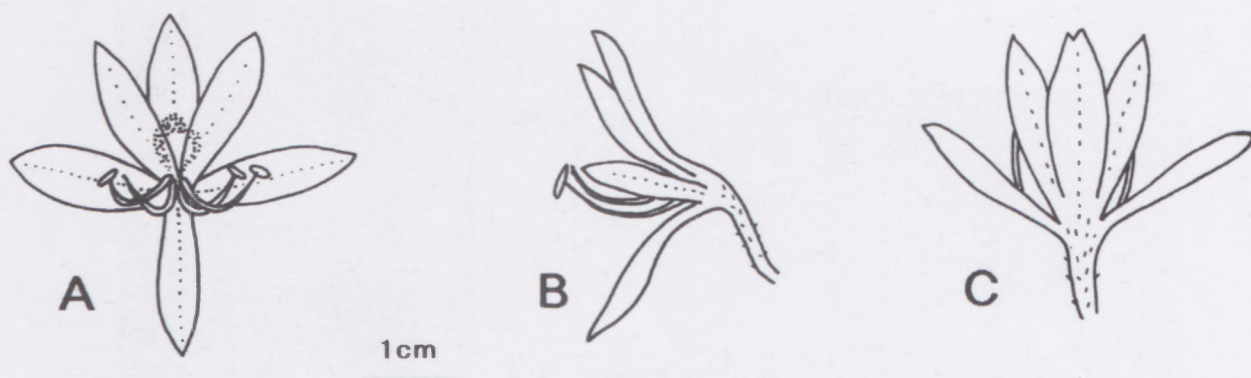


FIGURE 6.—*W. parviflora* flower structure. A, front view of left-handed flower showing narrow tepals characteristic of this species; B, side view; C, rear view.

Status: locally common, but with a sparse, scattered distribution. Due to the nature of its habitat, *W. brachyandra* may well become endangered, as swampy, moist areas are frequently drained for agriculture, building, etc.

Vouchers: *Compton 16359* (NBG); *Salter 8718* (NBG), *9046* (BOL).

4. *Wachendorfia parviflora* W.F. Barker in *Journal of South African Botany* 15: 39 (1949); W.F. Barker: 207 (1950). Type: Cape Peninsula, Camps Bay, *Salter 7457* (NBG, holo.!).

Rhizomatous perennial herb, 0.1–0.4 m tall, usually dwarf, 0.1–0.2 m. **Rhizome** small globose-ovoid, oblong, 5–25 mm in diameter. **Leaves** annual, erect or spreading, linear to lanceolate, usually falcate and longer than inflorescence, blue-green, softly hairy, up to 360 × 25 mm. **Leaf anatomy:** palisade layer one cell thick; cuticle with intermediate lignification; sclerenchyma caps well developed; subsidiary cells rectangular; mucilage canals small. **Culm** short (usually less than 0.2 m); culm, peduncles and pedicels covered in short glandular hairs. **Inflorescence** a very short, dense panicle; peduncles very short, densely clustered on axis. **Bracts** herbaceous, green, erect, often produced beyond the flowers. **Tepals** dull yellow, fading brownish purple, segments narrow, 15–25 × 3–6 mm, upper segments usually broader than the rest, lowermost tepal isolated. **Stamens:** two thirds length of tepals, 10–12 mm long; anthers 1.5–2.0 × 0.5 mm. **Style:** two-thirds length of tepals, 11 mm long. **Fruit** a dry capsule, broader than long, 6–7 × 11–14 mm; carpels obtuse, covered in glandular hairs. **Seeds** globose, coarsely hairy, 2–4 mm in diameter. Figure 6.

Flowering time: early August to late September, with a peak in early September.

Distinguishing features: dwarf habit; erect herbaceous bracts; tepals very narrow.

Distribution and habitat: *W. parviflora* is essentially a species of the western Cape, ranging from Nieuwoudtville to the Cape Peninsula and McGregor (Figure 7). There is a record from near Soebatsfontein and another from 15 km east of Hondeklipbaai (3017BB), which suggests that this species probably occurs all the way up the west coast as least as far north as Hondeklipbaai. This area is under-

collected (Gibbs Russell *et al.* 1984) and it may be more common and widespread in the area.

W. parviflora grows on both sandstone and granite derived soils, and there are a few records from shale areas. The species is found at altitudes ranging from 15–±500 m a.s.l. in habitats ranging from dry, sandy hollows in coastal fynbos to moist, rocky ledges in thick mountain fynbos. It is often found in association with *W. paniculata*.

Status: uncertain, probably uncommon and sparse throughout its range. Appears to be replaced by *W. paniculata* in many apparently suitable areas.

Vouchers: *W.F. Barker 4600* (NBG), *W.F. Barker 9-8-1935* (BOL); *Hanekom 1168* (PRE); *Johnson 236* (NBG); *Salter 7457* (NBG).

DETAILED MORPHOLOGICAL OBSERVATIONS

Rhizome

Wachendorfia possesses a distinctive rhizome, containing a red fluid rich in arylphenalenone pigments. The air-dried rhizome varies in diameter from 5–50 mm, although the fresh rhizomes may be twice this size. The shape is usually spherical to ovoid, although irregular shapes may occur. An air-dried rhizome is usually covered by a papery tunic composed of the dry leaf bases.

