Systematic studies in the tribe Amaryllideae (Amaryllidaceae)

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"This is a beautiful country for studying the graduation of Botanical species -- the families are so rich in species. I am little or nothing of a Botanist -- but with one feature it is impossible not to be struck - viz that when you find a species which fills up as you fancy a wanting link between two others - it does not *merely* fill it, but does so with the superaddition of some new characters - or some analogy with a 3d species which the others do not offer."

Sir John Herschel
writing from Feldhausen, Claremont, Cape of Good Hope, to Charles Lyell, February 20th, 1836.

Abstract

Systematic studies in the tribe Amaryllideae (Amaryllidaceae). D.A. Snijman, Compton Herbarium, National Botanical Institute, Private Bag X7, Claremont 7735, South Africa.

The phylogeny of the African Amaryllideae is presented as a basis for classification and an enquiry into the tribe's evolution. The focus is on the monotypic *Kamiesbergia* Snijman and *Carpolyza* Salisb., *Hessea* Herbert (nine species), *Namaquanula* D. & U. Müller-Doblies (three species) and *Strumaria* Jacq. (23 species), for which a full taxonomic treatment is given. The phylogenetic data are used to assess the biotic history of south western Africa; to analyse the constraints and potentialities available to taxa for reproductive strategies; and to gauge putative modes of lineage diversification. Data from bulb and leaf morphology, floral anatomy, pollen, external seed morphology and chromosome cytology were analysed cladistically. The strict consensus tree for Amaryllideae provided a template to trace character evolution. The strict consensus trees for *Namaquanula, Hessea* and *Strumaria* provided the basis for the cladistic biogeographic analysis, and identified sister-groups for analysing patterns of lineage diversification. The phylogenetic hypothesis indicates that, as previously circumscribed, subtribe Crininae Traub is paraphyletic. The emended Crininae includes *Crinum* L., *Boophane* Herbert *pro parte, Ammocharis* Herbert and *Cybistetes* Milne-Redhead & Schweickerdt. Strumariinae Traub ex D. & U. Müller-Doblies is incorporated into Amaryllidinae, which now includes *Amaryllis* L., *Nerine* Herbert, *Brunsvigia* Heist., *Boophane pro parte*, *Kamiesbergia, Namaquanula, Hessea, Carpolyza* and *Strumaria*. *Tedingea* D. & U. Müller-Doblies, *Bokkeveldia* D. & U. Müller-Doblies and *Gemmaria* Salisb. are placed into synonymy under *Strumaria*. The cladistic biogeographic analyses resulted in conflicting patterns. Although uninformative in themselves they may provide a basis for future comparative studies. Rapid lineage diversification is hypothesised for *Strumaria* through peripheral isolation. Large scale allopatry and founder events are hypothesised for *Hessea.* In Amaryllidinae the derived stomatose seed is hypothesised to be a key innovation which promoted the evolution of other xerophilous characters: hysteranthous leaves, autumn-flowering, small plant size and few leaves. This permitted rapid diversification in the Mediterranean-type climate of southern Africa. The more slowly developing seed of Crininae is interpreted as a constraint to the occupancy of the Mediterranean-type climatic region. Crininae evolved rapidly in the summer-rainfall regions of Africa, where the speciose *Crinum* evolved the contrasting hydrophilic habit as a drought-avoidance strategy.

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LIST OF REVISED GENERA, UNPUBLISHED NEW TAXA AND NEW COMBINATIONS USED IN THIS THESIS

Hessea Herbert

- *H. stellaris* (Jacq.) Herbert
- *H. breviflora* Herbert
- *H. pusilla* Snijman
- *H. speciosa* Snijman, *sp. nov.*
- *H. pilosula* D. & U. Müller-Doblies
- *H. incana* Snijman
- *H. cinnamomea* (L'Hérit.) Durand & Schinz
- *H. monticola* Snijman
- *H. undosa* Snijman

Namaquanula D. & U. Müller-Doblies *emend.* Snijman

Subgenus **Namaquanula**

- *N. bruce-bayeri* D. & U. Müller-Doblies

Subgenus **Myophila** Snijman, *subgen. nov.*

- *N. mathewsii* (W.F. Barker) Snijman, *comb. nov.* (= *Gemmaria mathewsii* (W.F. Barker) D. & U. Müller-Doblies)
- *N. pulcherrima* (D. & U. Müller-Doblies) Snijman, *comb. nov.* (= *G. pulcherrima* D. & U. Müller-Doblies).

Strumaria Jacq.

Subgenus **Tedingea** (D. & U. Müller-Doblies), Snijman *stat.nov.*

- *S. tenella* (L.f.) Snijman, *comb. nov.* (= *Tedingea tenella* (L.f.) D. & U. Müller-Doblies)
- *S. tenella* subsp. *orientalis* Snijman, subsp. nov.
- *S. pygmaea* Snijman, *nom.nov.* (= *Hessea spiralis* Baker)

Subgenus **Strumaria**

- *S. bidentata* Schinz
- *S. phonolithica* Dinter
- *S. barbarae* Obermeyer
- *S. hardyana* D. & U. Müller-Doblies
- *S. truncata* Jacq.

Subgenus **Gemmaria** (Salisb.) Snijman, *stat. nov.*

Section **Cryptomeria** Snijman, sect. *nov.*

- *S. picta* W.F. Barker (= *Bokkeveldia picta* (W.F.Barker) D. & U. Müller-Doblies)

Section **Gemmaria**

- *S. unguiculata* (W.F. Barker) Snijman, *comb. nov.* (= *Gemmaria unguiculata* (W.F. Barker) D. & U. Müller-Doblies)
- *S. karoopoortensis* (D. & U. Müller-Doblies) Snijman, *comb. nov.* (= *G. karoopoortensis* D. & U. Müller-Doblies)
- *S. karooica* (W.F. Barker) Snijman, comb. nov. (= *G. karooica* (W.F. Barker) D. & U. Müller-Doblies)
- *S. massoniella* (D. & U. Müller-Doblies) Snijman, comb. nov. (= *G. massoniella* D. & U. Müller-Doblies)
- *S. chaplinii* (W.F. Barker) Snijman, comb. nov. (= *G. chaplinii* (W.F. Barker) D. & U. Müller-Doblies)
- *S. gemmata* Ker-Gawl. = (*G. gemmata* (Ker-Gawl.) Salisb. ex D. & U. Müller-Doblies)
- *S. merxmuelleriana* (D. & U. Müller-Doblies) Snijman, *comb. nov.* (= *G. merxmuelleriana* D. & U. Müller-Doblies)
- *S. leipoldtii* (L.Bolus) Snijman, *comb. nov.* (= *G. leipoldtii* (L.Bolus) D. & U. Müller-Doblies)
- *S. villosa* Snijman, *sp. nov.*
- *S. discifera* Marloth ex Snijman, *sp. nov.*
- *S. discifera* subsp. *bulbifera* Snijman, subsp. nov.

Section **Bokkeveldia** (D. & U. Müller-Doblies) Snijman, stat. nov.

- *S. watermeyeri* L.Bolus (= *B. watermeyeri* (L.Bolus) D. & U. Müller-Doblies)
- *S. salteri* W.F.Barker (= *B. salteri* (W.F.Barker) D. & U. Müller-Doblies)
- *S. perryae* Snijman, *sp. nov.*
- *S. pubescens* W.F.Barker (=*B. pubescens* (W.F.Barker) D. & U. Müller-Doblies)
- *S. aestivalis* Snijman, *sp. nov.*

Subtribe **Crininae** Traub ex Snijman

Chapter 1.

INTRODUCTION

The tribe Amaryllideae is among the largest of the nine tribes recognised by Dahlgren *et al.* (1985) in the cosmopolitan family Amaryllidaceae. Amaryllideae is distributed throughout sub-Saharan Africa but is most speciose in southern Africa. Only the large genus *Crinum* is pantropical.

The rich diversity of this tribe in southern Africa (± 120 species), particularly in the winter-rainfall region, offers abundant opportunity for phylogenetic studies. Despite this, few modern systematic treatments of representative genera are available and no phylogeny of the tribe has been published. The most extensive taxonomic study is that of Verdoorn (1973) on *Crinum* in southern Africa. Other revisions include *Ammocharis* and *Cybistetes* (Milne-Redhead & Schweickerdt 1939), *Brunsvigia* (Dyer 1950, 1951), *Crinum* in tropical Africa (Nordal 1977, Nordal & Wahlstrøm 1980) and most recently a review of *Hessea, Strumaria* and related genera (Müller-Doblies 1985). Noteworthy are the problems posed to such studies by the floral biology of the tribe. Many valuable floral characters become cryptic in the dried state or are entirely lost. Moreover, most species from the semi-arid to arid, south-western regions of Africa often flower erratically and for short periods. Thus floral data for the tribe are often not readily accessible.

The present study stems from the perception that Amaryllideae constitutes a group rich in evolutionary patterns. Phylogenetic data constitute a powerful tool for testing hypotheses of macroevolution (Vrba 1985). Thus several examples of how phylogenetic systematics can be used to examine patterns and processes of macroevolution have recently been reviewed (Funk & Cracraft 1985, Funk & Brooks 1990). In view of the growing interest in what phylogenetic studies might indicate about evolution in general, this study aims to provide a phylogenetic basis or reference system to the evolutionary relationships of the tribe Amaryllideae, from which the evolutionary history can be reconstructed. The systematic focus is on the generic complex confined to the winter and autumn-rainfall regions of southern Africa: a group which is referred to in current literature as Strumariinae (Müller-Doblies 1985).

In particular this study has eight major objectives.

(1) The presentation of an empirically based, explicit hypothesis of the phylogenetic relationships of the genera in Amaryllideae.

(2) A re-examination of the current infrageneric classification of Amaryllideae (Müller-Doblies 1985, Traub 1970); and the presentation of a classification system which best reflects the cladistic relationships of the genera.

(3) An analysis at species level of the phylogenetic relationships in the generic complex Strumariinae *sensu* D. & U. Müller-Doblies (1985); and the establishment of an

appropriate system of classification to reflect the phylogenetic relationships.

(4) An assessment of the biotic history of the semi-arid, winter-rainfall region of southern Africa, using the phylogenetic relationships expressed in the Strumariinae as biogeographic indicators.

(5) An examination, with reference to the hypothesised phylogeny of Amaryllideae, of some of the life history traits developed among its genera, particularly within the species-rich clades.

(6) The identification of putative modes of speciation based on the distribution areas of the species under study and their phylogenetic relationships.

(7) The presentation of an hypothesis on the evolution of the tribe, which draws from the geographical patterns and patterns of character change shown by its genera, and which focuses on the taxa confined to the winter and autumn-rainfall regions of southern Africa.

(8) The provision of keys and full descriptions to the genera studied at species level.

Chapter 2.

MATERIAL AND METHODS

The classification by D. & U. Müller-Doblies (1985) of the subtribe Strumariinae formed the basis of this study at species level. Their generic names and binomials are referred to in the cladistic analysis but because the results of my analyses made it necessary to emend their taxonomic concepts, I have used my new combinations throughout this work. These are listed with synonyms on page XI and in Tables 4.8 & 4.9. The application of the name *Amaryllis belladonna* L. to the south-western Cape species included in this study, rather than to the American genus *Hippeastrum* Herbert, complies with the recent report of the International Nomenclatural Committee (Brummitt 1987). The tribe Amaryllideae as used here is equivalent to Crineae *sensu* Traub (1957, 1965, 1970). Herbert's (1821) original spelling of the genus *Boophane* is used throughout this work pending its acceptance as a name in current use at the XVth International Botanical Congress.

Information on the general morphology of *Crinum* L., *Boophane* Herbert, *Cybistetes* Milne-Redhead & Schweickerdt, *Ammocharis* Herbert, *Amaryllis* L., *Brunsvigia* Heist. and *Nerine* Herbert was taken from literature, as well as from living and dried material at the Kirstenbosch Botanic Garden and the Compton Herbarium (NBG). Data for *Kamiesbergia* Snijman, *Hessea* Herbert, *Namaquanula* D. & U. Müller-Doblies, *Carpolyza* Salisb. and *Strumaria* Jacq. *sensu lato* which includes *Bokkeveldia* D. & U. Müller-Doblies, *Gemmaria* Salisb. and *Tedingea* D. & U. Müller-Doblies came primarily from living collections at Kirstenbosch, where all the described species and several new species are currently cultivated. With the exception of *Hessea cinnamomea, H. monticola* and *H. undosa*, all the remaining taxa flowered regularly in cultivation.

Bulbs of 17 species of *Nerine* and nearly all the species of *Kamiesbergia, Hessea, Namaquanula, Carpolyza* and *Strumaria* were dissected scale by scale under a stereomicroscope and records were kept of the periodic growth of the leaves.

Flowers for anatomical study were fixed in FAA (90 ml ethanol (70%); 5 ml glacial acetic acid; 5 ml formaldehyde), subsequently dehydrated in an ethanol-xylol series, embedded in wax and cut with a rotary microtome at 10-15 μm. Serial sections were stained with safranin and either fast green or alcian blue, and examined by means of light microscopy.

For the examination of whole pollen grains by scanning electron microscopy (SEM), fresh nonacetolyzed pollen was dehydrated in ethanol and critical point dried before sputter-coating with Au/Pd. Photographs were taken with a Cambridge S200 scanning electron microscope at 10 kV.

Seeds were studied from fresh material by preparing temporary mounts of the testa for light microscopy. Material fixed in FAA was also prepared for SEM and photographed at 10 kV.

Chromosome data were gathered from actively growing root tips pretreated with saturated alphabromonaphthalene at 4^{o}C for 24 hours and fixed in 1:3 acetic acid/ethanol.

The roots were hydrolysed in normal hydrochloric acid at 60^{o}C for six minutes, stained with Feulgen for 30 minutes, counter stained with 2% aceto-orcein and then squashed. The slides were made permanent using the liquid CO_2 method. Photographs were taken with a Zeiss photomicroscope and drawings were made with the aid of a Wild drawing tube at an original magnification of 3 300 x.

For the cladistic analysis, the program Hennig 86 (Farris 1988) was used, and run on a microcomputer. The implicit enumeration (ie*) which provides exhaustive and minimal options (Platnick 1989) was used to generate trees for small data sets (25 taxa or less), while the branch-breaker (bb) option was used for larger data sets (38 taxa). The term homoplastic has been chosen from the words currently advanced as the adjective of "homoplasy", following the recommendation of Clark (1986). For the cladistic biogeographic analyses the program COMPONENT (Page 1989) was used.

I have seen all the species belonging to *Kamiesbergia, Hessea, Carpolyza* and *Strumaria sensu lato* in the field, with the exception of the Namibian and Richtersveld species (*Namaquanula bruce-bayeri, Strumaria bidentata, S. hardyana, S. barbarae* and *S. phonolithica*). Apart from these northern species, the ecological information listed under all the remaining taxa is derived from my own field studies, undertaken from 1985 to 1990.

The taxonomic descriptions were prepared from a combination of living material at Kirstenbosch Botanic Garden and dried material from B, BM, BOL, K, NBG, PRE, SAM and WIND. For the sake of brevity, the foliage leaves are always described as leaves. The measurements given for the leaves and scapes refer only to their above-ground parts. All specimens are cited according to the degree reference system of Edwards & Leistner (1971).

The material examined for data on bulb morphology, floral anatomy, pollen morphology, seed morphology and chromosome cytology is listed in Appendices 1-6.

Chapter 3.
HISTORICAL OUTLINE

3.1 The classification of the tribe Amaryllideae

Nearly all the genera currently placed in Amaryllideae *sensu* Dahlgren *et al.* (1985) had been described prior to Herbert's (1837) major publication on the Amaryllidaceae. Genera subsequently placed in the tribe were *Cybistetes* (Milne-Redhead & Schweickerdt 1939), *Tedingea, Namaquanula, Bokkeveldia* (Müller-Doblies 1985) and *Kamiesbergia* (Snijman 1991).

Initially, Amaryllideae constituted a polyphyletic assemblage placed at various ranks: Amaryllideae (Salisbury 1866), Amaryllidiformes (Herbert 1837) and Amarylleae (Endlicher 1837, Bentham & Hooker 1883, Baker 1888). With the first subtribal delimitation of Amaryllideae, the genera under consideration in this study were divided among the Haemanthinae, Amaryllidinae and Crininae (Pax 1887, Pax & Hoffmann 1930). This system was maintained by Hutchinson (1934, 1935), who raised their rank to tribal status.

TABLE 3.1-- The major classifications of the Amaryllideae since 1957

Genera Authors	*Amaryllis, Crinum, Ammocharis, Cybistetes, Boophane, Nerine, Brunsvigia*	*Hessea, Carpolyza, Strumaria*	*Namaquanula, Tedingea, Gemmaria, Bokkeveldia, Kamiesbergia*
Traub 1957	Crineae Crininae	Strumariinae	
Traub 1962	Crineae	Hesseae	
Traub 1963	Crineae	Strumarieae	
Traub 1965, 1970	Crineae		
Dahlgren *et al* 1985	Amaryllideae		
D. & U. Müller-Doblies 1985	Crininae	Strumariinae	

Advances in the classification of Amaryllideae are largely attributable to the studies of Traub (1957), who first delimited the tribe Crineae (he chose to use the name *Amaryllis* exclusively for the South American genus which is now known as *Hippeastrum*), in what has proven to be a monophyletic assemblage. The initial diagnostic character used for the tribe was the presence of fibres which appear when the bulb scales are torn apart. This has since been corroborated by the autapomorphic unitegmic ovules and bisulculate pollen (Huber 1969, Schulze 1984). Within Crineae, Traub (1957) initially recognised two subtribes, the Crininae and Strumariinae, which he raised to the rank of two tribes, the Crineae and Hesseae (Traub 1962), and subsequently formalised as Crineae and Strumarieae (Traub 1963). This classification was modified yet again when Traub (1965, 1970) merged the tribe Strumarieae within the tribe Crineae. Most recently D. & U. Müller-Doblies (1985) reinstated Strumariinae at subtribal level. The various classifications published since 1957 are summarised in Table 3.1.

3.2 The classification of the genera in the subtribe Strumariinae

The relationships between the genera first placed in Strumariinae (*Carpolyza, Strumaria, Hessea*) have been much obscured in the past, as is reflected in the instability of previous classifications (Baker 1888, 1896, Herbert 1837, Kunth 1850, Salisbury 1866). After 1923 many new species of *Hessea* and *Strumaria* were published (Barker 1931, 1935, 1943, 1944, Bolus 1923, 1930, Dinter 1923, Obermeyer 1981). The only character used to separate the genera was flower form. Thus species with stellate flowers were placed in *Hessea* and those with funnel-shaped flowers in *Strumaria*.

The cytological data of Goldblatt (1976a) ultimately brought into question the then accepted distinction between *Hessea* and *Strumaria*. This evidence supported stylar characteristics and the presence of a perianth tube, rather than floral form as important generic characters, as was earlier inferred by Phillips (1951). Goldblatt (1976a) concluded that a re-evaluation of the generic relationships of the Strumariinae was necessary.

The most recent contribution to the classification of *Hessea, Strumaria* and the allied genus *Carpolyza* is that of D. & U. Müller-Doblies (1985). This study incorporated new data from bulb and anther morphology and re-established the importance of stylar characters. However, floral form remained heavily weighted. The previously circumscribed *Hessea* and *Strumaria* were split into three additional genera, *Tedingea, Bokkeveldia* and *Gemmaria;* and the monotypic genus *Namaquanula* was newly described. D. & U. Müller-Doblies' classification is significant in that much of the confusion between *Hessea* and *Strumaria* was overcome, but it is limited in that no phylogenetic scheme was presented. The only publications following this revision are descriptions of four new species of *Hessea* (Snijman 1989, in press), the new monotypic genus *Kamiesbergia* (Snijman 1991) and five new taxa in *Strumaria* (Snijman in press).

Chapter 4.
PHYLOGENETIC ANALYSIS

4.1 The study group: position, delimitation and taxa

The subtribe Strumariinae *sensu* D. & U. Müller-Doblies (1985) is based on several character states. Of these, the actinomorphic flower is the only characteristic found in all species. The remaining set of characters (two foliage leaves; an amplexicaul cataphyll; a more or less obsolete perigone tube; an anther connective which forms a sheath around the filament tip; and the style connate to the stamens) is not common to all the representatives and includes the arbitrarily defined condition of small-sized plants.

In view of this current definition of Strumariinae it was considered necessary at the outset to examine the purported integrity of the subtribe. Thus, to determine whether Strumariinae as constituted by D. & U. Müller-Doblies (1985) is a monophyletic group, rather than a paraphyletic or polyphyletic assemblage based on a single symplesiomorphic state, all genera of the tribe Amaryllideae *sensu* Dahlgren *et al.* (1985) were analysed.

Thereafter, the study group which was the focus of detailed analysis included all the species of the genera circumscribed within the Müller-Doblies' Strumariinae; *Namaquanula, Hessea, Carpolyza* and *Strumaria sensu lato* which includes *Bokkeveldia, Gemmaria* and *Tedingea*; the recently described *Kamiesbergia* (Snijman 1991); an undescribed species of *Hessea* (*H. speciosa*) and five undescribed species of *Strumaria* (*S. perryae, S. aestivalis, S. discifera* and *S. villosa*). The species concept used here is compatible with the phylogenetic species concept as defined by Nixon & Wheeler (1990), namely the smallest aggregation of populations or lineages diagnosable by a unique combination of character states in comparable individuals.

The tribe Amaryllideae as circumscribed by Traub (1965, 1970) and Dahlgren *et al.* (1985) is undisputedly monophyletic, based on the well established autapomorphy of bisulculate pollen grains (Dahlgren & Clifford 1982, Dahlgren *et al.* 1985, Erdtman 1966, Schulze 1984). All other tribes of the family have monosulculate pollen grains, a character state distributed throughout the petaloid monocotyledons (Dahlgren & Clifford 1982). A probable second autapomorphy appears to be the unitegmic ovules, as opposed to the plesiomorphous bitegmic state (Huber 1969). The distribution of unitegmic ovules needs to be examined further however, as data are known only for *Amaryllis belladonna, Boophane disticha* and *Nerine sarniensis* (= *N. curvifolia*) (Schlimbach 1924).

The genera used to determine the systematic position of the study group within Amaryllideae are listed in Table 4.2. Those genera which I suspected to be polyphyletic were subdivided into the largest-sized homogeneous species groups that could reasonably be considered monophyletic, an approach modelled on Crisp and Weston's analysis of leguminous tribes (Crisp & Weston 1987). *Strumaria sensu stricto* and the *Bokkeveldia* group match D. & U. Müller-Doblies' (1985) concept of the genera, *Strumaria* and

Bokkeveldia; and *Strumaria tenella* previously constituted the monotypic genus *Tedingea* D. & U. Müller-Doblies. The only taxa not analysed according to current taxonomic treatments were *Boophane, Hessea* and species of *Strumaria* constituting the *Gemmaria* group.

Boophane (5 spp.) has been defined in past literature (Baker 1888, 1896, Dyer 1976, Herbert 1837, Milne-Redhead & Schweickerdt 1939, Phillips 1951) by two apparently homoplastic character states (dry, triquetrous capsules and pedicels which elongate in fruit), which also occur in *Brunsvigia* and *Cybistetes* respectively; as well as two arbitrarily defined character states (low ovule number and high flower number). In the analysis *Boophane guttata* and *Boophane flava* were grouped together by their uniquely speckled leaves and bristled leaf margins. The autapomorphy of the leaf arrangement (erecto-patent and fan-shaped) was used to group *Boophane disticha* with *Boophane haemanthoides,* whereas *Boophane pulchra* was treated separately, without a known autapomorphy.

Hessea spiralis, which here has the new name *Strumaria pygmaea*, has remained the least known of all the Strumariinae species (see Baker 1896, Müller-Doblies 1985). Now that the species has been rediscovered, its systematic position is re-evaluated. This diminutive species lacks the centrifixed anthers common to all other species of *Hessea sensu* D. & U. Müller-Doblies (1985), thus it was maintained as a separate species in the analysis of Amaryllideae.

Gemmaria (10 spp.) was defined by D. & U. Müller-Doblies (1985) by the character state: style thickened and forming a disc which passes into the stamens. I differ in my interpretation of this character in *G. pulcherrima* and *G. mathewsii*. In both these species the disc is green and papillose, contrasting with the pink to red style, whereas the disc in all other species of the *Gemmaria* group is smooth, always white to pink and concolorous with the style. On this basis I treated them as separate characters (22, 23, Table 4.3), and to test this hypothesis by means of congruence with other characters (Patterson 1982), *G. pulcherrima* and *G. mathewsii* were excluded from the *Gemmaria* group and treated separately for the analysis at generic level, under the new name: the *Namaquanula mathewsii* group.

Subsequent analyses were confined to determining the species relationships within the study group. Not all the species recognised in the taxonomic treatment by D. & U. Müller-Doblies (1985) were included in the analysis. *Hessea longituba* D. & U. Müller-Doblies, *H. brachyscypha* Baker and *H. zeyheri* Baker are included under *H. breviflora* Herb.; *H. weberlingiorum* D. & U. Müller-Doblies and *H. cinnabarina* D.& U. Müller-Doblies are grouped under *H. stellaris* (Jacq.) Herb.; and *Strumaria linguifolia* Jacq., *S. rubella* Jacq. and *S. angustifolia* Jacq. are treated as synonyms of *S. truncata* Jacq. *Strumaria undulata* Jacq., a doubtful species, was excluded entirely.

4.2 The outgroups

Traub (1962, 1963) divided Amaryllidaceae, as currently circumscribed (Dahlgren et al. 1985, Huber 1969, Schulze 1984) into two 'infrafamilies'. Among the tribes placed in the 'infrafamily' Amarylloidinae are Amaryllideae (= Crineae *sensu* Traub 1957, 1965, 1970), Haemantheae and Hippeastreae *sensu* Dahlgren *et al.* (1985) (= Zephyrantheae and Amarylleae *sensu* Traub 1962, 1963). On the basis of evidence gained from vegetative data, Arroyo & Cutler (1984) state that *Amaryllis* cannot be considered phylogenetically close to *Hippeastrum* since a few important structural features distinguish them. However, they converge florally and it is these similarities which have caused much of the confusion between *Amaryllis* and *Hippeastrum* in past literature (Sealy 1939, Traub & Moldenke 1949, Uphof 1938). In view of these similarities and differences *Hippeastreae* was chosen as an outgroup for the initial polarity hypotheses for all genera of Amaryllideae.

All characters defined for the analysis were applicable to the outgroup and ingroup with the exception of the non-phytomelanous seed coat of Amaryllideae. Haemantheae was used as a second outgroup in order to critically examine the effect of changing the polarity of floral symmetry; and this was finally used in combination with Hippeastreae as a further test of the relationships.

For the analysis of species relationships within the study group, *Nerine* was chosen as the outgroup. As can be seen from the analysis of genera within Amaryllideae (Figures 4.12 & 4.13), *Nerine* was placed within a clade which includes the study group. Data were derived from the large living collection of *Nerine* at the Kirstenbosch Botanic Garden.

None of the outgroups has a resolved phylogeny: a precondition which favours precise delimitation of character states in the ingroup (Stevens 1991). Thus if future studies reveal that outgroup variation is not as extensive and continuous as ingroup variation, the delimitation here of the states in the ingroups may require reconsideration (see Stevens 1991).

4.3 Character analysis

Neff (1986) argues that the greatest potential deficit of phylogenetic analysis is the failure to treat characters themselves as hypotheses, which are subject to test prior to their use at the higher level of cladistic analysis. Thus the primary goal of character analysis should be to analyse observations thoroughly at the level where they are low level hypotheses, so that fewer false hypotheses pass through to act as contradictory data in the cladistic analysis. To this effect I have attempted to reflect as clearly as possible how much evidence was gathered to support the definition of characters and the source of the evidence upon which an estimate of each state was made.

The characters and their states used in the analysis are enumerated in Tables 4.1, 4.3 & 4.6. All characters, were polarised using the outgroup comparison method (Watrous

& Wheeler 1981). The analyses at generic level are based on a much smaller data set than the analyses undertaken on the study group at species level, since several characters were unavailable for genera outside the study group. Stevens (1991) advocates that explicit justification for the delimitation of character states should be given as a matter of course in all phylogenetic studies. Thus, at the cost of lowering the resolution of the phylogeny, all characters varying extensively within the terminal units and whose delimitation could not be justified, were excluded. The characters selected do not show great environmental plasticity and are not related logically with one another which can result in data redundancy. According to the standard practice of avoiding any possible source of bias to the consistency index of cladograms (Kluge 1989, Sanderson & Donoghue 1989), derived character states which occurred in only one terminal taxon (autapomorphies) were ommitted from the computations but subsequently inserted on the cladograms. Measurement data (character 8, 9, Tables 4.3, 4.6) were partitioned using the method of Almeida & Bisby (1984) and are shown in Appendix 2.

In the following discussion of characters selected for the analyses emphasis is placed on the study group. Character 6 in Table 4.1 (capsule dehisence) and characters 12 & 13 in Table 4.3 (tepal margin and position) are considered self explanatory and are not discussed below. The material examined for data on bulb morphology, floral anatomy, pollen morphology, seed morphology and chromosome numbers is listed in Appendices 1-6.

4.3.1 Bulb morphology

Bulb morphology in *Namaquanula, Hessea, Carpolyza* and *Strumaria sensu lato* was studied in detail by D. & U. Müller-Doblies (1985) and was shown to be taxonomically useful. Apart from the work of Arroyo (1984) on a few species of *Crinum, Nerine* and *Amaryllis*, little else has been published on the bulb morphology of Amaryllideae. In view of the paucity of data thus far available for the tribe, this set of characters is limited here to the analysis of species within the study group.

The outer bulb scales in all species of the study group are modified into brown or tan, fibrous tunics with a parchment-like texture. *Namaquanula bruce-bayeri* differs by its secondarily cartilagenous bulb tunics which become brittle with age. Although cartilagenous tunics occur rarely in the study group, they are found in most species of *Brunsvigia, Boophane flava* and *Boophane guttata*. A characteristic of all bulbs in Amaryllideae are the minute extensible fibres which are produced when the scales are torn apart (Dahlgren *et al.* 1985, Traub 1957, 1962, 1963, pers. obs.). These are probably the remnants of the helically thickened cells reported previously in the leaves of *Amaryllis, Crinum, Nerine, Boophane* and *Brunsvigia* (Arroyo & Cutler 1984).

The inner bulb scales (character 0, Tables 4.3 & 4.6) are distinctly yellow in several, although not all, species placed in the *Gemmaria* group. This character state was used to substantiate the delimitation of the genus *Gemmaria* from *Bokkeveldia* (Müller-Doblies 1985) but the condition has since been found in bulbs of *Strumaria pubescens* (= *Bokkeveldia pubescens*) as well as *S. aestivalis* (pers. obs.).

The morphology of the bulb tunics in the study group is quite variable and can be summarised in the following arrangements (characters 1 & 2, Tables 4.3 & 4.6). In each of the following cases the prophyll is two-keeled, adaxial, non-sheathing and bladeless. The foliage leaves are bifacial and distichously arranged.

(1) In each shoot generation, the prophyll is followed by a series of amplexicaul foliage leaves and an innermost, non-amplexicaul foliage leaf. This pattern is present in *Kamiesbergia, Carpolyza, Strumaria tenella, S. hardyana* and *S. picta*. In *S. picta*, however, the vegetative sequence differs uniquely by two of the leaves (other than the prophyll), either at the beginning or end of the sequence, not producing blades (pers. obs.). (2) The prophyll is succeeded by an amplexicaul cataphyll (bladeless foliage leaf), a series of amplexicaul foliage leaves and an innermost, non-amplexicaul foliage leaf. This arrangement exists in most species of *Hessea* and the species of *Strumaria* previously placed in *Bokkeveldia* and *Gemmaria*. (3) In *Namaquanula bruce-bayeri* the prophyll is deficient and the shoot generation is reduced to occasionally four, but mostly three or less foliage leaves. All are amplexicaul, apart from the innermost non-amplexicaul leaf. D. & U. Müller-Doblies (1985) reported finding only two leaves per shoot generation in this species and placed it amongst the most reduced bulb types in Amaryllidaceae. However, bulbs collected more recently (*Van Berkel 549*, NBG), had up to two more leaves than the number originally reported (pers. obs.).(4) The prophyll is lacking. The series consists of an amplexicaul cataphyll, succeeded by several to one amplexicaul foliage leaves and a non-amplexicaul foliage leaf in the innermost position. This arrangement recurs in different genera (*Hessea cinnamomea, Namaquanula mathewsii, N. pulcherrima, Strumaria truncata, S. pygmaea* and *S. bidentata*).

In all species with an amplexicaul cataphyll, this extends above ground only in *S. truncata* and *H. breviflora*. When first exposed to light the sheathing cataphyll turns red but soon becomes brown and whithers back.

The growth pattern (character 2, Table 4.1) within species of the study group is extremely regular. Only one shoot generation per growing season is produced. Foliage leaves usually commence growth shortly after flowering. The growth rate is initially rapid until a plateau is reached, when approximately five months later the leaves die back. The bulbs become dormant during the seasonal drought. *Kamiesbergia* is the only taxon which deviates from this annual growth pattern. Several bulbs of *Kamiesbergia* have been observed, in the wild and in cultivation, with green foliage leaves during the summer drought. The growth pattern thus seems to be extended, in that some bulbs lack a dormant phase between successive shoot generations. In contrast, *Ammocharis* has an intercalary meristem (Troll 1954) and the leaves grow out again at the end of the dormant period. This is also a feature of *Cybistetes* (Milne-Redhead & Schweickerdt 1939) and to some extent *Crinum* (Verdoorn 1973).

4.3.2 Foliage leaves

For the analysis at generic level, only leaf pubescence, was considered sufficiently consistent to be of value. However, at species level, a few additional characters (0 & 1, Table 4.1; 3, 4 & 5, Tables 4.3 & 4.6; 6, Table 4.6) were used. All species of *Strumaria sensu stricto* have erect leaves arranged in a fan, a state derived from the plesiomorphic state of opposite phyllotaxis. Leaf position is variable amongst species of the *Bokkeveldia* and *Gemmaria* groups. Leaves which have the novel condition of being appressed to the ground occasionally become more upright in cultivation, but for the analysis, the derived leaf habit was coded according to observations in the field.

The species included in the *Bokkeveldia* and *Gemmaria* group have leaves which are more or less pubescent. The hairs are soft, simple and uniseriate and range in length from 0.2 mm (in *S. merxmuelleriana*) to 6 mm long (in *S. chaplinii*). The leaves are either entirely covered with hairs or only sparsely so. Pubescence dimishes in the adults of the *Bokkeveldia* group and certain species of the *Gemmaria* group (character 6, Table 4.6) but it is always present in the juveniles of both groups. Leaf surface pubescence is found nowhere else in Amaryllideae apart from *Hessea pilosula* and *H. incana*, which are puberulous, and *Brunsvigia radula* which has bristly trichomes covering the adaxial leaf surface. Leaf margins in *Crinum*, *Ammocharis* and *Cybistetes* have multiseriate and branching cartilagenous cilia (Arroyo & Cutler 1984), while in *Boophane flava* and *Boophane guttata* they are bristly. *Strumaria watermeyeri* is exceptional in having glabrous leaves with margins covered by viscose papillae to which sand grains adhere. Stickiness on leaves is also more or less developed in *Namaquanula bruce-bayeri* and *Strumaria bidentata*. In contrast to *S. watermeyeri* the stickiness is evenly laid down over the entire leaf.

A reduced number of foliage leaves is evident in *Namaquanula, Hessea* and the *Gemmaria* and *Bokkeveldia* groups, but leaf number was avoided for the analyses because of the absence of gaps in the continuum.

4.3.3 Inflorescence

The inflorescence of Amaryllideae is typical of the family. The solid, naked scape is terminated by two equitant spathe valves (Arroyo 1984), which subtend a reduced series of helicoid cymes (Müller-Doblies 1977). Two variables influence the overall shape of the inflorescence at anthesis, namely the length of the pedicels and the size of the flowers. The appearance of the inflorescence can alter still further thereafter, mostly by the elongation of the pedicels and to a lesser extent by the elongation of the capsule. The character, pedicel length relative to perigone length at anthesis, has been adopted here as a measure to reflect the inflorescence's clustered or spreading appearance (character 3, Table 4.1; 8, Table 4.3; 9, Table 4.6). The states recognised are: pedicels shorter than the perigone and pedicels longer than the perigone at anthesis. Overlap was relatively slight in *Carpolyza, H. pusilla* and *S. bidentata* (see Appendix 2).

The pedicels (character 7, Table 4.3; 8, Table 4.6) in most Amaryllideae are stiff, thereby supporting the flowers in a spreading position. Only in some species of *Strumaria sensu stricto* are the pedicels sufficiently lax for the flowers to be pendulous (*S. barbarae, S. hardyana* and *S. truncata*). In contrast, the lax appearance of the flowers of *Crinum* is due to the curvature of the perigone tube, rather than the pedicel. The fleshy green pedicels of *S. pygmaea* have developed a novel function as assimilatory structures. The filiform leaves of *S. pygmaea* remain insignificant throughout the growing season and it appears that the photosynthetic function is shared by the persistent infructescence, the pedicels of which remain green until the leaves die back.

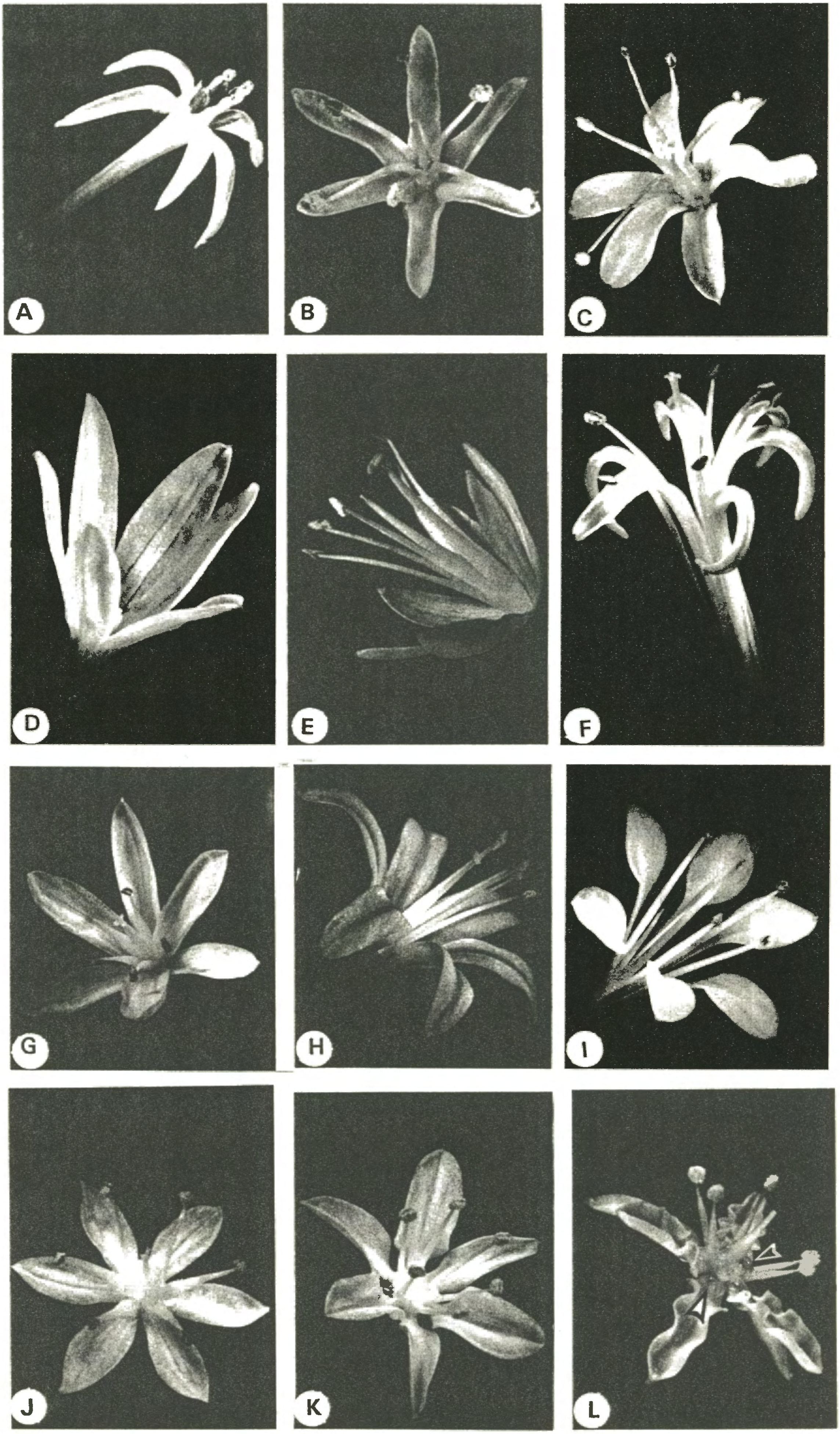
The development of the scape follows two distinct patterns (characters 4 & 5, Table 4.1; 6, Table 4.3; 7, Table 4.6), which effect different strategies of seed dispersal. A sclerenchymatous sheath is present beneath the cortex in all genera of Amaryllideae (Arroyo & Cutler 1984, pers. obs.), however, the scapes either remain flexuose, or become increasingly rigid after anthesis. Scapes which remain flexuose, remain attached to the bulb, releasing the seeds as individual units *(Amaryllis, Crinum, Ammocharis, Strumaria sensu stricto*). Scapes which become rigid, rapidly detach either at ground level, *(Brunsvigia, Boophane guttata* group, *Hessea, Kamiesbergia, Namaquanula,* the *Gemmaria* group and most species of the *Bokkeveldia* group), or at the top of the scape (*Boophane disticha* group, *Cybistetes*), and the entire infructescence is released as a single unit which is dispersed through tumbling. This process of dispersal, termed anemogeochory, occurs in many arid areas worldwide (Van der Pijl 1982).

4.3.4 Flowers

Both actinomorphic and zygomorphic flowers are present in Amaryllideae (character 7, Table 4.1). The character analysis indicated that actinomorphic flowers are consistent in three groups of the tribe (the *Boophane disticha* group, *Cybistetes* and Strumariinae *sensu* Müller-Doblies). Tendencies towards actinomorphy are present in several other genera of Amaryllideae (*Crinum, Cybistetes, Boophane guttata* and *Boophane pulchra*), but despite differences in the degree of zygomorphy, the flowers of these taxa were all coded as zygomorphic for lack of any other criterion for partitioning floral symmetry.

Within the study group flowers are either symtepalous or choritepalous. In both the symtepalous and choritepalous categories, species have open, spreading perigones as well as narrow, funnel-shaped perigones (Figure 4.1). Thus flowers at anthesis are either stellate, funnelform, or campanulate (character 9, Table 4.3; 10, Table 4.6). As no

FIGURE 4.1-- Mature floral form. A, *Kamiesbergia stenosiphon;* B & C, *Hessea breviflora;* D, *Carpolyza spiralis*; E, *Strumaria truncata*; F, *S. phonolithica*; G, *S. picta*; H, *S. salteri*; I, *S. watermeyeri;* J, *S. tenella*; K, *S. unguiculata*; L, *S. gemmata*, in which nectar droplets in axils between inner filaments and style, and false nectar spots on tepals below the filaments are indicated.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transformation series connecting these flower shapes could be developed, the character states were treated as nonadditive in the analysis. This was done despite the reservations expressed by Mickevich & Weller (1990) of the current use of this method in cladistic program packages. *Kamiesbergia* has somewhat hypocrateriform flowers due to an extensive narrow perigone tube, a condition which occurs nowhere else in the study group (Figure 4.1a).

Flower colour in the tribe ranges predominantly from pink to white, usually with darker streaking. Only a few species have red flowers and even fewer have pale lemon flowers. Verdoorn (1973) was the first to draw attention to differences in colouring among the ageing flowers of certain Amaryllideae. She noted that floral pigmentation in most species of *Crinum* is accentuated with age, whereas the colour is lost and the flowers turn brown in a few species. Colour changes at senescence are also a feature of the study group (character 8, Table 4.1; 10, Table 4.3). Loss of floral pigmentation is consistent in *Hessea, Kamiesbergia* and *Namaquanula.* In species of all the other genera, flower colour is enhanced with age (pers. obs.).

The interpretation of the perigone tube (character 11, Tables 4.3 & 4.6) is somewhat complex due to its extension and fusion with the androecium in some species. A perigone tube is clearly present in *Kamiesbergia, Namaquanula bruce-bayeri* and *Carpolyza;* in *Hessea* only a few species are symtepalous; whereas the tepals are free from each other in *Strumaria sensu lato.* D. & U. Müller-Doblies (1985) refer to the tube in *Hessea* as a winged-tube ("pterotubus"), which they regard as a derived structure. This increment is the result of vertical growth in the tepal/stamen confluence region, thus creating the winged appearance of the tube. Only two species of *Hessea* (*H. stellaris* and *H. breviflora*) have the plesiomorphous smooth symtepalous region present below the tepal/stamen confluence. All the remaining *Hessea* species have only the tubular component formed by the tepal/stamen confluence. This trend towards a reduction of the symtepalous tube and its replacement by a tubular component from the tepal/stamen confluence is also found in *Nerine.* However, since the tepals in *Nerine* taper proximally, the tube does not appear to be winged.

4.3.5 Stamens

The stamens in Amaryllideae are epitepalous. The adnation is clearly evident in species with well developed perigone tubes but less so in the choritepalous species where the adnation is much reduced (as in the *Gemmaria* group). The stamens are either separate or variously connate proximally (characters 9, Table 4.1; 14, Table 4.3). The connation in most genera extends only shortly above the tepal/stamen confluence (*Nerine, Brunsvigia, Boophane guttata, Boophane flava, Boophane pulchra, Kamiesbergia* and *Namaquanula*), but in certain species of *Hessea* (*H. breviflora* and *H. stellaris*) the connation is sufficiently elongated to form a distinct staminal tube reaching well above the tepal/stamen confluence (Figure 4.1C). In *Namaquanula mathewsii* and *N. pulcherrima* the bases of the filaments are dorso-ventrally flattened and they are fused to each other laterally, to form a very low connate ring up to 0.2 mm high (Figure 4.2B). In the analysis this has been hypothesised as the ultimate stage in reduction of the staminal connation. This pattern is constant in populations of *N. mathewsii* but is more variable in *N. pulcherrima.* The stamens in *Amaryllis* are connate but lack a distinct ring above the tepal stamen confluence.

Separate stamens are less common in the tribe. The interpretation of the stamens in *Carpolyza* and the species of *Strumaria* previously placed in *Gemmaria, Tedingea* (Figure 4.2) and *Bokkeveldia* (Figure 4.3) as separate from each other, is unproblematical, but in *Strumaria sensu stricto* it is more complex. Although separate in *S. bidentata,* (Figure 4.4) the stamens in the remaining four species of *Strumaria sensu stricto* are proximally connate (*S. barbarae, S. phonolithica, S. hardyana* and *S. truncata*). Serial sections of the different floral forms of *S. truncata,* however, indicated a transition series in which the separate stamens, which are proximally adnate to the style, become connate to each other (Figure 4.4). The staminal tube is interpreted as a secondary development and not homologous with that of other genera of Amaryllideae. Thus the staminal connation in species of *Strumaria sensu stricto* is treated independently from the staminal connation present in other genera of Amaryllideae (character 15, Table 4.3; 12, Table 4.6).

The androecium is variously adnate to the style in *Carpolyza* and *Strumaria sensu lato* (Figures 4.2, 4.3 & 4.4), and is a unique feature. The position of the adnation separates *Carpolyza* from *Strumaria sensu lato* but quantitative alterations and shifts in proportion contribute to the different patterns among *Strumaria sensu stricto,* and the *Bokkeveldia* and *Gemmaria* groups. Only the inner whorl of stamens is adnate proximally to the style in *Carpolyza.* Adnation of all the stamens to the style is the basic pattern in *Strumaria sensu lato* (character 10, Table 4.1). The adnation is vertically extended in most species of *Strumaria sensu stricto* and the *Bokkeveldia* group (reaching up to 4 mm in some species), or reduced to a small basal region in *S. tenella, S. pygmaea* and the *Gemmaria* group. Serial sections of representative flowers of these genera (Appendix 3), indicated that a more or less well developed efferent canal leads from each septal nectary to the sinus formed by the confluence of the inner filament with the style (Figures 4.2, 4.3 & 4.4). For the analysis no attempt was made to code the extent of stamen/style adnation, since this is expressed by character 21 & 14 (Tables 4.3 & 4.6): the shape of the nectar collection site. The secondary connation of the stamens to form a staminal tube, in which only the outer filaments remain adnate to the style, is illustrated for *S. truncata* (Figure 4.4). The stamens in all other genera of the tribe are quite free from the style. Because of the evident stepwise development from: (0) stamens free from style; (1)

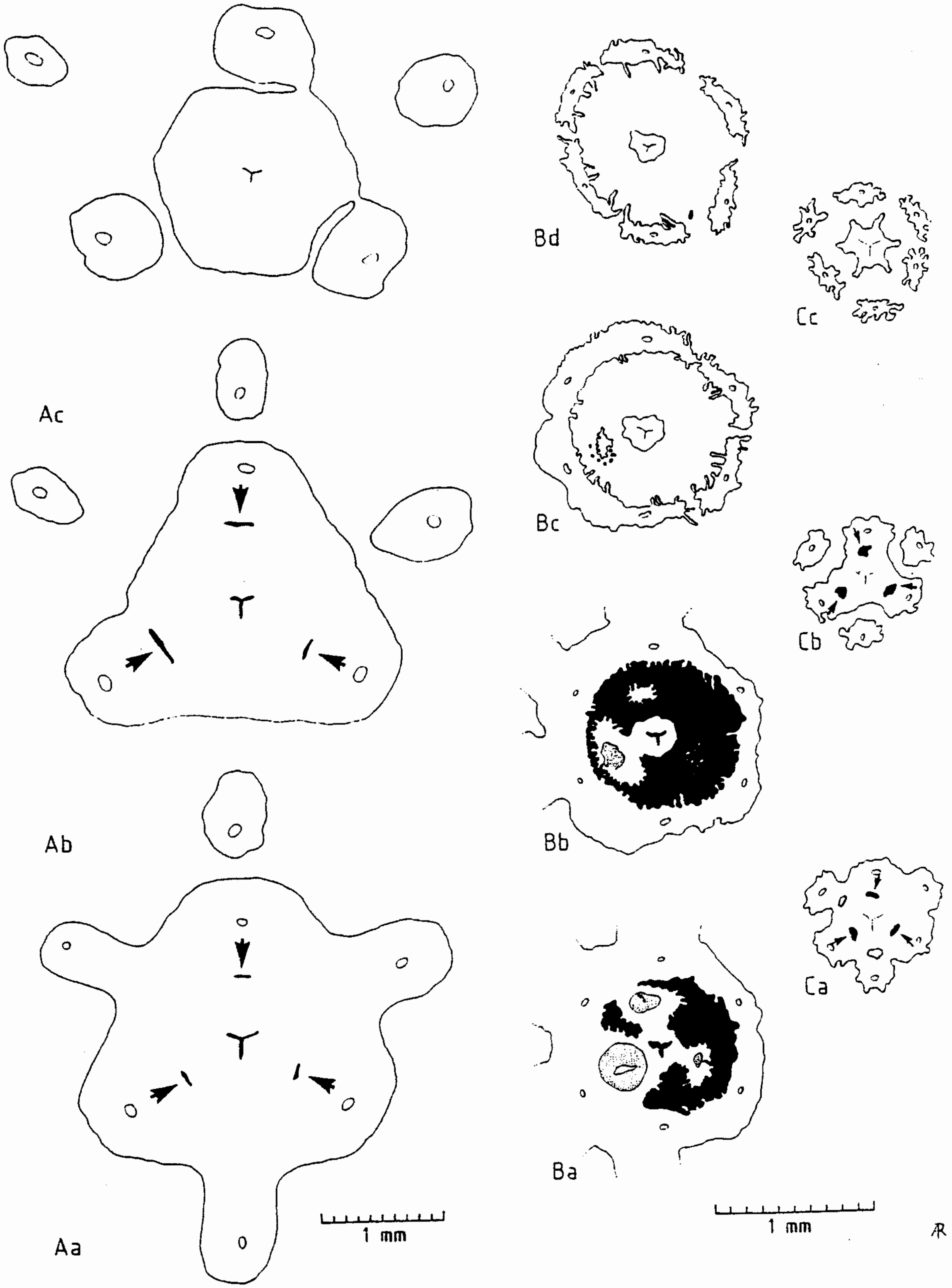

FIGURE 4.2– Transverse section series through filaments and style of mature flowers of *Strumaria* and *Namaquanula* species. Efferent canals for nectar are indicated by arrows. A, *S. gemmata, Vlok 956;* **Aa**, all filaments adnate to broadened style proximally; **Ab**, outer filaments free, efferent canals increasing in width; **Ac**, inner filaments freeing from style. **B**. *N. pulcherrima, Snijman 1022*; **Ba-Bb**, filaments connate into a low proximal ring, pulvini protruding above sunken ovary dome; **Bc-Bd**, filaments, with inner surface bearing trichomes, becoming separate. **C**, *S. tenella, Snijman 856;* **Ca**, all filaments adnate to style proximally; **Cb**, outer filaments free from style; **Cc**, all filaments free from enlarged style.

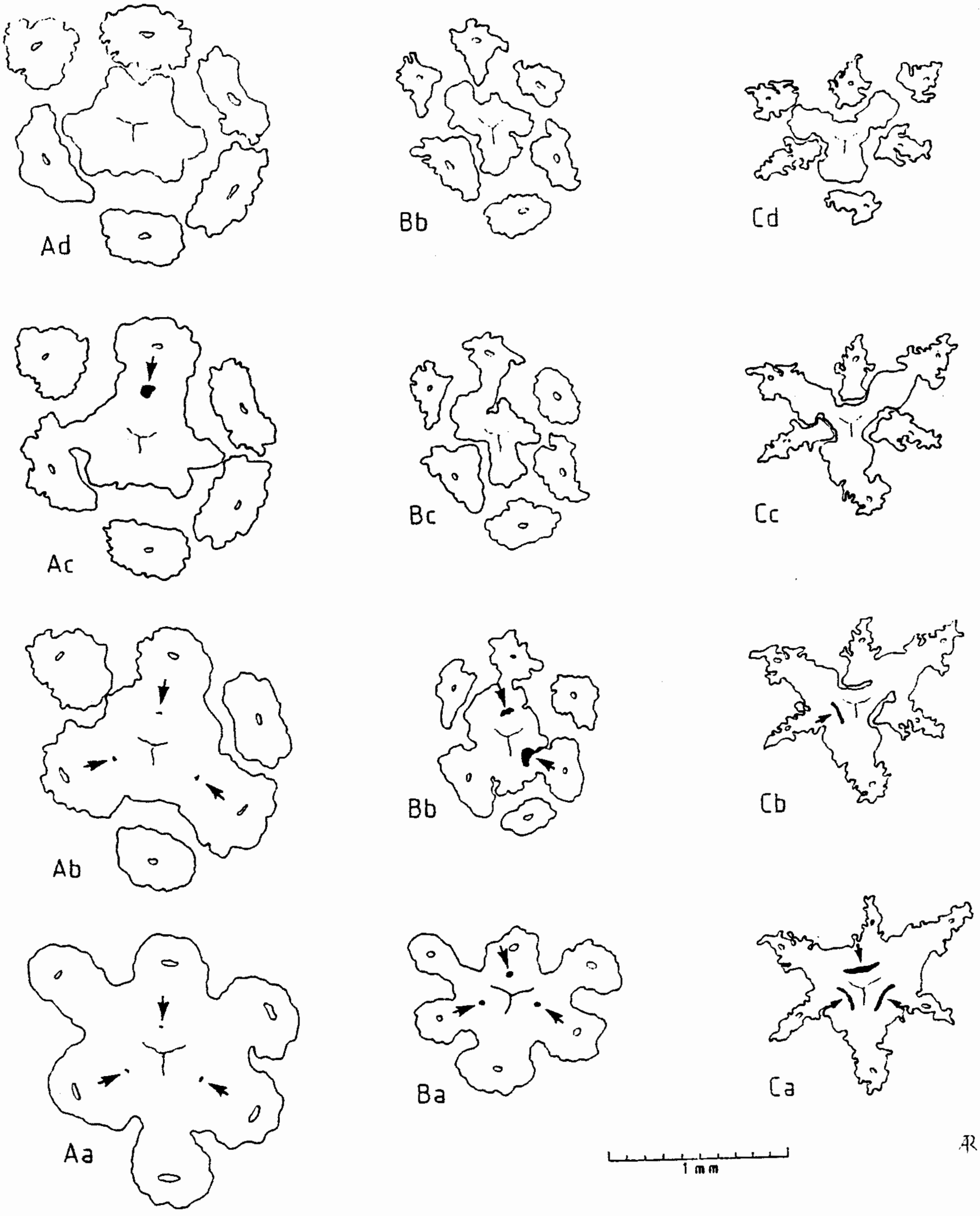

FIGURE 4.3-- Transverse section series through filaments and style of mature flowers of *Strumaria* species (subgenus Gemmaria). Efferent canals for nectar are indicated by arrows. **A**, *S. picta, Perry 1337,* **Aa**, all filaments adnate to style proximally; **Ab**, outer filaments free; **Ac**, inner filaments separating from style after efferent canals have increased in diam.; **Ad**, all filaments free distally. **B**, *S. salteri, Perry 1321, Snijman 254;* **Ba**, all filaments adnate to style proximally; **Bb**, outer filaments free and efferent canals enlarged; **Bc**, inner filaments separating from style; **Bd**, all filaments free distally. **C**, *S. pubescens, Snijman 1164*; **Ca**, all filaments adnate to style proximally and efferent canals tangentially widened; **Cb**, inner filaments separating from style; **Cc**, inner filaments free; **Cd**, all filaments free distally.