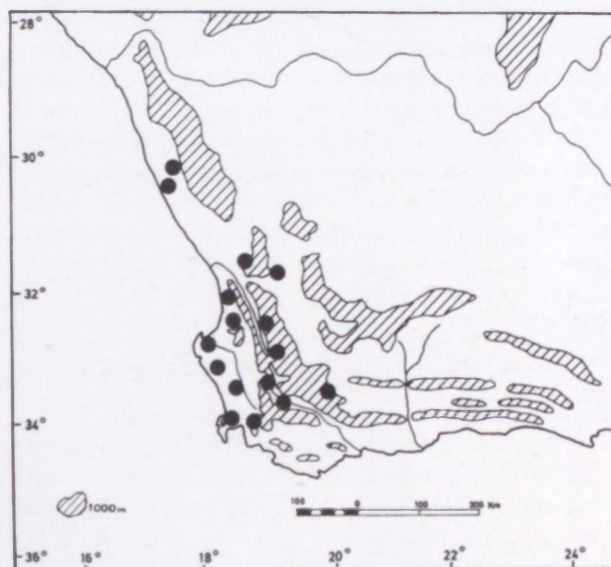


FIGURE 7.—Distribution of *W. parviflora*.

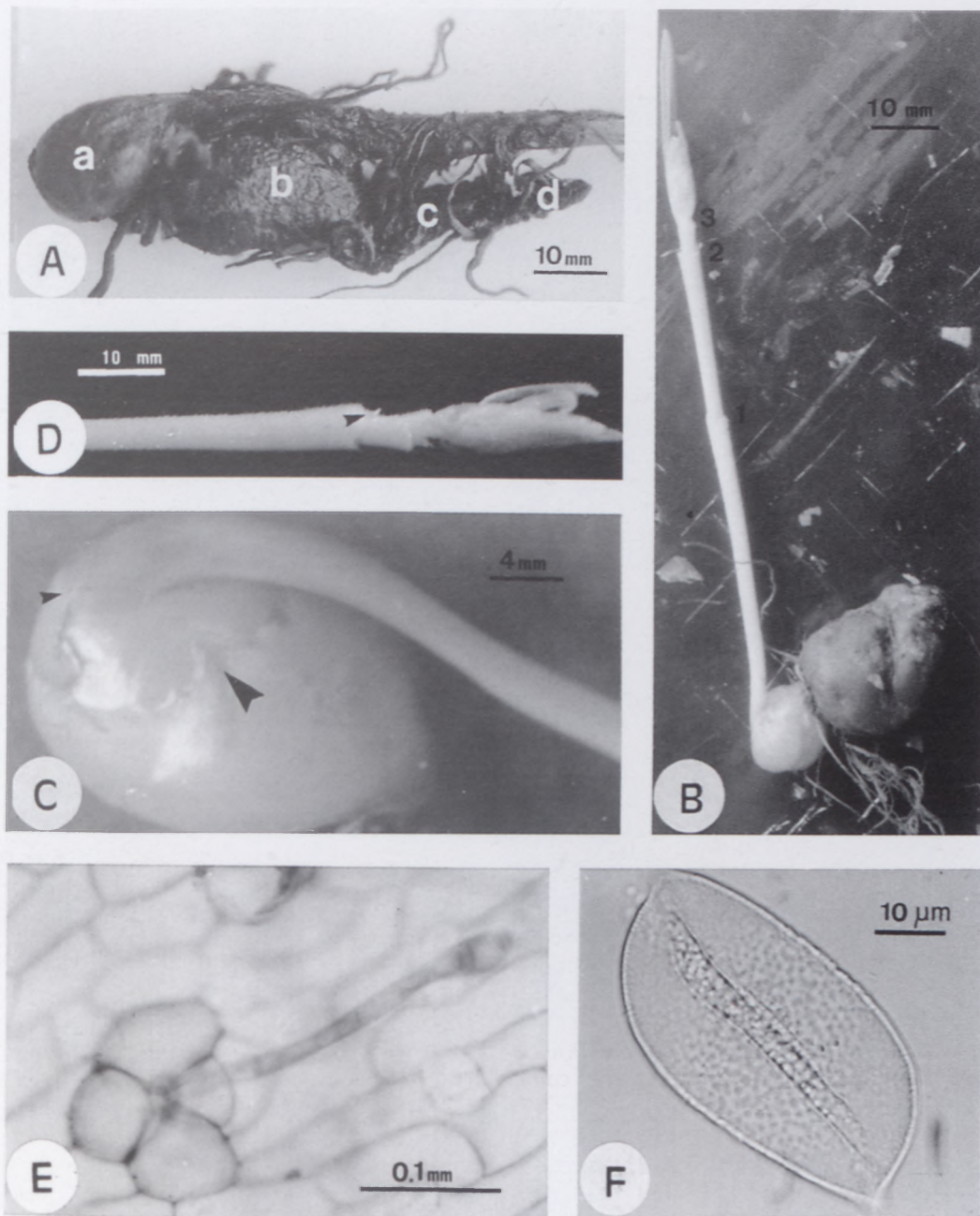


FIGURE 8.—A, *W. paniculata*: rhizome morphology, showing the three previous years' shrivelled rhizomes, separated in each case by a cluster of adventitious roots. a, active rhizome; d, three year old rhizome. B, *W. parviflora*: rhizome and culm with leaves removed. Culm nodes 1 and 2 with amplexicaul leaves; node 3 and onwards with spiral arrangement of leaves; nodes 2 and 3 with small sterile buds visible. C, *W. paniculata*: rhizome with all rhizome leaves removed; large node ringing middle of rhizome is node 2, axillary bud visible (large arrow); node 3 visible near base of culm (small arrow). D, E, *W. parviflora*: D, close up of young culm, nodes 2 & 3 visible, the sterile bud of node 2 arrowed; E, pileate epidermal hair, note four enlarged basal cells and multicellular hair construction. F, *W. paniculata*: light photomicrograph of pollen grain, illustrating central sulcus, proximal verrucae and micropore-pitted border.

A new rhizome is produced every year, with the previous year's rhizome remaining attached to the present year's rhizome. The old rhizome shrivels, until all that remains is the extensive system of vascular traces. Occasionally up to three old rhizomes may be found attached in sequence to the current rhizome. A cluster of thin, short adventitious roots sprouts from between each rhizome (Figure 8A, B).

Each rhizome has three nodes, each with a 'rhizome leaf' and an axillary bud (Figure 8C). The axillary buds are arranged distichously. Each axillary bud is capable of producing a new rhizome, although only one is actually produced. The new rhizome may be produced below or

to the side of the parent rhizome. This means that next year's rhizome will be exploring new soil, either deeper or some horizontal distance from the parent. This may be an important function given the absence of tap roots. The annual flowering shoot is formed by the apical bud, resulting in a sympodial growth form. *W. thyrsiflora* may produce stoloniferous lateral outgrowths from the main rhizome, some of which may ultimately extend several metres. These extended rhizomes are then capable of producing new ramets. Vegetative reproduction is common in monocots, and seems to be an important feature of *Wachendorfia*.

The rhizomes stain positive for starch. In *W. paniculata* and *W. parviflora* the amyloplasts are concentrated

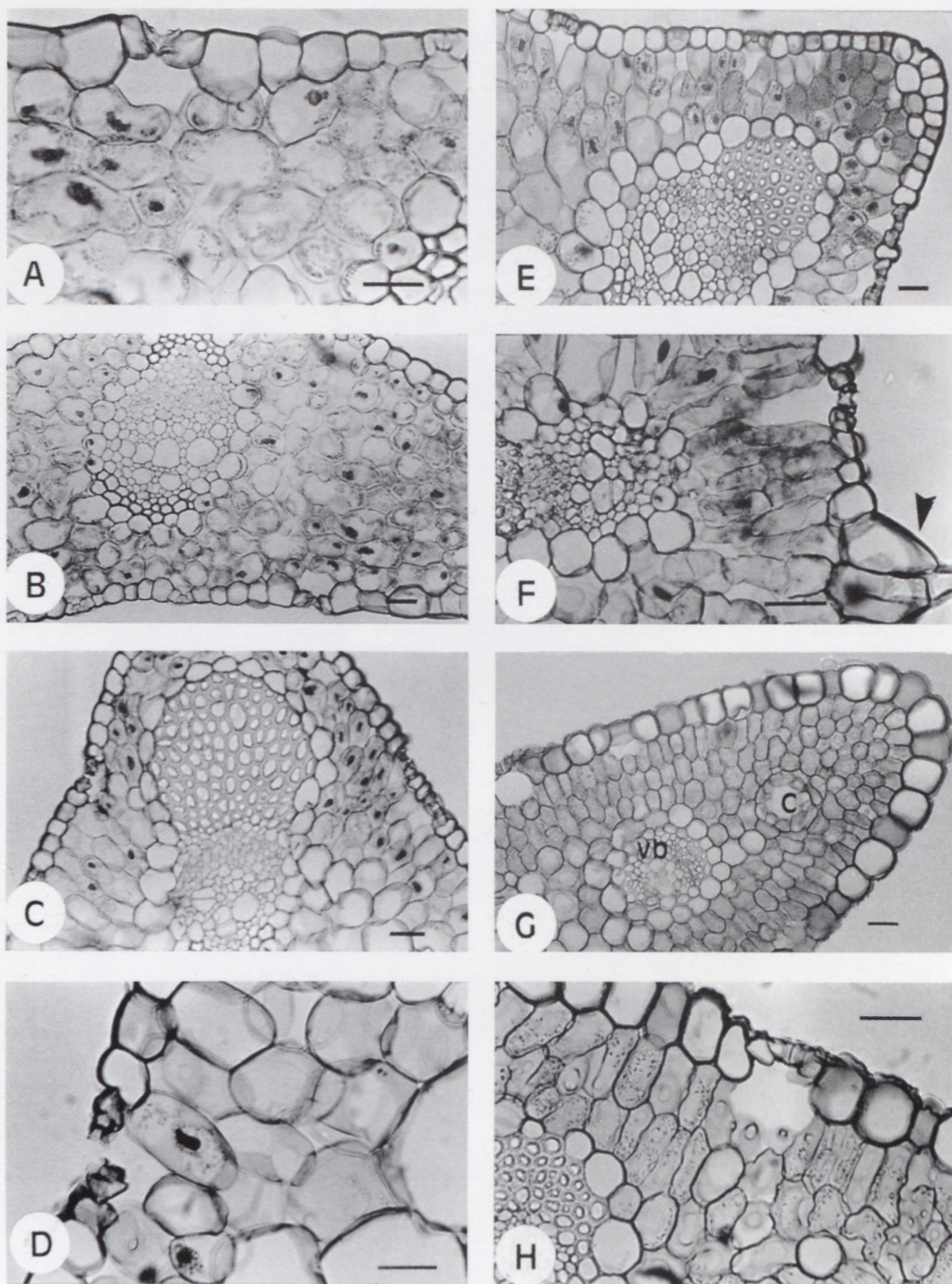


FIGURE 9.—Leaf anatomy of *Wachendorfia*; scale bar, 250 μm . A, B, *W. thyrsoflora*: A, leaf section illustrating kidney-shaped subsidiary cells and poorly defined palisade layer; B, vascular bundle with small sclerenchyma caps. C, D, *W. paniculata*: C, vascular bundle with large sclerenchyma caps; D, stoma with twin epidermal lips and single palisade layer. E, *W. brachyandra*: variable palisade width and bundle with large cap. F, *W. parviflora*: single palisade layer and trichome base with four swollen epidermal cells (arrowed). G, *Dilatris pillansii*: leaf edge with double palisade layer: c, mucilage canal; vb, horizontally aligned vascular bundle; spaces between densely packed cortical cells are the result of lobing. H, *D. pillansii*: stoma with twin epidermal lips and kidney-shaped subsidiary cells.

within the vascular stele, with almost none in the cortex. In *W. thyrsoflora* amyloplasts are equally common in the cortex and the stele. The reasons for this variation are unknown, but may be related to the persistence of the rhizome of *W. thyrsoflora*, resulting in an extremely long

underground organ.