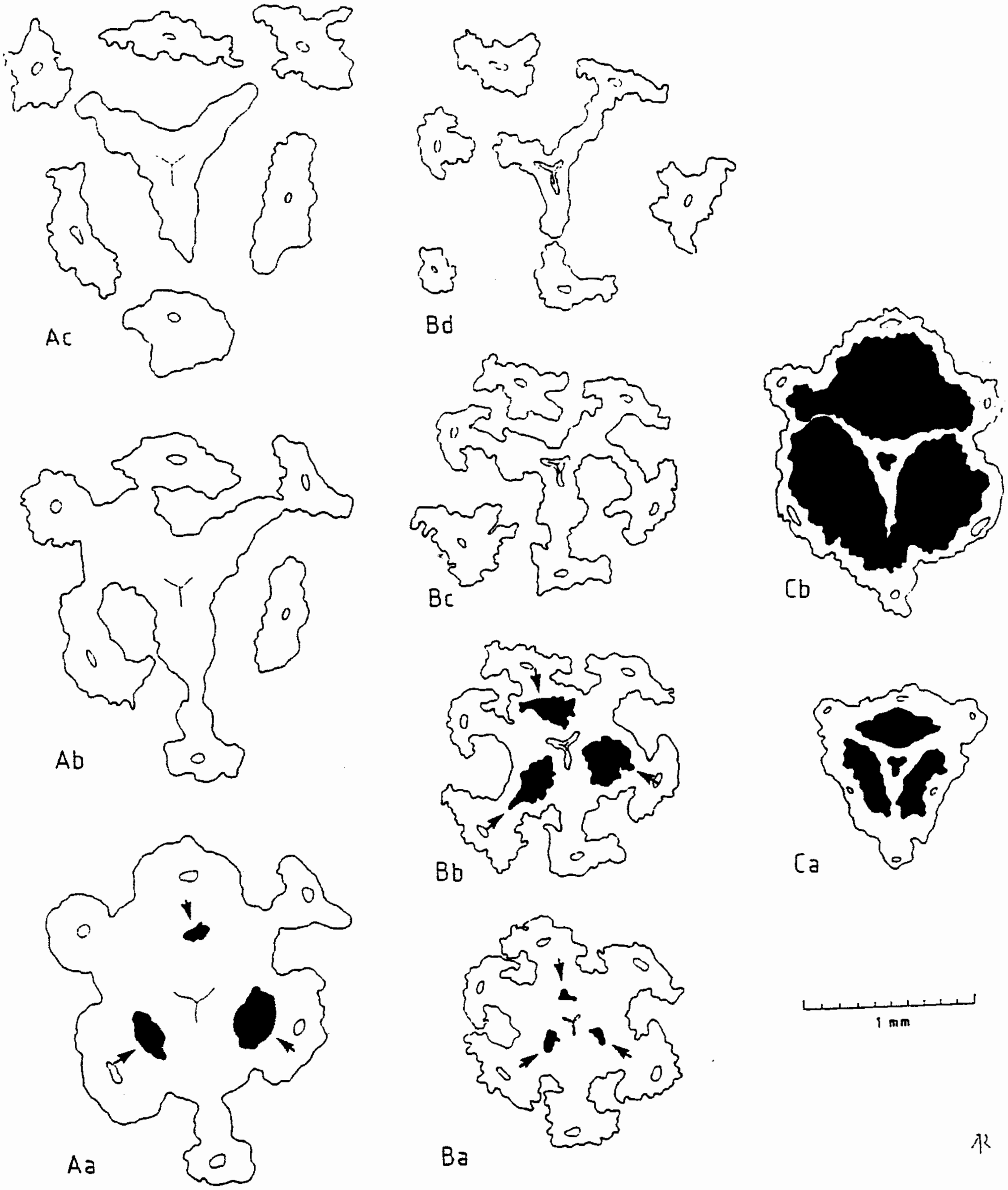

FIGURE 4.4– Transverse section series through filaments and style of mature flowers of *Strumaria* species (subgenus Strumaria). Efferent canals for nectar are indicated by arrows. A, *S. bidentata, Van Jaarsveld & Kuhn 3221;* Aa, all filaments adnate to style proximally, efferent canals large; Ab, inner filaments separating from style; Ac, all filaments free from style distally. B, *S. truncata, Duncan 257;* Ba, all filaments adnate to style proximally; Bb, efferent canals enlarged; Bc, inner filaments separating from style; Bd, all filaments free distally. C, *S. truncata, Barker 10192;* Ca, inner filaments laterally broadened and connate to outer filaments to form a tube, outer filaments adnate to winged edges of style, efferent canals replaced by large nectar wells; Cb, filament tube with enlarged circumference, separating from winged style.

both stamen whorls adnate to style; (2) both stamen whorls connate to each other and only the outer whorl adnate to the style; these character states have been treated as additive in the analyses of the study group.

In comparison to older taxonomic treatments, staminal dentation now has more limited use as a taxonomic character in Amaryllidaceae (Meerow 1989). I have used staminal dentation with equal circumspection. The absence or presence of staminal appendages in certain species is highly variable (Müller-Doblies 1985) but their presence in others is constant. The many species which are placed into synonymy under *Strumaria truncata* in this study, were originally characterised by different staminal teeth (Jacquin 1795). An examination of flowers within these taxa has since shown this feature to be unreliable (pers. obs.). In contrast, the numerous irregularly-shaped teeth midway along the length of the stamens in *S. bidentata* are consistently present and considered to be a unique feature of this species. The staminal appendages in *Namaquanula bruce-bayeri, N. mathewsii* and *N. pulcherrima* take the form of a solitary, inwardly-curved hook on each filament, with the ventral surface of the filament below each hook covered with trichomes (characters 12 & 13, Table 4.1; 16 & 17, Table 4.3) (Figure 4.2B). These hooks are short in *N. bruce-bayeri* and generally more prominent in *N. mathewsii* and *N. pulcherrima* but the ranges in length overlap, particularly in populations of *N. pulcherrima*. D. & U. Müller-Doblies (1985) maintained that the staminal hooks in *N. mathewsii* and *N. pulcherrima* are distinct from those of *N. bruce-bayeri* but failed to elaborate on whether they considered the characters to be homologous or not. I hypothesise that they are homologous structures.

4.3.6 Anthers

The anthers of Amaryllideae are linear-oblong to oblong, and range from dorsifixed to centrifixed. Anthers in *Hessea* and *Carpolyza* have been described repeatedly in past literature as "basifixed" (Baker 1888, 1896, Dyer 1976, Phillips 1951, Traub 1963), however this attachment has since been shown to be more specialised. The anther connective is formed into a tube, in which the distal tip of the filament is inserted and variously hidden (Müller-Doblies 1985). The relative lengths of the dorsal and ventral walls of the tubular connective enabled D. & U. Müller-Doblies to recognise three categories of anther attachment; dorsifixed anthers (relative lengths less than 50%); subcentrifixed anthers (relative lengths 50-75%); and centrifixed anthers (relative lengths more than 75%). Anthers are dorsifixed in most genera of Amaryllideae, subcentrifixed in *Carpolyza,* the *Gemmaria* and *Bokkeveldia* groups and centrifixed in *Hessea* (character 19, Table 4.3; 13, Table 4.6). *Kamiesbergia* differs uniquely as regards anther attachment. Unlike the usual medifixed position, the anthers of *Kamiesbergia* are attached to the filaments in the lower quarter of the connective (Figure 9.1). Both *Namaquanula bruce-bayeri* and *Kamiesbergia* lack a sheathed connective (character 18, Table 4.3).

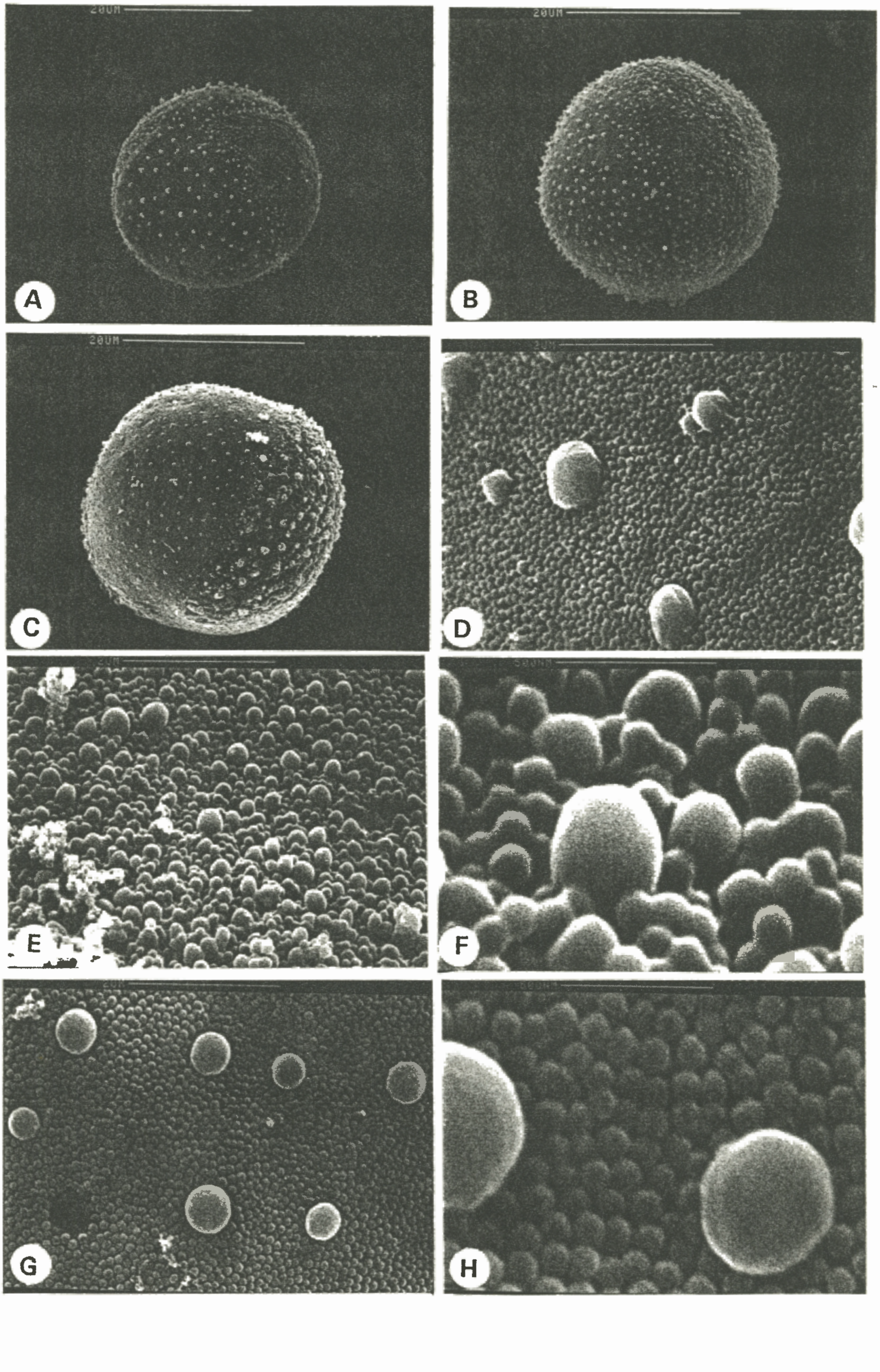

FIGURE 4.5-- Pollen morphology. Bisulculate pollen grains of: A, *Boophane disticha, Van Jaarsveld 5794*; B, *Kamiesbergia stenosiphon, Snijman 1175*; C, *Strumaria aestivalis, Perry 1991*; D-F, *Nerine huttonii, NBG 114/86*, showing surface ornamentation (D), and sulculus ornamentation (E & F); G-H, *Hessea stellaris, Goldblatt 6089*, showing gemmae and spinulae.

4.3.7 Pollen

The pollen grains of the tribe are consistently bisulculate (Erdtman 1966), isopolar, globose and biradial, with an intectate-columellate exine. Surface ornamentation is dimorphic and gemmate with scattered large spinulae (4--6 x the diameter of the gemmae), which decrease in size and increase in frequency toward the sulculus margins (Figure 4.5). This character was not used other than at tribal level. An analysis of pollen grain size is yet to be undertaken.

4.3.8 Nectaries

Published data on nectary position in Amaryllideae are available for *Amaryllis*, *Crinum* and *Hessea* (Daumann 1970, Singh 1972). The survey of this character has been extended since to *Brunsvigia, Nerine* and representative species of the study group (Manning unpub. ms.). Without exception the nectaries are septal. Daumanns' interpretation (Daumann 1970), of the anomalous androecial nectary situated on the abaxial surface of the filament base in *Strumaria gemmata (= Hessea gemmata)* could not be substantiated. Serial sections of *S. gemmata* flowers have shown that the nectaries line the septa in the distal half of the ovary and extend to the top of the prominent ovary dome (Figure 4.6A). Each septal nectary leads into a short efferent canal, which opens near the basal adaxial surface of each inner filament. A similar pattern was found in each of the species examined anatomically (Appendix 3). Species with the most prominent and widest ovary domes (*Strumaria gemmata* and *Namaquanula mathewsii*) appeared to have the largest nectaries (Figure 4.6), and species with the most extensive adnation of the inner stamens to the style have the longest efferent canals (*S. salteri*). The interesting trends apparent in the small set of species examined, indicate that the nectaries may yield potentially useful characters for future analyses.

Strumaria gemmata is the only species known in Amaryllideae with false-nectar spots in the form of shiny, solid, translucent hemispherical structures situated proximally on the adaxial surface of each tepal, below each filament (Figure 4.1L).

The sites for nectar collection (character 16, Table 4.1; 20, Table 4.3) and the shape of the collection sites (character 21, Table 4.3; 14, Table 4.6) have been used in the analyses. The plesiomorphic site for nectar collection is a central well around the base of the style. In contrast, nectar collects in three discrete sites, in the axils between the inner filaments and the style, in *Carpolyza* and *Strumaria sensu lato.* These specialised sites vary in depth and diameter. In most species (*Carpolyza, S. tenella, S. pygmaea* and the *Bokkeveldia* and *Gemmaria* groups), the axil between the inner filament and style is shallow and sinus-like, wherein nectar gathers and is held as a single droplet (Figure 4.1L). Through lengthwise extension of the stamen/style adnation, as well as radial extension of the confluence of the style with the outer filaments, the volume of the concavity between the inner filaments and style has been increased, and deep nectar wells have developed.

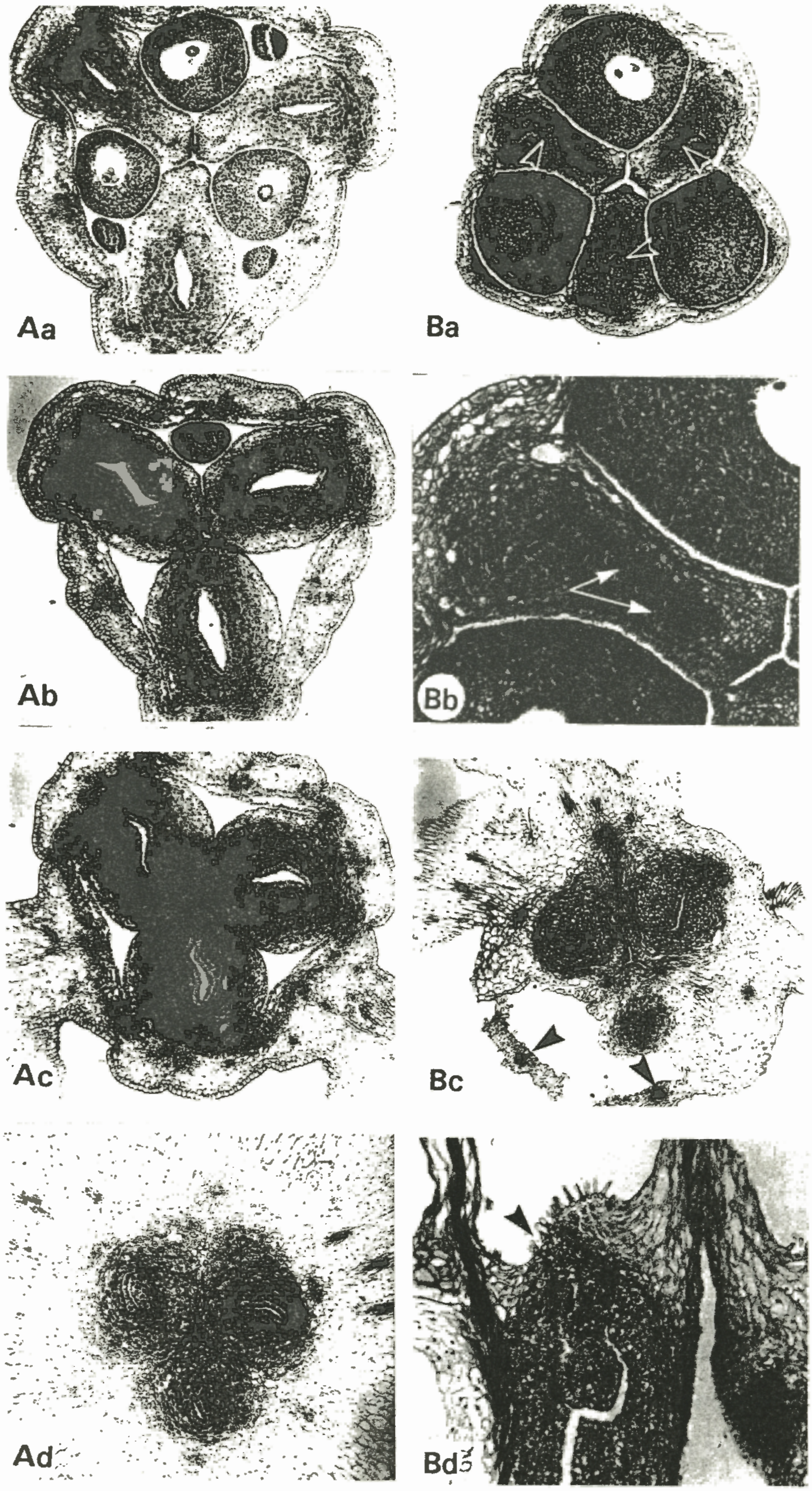

FIGURE 4.6-- Nectary morphology. Transverse (Aa-Bc) and longitudinal (Bd) sections through the ovary of *Strumaria* and *Namaquanula* species. **A**, *S. gemmata, Vlok 956;* **Aa**, midway up ovary; **Ab**, near top of ovary; **Ac**, nectary in sterile portion of ovary dome at level of outer tepal attachment; **Ad**, nectary at level of inner tepal attachment (x100). **B**, *N. mathewsii, Snijman 840*; **Ba**, midway up ovary; **Bb**, nectary detail (x 250) showing 3-4-layered nectary parenchyma and palisade-like epithelial cells; **Bc**, nectary in sterile portion of ovary dome, note that the outer and inner filaments are free from the nectary (x 100); **Bd**, exit of nectary from abaxial rim of trichome-covered pulvinus on ovary dome (x 200).

Such nectar wells are present in *Strumaria barbarae, S. phonolithica, S. hardyana, S. truncata* (Figure 4.4C) and the more distantly related *S. aestivalis*. Surface tension is sufficient to hold nectar in position, even in the wells of the pendulous flowers of *S. barbarae, S. hardyana* and *S. truncata*.

Namaquanula mathewsii and *N. pulcherrima* differ from all other species of the subtribe by having three raised papillate areas, referred to in this work as pulvini (Figures 4.2B & 4.6Bd) present on the ovary dome between the inner filaments and the style (character 22, Table 4.3). Nectar egresses on the abaxial rim of these pulvini and accumulates all around the staminal ring. This is regarded as an extreme form of the basic pattern in which nectar gathers centrally around the style.

4.3.9 Style

Style form (character 15, Table 4.1; 23, Table 4.3; 15, Table 4.6) in Amaryllideae is typically slender. As first suggested by Goldblatt (1976a), the variously enlarged style in species of *Strumaria sensu lato* constitutes a unique, derived character for the genus. The proximal swelling, which takes many forms, reaches at most half the style length (character 24, Table 4.3; 16, Table 4.6). The series of style forms has been divided into three categories, each defined by its symmetry about a horizontal axis, which was placed a quarter of the distance from the bottom to the tip of the style. Thus the styles are described as: distinctly thickened upwards to almost midway along their length (*S. tenella, S. pygmaea, S. bidentata, S. picta* and *S. discifera*); more or less equally thickened in the lower half (most species of the *Bokkeveldia* group and *Strumaria sensu stricto*); or distinctly broadest near the base (the *Gemmaria* group). These categories do not accommodate the various sculptural patterns present on the swellings, but mostly these are variable within species. Due to uncertainty in interpreting transformation within the series, this character was treated as non-additive.

The flowers of the study group are typically protandrous and the style rapidly elongates and branches after anthesis. The length of the style-branches, as well as the degree of recurving, differs somewhat among species at maturity. *Strumaria sensu lato* and *Kamiesbergia* tend to have papillae covering most of the adaxial surface whereas in *Hessea* the style branches tend to lack papillae proximally. In *Namaquanula bruce-bayeri* the branches are much reduced and the style apex appears truncate. A survey of the style apex in the outgroup *Nerine* showed it to be equally variable, ranging from capitate to three-lobed. No attempt was made to use this character in the analysis.

4.3.10 Ovules and seeds

The ovules of the study group are subglobose, anatropous and borne on axile placentae. Ovule number in the study group is mostly less than seven per locule.

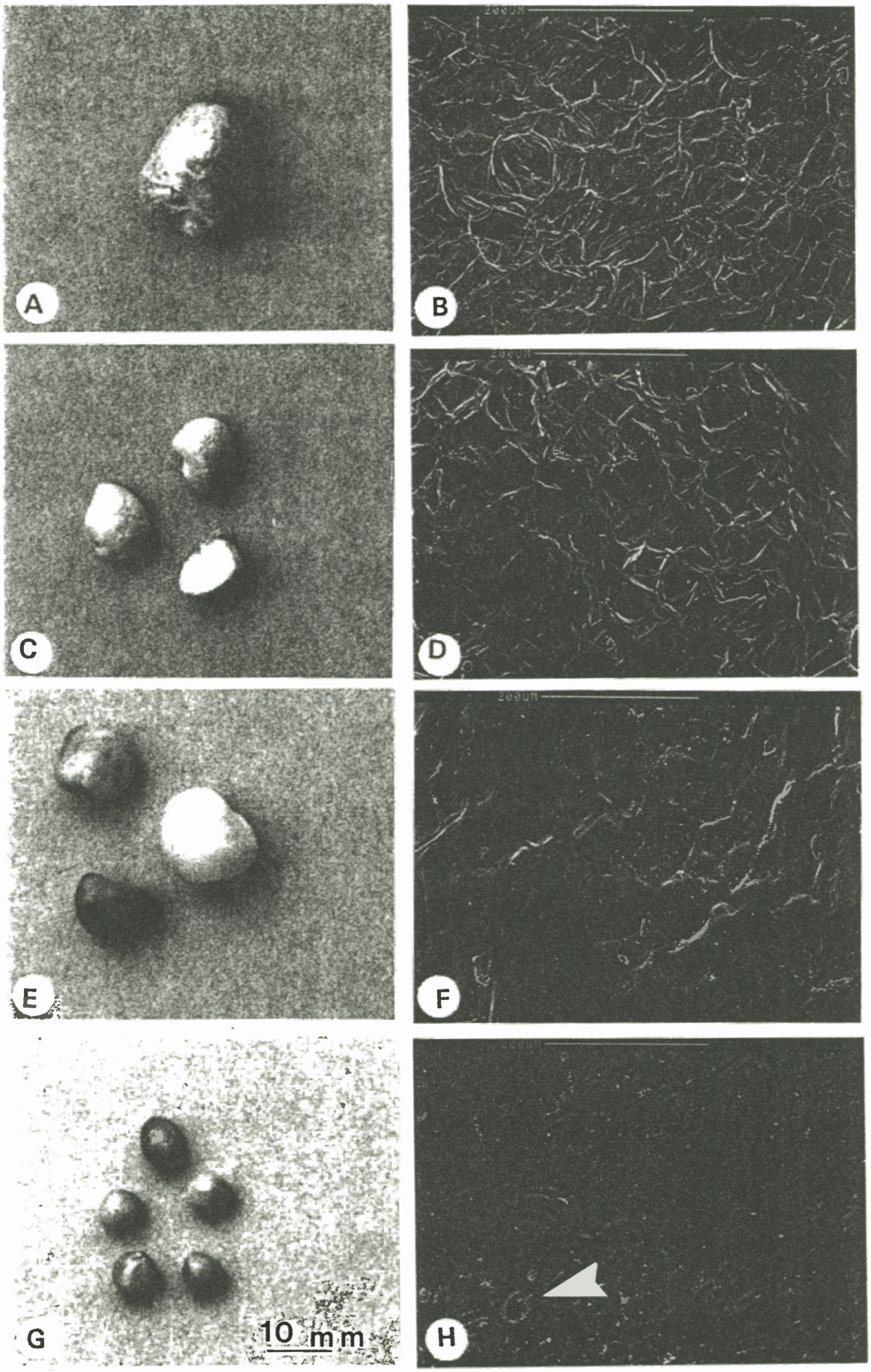

FIGURE 4.7-- Mature seed and testa morphology. A & B, *Crinum variabile, NBG 892/82,* showing detail of corky testa; C & D, *Ammocharis coranica,* KG 268/89, showing detail of corky testa; E & F, *Amaryllis belladonna, Snijman s.n.,* showing detail of smooth cuticle; G & H, *Boophane flava, Perry 1128,* showing detail of stomatose testa.

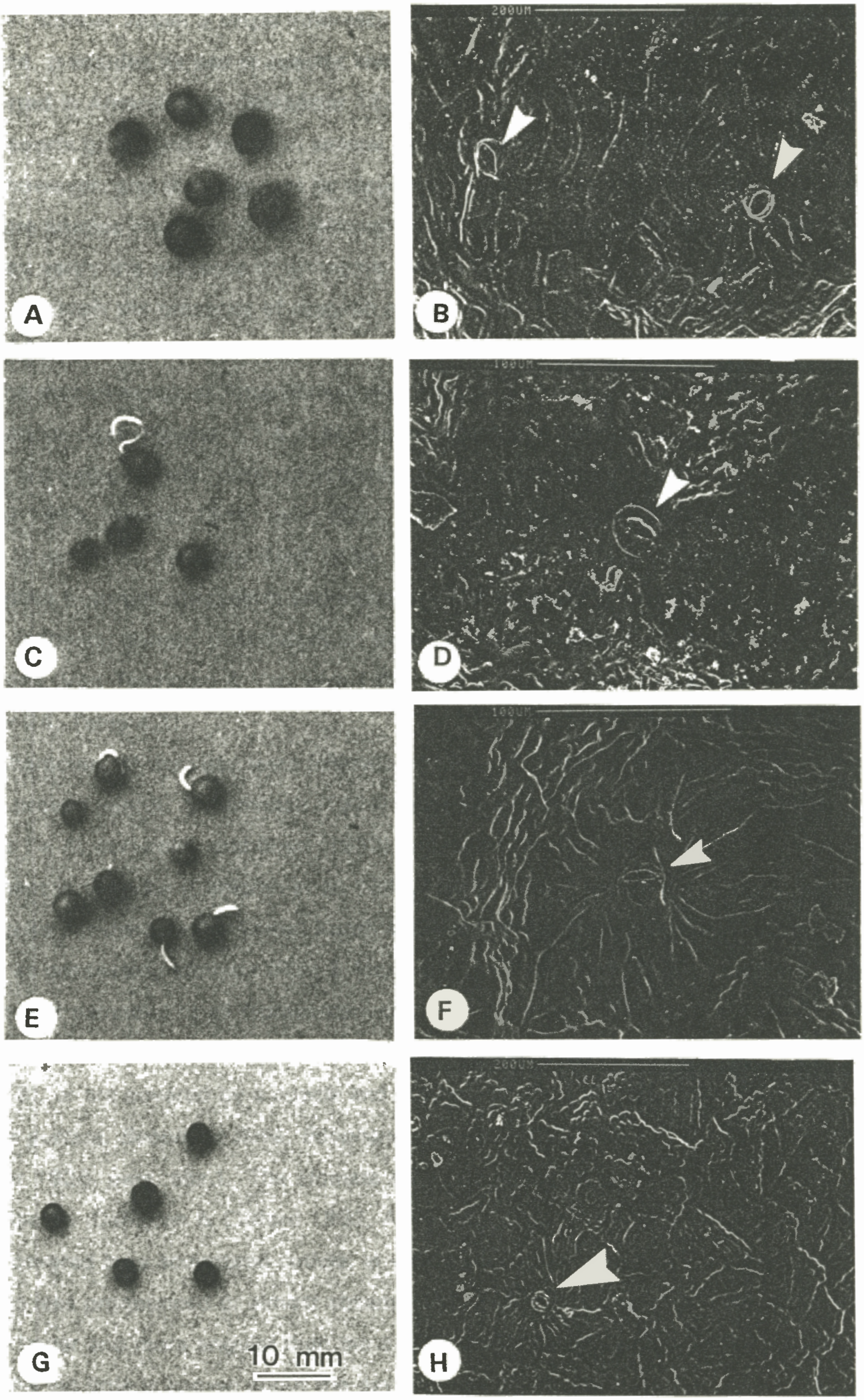

FIGURE 4.8-- Mature seed and testa morphology. A & B, *Brunsvigia orientalis*, *Snijman s.n.*, showing detail of stomatose testa; C & D, *Nerine filifolia*, *NBG 877/75*, showing detail of stomatose testa; E & F, *Strumaria truncata*, *Perry 1057*, showing detail of stomatose testa; G & H, *Hessea breviflora*, *Williamson 3431*, showing detail of stomatose testa.

Variation in number within a single inflorescence from the outermost to innermost flowers of the cyme, precludes its use at species level. Both unitegmic and ategmic ovules have been reported in Amaryllideae (Markötter 1936, Prillieux 1858, Schlimbach 1924, Tomita 1931). Reports of ategmic ovules in several dicotyledonous families have been proved incorrect however, and they may yet be disproved in Amaryllidaceae (Maheshwari 1950). Thus, future studies may lead to the reinterpretation of the ategmic ovules as unitegmic and thereby verify the presence of unitegmic ovules throughout the tribe. Alternatively, they may establish the presence of ategmic ovules within *Crinum* as a derived condition (Bouman 1984).

The mature seeds of Amaryllideae are chlorophyllous, fleshy and lack a phytomelanous coat (Figures 4.7 & 4.8). An exception is *Amaryllis belladonna* in which the seeds are white or pink, with chlorophyllous tissue present only in the embryo (Markötter 1936, Marloth 1915, pers. obs.). Loss of developmental complexity presents problems in assessing similarity (Neff 1986, Stevens 1984, Weston 1988). The absence of chlorophyll from the endosperm and integument of *Amaryllis* is treated here as a derived condition following current hypotheses on trends in the evolution of seeds of the dicotyledons (Von Teichman & Van Wyk 1991) and is thus regarded as an autapomorphy (character 24, Table 4.1).

Characters of the seed testa (characters 17 & 18, Table 4.1), which could be easily sampled, proved useful. Schlimbach (1924) reported stomata on the seeds of *Nerine sarniensis* (= *N. curvifolia*) and Boyd (1932) recorded them in *Carpolyza spiralis*, a novel development in the tribe (Dahlgren *et al.* 1985, Huber 1969). Elsewhere in the family only *Hymenocallis occidentalis* (Le Conte) Kunth and *Eucrosia* Ker-Gawl. have also been recorded as possessing stomata (Flint & Moreland 1943, Meerow 1987). A survey of this character was extended to all representatives of Amaryllideae. The testas are either corky and lack stomata (*Crinum, Cybistetes, Boophane disticha, Boophane haemanthoides*) (Figure 4.8), or are covered by a cuticle and possess stomata (*Nerine, Brunsvigia, Boophane guttata, Boophane flava, Boophane pulchra* and all members of the study group) (Markötter 1936, pers. obs.). The stomata are anomocytic, as is typical for Amaryllidaceae (Dahlgren & Clifford 1982, Arroyo & Cutler 1984), and the surrounding cells are covered by a sculptured cuticle, in which the central striations vary from thick and sinuous to less pronounced or almost absent (Figure 4.8). Seeds with a corky testa are generally larger and more angular than the ovoidal-shaped seeds with stomata (Figures 4.7 & 4.8). As yet little is known about the development of the seed coat. In this analysis the presence of an unspecialised cutinous testa is hypothesised as the basic condition which gave rise to two derived conditions: a corky testa in one group and a stomatose testa in the other.

4.3.11 Chromosome cytology

Chromosome numbers (character 19, Table 4.1; 25, Table 4.3; 17 & 26, Table 4.6) in Amaryllideae are well known, largely due to the work of Gouws (1949), Wilsenach (1965), Jones & Smith (1967), Goldblatt (1972, 1976a) and Nordal & Wahlstrøm (1980). A karyotype of $x = 11$ characterises most genera and is considered basic in the tribe (Goldblatt 1976a), as well as the family (Inariyama 1937, Meerow 1984, Satô 1938, Wilsenach 1965). Species of *Carpolyza* and *Strumaria sensu lato* (of which some were previously treated as *Hessea* species by Goldblatt (1976a)) have a reduced base number of $x = 10$ (Goldblatt 1976a, Müller-Doblies *et al.* 1987, pers. obs.). The only exception in *Strumaria* is *S. pygmaea* which has $x = 11$.

In general, Amaryllideae with $x = 11$ display an underlying uniformity in their chromosome phenotypes. The karyotypes comprise a pair of large metacentric chromosomes; six pairs of medium-sized metacentric to submetacentric chromosomes, of which one is sometimes a SAT chromosome pair; and four pairs of shorter metacentric or occasionally submetacentric chromosomes. As can be seen from Figure 4.9, slight variations in relative arm lengths exist between the *Hessea* species examined. The pair of large metacentrics, which are widespread in the tribe, are absent in *Kamiesbergia*, *Hessea breviflora* and *H. stellaris*, and replaced by a pair of acrocentric to submetacentric chromosomes. *Strumaria pygmaea* shows the greatest bimodality and differs from the basic pattern in having one large metacentric pair; two medium submetacentric pairs and eight short submetacentric pairs (Figure 4.10F). This karyotype has been treated as an autapomorphy in the analyses.

The chromosome complement in species with $x = 10$, consists of one pair of large metacentric chromosomes; five somewhat shorter metacentric pairs, one pair of which may be characterised by a large satellite on each chromosome; and four short metacentric pairs (Figure 4.10). Müller-Doblies *et al.* (1987) claimed that differences in the mean arm ratio of the largest chromosome among species of the subtribe Strumariinae support their generic delimitation. Jones & Smith (1967) stress that the chromosome types in *Crinum* do not form a highly rigid pattern. The large chromosomes of *Hessea* also proved variable. Thus the purported value of the relative arm lengths of the large chromosome as a taxonomic character does not seem plausible.

In the study group, B chromosomes occurred in *Hessea breviflora* ($2n = 22 + 1 - 3B$) (Goldblatt 1976a), *Strumaria truncata* ($2n = 20 + 1 - 2B$) (Goldblatt 1976a), S. *discifera* ($2n = 20 + 1B$) and S. *villosa* ($2n = 20 + 2B$) (Figure 4.11). The size of the B chromosomes more or less approximates the length of either arm of the short metacentric chromosomes. The centromeres of the B chromosomes in *H. breviflora* are clearly telocentric and in *S. discifera* and S. *villosa* they appear to be median.

Chromosome data were obtained from Goldblatt (1976a, unpub. data), as well as from the material studied in Appendix 6.

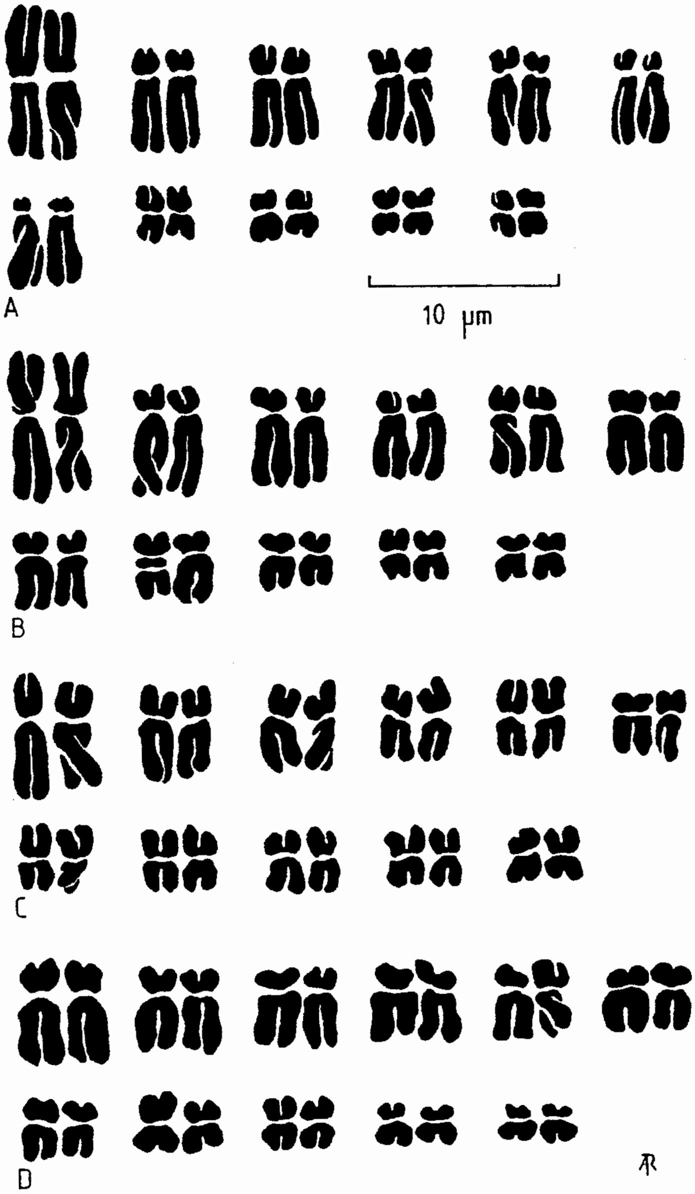

FIGURE 4.9-- Karyotypes of *Namaquanula* and *Hessea* species, 2n = 22. A, *N. bruce-bayeri, Van Berkel 552*; B, *H. pilosula, Snijman 1131*; C, *H. breviflora, Van Jaarsveld 5305*; D, *H. stellaris, Goldblatt 6089.*

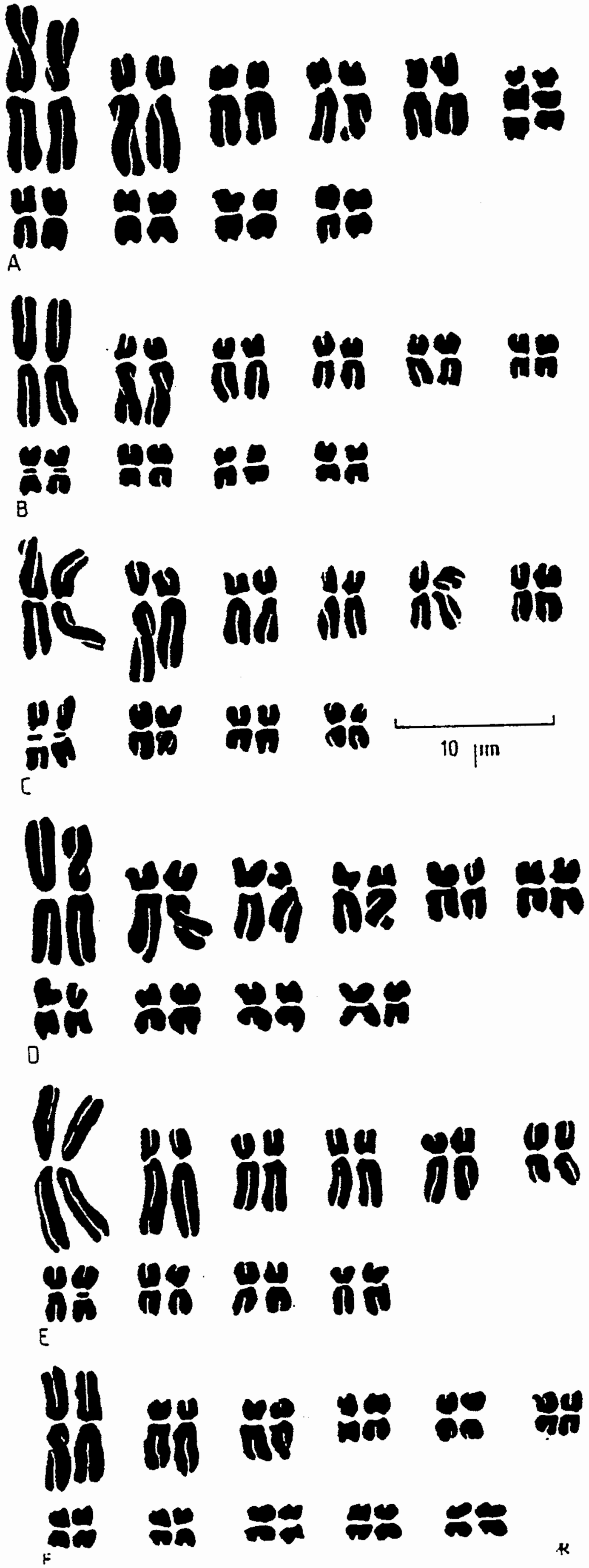

FIGURE 4.10– Karyotypes of *Strumaria* species, 2n = 20 and 2n = 22. A, *S. watermeyeri* subsp. *botterkloofensis*, *Snijman 1079*; B, *S. discifera*, *Perry & Snijman 2042*; C, *S. karoopoortensis*, *Perry 1278*; D, *S. merxmuelleriana*, *Snijman 306*; E, *S. chaplinii*, *Duncan 28*; F, *S. pygmaea*, *Snijman 862*.

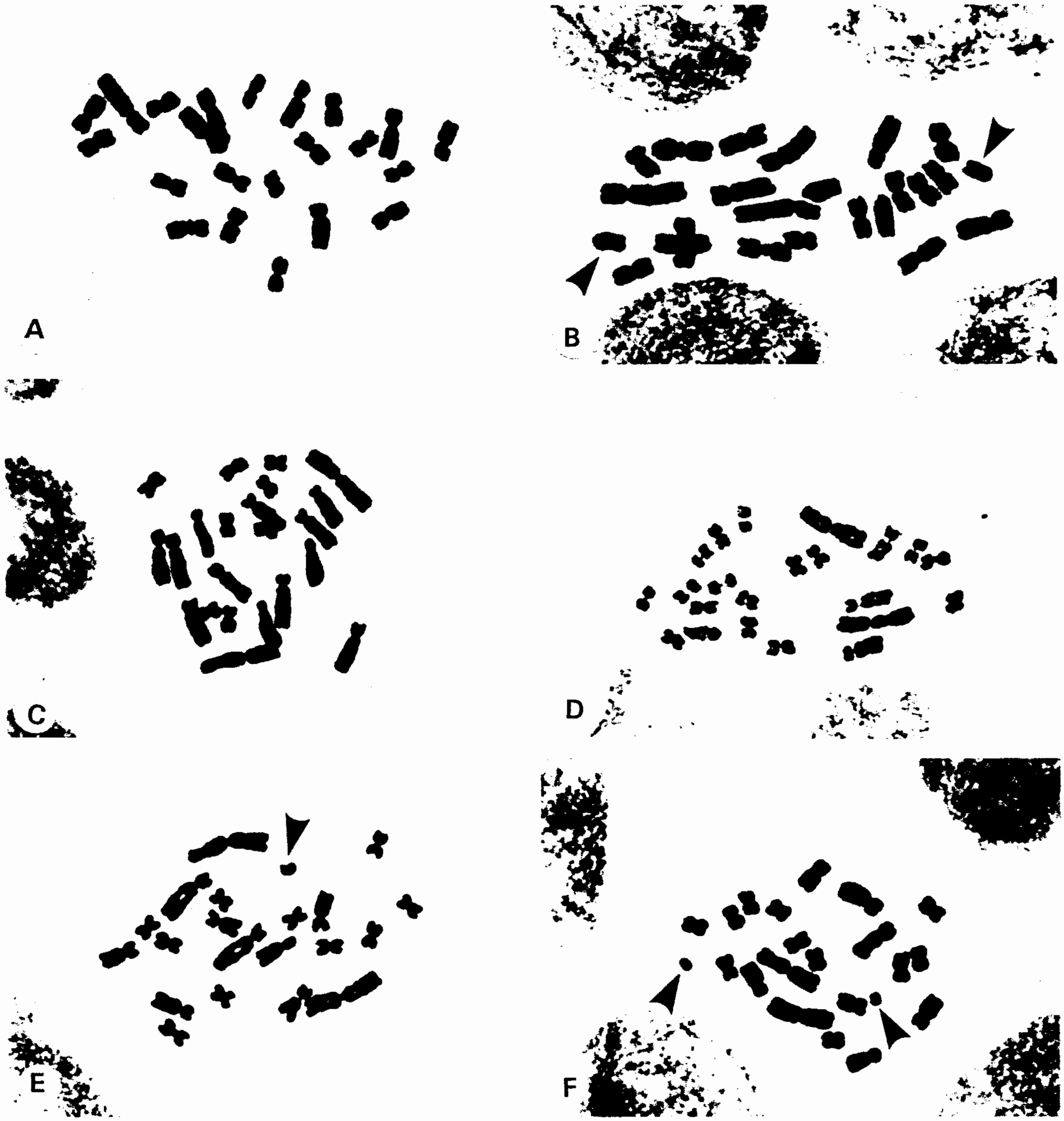

FIGURE 4.11-- Somatic chromosomes of *Hessea, Namaquanula* and *Strumaria* species. Arrows indicate B chromosomes. A, *H. breviflora, Barker 2868*, 2n = 22; B, *H. breviflora, Perry 690*, 2n = 22 + 2B (arrowed); C, *N. bruce-bayeri, Van Berkel 552*, 2n = 22; D, *S. pygmaea, Snijman 862*, 2n = 22; E, *S. discifera, Snijman 261*, 2n = 20 + 1B; F, *S. villosa, Perry 1544*, 2n = 20 + 2B (X 1500).

4.3.12 *A posteriori* examination of characters

After generating an initial set of cladograms, re-examination of some character states was undertaken to finalise their coding. The procedure was limited to an informal reconsideration of character states without recourse to the more rigorous techniques of transmodal character determinations (Mickevich & Weller 1990).

4.4 Cladistic analysis

4.4.1 Analysis of the genera of Amaryllideae

Twenty characters were defined for the analyses of the genera, species groups and species of Amaryllideae (Table 4.1). These were transformed into a data matrix (Table 4.2) and analysed with the use of Hennig 86 (Farris 1988). With Haemantheae as the outgroup the ie* option gave 55 minimal-length cladograms of 32 steps, and a consistency index of 0.68. The strict consensus tree is shown in Figure 4.12a. The robustness of this consensus tree was examined by manipulation of the data to reflect the use of Hippeastreae as the outgroup. The ie* option gave 330 minimal-length cladograms of 32 steps and a consistency index of 0.68. The strict consensus tree is shown in Figure 4.12b. Two major clades are present in both trees: one containing *Crinum, Ammocharis, Cybistetes* and the *Boophane disticha* group; the other containing *Nerine, Brunsvigia,* the *Boophane guttata* group, *Boophane pulchra* and the study group. Only the placement of *Amaryllis* differed between the two and either formed one branch of an initial trichotomy or fell within the clade close to *Nerine* and *Brunsvigia.*

When both Haemantheae and Hippeastreae were used as a combined outgroup *Amaryllis* again fell within the clade with *Nerine* and *Brunsvigia*. Since this resolution is in agreement with that given in Figure 4.12a, only Haemantheae was used as the outgroup in subsequent analyses. As a means of choosing among the multiple equally parsimonious cladograms, the xsteps w routine of successive approximations character weighting was applied: a technique which selects cladograms based on the set of most consistent characters (Carpenter 1988). The ie* option using the weighted data set gave 3 trees and a strict consensus tree as shown in Figure 4.13. Characters are mapped on the consensus tree in Figure 4.18. Comparison of the three minimal-length trees in Figure 4.13 showed that their differences were due to the weakness of character 3, which in turn reflects the problem experienced in delimiting this character (pedicel/perigone length) into two discrete states.

No matter how the data were manipulated the study group was only ever resolved as a monophyletic group within a clade containing *Nerine, Brunsvigia, Boophane pulchra* and the *Boophane guttata* group. The only synapomorphy for the study group in Figure 4.18 is actinomorphic flowers, a homoplastic character. The synapomorphies for each of the clades at the initial dichotomy of Figure 4.18 are: a corky, dry testa for the clade containing *Crinum, Ammocharis, Cybistetes* and the *Boophane disticha* group; and the

TABLE 4.1-- Characters used for the cladistic analyses of genera and species groups of Amaryllideae. The numbers correspond to the data matrix in Table 4.2 and the cladogram in Figure 4.18. (Higher scores indicate relative apomorphy. Autapomorphies at the end of the list were not used in the analysis but were later inserted on the cladogram.)

CHARACTER	STATE
Leaves	
0. Foliage leaf vestiture	0 = glabrous, 1 = pubescent (at least in juveniles).
1. Foliage leaf margins	0 = without cartilagenous teeth, 1 = with cartilagenous teeth.
2. Growth in each leaf	0 = limited to one season, 1 = punctuated growth flushes occurring in the previous and current season.
Inflorescences	
3. Relative pedicel/perigone lengths at anthesis	0 = shorter than perigone, 1 = longer than perigone.
4. Infructescence habit at seed set	0 = scape persistent, 1 = scape detaching proximally.
5. Infructescence habit at seed set	0 = flower cluster persisting to scape, 1 = flower cluster detaching from scape.
6. Capsule	0 = indehiscent, 1 = dehiscent.
7. Floral symmetry	0 = actinomorphic, 1 = zygomorphic.
8. Flower colour at senescence	0 = pigmentation accentuated, 1 = pigmentation lost.
9. Staminal connation	0 = separate, 1 = connate.
10. Staminal adnation	0 = free from style, 1 = inner stamens adnate to style, 2 = all stamens adnate to style, 3 = stamens fused into a tube and outer filaments adnate to style.
11. Lateral filament appendages	0 = never developed, 1 = developed at least in some species.
12. Ventral filament hook	0 = absent, 1 = present.
13. Ventral surface of filaments	0 = smooth, 1 = covered with trichomes proximally.
14. Anther attachment	0 = otherwise, 1 = in a distinct sheath formed by the anther connective. (Dorsal wall 50-100% ventral wall.)
15. Style form	0 = slender, 1 = inflated, thickened or winged proximally.
16. Nectar collection sites	0 = in a central well around the style, 1 = in axils between inner filaments and style.
Seeds	
17. Nonphytomelanous testa	0 = a thin cuticle, 1 = dry and corky.
18. Testa	0 = without stomata, 1 = with stomata.
Cytology	
19. Basic chromosome number	0 = 11, 1 = 10.
Autapomorphies	
20. Leaf markings	0 = unmarked, 1 = speckled with red.
21. Stamen length	0 = equal, 1 = dimorphic.
22. Anther attachment	0 = medifixed, 1 = attached near base of connective.
23. Seed testa	0 = clear, 1 = rose pink.
24. Seed endosperm and integument	0 = chlorophyllous, 1 = nonchlorophyllous.
25. Pollen grain	0 = monosulculate, 1 = bisulculate.

TABLE 4.2-- Data matrix for Amaryllideae with Haemantheae and Hippeastreae as the outgroups. (Question marks indicate inapplicable or unknown character states.) Character 10 was treated as additive. The characters correspond to TABLE 4.1.

Taxon	Character states				Abbre-viation
	0 0	0 5	1 0	1 5	
Hippeastreae	00000	01101	00000	00?00	HIPP
Haemantheae	00000	00000	00000	0000?	HAEM
Crinum	01100	00100	00000	00100	CRIN
Boophane disticha group	00000	10000	00000	00100	DIST
Ammocharis	01100	00000	00000	00100	AMMO
Cybistetes	01100	10100	00000	00100	CYBI
Amaryllis	00000	01101	00000	00000	AMAR
Carpolyza	00011	01000	10001	01011	CARP
Strumaria tenella	00011	01000	20000	11011	TENE
Strumaria sensu stricto	00000	0100?	30000	11011	STRU
Bokkeveldia group	10011	01000	20001	11011	BOKK
Gemmaria group	10011	01000	20001	11011	GEMM
Nerine	00001	01101	01000	00010	NERI
Brunsvigia	00011	01101	01000	00010	BRUN
Boophane pulchra	00001	01101	00000	00010	PULC
Kamiesbergia	00011	01011	00000	00010	KAMI
Boophane guttata group	00011	011?1	00000	00010	GUTT
Hessea	00011	01011	00001	00010	HESS
Namaquanula bruce-bayeri	00011	01011	00110	00010	BRUC
Namaquanula mathewsii group	00011	01011	00111	00010	MATH
Strumaria pygmaea	00011	01000	20000	1101?	PYGM
Weights:*	111 00024	1 1 00204	1111 00000	11111 00000	

*Weights obtained by successive approximations character weighting using the xsteps w sequence.

presence of a dehiscent capsule for the largest clade consisting of *Amaryllis, Brunsvigia, Boophane pulchra,* the *Boophane guttata* group and the study group. Other apomorphies which corroborate the dehiscent capsule are zygomorphic flowers and proximally connate stamens, both of which have one subsequent reversal.