The xylem elements have an amphivasal arrangement, which is similar to that reported for the Restionaceae by Linder (1990).

Leaf morphology

Although the plicate leaves of *Wachendorfia* are distinctive, they often show considerable intraspecific variation. The colour varies from dark green through to light yellow-green, and is often a function of leaf age. The shape may vary within a species, some populations of *W. paniculata* having almost needle-like leaves, and others having broad, falcate leaves. *W. thyrsoflora* usually has large ensiform leaves, whereas *W. brachyandra* has lanceolate or falcate leaves. *W. parviflora* is normally characterised by falcate leaves, but may frequently have lanceolate leaves. *W. thyrsoflora* has distinctly longer and broader leaves than any of the other species (up to 900 × 80 mm). The other three species show much interplant variation in leaf size, but are all within approximately the same range, up to 400 × 40 mm. There seems to be some altitudinal variation in leaf size and shape in *W. paniculata*, with specimens growing at high altitudes tending to have extremely long, narrow, linear leaves.

Wachendorfia leaves originate from both the rhizome and the culm. There are usually three large rhizome leaves, arising from the three rhizome nodes (Figure 8C). These leaves sheath the culm at the base. The culm leaves fall into two types: the lowest two are amplexicaul and opposite, whereas those further up the stem are spirally arranged (Figure 8D). The lower leaves thus give the distinct impression of being two-ranked. The leaves are always firm in texture, longitudinally plicate and entire. The leaves of *W. thyrsoflora* and *W. brachyandra* are always glabrous or very nearly so, while those of *W. parviflora* are distinct in having a dense coating of numerous short hairs (Figure 8E). *W. paniculata* leaves vary from being nearly glabrous to densely hairy with long white hairs. Within-plant variation in leaf hairiness is small, although within-population variation may be great in this species. There is no obvious ecological reason for the difference in leaf hairiness within the species, as it does not seem to follow a gradient of rainfall, altitude or any other single factor.

The dense leaf hairs in *W. parviflora* are of two types. Pointed, unicellular hairs are by far the most common, outnumbering the pileate, tricellular hairs by about 5:1. Adaxial and abaxial leaf surfaces are equally hairy. Four or occasionally five large epidermal cells support the base of each hair. The unicellular hairs taper to a point and appear to have hollow bases, whereas the tricellular hairs have small terminal cap cells that may be glandular (Figure 8E).

The two species confined to permanently damp habitats (*W. thyrsoflora* and *W. brachyandra*) have glabrous leaves, whereas the two dryland species (*W. paniculata* and *W. parviflora*) usually have hairy leaves.

Leaf anatomy

The leaf anatomy of *Dilatrix pillansii* W.F. Barker, *D. corymbosa* Berg., and the four species of *Wachendorfia*, was examined. *Wachendorfia* leaves are plicate, and both thinner and wider than the narrow, rigid leaves of *Dilatrix*, which have a number of special associated features.

The palisade layer in *Dilatrix* is two cells wide (Figure 9H), which is a similar arrangement to the twin layer of columnar palisade cells in *Conostylis* R. Br. (Green 1959). *Lachnanthes* Ell. lacks a palisade layer altogether (Simpson & Dickison 1981). There is thus a range of palisade structures within the family. The Cape genera reflect this variation well, with *Dilatrix* having a two cell layer, *W. thyrsoflora* without a distinct layer (Figure 9A), and the other *Wachendorfia* species with either a one or a two cell layer (Figures 9C–F). Cortical air spaces are absent in *Dilatrix* and the cortical cells are lobed (Figure 9H). All *Wachendorfia* species have air spaces between the isodiametric cortical cells (Figures 9A–F).

The epidermal cuticle is thick in *Dilatrix*, *W. thyrsoflora* and *W. paniculata*, but is noticeably thinner in *W. parviflora* and *W. brachyandra*. Lignification of the epidermal layer is light in all taxa bar *W. parviflora*, in which extensive lignification is evident (Figure 9A–H).

Stomata in *Dilatrix* and *Wachendorfia* species are paracytic. The epidermal lip has a well-developed upper component and a lower lip of about half the length of the upper. This double epidermal lip is also recorded in *Lachnanthes* (Simpson & Dickison 1981). Green (1959) made no mention of these epidermal lips in his study of the Australian genus *Conostylis*, although his drawings show slight spurs on the outer edges of the stomata. *Dilatrix* has a kidney-shaped subsidiary cell (Figure 9H), a feature which it shares with *W. thyrsoflora*. All other *Wachendorfia* species have rectangular subsidiary cells. Stomata appear to be equally common on both sides of the leaf and are very slightly sunken relative to the epidermal layer. Large substomatal cavities are present in all taxa.

In *Wachendorfia*, the large first order vascular bundle within the extreme edge of the leaf closest to the culm, lies horizontally (i.e. tangential to the culm axis), whereas all others in the leaf are vertically orientated (i.e. radial to the culm axis). This feature is also found in *Conostylis* (Green 1959). This may be the result of the leaf sheathing around the rhizome and the culm, thus flattening one edge of the leaf and distorting the apparent bundle position. Sclerenchyma cap development in the vascular bundles is very variable. *W. thyrsoflora* has poorly developed caps, whereas in *Dilatrix* and *W. parviflora* they are well-developed. This feature is variable in both *W. brachyandra* and *W. paniculata*, and in the latter the bundles may be exceptionally well developed.

W. thyrsoflora has larger leaf cortex mucilage canals than the other species in the genus. This may be an allometric feature associated with the overall large size of the species or the result of ecological or phylogenetic factors. We suggest that it does have ecological relevance, as the various species' leaf sections were taken from leaves of the same size (thus reducing any allometric effects), and *W. thyrsoflora* is unique in being confined to permanently damp sites. Large quantities of mucilage can be seen in cut sections of *W. thyrsoflora* leaves and most of this appears to come from the large canals in the leaf. *Dilatrix* has a single large canal within the leaf (Figure 9G), and this is always located in the side of the leaf closest to the aerial stem. There are a number of other smaller canals scattered throughout the leaf cortex which may act as mucilage ducts.

Floral morphology

Considerable interplant and interpopulation variation occurs in the length of the inflorescence, the number of cymes produced, the number of flowers in a cyme, the size and colour of the flowers, the degree of perianth spreading, and the size of the nectaries.

Wachendorfia flowers are enantiomorphic. The style of some flowers is sharply directed to the right, whereas in other plants it is deflected to the left (Figure 2). In both cases, one of the three stamens is borne close to the style, the other two are deflected in the opposite direction. *Dilatrix* is also enantiomorphic, but differs in that both left- and right-handed flowers may be found on the same inflorescence.

The upper three tepals in *Wachendorfia* have pale markings surrounded by dark rings which may act as nectar guides. There is much interplant variation in the contrast, size, and shape of these markings. Large 'semi-extrafloral' nectaries are formed by the bases of the outer upper and the two adjacent inner tepals, one being present on each side of the flower. These are elongated into spurlike structures clearly visible on the outside edges of the flowers. Significant quantities of nectar are produced, which may persist even after the flower itself has withered. Nectar is also produced long before the flower is open. Sugar concentration in an open flower is about 20%, rising to 50% in a withered flower (Ornduff & Dulberger 1978).

The genus is essentially spring flowering, although there are some intra- and interspecific differences worth noting. High altitude forms of *W. paniculata* are noted for their late flowering. The species has an extremely long flowering period, and this may be attributed to the varied habitats in which the species is found. *W. thyrsoflora* is often found flowering in late summer. This might be a reflection of its moist habitat, as severe moisture stress is unlikely, perhaps allowing this species to flower much later than the other species which favour drier habitats. *W. parviflora*

is interesting in that it flowers early, with no flowering recorded later than September. It is often the only species of the genus in flower in early August.

The three dryland species can be separated on flower structure. In Figure 10 three floral measurements are plotted for *W. parviflora*, *W. brachyandra*, and *W. paniculata*. On the y-axis a ratio of stamen (= style) length over maximum tepal length for each flower is plotted, (demonstrating the distinctness of *W. brachyandra*), and on the x-axis the maximum tepal width recorded for each flower is given (demonstrating the distinctness of *W. parviflora*). *W. thyrsoflora* is a very distinct species in many different ways (habitat, size, anatomy), and for this reason is not included in this analysis. The figure illustrates how the three species can be separated by a combination of floral characters, but it should be noted that it does not demonstrate the existence of clearcut phenetic groups.

Pollen

Erdtman (1966) recognized three pollen types within the Haemodoraceae. Six genera, including both *Dilatrix* and *Wachendorfia*, are characterized by monosulcate pollen (20–90 μm long) with a 'usually not very distinct' exine stratification and sexine pattern. *Barberetta* was not studied by Erdtman (1966). Simpson (1983) published a systematic palynological survey of the Haemodoraceae, in which the pollen was investigated by light microscopy, and both scanning and transmission electron microscopy, thus allowing a detailed characterisation of the wall structure. He included two species of *Dilatrix*, *Wachendorfia thyrsoflora* and *Barberetta* in his study, and his observations provide a useful descriptive base for the present study which included the other three species of *Wachendorfia*.

Dilatrix pillansii and *D. corymbosa* possess very similar pollen grains, are monosulcate and heteropolar, with verrucate to baculate non-apertural sculpturing and gemmate to psilate apertural sculpturing (Figure 11A). Grains are approximately 50 μm long (polar) and 25 μm wide (equatorial). The exine surface appears to be quite