Phytomelanous seeds are considered synapomorphic for Asparagales (Dahlgren & Rasmussen 1983), and the lack of phytomelan may be secondary. Thus the dry, corky, non-phytomelanous seed coat present in *Crinum, Ammocharis, Cybistetes* and the *Boophane disticha* group is interpreted here as a specialised development. On this basis the clade containing *Crinum* and its allies is accepted as well defined. The presence of stomata on the testa which defines all genera, except *Amaryllis*, in the second major clade has been rarely reported in Amaryllidaceae and is unargueably a derived state. Consequently, the clade which it supports is also accepted with a high degree of confidence, based on the criterion of experience and knowledge of the characters and the

```
ie length 32 ci 68 ri 87 trees 55
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tsave file 0 from ie 55 trees
nelsen file 0 from ie 55 trees
tplot file 0 from nelsen 1 tree
    ╒═0haem
├═30┤   ╒═2dist
    ├═28┤   ╒═3ammo
    │   ╘═26┤   ╒═1crin
    │       ╘═24╧═4cybi
    │   ╒═5amar
    ╘═29┤   ╒═11neri
        ╘═27╪═12brun
            ├═13pulc
            ├═15gutt
            │   ╒═14kami
            ╘═25╪═16hess
                │   ╒═17bruc
                ├═23╧═18math
                │   ╒═6carp
                ╘═22┤   ╒═7tene
                    ╘═21╪═8stru
                        ├═19pygm
                        │   ╒═9bokk
                        ╘═20╧═10gemm
```

A

```
ie length 32 ci 68 ri 87 trees 330
tsave cinout14
tsave file 0 from ie 330 trees
nelsen file 0 from ie 330 trees
tplot file 0 from nelsen 1 tree
    ╒═0hipp
├═28╪═5amar
    │   ╒═2dist
    ├═26┤   ╒═1crin
    │   ╘═24╪═3ammo
    │       ╘═4cybi
    │   ╒═11neri
    ╘═27╪═12brun
        ├═13pulc
        ├═15gutt
        │   ╒═14kami
        ╘═25╪═16hess
            │   ╒═17bruc
            ├═23╧═18math
            │   ╒═6carp
            ╘═22┤   ╒═7tene
                ╘═21╪═8stru
                    ├═19pygm
                    │   ╒═9bokk
                    ╘═20╧═10gemm
```

B

FIGURE 4.12-- Cladistic computations using the ie* option of the genera and species groups of the tribe Amaryllideae based on the unweighted data in Table 4.2. **A**, Strict consensus tree with Haemantheae as the outgroup; **B**, strict consensus tree with Hippeastreae as the outgroup.

```
ie length 188 ci 91 ri 97 trees 3
tsave cinout28
tsave file 0 from ie 3 trees
tplot file 0 from ie 3 trees
```

```
ie length 188 ci 91 ri 97 trees 3
tsave cinout30
tsave file 0 from ie 3 trees
nelsen file 0 from ie 3 trees
tplot file 0 from nelsen 1 tree
```

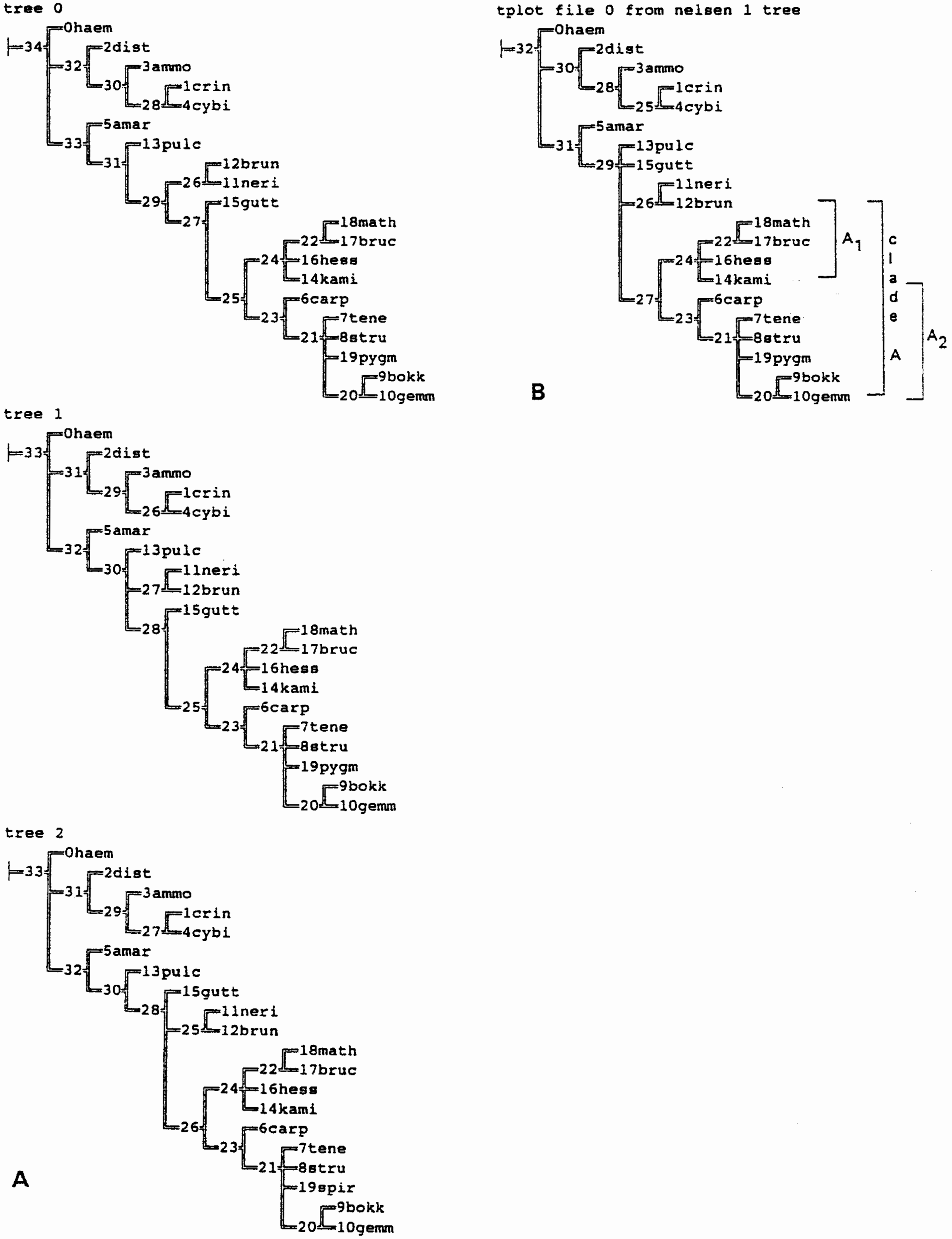


FIGURE 4.13– Cladistic computations using the ie* option of the genera and species groups of the tribe Amaryllideae based on the weighted data in Table 4.2 with Haemantheae as the outgroup. A, All the minimal-length trees; B, strict consensus, tree.

group (see Linder 1991a). The dehiscence of the capsule is considered sufficient to support the inclusion of *Amaryllis* with *Nerine* and its allies. It is the only taxon in the clade with an unspecialised seed cuticle and the lack of chlorophyllous tissue from the endosperm and integument (Markötter 1936).

4.4.2 Analysis of all known species of the study group

Subsequent analyses at the species level focused on clade A of the consensus trees in Figure 4.13B (the study group of *Kamiesbergia, Namaquanula, Hessea, Strumaria, sensu lato* and *Carpolyza*). Characters used in the analysis of all 37 species, with *Nerine* as the outgroup, are listed in Table 4.3. The data matrix is shown in Table 4.4. Because the ie option was considered to be prohibitively time consuming for exhaustive analyses on such a large data set, only the mhennig* bb (branch-breaker) option was used to examine the internal structuring of the study group. This algorithm calculated over 100 cladograms of minimal length 55, and CI 0.56. The consensus tree is shown in Figure 4.14a.

The plausibility of the synapomorphies defining the clades formed by the first dichotomy were examined. Apart from the homoplastic synapomorphy, scape detaching proximally at seed set (character 6), subclade A_1 is also defined by the strong character 10 (flowers turning brown with age), which although not unique in the tribe is recorded elsewhere only in *Crinum*. Subclade A_2 of this tree is defined by the two unique characters 14 and 20 (stamens separate; and nectar collecting in three discrete sites) and the strong character 25 ($x = 10$) which evolved only once in the tribe and has only one subsequent reversal to the bimodal karyotype of $x = 11$ in *S. pygmaea*. Moreover, both clades formed at the initial dichotomy proved to be congruent with segments A_1 and A_2 obtained from a different data set for the genera of Amaryllideae (Figure 4.13). Thus the division of the study group into two clades at species level appeared satisfactory. Removal of the extremely homoplastic characters 0, 9 and 24 resulted in greater resolution above node 48 of the strict consensus tree as shown in Figure 4.14b; this being obtained from 6 minimal-length cladograms of 41 steps and with a consistency index of 0.63. The procedure nevertheless lacked the power to resolve the species relationships in both segments simultaneously. In an attempt to obtain greater internal resolution a separate set of analyses for each segment follows.

TABLE 4.3-- Characters used for the cladistic analysis of the 37 species of the study group. The numbers correspond to the data matrices in Tables 4.4 & 4.5 and the cladogram in Figure 4.19. (Higher scores indicate relative apomorphy. Characters treated as nonadditive are marked thus*. Autapomorphies at the end of the list were not used in the analyses but were later inserted on the cladogram. Characters marked in bold were used for the subsequent analysis of *Kamiesbergia, Hessea* and *Namaquanula*.

CHARACTER	STATES
Bulb and leaves	
0. Inner tunics of bulb	0, white; 1, yellow.
1. Prophyll	0 = non-amplexicaul and bladeless, 1 = amplexicaul and bladeless.
2. Second leaf of renewal bud	0 = an amplexicaul foliage leaf, 1 = bladeless and amplexicaul (cataphyll).
3. Foliage leaf arrangement	0 = opposite, 1 = flabelliform.
4. Foliage leaf position	0 = spreading, 1 = appressed to ground.
5.* Foliage leaf vesture	0 = glabrous, 1 = puberulous, 2 = pubescent (in juveniles at least).
Inflorescence	
6. Scape habit at seed set	0 = persistent, 1 = detaching proximally.
7. Pedicel habit at anthesis	0 = stiff, 1 = lax to pendulous.
8. Relative pedicel/perigone lengths	0 = shorter than the perigone, 1 = longer than the perigone.
Flowers	
9.* Flower shape at anthesis	0 = narrowly to widely funnelform, 1 = campanulate, 2 = stellate.
10. Flower colour at senescence	0 = pigmentation accentuated, 1 = pigmentation lost (turning brown).
11. Tepals	0 = symtepalous, 1 = choritepalous.
12. Tepal margins	0 = more or less smooth, 1 = distinctly crisped.
13. Tepal position	0 = spreading, 1 = rotate.
14. Staminal connation	0 = connate basally, 1 = separate.
15. Staminal adnation	0 = stamens entirely free from style, 1 = both staminal whorls adnate to style, 2 = both staminal whorls fused to each other and outer whorl adnate to style.
16. Ventral filament hook	0 = absent, 1 = present.
17. Ventral surface of filaments	0 = smooth, 1 = covered proximally with trichomes.
18. Anther attachment	0 = filament shortly sheathed by connective, 1 = filament not sheathed by connective.
19. Filament attachment in sheathed connective	0 = dorsifixed, 1 = subcentrifixed, 2 = centrifixed.
20. Nectar collection sites	0 = in central well around style, 1 = in axils between inner filaments and style.
21. Form of nectar collection site between inner filaments and style	0 = shallow hollows, 1 = deep wells.
22. Green ovary dome	0 = not raised, 1 = raised into three pulvini.
23. Style form	0 = more or less slender along its entire length, 1 = distinctly thickened, inflated or winged in lower half.
24.* Form of style swelling	0 = thickening upwards to ± midway along its length, 1 = ± equally thickened in lower region, 2 = broadest near base.
Cytology	
25. Basic chromosome number	0 = 11, 1 = 10.
Autapomorphies	
26. Bulb covering	0 = fibrous, 1 = cartilagenous.
27. Cataphyll colour	0 = not coloured, 1 = reddened.
28. Leaf surface	0 = not sticky, 1 = sticky.
29. Flower colour	0 = pink to white, 1 = yellow.
30. Stamen length	0 = equal, 1 = dimorphic.
31. Anther attachment	0 = medifixed, 1 = attached near base of connective.

TABLE 4.4-- Data matrix for all species of the study group with *Nerine* as the outgroup. The characters correspond to those in Table 4.3. (A question mark indicates unknown or inapplicable character states. Characters 5, 9 & 24 were treated as nonadditive.)

Taxon	Character states						Abbreviation
Char no.	0	0	1	1	2	2	
	0	5	0	5	0	5	
Nerine	00000	0000?	00000	00010	0?00?	0	NER
Carpolyza	00000	00010	00001	?0011	1000?	1	CAR
Strumaria tenella	00000	00012	01001	10010	10?10	1	TEN
S. pygmaea	01000	00012	01001	10010	10?10	?	PYG
S. bidentata	01010	00001	01001	10010	10?10	1	BID
S. phonolithica	???10	00000	?1001	20010	11?11	1	PHO
S. barbarae	???10	0?100	01001	20010	11?11	1	BAR
S. hardyana	00010	00100	01001	20010	11?11	1	HAR
S. truncata	01010	00100	01001	20010	11?11	1	TRU
S. picta	00000	20001	01001	10011	10?10	1	PIC
S. perryae	00100	21010	01001	10011	10?11	1	PER
S. salteri	00101	21010	01001	10011	10?11	1	SAL
S. watermeyeri	00101	?1000	01001	10011	10?11	1	WAT
S. pubescens	10100	21010	01001	10011	10?11	1	PUB
S. aestivalis	10100	21010	01001	10011	11?11	1	AES
S. discifera	00100	21012	01001	10011	10?10	1	DIS
S. karoopoortensis	10100	21012	01001	10011	10?12	1	KRP
S. unguiculata	00100	20012	01001	10011	10?12	1	UNG
S. gemmata	10101	21012	01101	10011	10?12	1	GEM
S. chaplinii	00101	21012	01001	10011	10?12	1	CHA
S. leipoldtii	00101	21012	01001	10011	10?12	?	LEI
S. villosa	10101	21012	01001	10011	10?12	1	VIL
S. karooica	10101	21012	01001	10011	10?12	1	KAR
S. massoniella	1??01	2?012	01001	10011	10?12	1	MAS
S. merxmuelleriana	10101	2?012	01001	10011	10?12	1	MER
Kamiesbergia	0000	0101?	1000	0000?	0?00?	0	KAM
Namaquanula bruce-bayeri	0?000	01010	10000	0110?	0?00?	0	BRU
N. pulcherrima	01000	01012	11010	01111	0?10?	0	PUL
N. mathewsii	01000	01012	11010	01111	0?10?	0	MAT
Hessea cinnamomea	01000	01012	11100	00012	0?00?	0	CIN
H. monticola	00100	01012	11100	00012	0?00?	0	MON
H. undosa	00100	0?012	11100	00012	0?00?	0	UND
H. pilosula	00100	11012	11000	00012	0?00?	0	PIL
H. incana	00100	11012	11000	00012	0?00?	0	INC
H. pusilla	00100	0?012	11000	00012	0?00?	0	PUS
H. stellaris	00100	01012	10000	00012	0?00?	0	STE
H. speciosa	00100	01012	11000	00012	0?00?	0	SPE
H. breviflora	00100	01012	10000	00012	0?00?	0	BRE
Char. no.	0	0	1	1	2	2	
	0	5	0	5	0	5	

```
mhennig length 55 ci 56 ri 88 trees 5
bb file 0 from mhennig 5 trees
bb length 55 ci 56 ri 88 trees 100 (overflow)
tsave sheout2
tsave file 0 from bb 100 trees
nelsen file 0 from bb 100 trees
tplot file 0 from nelsen 1 tree
```

```
mhennig length 41 ci 63 ri 91 trees 3
bb file 0 from mhennig 3 trees
bb length 41 ci 63 ri 91 trees 6
tsave sheout4
tsave file 0 from bb 6 trees
nelsen file 0 from bb 6 trees
tplot file 0 from nelsen 1 tree
```

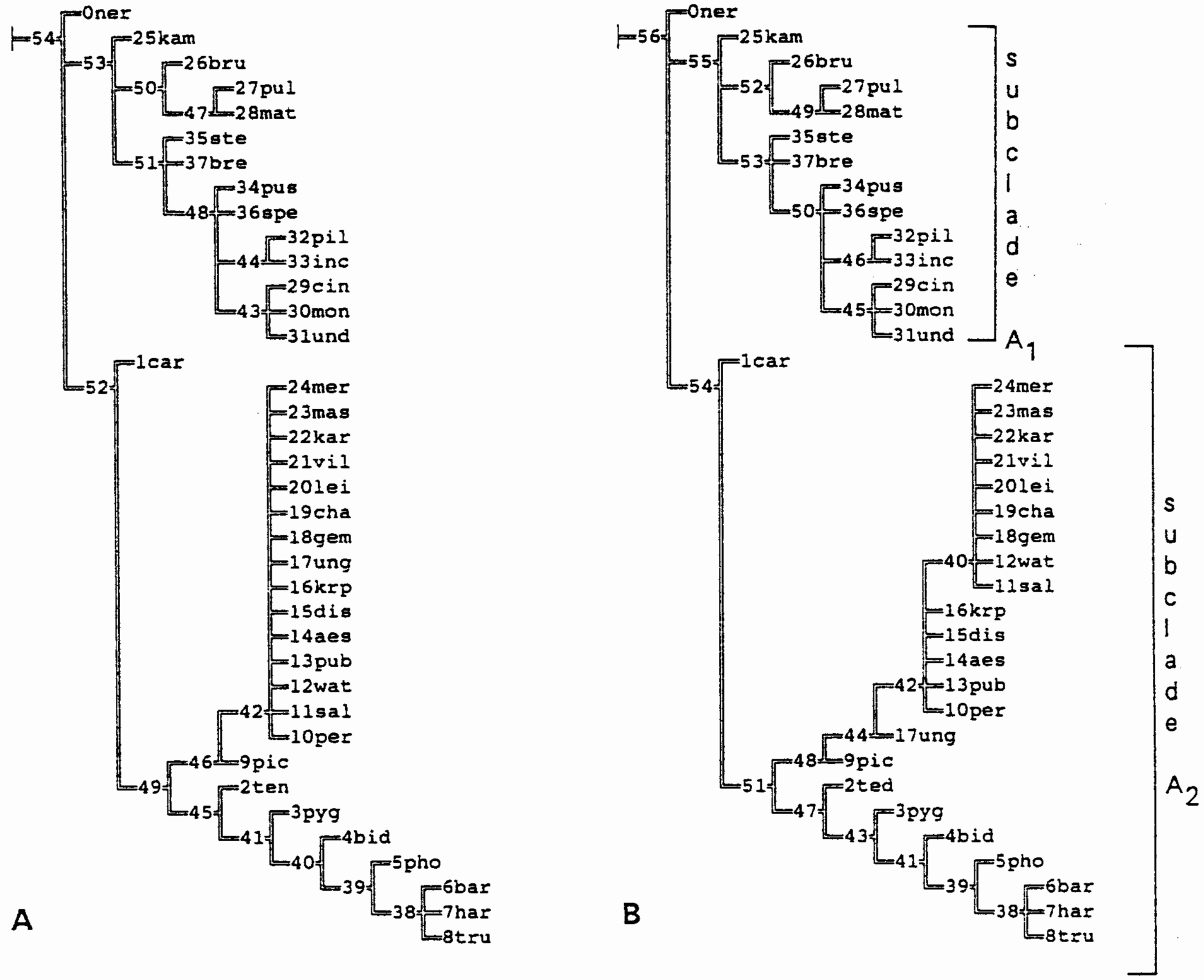


FIGURE 4.14-- Cladistic computations using the bb option of all known species of the study group based on the data in Table 4.4 with *Nerine* as the outgroup. A, Strict consensus tree using all characters; B, strict consensus tree after removal of homoplastic characters 0, 9 & 24.

4.4.3 Analysis of the species of *Kamiesbergia*, *Hessea* and *Namaquanula*

Thirteen species occur in the *Kamiesbergia*, *Namaquanula* and *Hessea* alliance. Only 11 characters from the comprehensive character list in Table 4.3 were applicable to these analyses using *Nerine* as the outgroup. The data set of 14 taxa by 11 characters is given in Table 4.5.

TABLE 4.5-- Data matrix for the species of *Kamiesbergia, Namaquanula* and *Hessea* using *Nerine* as the outgroup. The characters correspond to those marked in bold in Table 4.3. Question marks indicate inapplicable characters. Character 10, an autapomorphy for the group, was added to the resultant cladogram.

Taxon	Character states	Abbre-viation
Char no.	00011 11111 2	
	12512 36789 2	
Nerine	00000 00010 0	NER
Kamiesbergia	00000 0000? 0	KAM
Namaquanula bruce-bayeri	?0000 0110? 0	BRU
N. pulcherrima	10010 11111 1	PUL
N. mathewsii	10010 11111 1	MAT
Hessea cinnamomea	10011 00012 0	CIN
H. monticola	01011 00012 0	MON
H. undosa	01011 00012 0	UND
H. pilosula	01110 00012 0	PIL
H. incana	01110 00012 0	INC
H. pusilla	01010 00012 0	PUS
H. stellaris	01000 00012 0	STE
H. speciosa	01010 00012 0	SPE
H. breviflora	01000 00012 0	BRE

The ie* algorithm resulted in three minimal-length cladograms, of length 16 and CI 0.75 (Figure 4.15a). One of these trees (tree 2) has a topology identical to that of the strict consensus tree shown in Figure 4.15b.

Comparison of these three cladograms showed that the placement of *Kamiesbergia* was the only variable and hinged on the delimitation of character 18: the absence of a connective sheath in both *Namaquanula bruce-bayeri* and *Kamiesbergia*. The interpretation of loss of developmental complexity often presents problems in assessing similarity (Neff 1986, Stevens 1984, Weston 1988). Due to differences in the position of anther attachment among these species, the hypothesised independent loss of the anther connective sheath in *Kamiesbergia* and *Namaquanula bruce-bayeri,* is consistent with the resolution of the consensus tree (Figure 4.15b). The topology remained unchanged from that attained by the simultaneous analysis of all species of the study group (Figure 4.14).

TABLE 4.6-- Characters used for the cladistic analyses of the species of *Carpolyza* and *Strumaria sensu lato.* The numbers correspond to the data matrix in Table 4.7 and the cladogram in Figure 4.20. (Higher scores indicate relative apomorphy. Characters treated as nonadditive are marked thus*. New or redefined characters are marked thus +. Autapomorphies at the end of the list were not used in the analysis but were later inserted on the cladogram.)

CHARACTER	STATES
Bulb and leaves	
0. Inner tunics of bulb	0 = white; 1 = yellow.
1. Prophyll	0 = non-amplexicaul and bladeless, 1 = amplexicaul and bladeless.
2. Second leaf	0 = an amplexicaul foliage leaf, 1 = an amplexicaul cataphyll.
3. Foliage leaf arrangement	0 = opposite, 1 = flabelliform.
4. Foliage leaf position	0 = spreading, 1 = appressed to ground.
5.+ Foliage leaf vesture	0 = glabrous, 1 = more or less pubescent (in juveniles at least).
6.+ Pubescence in adults	0 = a few short scabrid trichomes, 1 = long and soft.
Inflorescence	
7. Scape habit at seed set	0 = persisting, 1 = detaching proximally.
8. Pedicel habit at anthesis	0 = stiff, 1 = lax to pendulous.
9.+ Relative pedicel/perigone lengths at anthesis	0 = shorter or more or less equalling the perigone, 1 = at least twice as long as the perigone.
Flowers	
10.* Flower shape at anthesis	0 = narrowly to widely funnelform, 1 = campanulate, 2 = stellate.
11. Tepals	0 = symtepalous, 1 = choritepalous.
12. Staminal adnation	0 = both staminal whorls adnate to style, 1 = both whorls fused to each other and outer whorl only adnate to style.
13. Filament attachment in anther sheath	0 = dorsifixed, 1 = subcentrifixed.
14. Form of nectar collection site.	0 = shallow hollows between inner filament and style, 1 = deep wells between inner filament and style.
15. Style form	0 = more or less slender throughout, 1 =thickened, winged or inflated proximally.
16.* Form of style swelling in the	0 = thickening upwards to ± midway along its length, 1 = more or less equally thickened in lower half, 2 = broadest near base.
Cytology	
17. Basic chromosome number	0 = 11, 1 = 10.
Autapomorphies	
18. Cataphyll colour	0 = not coloured, 1 = reddened.
19. Leaf surface	0 = otherwise, 1 = pustulate and glandular.
20. Leaf surface	0 = otherwise, 1 = sticky over entire surface.
21. Pedicels	0 = drying with age, 1 = remaining green and fleshy.
22. Flower colour	0 = pink to white, 1 = lemon yellow.
23. Tepals	0 = without false nectar spots, 1 = with false nectar spots.
24. Tepals	0 = not clawed, 1 = distinctly clawed.
25. Staminal adnation	0 = otherwise, 1 = inner stamens adnate to style.
26. Karyotype for basic number (x = 11)	0 = not bimodal, 1 = bimodal.

TABLE 4.7-- Data matrix for species of *Carpolyza* and *Strumaria sensu lato* with *Nerine* as the outgroup. The characters correspond to those in Table 4.6. (Question marks indicate unknown or inapplicable states.) Characters 10 & 16 were treated as nonadditive.

Taxon	Character states				Abbre-viation
Char no.	0 0	0 5	1 0	1 5	
Nerine	00000	0??00	?0?0?	0?0	NER
Carpolyza	00000	0?000	00?10	0?1	CAR
Strumaria tenella	00000	0?001	21000	101	TEN
S. pygmaea	01000	0?001	21000	10?	PYG
S. bidentata	01010	0?000	11000	101	BID
S. phonolithica	???10	0?000	01101	11?	PHO
S. barbarae	???10	0??10	01101	11?	BAR
S. hardyana	00010	0?010	01101	111	HAR
S. truncata	01010	0?010	01101	111	TRU
S. picta	00000	10000	11010	101	PIC
S. perryae	00100	11100	01010	111	PER
S. salteri	00101	10100	01010	111	SAL
S. watermeyeri	00101	??100	01010	111	WAT
S. pubescens	10100	11100	01010	111	PUB
S. aestivalis	10100	11101	01011	111	AES
S. discifera	00100	11101	21010	101	DIS
S. karoopoortensis	10100	10101	21010	121	KRP
S. unguiculata	00100	10001	21010	121	UNG
S. gemmata	10101	1?101	21010	121	GEM
S. chaplinii	00101	11101	21010	121	CHA
S. leipoldtii	00101	11101	21010	12?	LEI
S. villosa	10101	11101	21010	121	VIL
S. karooica	10101	10101	21010	121	KAR
S. massoniella	1??01	10?01	21010	12?	MAS
S. merxmuelleriana	10101	10?01	21010	121	MER
Weights:*	11 20004	1 1 02402	11 40043	1 1 060	

* Weights obtained by successive approximations character weighting using the xsteps w sequence.

4.4.4 Analysis of the species of *Carpolyza* and *Strumaria sensu lato*.

For the analysis of the 24 species which fall within subclade A_2 of the consensus tree for Amaryllideae (Figure 4.13), the characters in Table 4.3 were slightly redefined and one further character was added. The characters redefined for these analyses, with *Nerine* as the outgroup, are listed in Table 4.6. The data matrix for 18 characters and 25 taxa is given in Table 4.7.

The ie* option resulted in 27 cladograms of minimal-length 35, and CI 0.57. The strict consensus tree is shown in Figure 4.16a. *Carpolyza* resolved as a sister group to the rest of the ingroup. As an additional test of the internal structure of the ingroup, *Carpolyza* was thus assigned to the outgroup. The ie* algorithm resulted in 9 cladograms of minimal

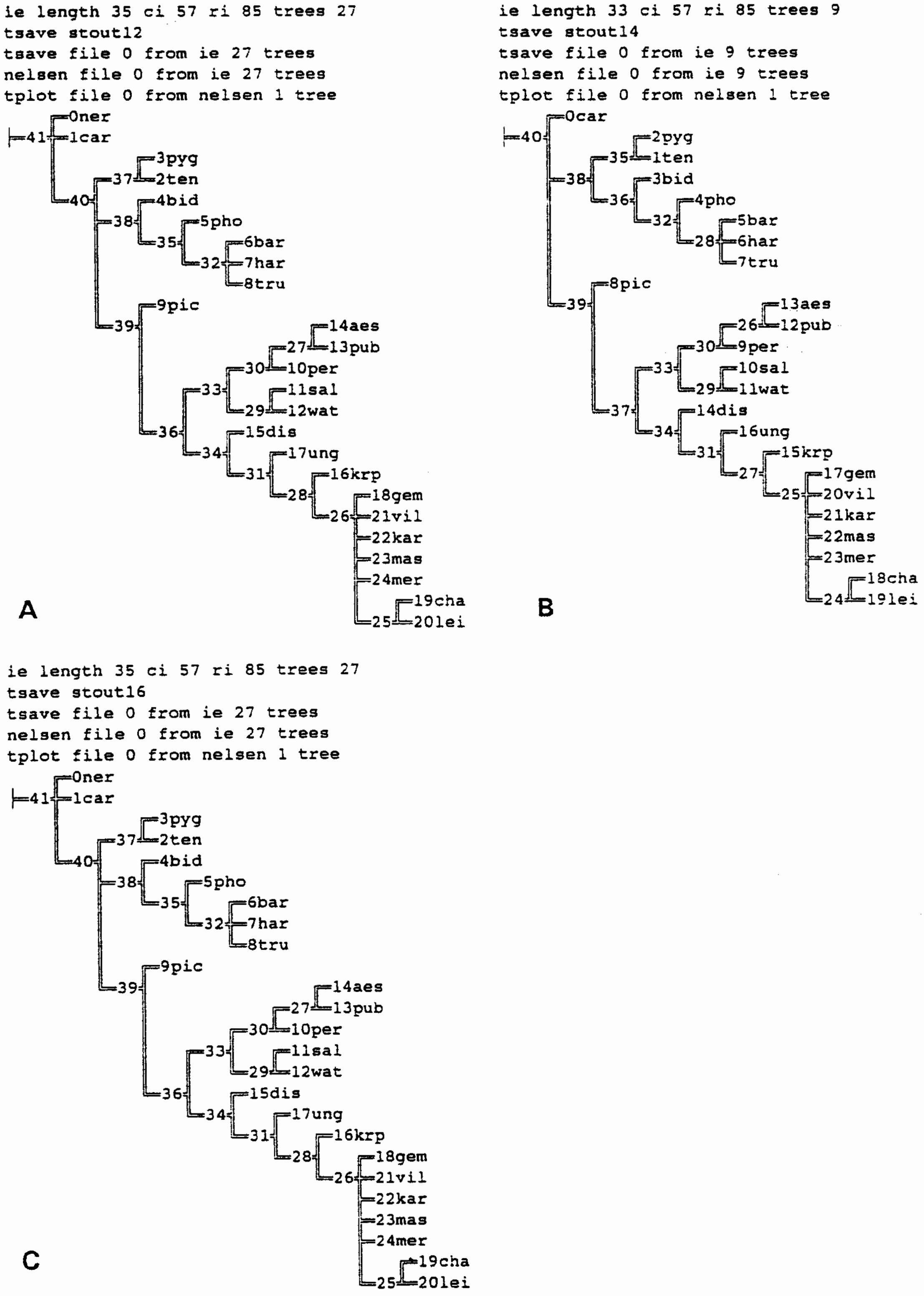
```
ie length 16 ci 75 ri 82 trees 3
tsave hesh12
tsave file 0 from ie 3 trees
tplot file 0 from ie 3 trees
tree 0
     ┌═0ner
├═21═┤    ┌═2bru
     ├═19═┤    ┌═3pul
     │    └═17═┴═4mat
     │    ┌═1kam
     └═20═┤    ┌═11ste
          └═18═┼═13bre
               │    ┌═10pus
               └═16═┼═12spe
                    │    ┌═8pil
                    ├═15═┴═9inc
                    │    ┌═5cin
                    └═14═┼═6mon
                         └═7und
tree 1
     ┌═0ner
├═21═┤    ┌═1kam
     ├═19═┤    ┌═2bru
     │    └═17═┤    ┌═3pul
     │         └═14═┴═4mat
     │    ┌═11ste
     └═20═┼═13bre
          │    ┌═10pus
          └═18═┼═12spe
               │    ┌═8pil
               ├═16═┴═9inc
               │    ┌═5cin
               └═15═┼═6mon
                    └═7und
tree 2
     ┌═0ner
├═20═┼═1kam
     │    ┌═2bru
     ├═18═┤    ┌═3pul
     │    └═16═┴═4mat
     │    ┌═11ste
     └═19═┼═13bre
          │    ┌═10pus
          └═17═┼═12spe
               │    ┌═8pil
               ├═15═┴═9inc
               │    ┌═5cin
               └═14═┼═6mon
                    └═7und
```

A

```
ie length 15 ci 80 ri 86 trees 3
tsave hesh8
tsave file 0 from ie 3 trees
nelsen file 0 from ie 3 trees
tplot file 0 from nelsen 1 tree
     ┌═0ner
├═20═┼═1kam
     │    ┌═2bru
     ├═18═┤    ┌═3pul
     │    └═16═┴═4mat
     │    ┌═11ste
     └═19═┼═13bre
          │    ┌═10pus
          └═17═┼═12spe
               │    ┌═8pil
               ├═15═┴═9inc
               │    ┌═5cin
               └═14═┼═6mon
                    └═7und
```

B

FIGURE 4.15-- Cladistic computations using the ie* option of the species of *Kamiesbergia, Hessea* and *Namaquanula* based on the data in Table 4.5 with *Nerine* as the outgroup. A, All the minimal-length trees; B, strict consensus tree.

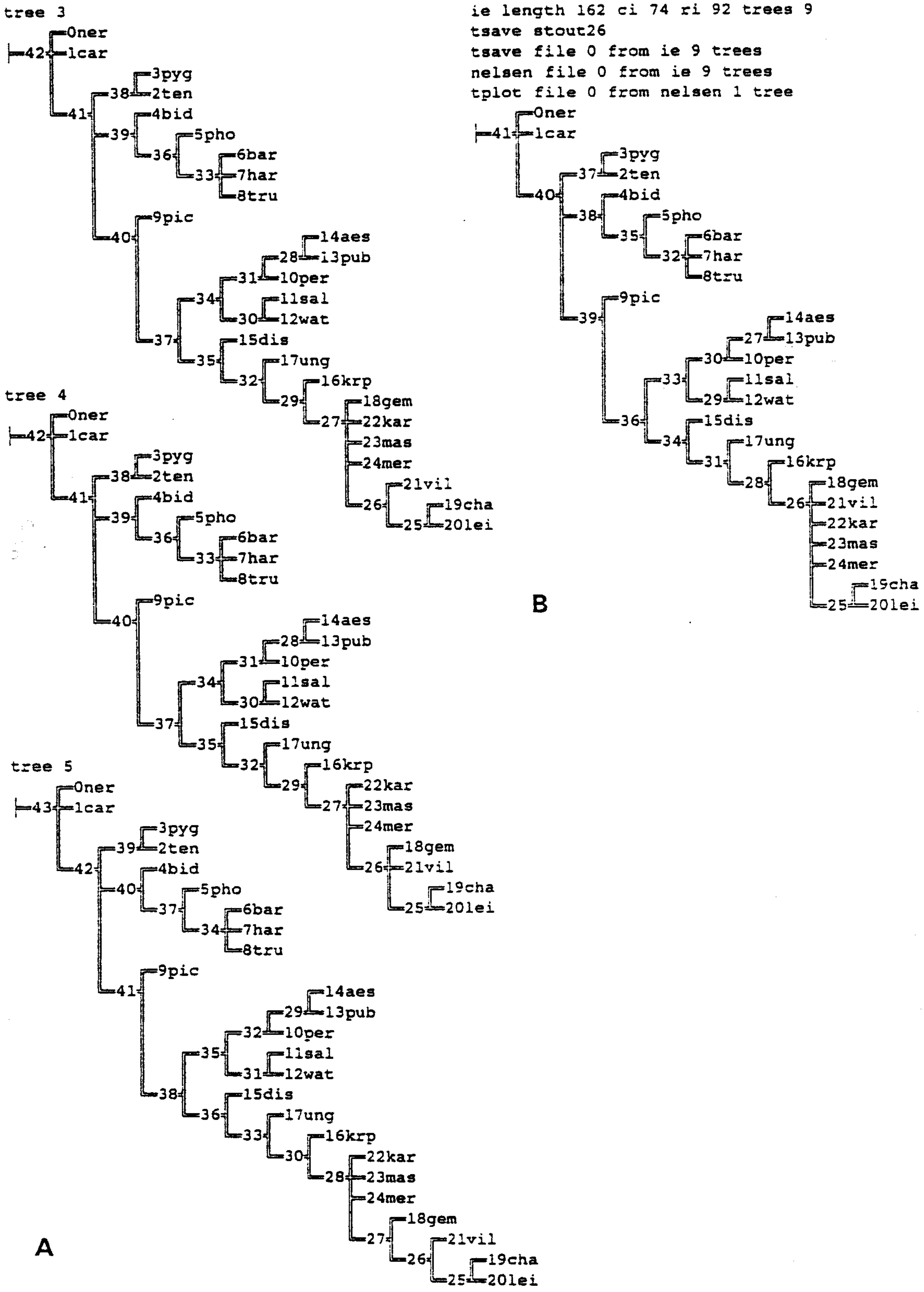


```
ie length 35 ci 57 ri 85 trees 27
tsave stoutl2
tsave file 0 from ie 27 trees
nelsen file 0 from ie 27 trees
tplot file 0 from nelsen 1 tree
```

```
ie length 33 ci 57 ri 85 trees 9
tsave stoutl4
tsave file 0 from ie 9 trees
nelsen file 0 from ie 9 trees
tplot file 0 from nelsen 1 tree
```

```
ie length 35 ci 57 ri 85 trees 27
tsave stoutl6
tsave file 0 from ie 27 trees
nelsen file 0 from ie 27 trees
tplot file 0 from nelsen 1 tree
```

FIGURE 4.16-- Cladistic computations using the ie* option of the species of *Carpolyza* and *Strumaria* based on the unweighted data in Table 4.7. **A**, Strict consensus tree with *Nerine* as the outgroup; **B**, strict consensus tree with *Carpolyza* as the outgroup; **C**, strict consensus tree with *Nerine* and *Carpolyza* as the outgroup.



```
ie length 162 ci 74 ri 92 trees 9
tsave stout26
tsave file 0 from ie 9 trees
nelsen file 0 from ie 9 trees
tplot file 0 from nelsen 1 tree
```

FIGURE 4.17-- Cladistic computations using the ie* option of the species *Carpolyza* and *Strumaria* based on the weighted data in Table with *Nerine* as the outgroup. A, Subset of minimal-length trees with initial trichotomy as in the strict consensus tree; B, strict consensus tree.

length 33 and CI 0.57. The consensus tree of this analysis is shown in Figure 4.16b. The number of clades formed by the initial division in the two consensus trees differs but the pattern within the clades is congruent.

Dorsifixed anthers are plesiomorphous in Amaryllideae. The synapomorphy at node 38 in Figure 4.16b has this plesiomorphous state by reversal from the subcentrifixed state which was specified by *Carpolyza* as the outgroup. The use of both *Nerine* and *Carpolyza* as the outgroups resolved this equivocal assessment. The result was a consensus tree (Figure 4.16c) in agreement with that in Figure 4.16a. In an attempt to reduce ambiguity in the data set and to obtain a grouping based on the most consistent characters, the xsteps w sequence of weighting was applied. The ie* option using *Nerine* as the outgroup generated 9 trees and a strict consensus tree as shown in Figure 4.17. Three of the minimal-length cladograms had a basal trichotomy as shown at node 40 of the consensus tree (Figure 4.17b). Within this subset of trees the only other variable was the placement of *S. gemmata.* This arose from the problem of treating the variable condition, in this species, of leaf pubescence (character 6, Table 4.6). Since decisions to score intermediate states as being apomorphic or plesiomorphic are questionable (Stevens 1991), leaf pubescence was treated as having missing data for *S. gemmata.* Because the minimal-length trees reflect the arbitrariness involved in choosing between these states for *S. gemmata*, the consensus tree was accepted as the best measure of the information content in the data set for the subsequent taxonomic classification and phylogenetic hypothesis.

4.5 Discussion

Controversy exists among systematists concerning the use in classifications of fundamental cladograms versus consensus trees based on the same data set (Anderberg & Tehler 1990, Carpenter 1988, Miyamoto 1985). This arises from conflicting needs. The most resolved parsimonious character distribution obtainable from a particular data set is most efficient for information content, transmission and retrieval (Farris 1979, 1982). However multiple phylogenetic hypotheses do not meet the demand of one taxonomic classification which seeks a less resolved hypothesis which two or more sets of evidence agree upon. Consensus cladograms are used for the phylogenetic hypotheses in the present study. As discussed by Kluge (1989) they are considered to be an efficient means of summarizing alternative hypotheses as well as being effective in focusing attention on multichotomies, which may be due to lack of data or conflict in the available evidence, and the need for further research.

The resultant cladistic pattern for the genera and species groups of Amaryllideae (Figure 4.18) indicates that *Amaryllis, Nerine, Brunsvigia*, the *Boophane guttata* group and *Boophane pulchra* are more closely related to the study group than they are to *Crinum, Cybistetes, Ammocharis* and the *Boophane disticha* group. Nodes **b** and **c** define relatively well corroborated clades, each with one nonhomoplastic synapomorphy: a corky testa at node b; and a dehiscent capsule at node c. Neither of the clades at nodes b and c are congruent with the subtribal classifications of Traub (1957) and D. & U. Müller-Doblies (1985) (Table 3.1). The result indicates that the subtribe Crininae *sensu* Traub (1957) is paraphyletic.

The study group, which corresponds with the subtribe Strumariinae *sensu* D. & U. Müller-Doblies forms a weakly corroborated monophyletic group at node h, defined by one synapomorphy (actinomorphic flowers). In order to reflect the phylogeny, minimum taxonomic decisions must be made to modify an existing classification (Wiley 1981), as long as the criterion of monophyly is met. Thus Linder (1991a) has argued for the need to assess which nodes are not likely to change with the addition of new data. Such nodes can be selected for formal naming, thereby establishing classifications that are maximally stable. Since the larger clade in which the study group is placed, is more strongly substantiated at node c by three characters of which one (dehiscent capsules) is non-homoplastic, the option of expanding the limits of the subtribe to include *Amaryllis, Nerine, Brunsvigia,* the *Boophane guttata* group, *Boophane pulchra* and *Kamiesbergia* is a preferred solution. In accordance with this change, the name Amaryllidinae takes precedence over the name Strumariinae, and the emended subtribe Crininae then constitutes a monophyletic group.

The monotypic *Amaryllis*, which is basal to the subtribe Amaryllidinae is defined by two derived conditions: the absence of chlorophyll from the endosperm and integument, and the less well defined autapomorphy of the rose-coloured pigment in the outer layer of the integument. Chemical tests by Markötter (1936) on this layer indicate that it differs from the brownish red pigment in seeds elsewhere in the tribe. The position of *Amaryllis* is thus comparable to that of the monotypic South American genus *Worsleya* (Traub) Traub, which is kept separate from *Hippeastrum* on the basis of its uniquely shaped seeds (Traub & Moldenke 1949).

The result of this analysis also indicates that the genus *Boophane,* as currently defined (Baker 1896, Barker 1963, Leighton 1947, Snijman 1983), is polyphyletic, which confirms the earlier speculation by Milne-Redhead & Schweickerdt (1939) that it is artificially delimited. *Boophane pulchra* lacks the synapomorphies of *Boophane guttata* and *Boophane flava* (leaves speckled with red and margins bristly) but has no known autapomorphy. Phenetically it is closest to *Brunsvigia* but further data are required before its transferance to this genus can be made. The relationship between *Nerine, Brunsvigia* and the *Boophane guttata* group is as yet poorly understood. A cladistic study at species level, together with the discovery of several new characters, should resolve this in the future.

Within the study group *Kamiesbergia, Hessea* and *Namaquanula* formed a clade at node i based on the loss of floral pigmentation at senescence (character 8), with the

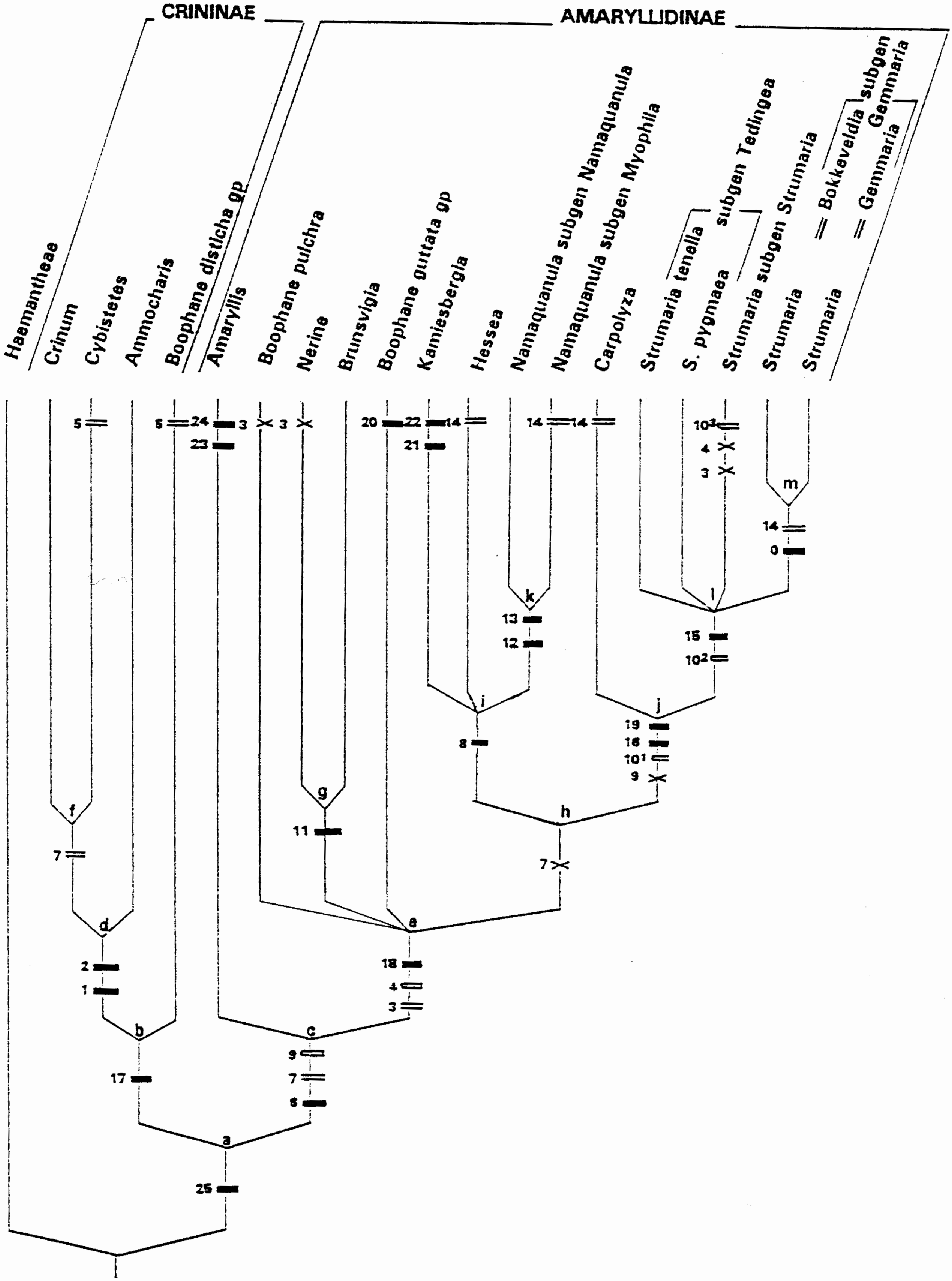


FIGURE 4.18-- Strict consensus tree of the genera of Amaryllideae. Representatives of the *Boophane disticha* group, *Boophane guttata* group, the *Bokkeveldia* group, the *Gemmaria* group and *Namaquanula mathewsii* group = subgenus Myophila, are given in Part 4.1. The characters are listed in Table 4.1. ▬ represents an apomorphy without homoplasy; ═ represents an apomorphy with a subsequent reversal, or successive states of a multistate character; = represents a parallelism; × reflects a reversal. The nodes are marked a-m.

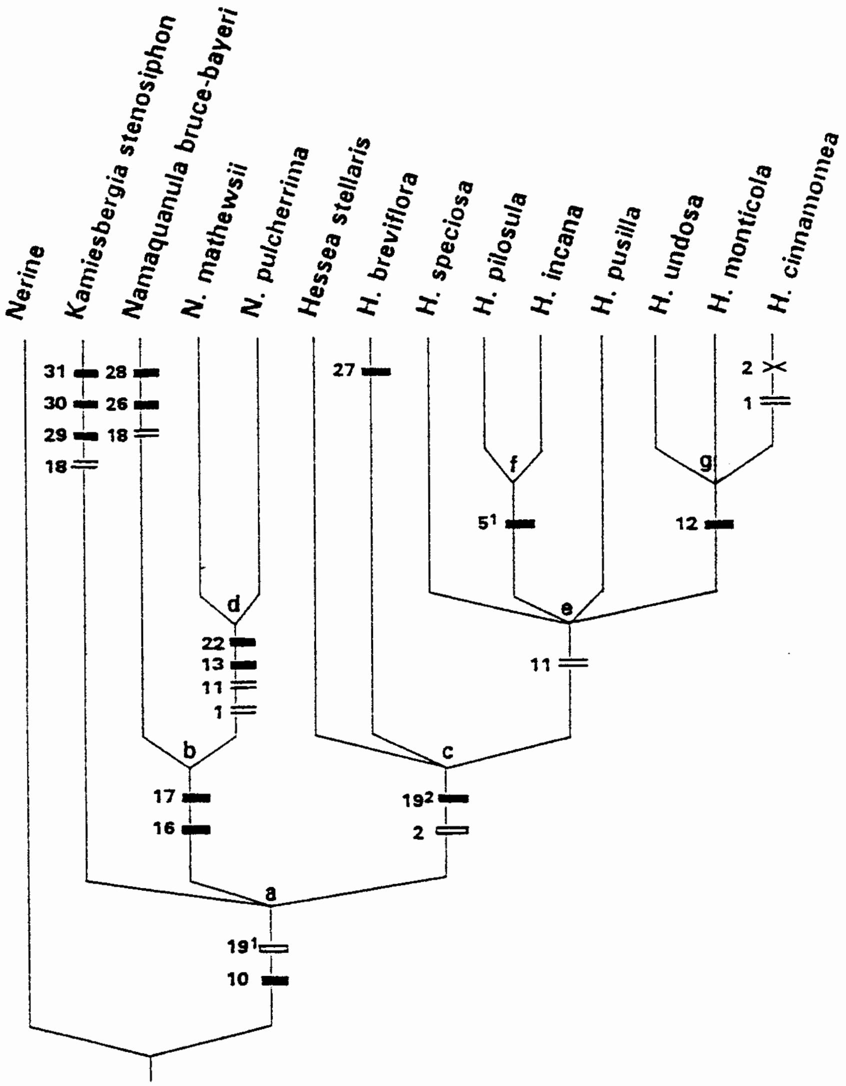


FIGURE 4.19-- Strict consensus tree of the species of *Kamiesbergia, Namaquanula* and *Hessea*. The characters are listed in Table 4.3.

▬ represents an apomorphy without homoplasy; ▭ represents an apomorphy with a subsequent reversal or successive states of a multistate character; = represents a parallelism; >< reflects a reversal. The nodes are marked a-g.

exception of *H. spiralis* (newly named *S. pygmaea*) which resolved in the clade containing *Strumaria* species. *Gemmaria,* as circumscribed by D. & U. Müller-Doblies (1985), also resolved as a polyphyletic genus in need of recircumscription. *Namaquanula mathewsii* and *N. pulcherrima* (*Gemmaria mathewsii* and *G. pulcherrima*) resolved as a sister group to *Namaquanula bruce-bayeri,* united by hooks and trichomes on the filaments.

As shown in Figure 4.19 *Kamiesbergia, Namaquanula* and *Hessea* resolved as a trichotomy: *Hessea* with the unique autapomorphy of centrifixed stamens; *Kamiesbergia* with four autapomorphies; and *Namaquanula* with two autapomorphies. Any hierarchic level can be applied in phylogenetic classification, as long as precise monophyly is maintained (Cracraft 1974, Wiley 1981). Thus the option of lowering the rank of the monophyletic groups in Figure 4.19 to subgeneric level and placing them in a large genus defined by the autapomorphy at node **a** (flowers losing their colour at senescence) was initially considered but ultimately rejected because I place less confidence in this character than those defining the three clades which it encompasses.

The relationship of *Namaquanula mathewsii* and *N. pulcherrima* to *N. bruce-bayeri* has a parallel in the tribe Pancratieae. *Namaquanula bruce-bayeri* has a distinct perigone tube and staminal tube. The perigone tube in *N. mathewsii* and *N. pulcherrima* is absent (character 11) and the staminal tube is reduced to a very low connate ring. The same reduction series has been described in Pancratieae, where the ultimate stages of reduction are evident in *Lapiedra* Lag. (Müller-Doblies 1978). The reduction to an obsolete perigone tube is also repeated in the genus *Hessea,* where all the species in the clade at node **e** (Figure 4.19) have choritepalous flowers (character 11).

Figure 4.20 indicates the cladistic relationships between species of *Carpolyza* and *Strumaria.* The monotypic genus *Carpolyza* resolved as a sister species to the rest of the ingroup based on the autapomorphy (character 25) of the inner filaments adnate to the style. The rest of the ingroup falls within a stable clade supported at node **b**, by two synapomorphies: one non-homoplastic (style variously swollen); and the other (choritepalous flowers) homoplastic elsewhere (in *Hessea, Namaquanula mathewsii* and *N. pulcherrima*). Above the trichotomy formed at node **b**, two further clades (at node **d** and **e**) are reliably supported by synapomorphies with no homoplasy: flabelliform arrangement of leaves at node **d**; and pubescent leaves at node **e**. The third clade (at node **c**) is only weakly upheld by two homoplastic characters (pedicels much longer than perigone and flowers stellate). The only clade congruent with the D. & U. Müller-Doblies' (1985) classification, is that defined at node **d**, which comprises the genus *Strumaria sensu stricto*. Elsewhere the result is at variance with the current classification.