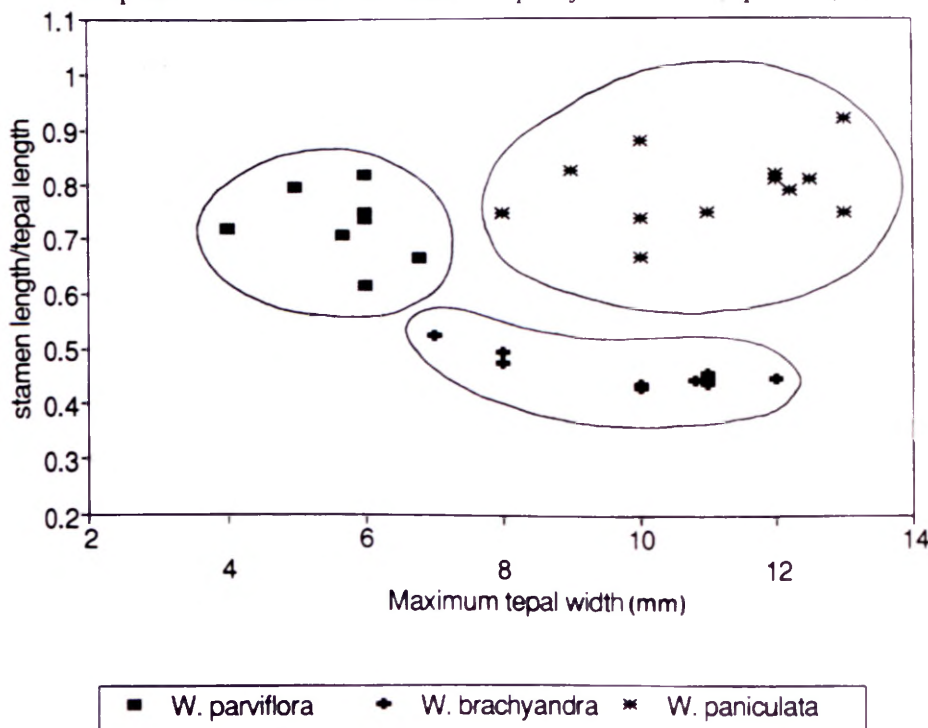


FIGURE 10. — Scatter diagram of the maximum tepal width against the ratio of stamen/petal length for *W. parviflora*, *W. brachyandra* and *W. paniculata*, showing how these species can be separated morphologically.

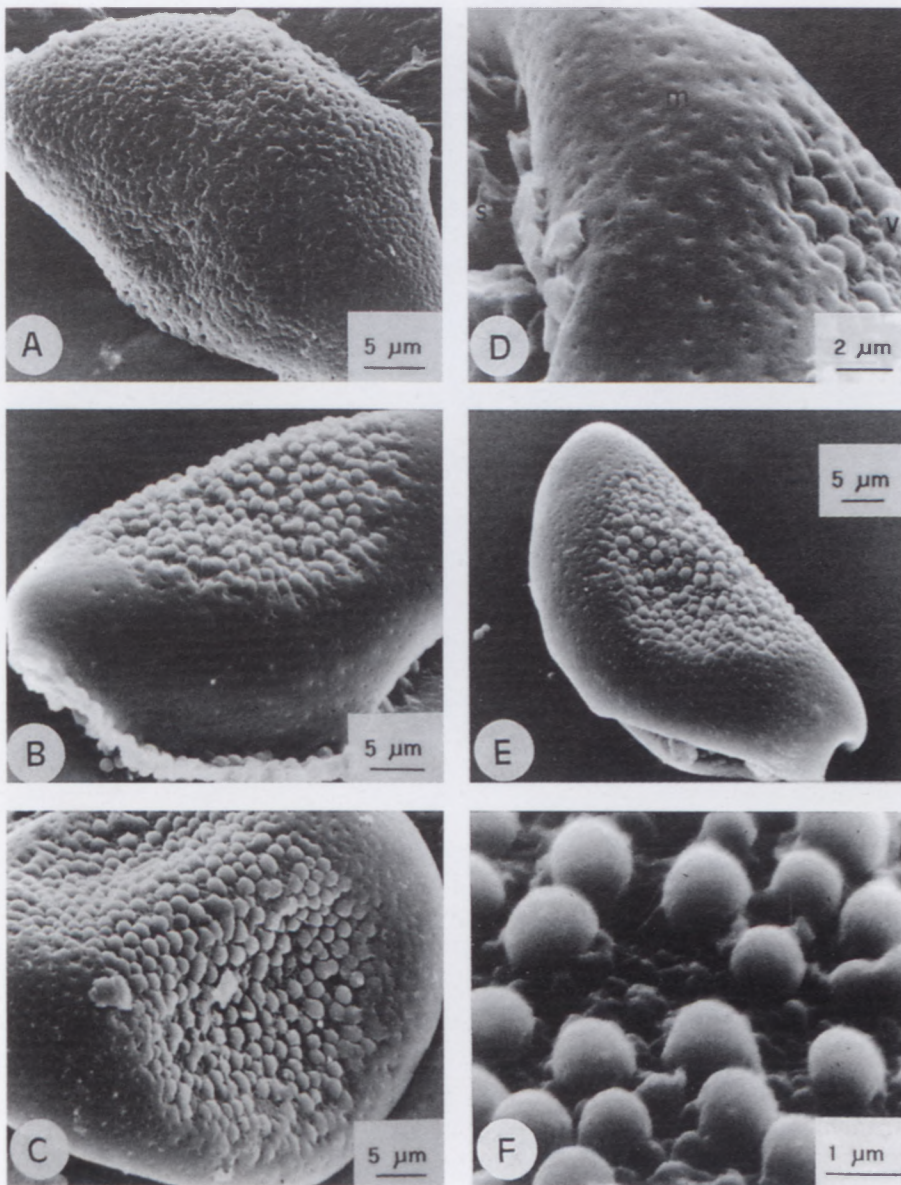


FIGURE 11.—Scanning electron micrographs of pollen grains. A, *Dilatris corymbosa*: reticulate exine. B, *W. thyrsoiflora*: broad micropore-pitted border. C, *W. parviflora*: verrucae patterning. D, *W. brachyandra*: v, verrucae; m, micropore-pitted border; s, sulcus. E, F, *W. paniculata*: E, heteropolar, boat-shaped grain; F, close-up of verrucae and granular secondary exine sculpturing beneath.

different from the exine of *Wachendorfia* pollen, as the verrucae seem to have coalesced to form a more continuous bumpy pattern. *Dilatris* also has a far less obvious micropore-pitted aperture border.