Although classified as monotypic, the genus *Tedingea* (referred to here as *S. tenella*) resolves as a sister species to *S. pygmaea* (= *Hessea spiralis*) at node **c**. The result also indicates that *S. picta* (= *Bokkeveldia picta*) is cladistically basal to the remaining taxa

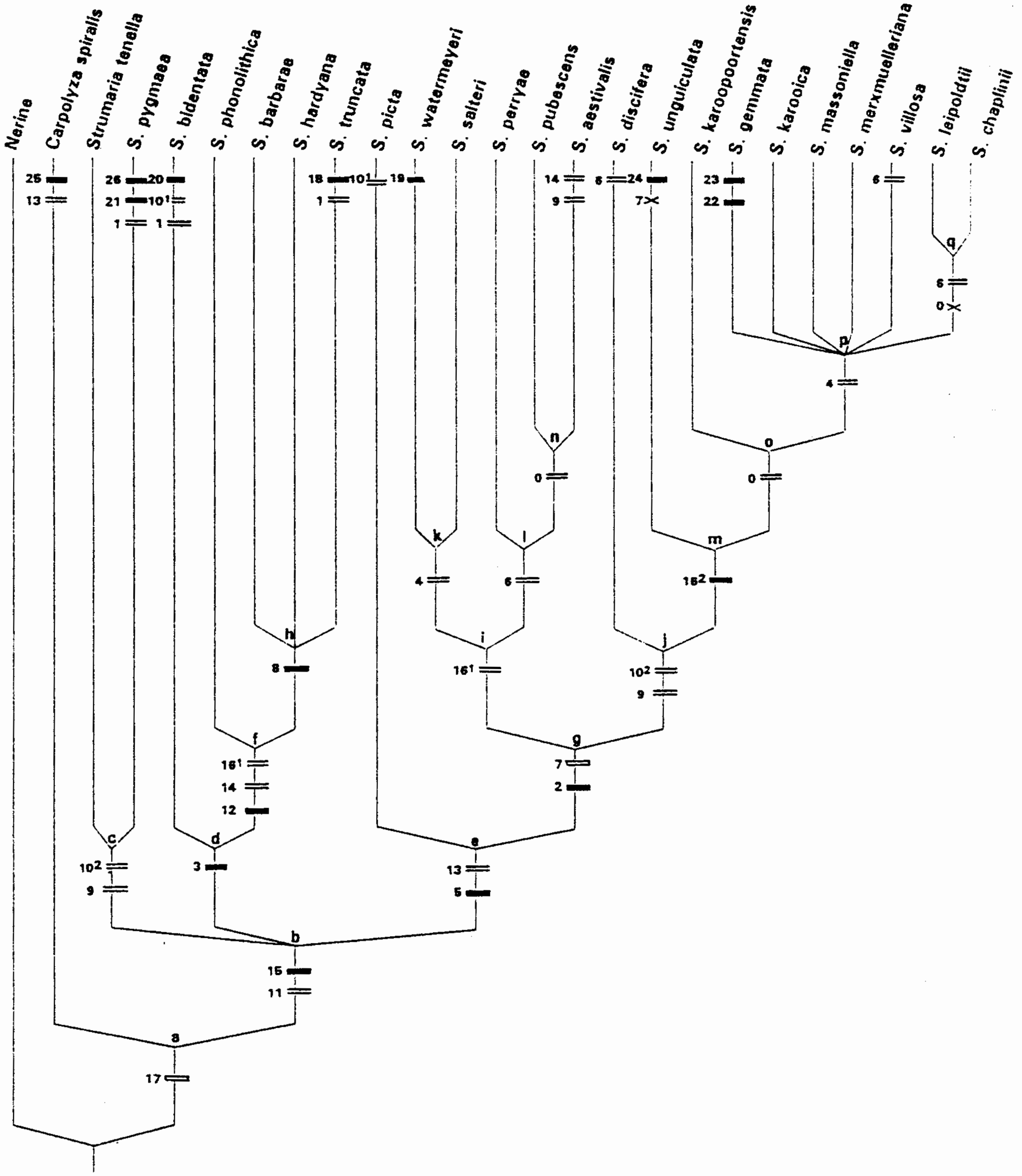


FIGURE 4.20-- Strict consensus tree of the species of *Carpolyza* and *Strumaria*. The characters are listed in Table 4.6. ▬ represents an apomorphy without homoplasy; ▭ represents an apomorphy with subsequent reversal or successive states of a multistate character; = represents a parallelism; ⤫ reflects a reversal. The nodes are marked a-q. Character 17 is replaced in *S. pygmaea* by the autapomorphous character 26.

with which it forms a monophyletic group. An autapomorphy for the taxa at node **g** is the presence of a cataphyll in a position subsequent to the prophyll (character 2) and the synapomorphy: scape abscising at anthesis (character 7). The synapomorphies at node j are stellate flowers and spreading umbels with long pedicels, both homoplasies which are also found at node **c**. The taxa of the *Gemmaria* group have the autapomorphy of the style being distinctly broadest near its base (at node **m**) as well as the homoplastic characters of yellow bulb tunics (node **o**); and leaves appressed to the ground (node **p**).

Bokkeveldia, as circumscribed by D. & U. Müller-Doblies (1985) is shown to be paraphyletic. The acceptance or rejection of paraphyletic groups in evolutionary classification has been hotly debated. Several authors (Ashlock 1984, Cronquist 1987, Duncan 1980) favour the recognition of paraphyletic groups or convex groups *sensu* Duncan (1980), since this allows greater flexibility in the interpretation of the cladistic results in relation to classificatory conclusions. This is contrary to Patterson (1982), Donoghue & Cantino (1988), Humphries & Chappill (1988) and Cracraft (1974), who argue that the most important development in systematics has been the recognition that strictly monophyletic groups are natural products of evolution. The fundamental goal of the systematist therefore, is the recognition of monophyletic groups, which will facilitate studies of the evolutionary process. Thus the formal recognition of *Gemmaria* from *Bokkeveldia* would not convey accurate information about all the decendants of *Bokkeveldia* and the genera would have no evolutionary connotations (Wiley 1981).

An assessment of the possible ways of reclassifying the ingroup to reflect monoplyletic assemblages led to the decision to relegate the groups formed at nodes **c**, **d** and **e** to subgeneric rather than generic rank, since node **c** is based on two homoplastic characters and is considered to be weak. Thus apart from the monotypic genus *Carpolyza*, which is retained, the rest of the ingroup is allotted to a single genus, for which the name *Strumaria* takes precedence.

The data nearly completely resolve the species relationships except for the polychotomy at node **p**. Incongruence may be due to mosaic evolution and/or investigator error (Kluge 1989) but re-examination of the characters responsible for the polychotomy suggests that the clade represents an assemblage of closely related sibling species with little differentiation. *Namaquanula mathewsii* and *N. pulcherrima*, although superficially similar to the species in this polychotomy, in that both have wide-open stellate flowers, showed a different pattern of relationship as shown in Figure 4.18.

The overall level of homoplasy present in the groups analysed is less than that found by Meerow (1989) in the South American genera *Eucharis* Planchon & Linden and *Caliphruria* Herbert. Sanderson & Donoghue (1989) found that the consistency index (the measure of homoplasy) obtained in analyses is highly correlated with the number of taxa included but does not show significant relationship to the number of characters utilised. In agreement with the results obtained by Sanderson & Donoghue (1989) the CI increased in the analyses as the number of taxa diminished: CI 0.57 for the analysis of *Strumaria* and *Carpolyza* with 25 taxa; CI 0.68 for the analysis of Amaryllideae with 20 taxa; and CI 0.75 for the analysis of *Hessea* and its allies involving 14 species.

4.6 Conclusions

The strict consensus trees generated by the cladistic analyses indicate that the subtribe Crininae, as previously circumscribed (Traub 1957), is paraphyletic. To reflect the derived working hypothesis, the subtribe Strumariinae is amplified to incorporate *Amaryllis, Nerine, Brunsvigia, Boophane* (comprising *B. guttata* and *B. flava* only) and the study group. As a result, the older name Amaryllidinae takes precedence over Strumariinae. The subtribe Crininae is reduced to include only *Crinum, Cybistetes, Ammocharis* and the species pair *Boophane disticha* and *B. haemanthoides*. The monophyletic subtribes are emended as shown in Table 4.8. Furthermore, the genus *Boophane* as previously circumscribed (Baker 1888, 1896, Dyer 1976, Herbert 1837, Milne-Redhead & Schweickerdt 1939, Phillips 1951) falls within both subtribes and is polyphyletic. A possible new generic name for *Boophane guttata* and *B. flava* is yet to be sought.

TABLE 4.8-- Revised classification of the tribe Amaryllideae derived from the results of the cladistic analyses in this study.

Subtribe Amaryllidinae

A monophyletic group defined by the autapomorphy of a dehiscent capsule, as well as the synapomorphy of stomatose seeds (except in *Amaryllis*).

Amaryllis L.
Nerine Herbert
Brunsvigia Heister
Boophane Herbert pro parte (as to *B. guttata* (L.) Herbert and *B. flava* W.F.Barker ex Snijman)
Kamiesbergia Snijman
Namaquanula D. & U. Müller-Doblies emend. Snijman
Hessea Herbert
Carpolyza Salisb.
Strumaria Jacq.

Subtribe Crininae Traub ex Snijman

A monophyletic group defined by the autapomorphy of a corky testa.

Crinum L.
Boophane Herbert pro parte (as to *B. disticha* (L.f.) Herbert and *B. haemanthoides* Leighton)
Ammocharis Herbert
Cybistetes Milne-Redhead & Schweickerdt

With respect to the hypothesised relationships within the study group the following conclusions are drawn about the status of the genera as circumscribed by D. & U. Müller-Doblies (1985) and Snijman (1991, in press).

(1) The newly described taxon *Kamiesbergia* (Snijman 1991) with four autapomorphies warrants recognition as a monotypic genus.

(2) *Gemmaria mathewsii* and *G. pulcherrima* (Müller-Doblies 1985) warrant incorporation into *Namaquanula*, which is divided here into two subgenera.

(3) With the exclusion of *H. spiralis*, the remaining species of *Hessea*, form a monophyletic group with autapomorphic centrifixed anthers.

(4) *Carpolyza* warrants maintenance as a monotypic genus.

(5) *Bokkeveldia* as previously circumscribed, (Müller-Doblies 1985) is paraphyletic. Thus the closely related genus *Gemmaria*, which was resurrected by D. & U. Müller-Doblies (1985)), cannot be retained.

(6) All the species of *Strumaria sensu stricto, Bokkeveldia, Gemmaria,* (except *G. mathewsii* and *G. pulcherrima*), *Tedingea* and *Hessea spiralis* form a robust monophyletic group based on the unique character of a swollen or winged style. Not every one of the three major clades formed within this monophyletic group is strongly supported. Thus it is concluded that *Bokkeveldia, Gemmaria* and *Tedingea* should be united with *Strumaria* under the latter name and three subgenera (subgenus *Tedingea,* subgenus *Strumaria* and subgenus *Gemmaria*) should be recognised. Subgenus Gemmaria is further divided into three sections. The epithet *S. spiralis* is already occupied, thus with the transferrance of *H. spiralis* to *Strumaria*, it is renamed *S. pygmaea*.

(7) Lastly it can be concluded that the four unpublished species (*S. perryae, S. aestivalis, S. discifera* and *S. villosa*) are correctly placed in the genus *Strumaria.*

Species groupings and genera emended as a result of the analysis are listed in Table 4.9. The new combinations are yet to be formally validated.

TABLE 4.9-- List of revised genera and new species combinations arising from the results of the cladistic analyses in this study.

1. ***Kamiesbergia*** Snijman
A monotypic genus defined by the autapomorphies, dimorphic stamens and anthers attached near base of connective.

2. ***Hessea*** Herbert
A monophyletic genus defined by the unique autapomorphy of centrifixed anthers.
H. stellaris (Jacq.) Herbert
H. breviflora Herbert
H. pusilla Snijman
H. speciosa Snijman, *sp. nov.*
H. pilosula D. & U. Müller-Doblies
H. incana Snijman
H. cinnamomea (L'Hérit.) Durand & Schinz
H. monticola Snijman
H. undosa Snijman

3. ***Namaquanula*** D. & U. Müller-Doblies *emend.* Snijman
A monophyletic genus defined by the autapomorphies of ventral filament hooks and trichomes proximally covering the ventral surface of the filaments.

3.1 Subgenus *Namaquanula*
N. bruce-bayeri D. & U. Müller-Doblies

3.2 Subgenus *Myophila* Snijman, *sub gen. nov.*
N. mathewsii (W.F. Barker) Snijman, *comb. nov.* (= *Gemmaria mathewsii* (W.F. Barker) D. & U. Müller-Doblies)
N. pulcherrima (D. & U. Müller-Doblies) Snijman, *comb. nov.* (= *G. pulcherrima* D. & U. Müller-Doblies).

4. ***Carpolyza*** Salisb.
A monophyletic genus defined by the autapomorphy of the inner filaments adnate to the style.
C. spiralis (L'Hérit.) Salisb.

5. ***Strumaria*** Jacq.
A monophyletic genus defined by the autapomorphy of the swollen or winged style.

5.1 Subgenus Tedingea (D. & U. Müller-Doblies) Snijman, *stat.nov.*
S. tenella (L.f.) Snijman, *comb. nov.* (= *Tedingea tenella* (L.f.) D. & U. Müller-Doblies)
S. pygmaea Snijman, *nom.nov.* (= *Hessea spiralis* Baker)

5.2 Subgenus Strumaria
S. bidentata Schinz
S. phonolithica Dinter
S. barbarae Obermeyer
S. hardyana D. & U. Müller-Doblies
S. truncata Jacq.

- 5.3 Subgenus Gemmaria (Salisb.) Snijman, *stat. nov.*
  - 5.3.1 Section Cryptomeria Snijman, sect. *nov.*
    - *S. picta* W.F. Barker (= *Bokkeveldia picta* (W.F.Barker) D. & U. Müller-Doblies)
  - 5.3.2 Section Gemmaria
    - *S. unguiculata* (W.F. Barker) Snijman, *comb. nov.* (= *Gemmaria unguiculata* (W.F. Barker) D. & U. Müller-Doblies)
    - *S. karoopoortensis* (D. & U. Müller-Doblies) Snijman, *comb. nov.* (= *G. karoopoortensis* D. & U. Müller-Doblies)
    - *S. karooica* (W.F. Barker) Snijman, comb. nov. (= *G. karooica* (W.F. Barker) D. & U. Müller-Doblies)
    - *S. massoniella* (D. & U. Müller-Doblies) Snijman, comb. nov. (= *G. massoniella* D. & U. Müller-Doblies)
    - *S. chaplinii* (W.F. Barker) Snijman, comb. nov. (= *G. chaplinii* (W.F. Barker) D. & U. Müller-Doblies)
    - *S. gemmata* Ker-Gawl. = (*G. gemmata* (Ker-Gawl.) Salisb. ex D. & U. Müller-Doblies)
    - *S. merxmuelleriana* (D. & U. Müller-Doblies) Snijman, *comb. nov.* (= *G. merxmuelleriana* D. & U. Müller-Doblies)
    - *S. leipoldtii* (L.Bolus) Snijman, *comb. nov.* (= *G. leipoldtii* (L.Bolus) D. & U. Müller-Doblies)
    - *S. villosa* Snijman, *sp. nov.*
    - *S. discifera* Marloth ex Snijman, *sp. nov.*
  - 5.3.3 Section *Bokkeveldia* (D. & U. Müller-Doblies) Snijman, stat. nov.
    - *S. watermeyeri* L.Bolus (= *B. watermeyeri* (L.Bolus) D. & U. Müller-Doblies)
    - *S. salteri* W.F.Barker (= *B. salteri* (W.F.Barker) D. & U. Müller-Doblies)
    - *S. perryae* Snijman, *sp. nov.*
    - *S. pubescens* W.F.Barker (=*B. pubescens* (W.F.Barker) D. & U. Müller-Doblies)
    - *S. aestivalis* Snijman, *sp. nov.*

Chapter 5.
BIOGEOGRAPHY

5.1 Theoretical outline

The patterns of spatial distribution attained by life on earth and the means by which these distributions were achieved are two essential concerns of biogeography (Rosen 1978). Descriptive or empirical biogeography is the analysis of pattern in present-day distributions, whereas historical biogeography is the study of the distribution of living organisms in time and space (Ball 1976, Rosen 1978). The historical component is sometimes regarded as ecological. However, the ecological time scale, which places demographic processes in the framework of tens to hundreds of generations, neglects evolutionary, major disjunctional and long-term temporal components, which together comprise the elements of historical biogeography (Humphries & Parenti 1986, Ricklefs 1989).

The theory and methodology of biogeography has received much attention in the past decade. Ball (1976) recognises two phases in the development of historical biogeography: a narrative phase and an analytical phase, each marked by a different set of methodologies of varying heuristic value.

In early biogeographical studies the concept of centre of origin in both the Linnean and Darwinian sense was accepted and used as if it were a conceptual model necessary and fundamental to historical analysis (Croizat *et al.* 1974). Thus the main focus for many biogeographers was the determination of a centre of origin for different taxa and a narrative explanation which invoked evolution and dispersal as causal agents for distribution (Humphries & Parenti 1986). This approach lacked empirical rigour. Several of the criteria recognised for determining such centres of origin assumed random or equal rates of dispersal and evolution among taxa (Rotramel 1973), and since these assumptions cannot be supported (see Vrba 1980), the validity of the results are doubtful. A further weakness of narrative explanations is that they are not sufficiently restrictive and therefore unfalsifiable (Ball 1976, Humphries & Parenti 1986).

In the panbiogeographic approach of Croizat the classical concept of centre of origin was changed to a more sophisticated one (Seberg 1986). Distributions of taxa are depicted on maps such that the disjunct parts of the distribution of every taxon are joined by lines connecting what were interpreted to be nearest neighbours. Each graphic pattern represents a track and tracks that coincide form standard or generalised tracks (Croizat *et al.* 1974). "Gates" are particular areas on the globe where standard tracks intersect and these were interpreted as places where geological revolutions initiated differentiation (Seberg 1986). Croizat's propositions for the causes of present distribution patterns possessed the problem common to all earlier solutions: they lacked a definition of relationship between areas (Humphries & Parenti 1986). Page (1987) later equated track analysis with the method of spanning tree biogeography using graph concepts, but still rejected the need for character data (Humphries & Seberg 1989).

The recognition of species and monophyletic sister-groups as the units for the study of evolution led to the consideration of the area relationship within properly reconstructed sister-group systems as the main method of analytical historical biogeography (Brundin 1972). This approach, which is referred to broadly as cladistic biogeography by Humphries & Parenti (1986), covers vicariance or phylogenetic biogeography. Whereas Croizat's tracks placed the co-ordinates of a group in space, which then led to an enquiry into factors of time and form, most cladistic biogeographers consider form to be an essential prerequisite to an enquiry into time and space (Humphries & Parenti 1986). Form and space are considered to be the only empirical parts of biogeography. Time is an inference (C.J. Humphries pers. comm.).

Arising from Croizat's generalised track concept is the principle of cladistic biogeography which states that one particular distribution pattern is insufficient to resolve decisively its cause (Seberg 1986). Thus with distribution data, the consideration is whether they conform to a general pattern of relationships shown by other groups of taxa endemic to the areas concerned (Platnick & Nelson 1978).

Area cladograms are produced by substituting for taxa the areas in which they occur. The justification for this procedure is the underlying assumption that the history of life has some generality with respect to the history of the earth's geography (Rosen 1978). The generality of the area cladograms can be examined by comparison with other groups in the same areas. Corroboration of a particular pattern is equivalent to a general statement for a relatively recent ancestry of the biotas under examination; a biota being defined as an assemblage of organisms restricted to the same place and time (Kluge 1988). By means of this approach a biogeographic hypothesis may be produced which meets the criteria of explanatory power, internal consistency, predictive power and the potential for falsification (Ball 1976).

Despite the advances inherent in cladistic biogeography a diversity of opinions exist on the methods that are most appropriate to analyse historical pattern. Current methods include component analysis (Humphries & Parenti 1986, Nelson & Platnick 1981, Page 1989), Brooks' parsimony analysis, BPA (Brooks 1985, Wiley 1988) and group compatability as implemented in CAFCA (Zandee & Roos 1988).

Most applications of the methods encounter problems of incongruence and unresolved statements in the derivation of general area cladograms. If the sister-group relationships are correct then incongruence may be attributable to a variety of historical reasons: extinction may result in missing taxa; species may have similar distributions but different histories; long-distance dispersal may result in non-vicariant area relationships; widespread taxa may represent failures to differentiate in areas that may be historically related or unrelated (Cracraft 1988, Humphries & Parenti 1986). Given the ambiguity caused by widespread taxa, three different interpretations about the cladistic relationship of areas sharing a widespread taxon have been proposed: Assumption 0 (Zandee & Roos 1987); Assumption 1 and Assumption 2 (Nelson & Platnick 1981).

Component analysis attempts to search for concordance among different clades in their shared patterns of common ancestry. The non-shared aspects of the various cladograms are treated as "noise", not pattern. With respect to biogeography, that pattern consists of shared area relationships, which are postulated to have a historical relationship. Assumption 1 or Assumption 2 may be implemented for component analysis if widespread species are present in the analysis. Under Assumption 1 it is assumed that whatever is true of a widespread taxon in one part of its range must also be true of the taxon in other parts of its range. Assumption 2 indicates that whatever is true of a widespread taxon in one part of its range might not be true of the taxon in other parts of its range.

Brooks' parsimony analysis is designed to reduce the complexity of multiple patterns to one or more most parsimonious hypotheses. It relies upon an analogy to methods in systematics. Both BPA and Zandee & Roos' method implement Assumption 0. Assumption 0 is based on the concept that the reconstructed phylogeny is the best possible estimate of the true phylogeny. It implies that if a species appears to be wrongly delimited and actually represents two or more species, the resulting species are assumed to be sister groups and should together represent a monophyletic group. Consequently the areas inhabited by each widespread species represent undisputable components.

Based on an example in South America, Cracraft (1988) argues that neither component analysis (Humphries & Parenti 1986, Nelson & Platnick 1981) nor biogeographic parsimony analysis (Brooks 1985, Wiley 1988, Zandee & Roos 1988) is intrinsically capable of resolving accurately the complexity of the history of continental biotas, but that both are useful methods for revealing the existence of biogeographic pattern. However, several studies using component analysis have been succesfully undertaken in Australia (Ladiges & Humphries 1986, Ladiges *et al.* 1987, Thiele & Ladiges 1988, Ladiges *et al.* 1989). The methods of cladistic biogeography are still being developed but, clearly, until more data become available the advantages and limitations of these methods remain poorly known (Page 1990).

5.2 Descriptive biogeography

In this analysis of present-day distribution patterns the focus is on the actinomorphic-flowered Amaryllidinae. Due to inadequate data, the distributions of the remaining genera of Amaryllideae and Crininae are limited to general descriptive outlines.

5.2.1 Distribution of the subtribes

As seen in Figure 5.1 the subtribe Crininae is widespread throughout sub-Saharan

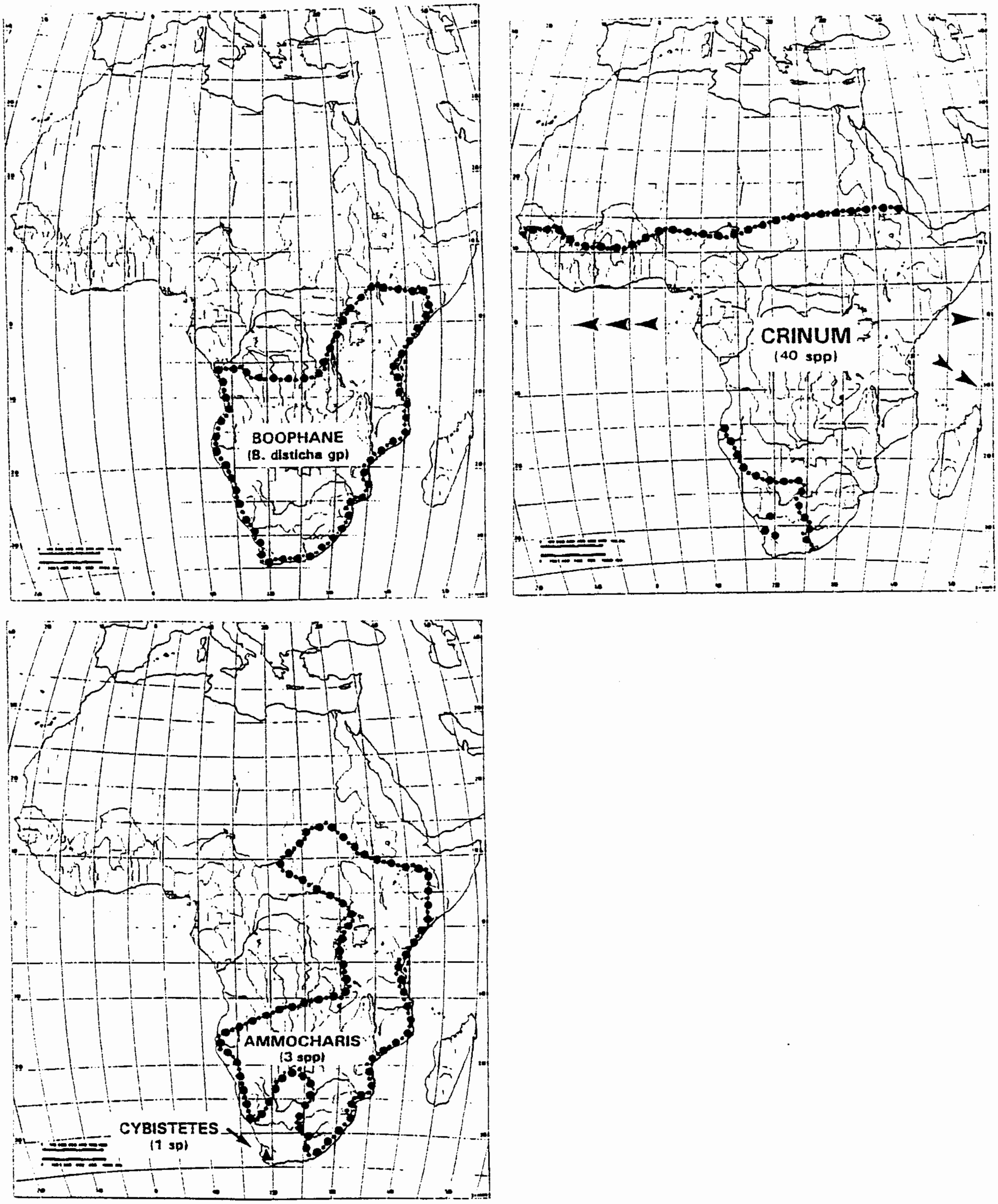


FIGURE 5.1– Distribution ranges of the genera of Crininae in Africa.

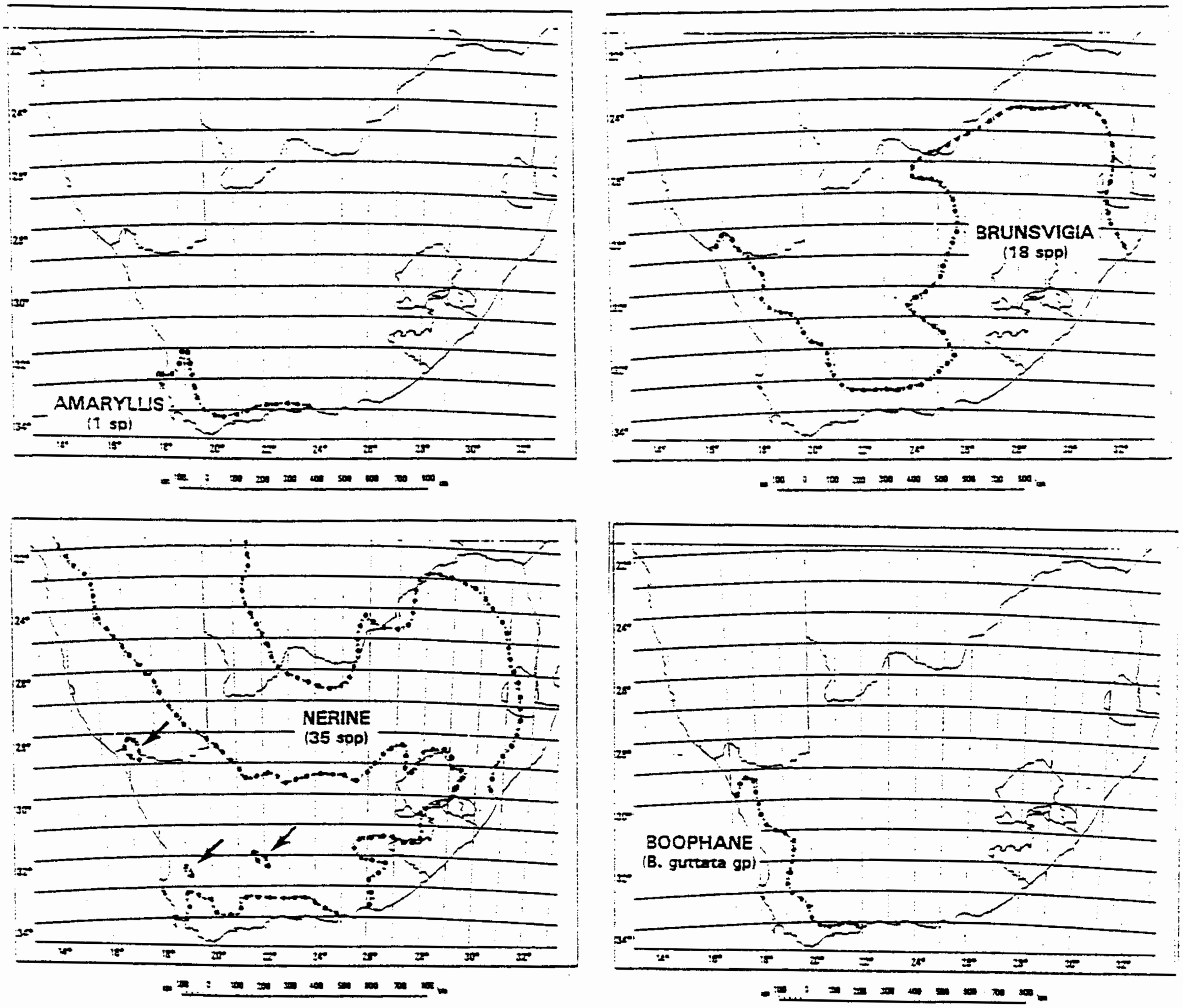


FIGURE 5.2-- Distribution ranges of the zygomorphic-flowered genera of Amaryllidinae in southern Africa.