Wachendorfia pollen is monosulcate and heteropolar, with a convex aperture wall consisting of widely separated, two-layered baculate exine elements, over a relatively thick two-layered, fibrillar intine (Simpson 1983). The concave non-apertural wall is proximally verrucate, with a granular appearance between the verrucae (Figure 11F). The verrucae thus appear to 'saddle' the pollen grain (Figures 8F; 11B–F). The aperture wall is encircled by a smooth border pitted with micropores (Figure 11B–F). The 'coarsely granular, distinctly convex operculum' noted by Erdtman (1966) is an aperture wall with an outer layer of closely spaced exine structural elements, a point noted by Simpson (1983). These apertures often disintegrate during acetolysis, probably because of the lack of continuous exine material between the elements. The grains are distinctly hemispheric in shape. All species have grains $40\text{--}50 \times 20\text{--}25 \mu\text{m}$. In all species the size of the exine verrucae is relatively constant, about $1 \mu\text{m}$ in diameter, and all species have the granular substance visible between the verrucae. This granular layer is the lower layer of the

two-layer exine. *W. thyrsoiflora* (Figure 11B) differs from the rest of the genus in that the distance between the sulcus and the start of the verrucae, i.e. the width of the micropore-pitted border, is twice as great as in the other species. There is thus no reliable way to identify *Wachendorfia* pollen, with the exception of that of *W. thyrsoiflora*, to species level.

The pollen of *Barberetta* is virtually identical to that of *Wachendorfia*. This suggests that *Barberetta* is more closely related to *Wachendorfia* than it is to *Dilatris*.

Seeds

The seeds of *Wachendorfia* are all ovoid or spherical, about 2 mm in diameter, and covered in numerous short hairs (Figure 12B–F). There is little interspecific variation, and they cannot be reliably used for species identification. Hair length and width shows very little variation. All the species have curious verrucae on the hairs (Figure 12E, F), and their function and origin is not known.

W. thyrsoiflora has the most distinctive seed, as they are large and somewhat kidney-shaped. When viewed in a

SEM, the hairs on the seed also have a greater density of verrucae than the hairs of other species. The seed dispersal biology is unknown, with hydrochory and anemochory possible. The seed of *W. thyrsoflora* has been observed floating on streams (pers. obs.), and as this species is generally associated with streams, hydrochory may be important here.

Pollination biology

The few studies on the evolutionary significance of

enantiomorphy have suggested that it is probably a feature which promotes outcrossing, that is, increases the level of intermorph pollination (Wilson 1887; Ornduff & Dulberger 1978). This conclusion is based on the findings that *W. paniculata* has a weakly developed self-incompatibility system, and that intermorph crosses produce more seeds than self-pollinations or intramorph pollinations. Selection for outcrossing cannot be the driving force behind the evolution of the *Dilatris* flower structure, as left- and right-handed flowers are found on the same plant. The



FIGURE 12. — Scanning electron micrographs of seed. A, *Dilatris viscosa* L.f.: disc-like seed with a central funicle and reticulate patterning. B, *W. brachyandra*: seed hairs often have relatively few verrucae. C, *W. paniculata*: typical raised funicle and hairy, oval seed. D, *W. brachyandra*: spherical seed with the usual central funicle(f). E, *W. parviflora*: seed hairs and verrucae. F, *W. thyrsoflora*: dense verrucae on its seed hairs.

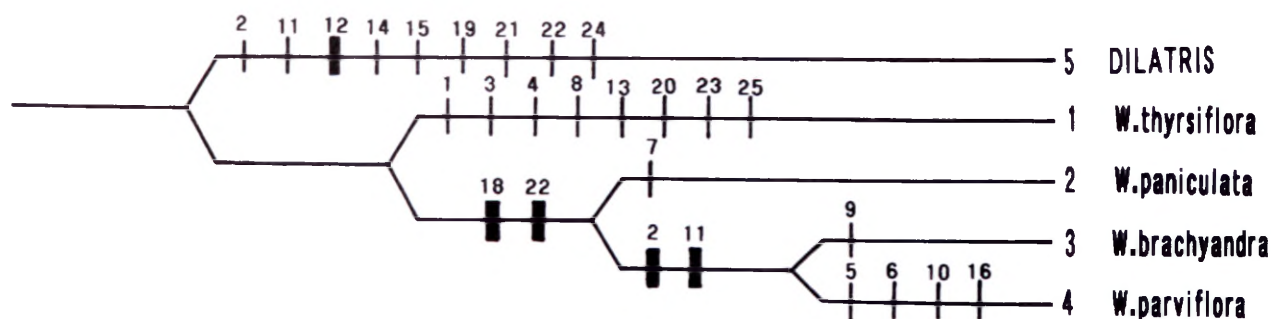


FIGURE 13.—Cladogram for the species in *Wachendorfia*. All characters are indicated; those that are phylogenetically informative are indicated by thicker lines. The length of the components indicates the patristic distances on the diagram. Character codes are given in Table 1, and the distribution of the characters in Table 2.

evolutionary history behind such a strange system is completely unknown (Ornduff & Dulberger 1978).

The seemingly wasteful production of large quantities of 'extrafloral' nectar, often prior to anthesis, is once again difficult to explain in evolutionary terms, and deserves further study. The nectaries open to the outside of the flower and nectar stealing is therefore very easy, as the 'thief' does not have to get anywhere near the pollen or stigmatic surfaces. Ants are seldom seen on the plants due to the glandular hairs on the stem, so the 'extrafloral' nectar does not appear to have any function in feeding 'ant guards' (see Faegri & Van der Pijl 1966).

The pollinators are unknown. This would be a rewarding field of study, as the unusual floral morphology may reflect interesting evolutionary/ecological interactions. One of the problems with the pollination syndrome is that in all species, except *W. brachyandra*, the stigma and anthers seem too far apart for most insects to touch when visiting the flower. We might predict that seed set would be greater in *W. brachyandra* than in the other species (ease of pollination), but preliminary observations do not support this prediction. There must therefore be some insects which can pollinate the other species. These insects would have to be significantly larger than the common honeybee, *Apis mellifera*, as this species is not able to reach the anthers. The carpenter bee, *Xylocopa caffra*, is large enough but it is very seldom seen on low growing *Wachendorfia*, as it tends to favour tall shrubs and small trees, e.g. *Virgilia oroboides*. The first author has seen tabanid flies (family Tabanidae) taking nectar from *W. parviflora* and *W. paniculata*, and in the process, the wings of this large-bodied fly touched the anthers. It is possible that this group of flies may be important pollinators of the genus due to their size and anthophilous behaviour, but more observations are needed. Other potential pollinators include numerous small beetles that appear to feed on the pollen. These beetles clamber over the anthers and may effect a degree of 'mess and soil' pollination.

Phylogeny and speciation

The most parsimonious cladogram is given in Figure 13. The patristic distances (i.e. the degree of divergence from its ancestor) of each component is indicated by the relative length of that component. All the characters, including the autapomorphies, have been indicated on the diagram. Phylogenetically informative characters are indicated by thicker lines.

W. thyrsiflora is basal in the genus and has many more autapomorphies than any of the other species, indicated by the long patristic distance from its basal node. This suggests that *W. thyrsiflora* has diverged morphologically from the rest of the genus. It also occupies the most peculiar habitat, in perennially wet marshes and along streams, whereas the other species are all in habitats that are at least seasonally dry, and the morphological divergence may reflect this habitat specialisation.

The remaining three species occupy relatively similar habitats, and also show relatively low patristic differences between them. *W. paniculata* has a wide ecological and geographical range, but is restricted to well-drained habitats. *W. brachyandra* is restricted to the southwestern Cape, where it occurs in seasonally wet places and forest margins. There is no evidence to date of it occurring with any of the other species, but the stamen-petal ratio may reflect a pollination isolation mechanism.

W. parviflora is often found occurring with *W. paniculata* and appears to be ecologically very similar. However, there is a temporal separation in the flowering time, with *W. parviflora* flowering earlier than *W. paniculata*. This suggests that *W. parviflora* may be a neotenus form of *W. paniculata*. Morphologically, the hairy leaves and narrow tepals may be juvenile structures (although this has not been substantiated with ontogenetic studies on *W. paniculata* and *W. brachyandra*). The speciation mechanism that may lead to such a neotenus form is obscure. Unfortunately this species has not been investigated cytologically, so the possibility of cytological reorganization underlying this evolution is not excluded.

The short patristic distance between the ancestral node and *W. paniculata* suggests that the ancestral habitat of *Wachendorfia* was well-drained. Conversely, the large patristic distance to *W. thyrsiflora* suggests that its perennially wet habitat is a derived habitat. It is interesting that the diversification in the genus occurred in the dryland clade, rather than the marshland clade. Although the total patristic distances of the *W. thyrsiflora* clade and the *W. paniculata* clade are the same, the *W. paniculata* clade, because it contains three species, has a much wider range of variation. This is expressed morphologically by the different taxa showing different patristic values, phenologically by the much wider range of flowering times and ecologically by the range of substrates and moisture regimes. The total geographical ranges of the two clades are the same. These results would caution against auto-

matically assuming that because the wetland taxon is taxonomically isolated, it represents the ancestral habitat.

CONCLUSIONS

Wachendorfia consists of three well-defined species and a fourth extremely variable species. This latter species, *W. paniculata*, has been the cause of much confusion in the past: at least seven specific names were given to the various forms. This variation is continuous, making the recognition of intraspecific taxa totally arbitrary. There is never any real geographic separation of these forms, so the use of subspecific or varietal rank would be inappropriate (Stuessy 1990). However, there is a form that shows a type of geographical separation along with a distinctively lax morphology (*W. paniculata* form 2). Although this form is confined to the mountains between Ceres and Pakhuis Pass, it is not the only form in the area, so subspecific rank would not be appropriate (no allopatry).

Linder (1990) found that 'using only macro-morphological structures at specific level in the Restionaceae only reflects a portion of the available information and reliance on such a small portion of the available data set may lead to mistakes when assessing the relationships among species'. The present study supports this view and we feel that the reliance on macro-morphological features is often the reason for inadequate, confusing species delimitations within *Wachendorfia*. The present study assessed not only macro-morphological variation within *Wachendorfia*, but also pollen and seed coat features, rhizome storage products, and basic features of leaf anatomy. It is hoped that this broader data base strengthens the proposed classification of *Wachendorfia*.

The cladistic analysis suffered from a lack of informative characters and the resulting cladogram should be interpreted with caution. However, the diagram of patristic distances (Figure 11) illustrates the difference between the habitat specialist (*W. thyrsoflora*) and the habitat generalists, the former having many more derived traits, suggesting that ecological specialization has occurred. *W. parviflora* is notable for the number of derived characters that support the idea of it being a neotenus species.

The reproductive biology is not sufficiently well known to understand the evolution of the peculiar form of floral enantiomorphy in *Wachendorfia*. Although there is a phylogeny at generic level (Simpson 1990) the functional purpose of enantiomorphy and extrafloral nectaries is not understood. This may well be linked closely to the pollination biology in the genus.

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