Africa (Baker 1898, Nordal 1982). Only *Crinum* extends beyond the continent into the tropics and temperate regions of the Old and New Worlds (Nordal & Wahlstrøm 1980, Verdoorn 1973). The *Boophane disticha* group, which includes *B. haemanthoides*, has two known species distributed allopatrically throughout sub-Saharan Africa. *Ammocharis* has three allopatric species distributed from east Africa through southern central Africa to southern Africa (Milne-Redhead & Schweickerdt 1939, Nordal 1982); whereas the monotypic *Cybistetes* is confined to the south-western Cape. With the exception of *Cybistetes* and *Boophane haemanthoides*, the distribution patterns of Crininae coincide predominantly with a summer-rainfall pattern.

In contrast, the subtribe Amaryllidinae is restricted entirely to southern Africa (Figure 5.2). Only *Brunsvigia* is equally distributed in the winter and summer-rainfall areas in the west and east respectively. The remaining genera are more or less restricted to either the summer or the winter-rainfall regimes; *Nerine* in the summer-rainfall area with a few outliers in the winter-rainfall area; and *Amaryllis* and the *Boophane guttata* group of two species in the winter-rainfall area.

5.2.2 Distribution of the actinomorphic-flowered Amaryllidinae

The genera of the actinomorphic-flowered Amaryllidinae occur throughout south western Africa, from southern Namibia, through to the north-western and south-western Cape into the Little Karoo and Great Karoo, and the eastern Orange Free State at the eastern-most limit. This western half of southern Africa is semi-arid, with a median annual rainfall of less than 500 mm, and includes both autumn-rainfall and winter-rainfall zones (Zucchini & Adamson 1984).

Strumaria, the largest genus of the actinomorphic-flowered Amaryllidinae, with 23 species, has the most widespread distribution (Figure 5.3a) and has only two species which extend marginally into the summer-rainfall region: *S. tenella* (disjunct between the winter-rainfall region of the Cape and the eastern Orange Free State and Lesotho) and *S. gemmata* (southern Cape and eastern Great Karoo). Most species show high fidelity to open, seasonal, relatively moist sites usually amongst rocks along stream banks or seepage zones. These microhabitats are highly discontinuous from the regional environment, where the vegetation cover comprises low, succulent or small-leaved xerophytic shrublands.

The highest species concentrations (based on the number of species per 30' x 30' square) are in the uplands of Namaqualand near Springbok (grid 2917) and the Bokkeveld Mountain escarpment (grid 3119) (Figure 5.3a). A remarkably high number of species have restricted distributions. Eight species (35%) are known to occur in only one 30' square and ten species (43%) are known to occur in two to three 30' squares. These narrowly endemic species are allopatric except in grids 2917 BA (*S. villosa* and *S. merxmuelleriana*) and 3119 CA (*S. picta* and *S. watermeyeri*), where the co-occurring

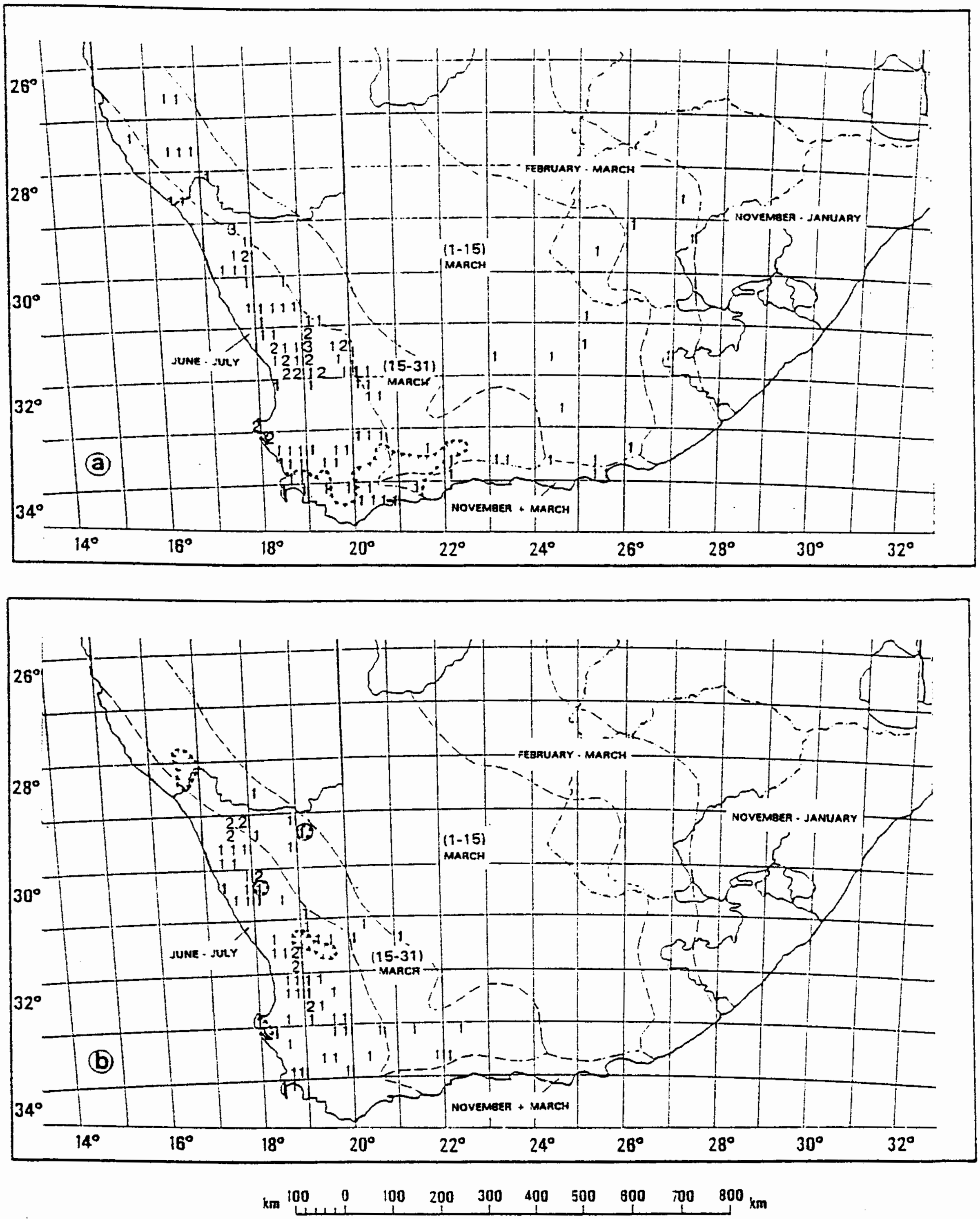


FIGURE 5.3– Distribution ranges and the frequency of species per 30' x 30' square in the actinomorphic-flowered Amaryllidinae. Evenly broken lines delineate regions with different periods of maximum rainfall (from Zucchini & Adamson 1984, Figure 6.6). A, Range of *Carpolyza* (TTT), numbers refer to frequency of *Strumaria* species; B, ranges of *Namaquanula* (TTT), *Kamiesbergia* (☉), numbers refer to frequency of *Hessea* species.

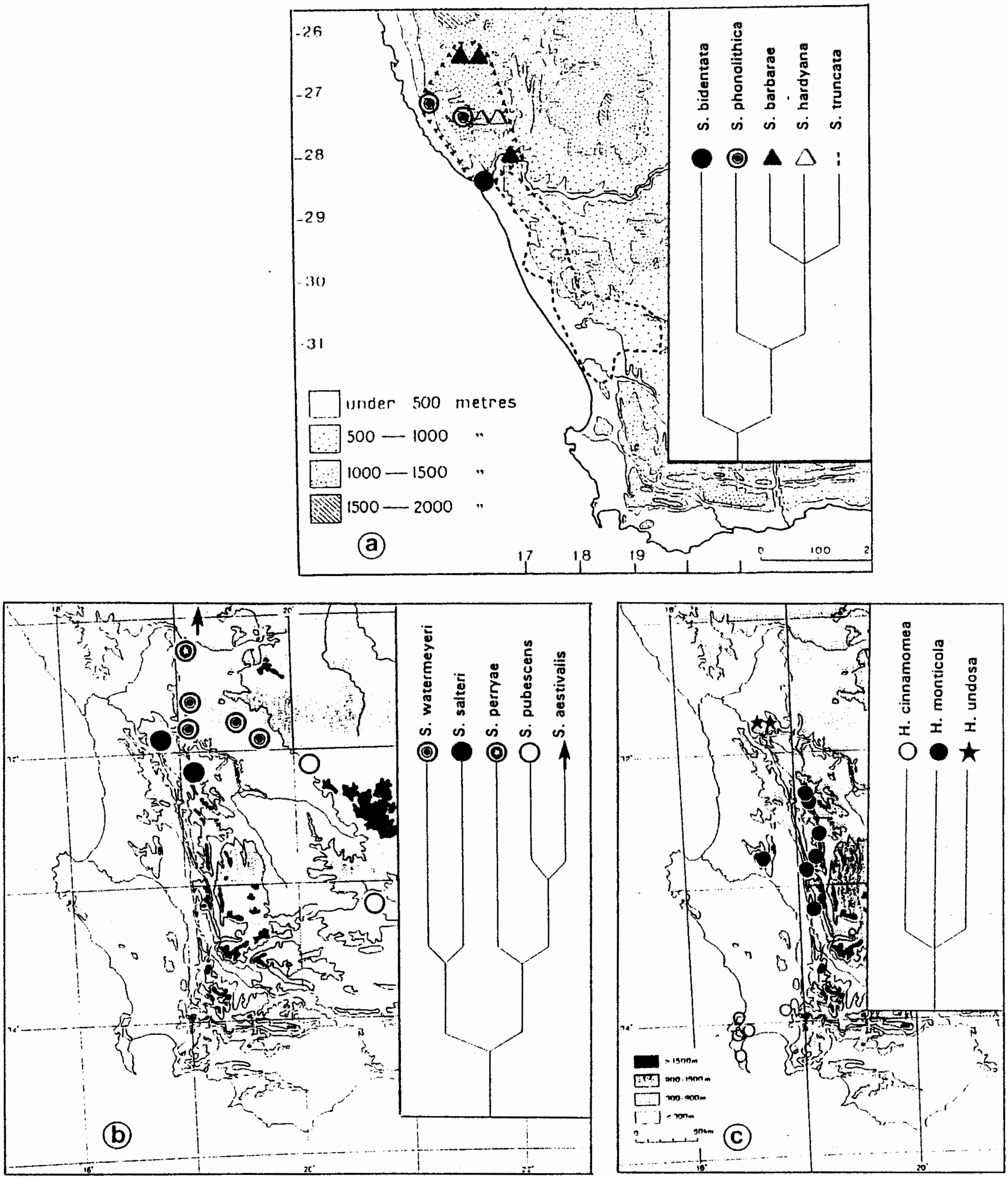


FIGURE 5.4-- Distribution patterns of selected clades of *Strumaria* and *Hessea*. **A,** Subgenus *Strumaria*; **B,** section Bokkeveldia subgenus Gemmaria; **C,** sister-species of *Hessea* known from the Cape Fold Mountains.

species are nevertheless restricted to specific edaphic sites. The extremely restricted distribution of species is a feature of many genera in the Cape flora (Bremer 1976, Goldblatt 1976b, Karis 1989, Levyns 1954, Oliver 1991, Rourke 1969, 1972, Weimarck 1934, 1940) but has not previously evoked comment for the karroid regions.

A phytogeographical centre, which has consistently been recognised in other genera (Bruyns 1989, Hartmann 1987, Moffett 1978), but more widely circumscribed than the original delimitation of Nordenstam (1969), is the Gariep Centre, located in the Richtersveld and the southernmost region of Namibia. Four closely related species (*S. bidentata, S. phonolithica, S. barbarae* and *S. hardyana*) are endemic to this area (Figure 5.4a). Although each of these species is localised within this somewhat enlarged Gariep Centre, no one species occurs over the entire range; a pattern similar to that found by Hartmann (1987) in Mesembryanthemaceae.

The well corroborated clade diagnosing section Bokkeveldia shows the sister-species *S. watermeyeri* and *S. salteri* distributed allopatrically on the Bokkeveld escarpment, Nardouwsberg and northern Cedarberg, a phytogeographical area equivalent to the Gifberg-Bokkeveld subcentre, identified by several genera of Iridaceae (Goldblatt 1985). These species in turn form a sister-group to *S. perryae, S. pubescens* and *S. aestivalis*. *Strumaria pubescens* falls within the area of endemism identified by Weimarck (1941) as the Hantam-Roggeveld subcentre; *S. perryae* occurs at the northern extreme of the Bokkeveld escarpment; and the outlying *S. aestivalis* is restricted to the Langberg in the north near Loeriesfontein (Figure 5.4b).

Carpolyza, a monotypic genus which is closely related to *Strumaria* is restricted to the south-western Cape and southern Cape, always in seasonally moist sites (Figure 5.3a).

Hessea, with only nine species, is less widespread than *Strumaria* and is entirely restricted to the winter and autumn-rainfall regions of southern Africa (Figure 5.3b). Like *Strumaria* it spans the Karoo-Namib Region and the Capensis Region; phytochorological regions defined by Werger (1978). Habitats are seasonally moist sites provided by seasonal washes and rocky situations. Unlike *Strumaria* most species favour sandy soil and only one species (*H. stellaris*) occupies the loamy clay soils derived from shales of the Cape Supergroup and Karoo Sequence. The presence of a few species of *Hessea* on the mountains of the south-western Cape suggests that the low fertility of the substrates of the Cape Fold Mountains forms less of a barrier to *Hessea* than to *Strumaria.*

No marked areas of species richness are evident. Species are mostly widespread and allopatric. In comparison to *Strumaria* only three species (*H. incana, H. pusilla, H. undosa*) are known from only one or two 30' squares. A noteworthy phytogeographic pattern is shown by the closely related species *H. undosa, H. monticola* and *H. cinnamomea,* which span centres of endemism identified by other groups (Figure 5.4c): the Gifberg-Bokkeveld Mountain Subcentre (Goldblatt 1985), the Cedarberg Subcentre (Goldblatt 1985, Weimarck 1941) and the Cape Peninsula Subcentre (Weimarck 1941).

Hessea monticola and *H. cinnamomea* are both fire opportunists, with profuse, post-fire flowering in autumn or winter and long, fire-free sterile intervals which may last from six to 40 years. In contrast *H. undosa*, which occupies persistently open sites amongst the dry fynbos community of the Gifberg, flowers annually without fire.

Namaquanula, closely related to *Hessea*, has only three widely disjunct allopatric species. These are located near the mouth of the Orange River, which is equivalent to Nordenstam's (1969) Gariep centre; the Bokkeveld Mountains near Nieuwoudtville; and the west coast near Langebaan (Figure 5.3b), each in distinct edaphic habitats.

Kamiesbergia, the monotypic genus allied to *Hessea* and *Namaquanula* is narrowly distributed on the eastern limit of the distribution area of *Hessea*, in western Bushmanland (Figure 5.3b), where it is restricted to crevices in exposed granite domes.

5.3 Cladistic biogeography

The first model of area relationships in southern Africa, derived from cladistic biogeographical methods, was that of Anderberg (1986), based on the 'ancestral species map' method of Wiley (1981), the results of which are difficult to compare with other data. Those based on component analysis are Bruyns & Linder (1991), Kurzweil *et al.* (1991) and Griswold (1991). Other limited examples are shown by Bremer (1978), Wanntorp (1988) and to some extent Karis (1989). Thus far, just one cladistic biogeographical analysis has been undertaken for the winter-rainfall region of southern Africa (Bruyns & Linder 1991). Now that cladograms for the species of *Namaquanula, Hessea* and *Strumaria* are available, a further cladistic analysis of the south western region of Africa is undertaken. For such an analysis no assumptions about the age of the group, their present or previous dispersal ability or activity are required (Humphries & Parenti 1986).

5.3.1 Area cladogram for *Namaquanula* and *Hessea*

The areas in which each of the *Namaquanula* and *Hessea* species occur have been placed on the strict consensus tree shown in Figure 4.19. The areas (A ....G) are defined by the distribution ranges of the broadest allopatric species, following the method of Ladiges *et al.* (1987). Distributions representing two or more closely allopatric species within a general geographic area are given numbered subscripts. The areas are mapped on Figure 5.5a and listed for each species, with accompanying habitat data in Table 5.1.

The size of the distribution areas varies greatly. *Namaquanula bruce-bayeri* and *N. mathewsii* have restricted endemic ranges near the Orange River Mouth and on the west coast respectively and are represented by Areas A and C. *Hessea stellaris* has a widespread distribution from near Loeriesfontein to Oudtshoorn but as it does not overlap any other species of *Hessea* or *Namaquanula* it is also represented by a single area on the

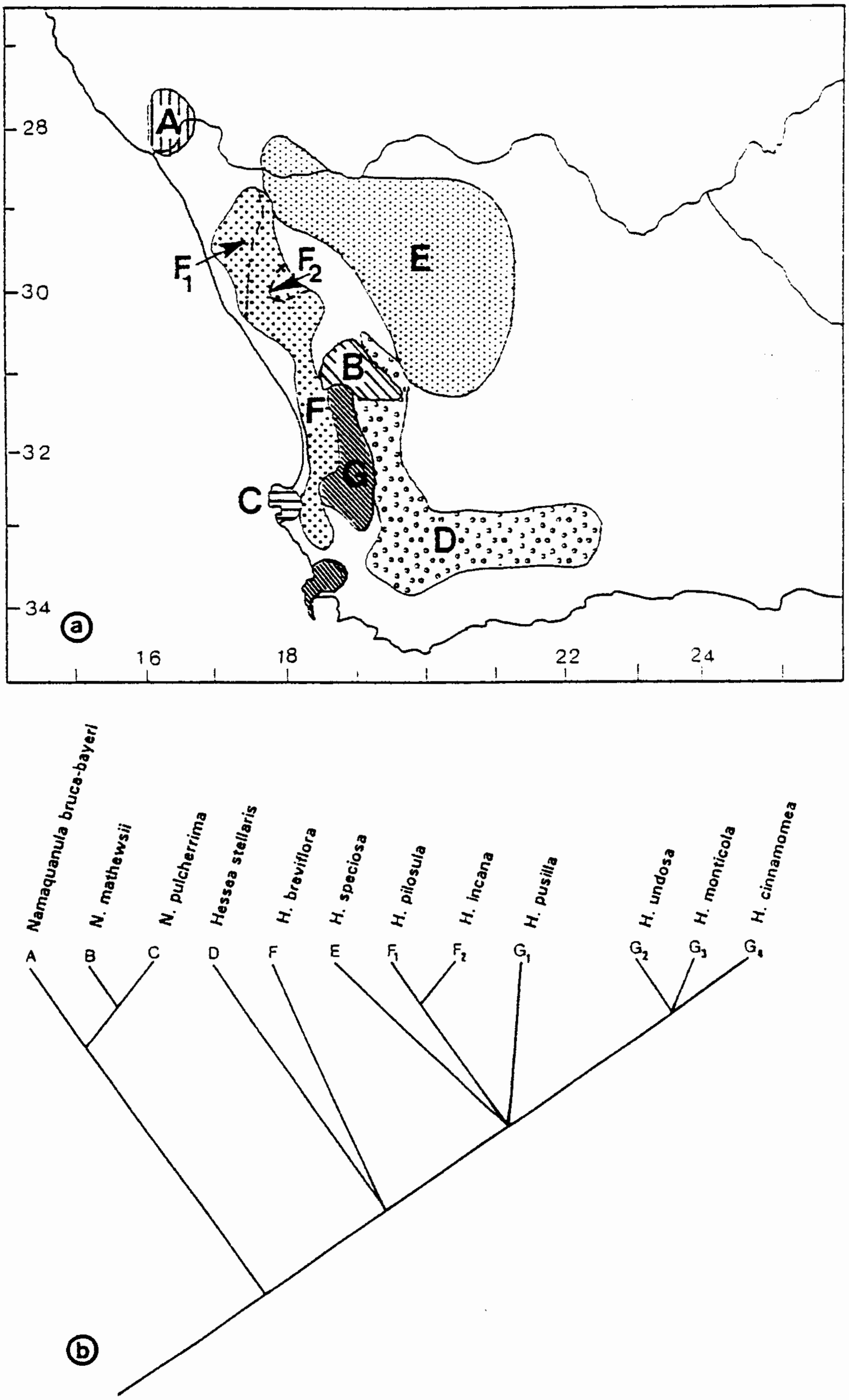


FIGURE 5.5-- Areas and area cladogram defined by *Hessea* and *Namaquanula* species. **A**, Areas defined by species listed in Table 5.1; **B**, area cladogram based on the strict consensus tree in Figure 4.19.

cladogram (area D). *Hessea speciosa* defines Area E (Bushmanland) and *N. pulcherrima* defines area B, the high-lying plateau between Nieuwoudtville and Calvinia in the north-western Cape. The trichotomy made up of the species *H. undosa*, *H. monticola* and *H. cinnamomea* determines area G, namely the western Cape Fold Mountains from the Gifberg along the Cedarberg and Piketberg to the Cape Peninsula. Area F is the most complex area. The boundaries are defined by *H. breviflora* which extends from near Springbok in the north to near Malmesbury in the south-western Cape and eastwards across the coastal lowlands to the first escarpment which runs parallel to the west coast. Two species are sympatrically nested in this area, *H. pilosula* which defines area F_1, and *H. incana*, which is narrowly endemic on the Kamiesberg, defines area F_2.

TABLE 5.1-- Areas and habitats of *Namaquanula* and *Hessea*

Species	Area and habitat
Namaquanula	
N. bruce-bayeri	Area A. Alluvial gravel on flats or low hills near Orange River Mouth.
N. pulcherrima	Area B. Heavy clay loam on lower western foothills of Bokkeveld escarpment as well as elevated plateau between Nieuwoudtville and Calvinia.
N. mathewsii	Area C. Coastal shallow calcareous soils over limestone near Saldanha Bay.
Hessea	
H. stellaris	Area D. Loamy and sandy soil of Little Karoo, the foothills bordering the western Tanqua Karoo northwards to Loeriesfontein.
H. breviflora	Area F. Loamy or sandy soil on or around rocky outcrops throughout Namaqualand and lower slopes of Olifants River Mountains.
H. speciosa	Area E. Deep red sands and friable loams of Bushmanland.
H. pilosula	Area F_1. Deep red terrestrial sands on west coast and near Springbok.
H. incana	Area F_2. Elevated sandy plains between granite domes on the Kamiesberg.
H. pusilla	Area G_1. Deep white sand on sandstone sheets, northernmost end of Bokkeveld Mountains.
H. undosa	Area G_2. Seasonally waterlogged shallow sand or rock sheets, Gifberg.
H. monticola	Area G_3. Seasonally waterlogged loamy slopes or plains, Cedarberg and Piketberg.
H. cinnamomea	Area G_4. Seasonally waterlogged peaty lowlands on the Cape Peninsula.

The area cladogram obtained from *Namaquanula* and *Hessea* is shown in Figure 5.5b.

5.3.2 Area cladogram for *Strumaria*

The area in which each species of *Strumaria* occurs has been placed on the strict consensus tree shown in Figure 4.20. The areas (A, ..., J) are more or less comparable to those used in the area cladogram of *Hessea* and *Namaquanula* but do not correspond exactly (Figure 5.5). Those pertaining to subgenus Tedingea have been omitted because that clade only expresses a two-taxon statement, and since a two-taxon statement is consistent with all possible patterns it cannot corroborate or falsify any pattern. Areas A_1 to A_4 are defined by the distributions of *S. bidentata, S. phonolithica, S. barbarae* and *S. hardyana* respectively in southern Namibia and the Richtersveld, as shown in Figure 5.4a. Area B is defined by *S. discifera* and has *S. picta* (area B_1) sympatrically nested within it. Area C is defined by the species pair *S. chaplinii* and *S. leipoldtii* on the west coast and area D is defined by *S. gemmata*. *Strumaria truncata* defines area F, the large area known as Namaqualand but also extends into area B. Two taxa are sympatric in area F, namely *S. villosa* and *S. merxmuelleriana*, in the uplands near Springbok. These species define areas $F_{1.1}$ and $F_{1.2}$ respectively. Area G is determined by *S. watermeyeri* and *S. salteri* on the Cape Fold Mountains between the Bokkeveld Mountains and the Pakhuis Mountains, while area H on the south-western periphery of the Tanqua Karoo is defined by the sister species *S. unguiculata* and *S. karoopoortensis.* Area I is defined by *S. karooica* on the Roggeveld escarpment and has *S. pubescens* sympatrically distributed within it. Area J is defined by *S. massoniella* and contains *S. aestivalis.* Area E (Bushmanland) is missing from this analysis since *Strumaria* is not represented here.

The areas are mapped on Figure 5.6a and listed with species and habitats in Table 5.2.

5.3.3 Component analysis of *Namaquanula, Hessea* and *Strumaria*

Comparison of the area cladograms of *Namaquanula, Hessea* (Figure 5.5b) and *Strumaria* (Figure 5.6b) indicates that each is lacking in some information as they have unresolved area relationships and incongruent distribution patterns. Nelson & Platnick's (1981) component analysis has the potential power to assess the variation among the patterns and give a single rigorous result. Thus, with the use of this method, it may be possible to show that although each group has a unique pattern of area relationships, each pattern has the same biogeographical history (Humphries & Parenti 1986).

For component analysis I have employed the method of Ladiges *et al.* (1987) which assumes that the narrowly sympatric areas reflect the same occurrences as the broader areas in which they occur (for example B_3 can be treated the same as B), so that reduced area cladograms can be attained. Furthermore for the *Hessea* data, area D and E were combined to avoid the prohibitively long computations induced by a unique area. Similarly, for the *Strumaria* data the unique area H was included in D.

TABLE 5.2-- Areas and habitats of *Strumaria* subgenus *Strumaria* and subgenus *Gemmaria*

Species in major clades	Area and habitat
Subgenus *Strumaria*	
S. bidentata	Area A_1. Sandy flats adjacent to Orange River Mouth.
S. phonolithica	Area A_2. Steep mountain slopes amongst phonolite chips, southern Namibia.
S. barbarae	Area A_3. Exposed limestone screes, southern Namibia.
S. hardyana	Area A_4. Shale and limestone crevices on mountain slopes, southern Namibia.
S. truncata	Area F. Shale or granite-derived soils on gentle slopes or plains, Namaqualand.
Subgenus *Gemmaria*	
S. picta	Area B_1. Heavy loamy soils on eastern foothills of Bokkeveld Mountains.
S. discifera	Area B. Heavy loamy soils on gentle slopes between the Bokkeveld Mountains and Roggeveld Escarpment.
S. unguiculata	Area H. Loamy soils amongst slate chips on north-facing slopes of Doornrivier Valley.
S. karoopoortensis	Area H. Loamy soils on an isolated shale outcrop in the arid southern Tanqua Karoo.
S. gemmata	Area D. Loamy soils, stony slopes or flats, Little Karoo, southern Cape and Great Karoo.
S. karooica	Area I. Heavy loamy soils on rocky flats, Roggeveld escarpment.
S. massoniella	Area J. Sandy arid, elevated plains, Loeriesfontein to eastern Kamiesberg.
S. merxmuelleriana	Area $F_{1.1}$. Sandy elevated sites near Springbok.
S. chaplinii	Area C. Coastal granite outcrops near Saldanha Bay.
S. leipoldtii	Area C. Loamy soil on rock outcrops edging seasonal river, Lamberts Bay.
S. villosa	Area $F_{1.2}$. Exposed patches of quartz pebbles overlying weathered granite soil, near Springbok.
S. watermeyeri	Area G. Shallow sandy soil on exposed sandstone sheets, Bokkeveld Mountains.
S. salteri	Area G. Sandy pockets on sandstone outcrops on Nardouw and Pakhuis Mountains.
S. perryae	Area B_3. Loamy flats, northern Bokkeveld Mountains.
S. pubescens	Area D. Shaley rock ledges, S facing slopes, Roggeveld escarpment.
S. aestivalis	Area J. Shaley banks of seasonal stream, Langeberg.

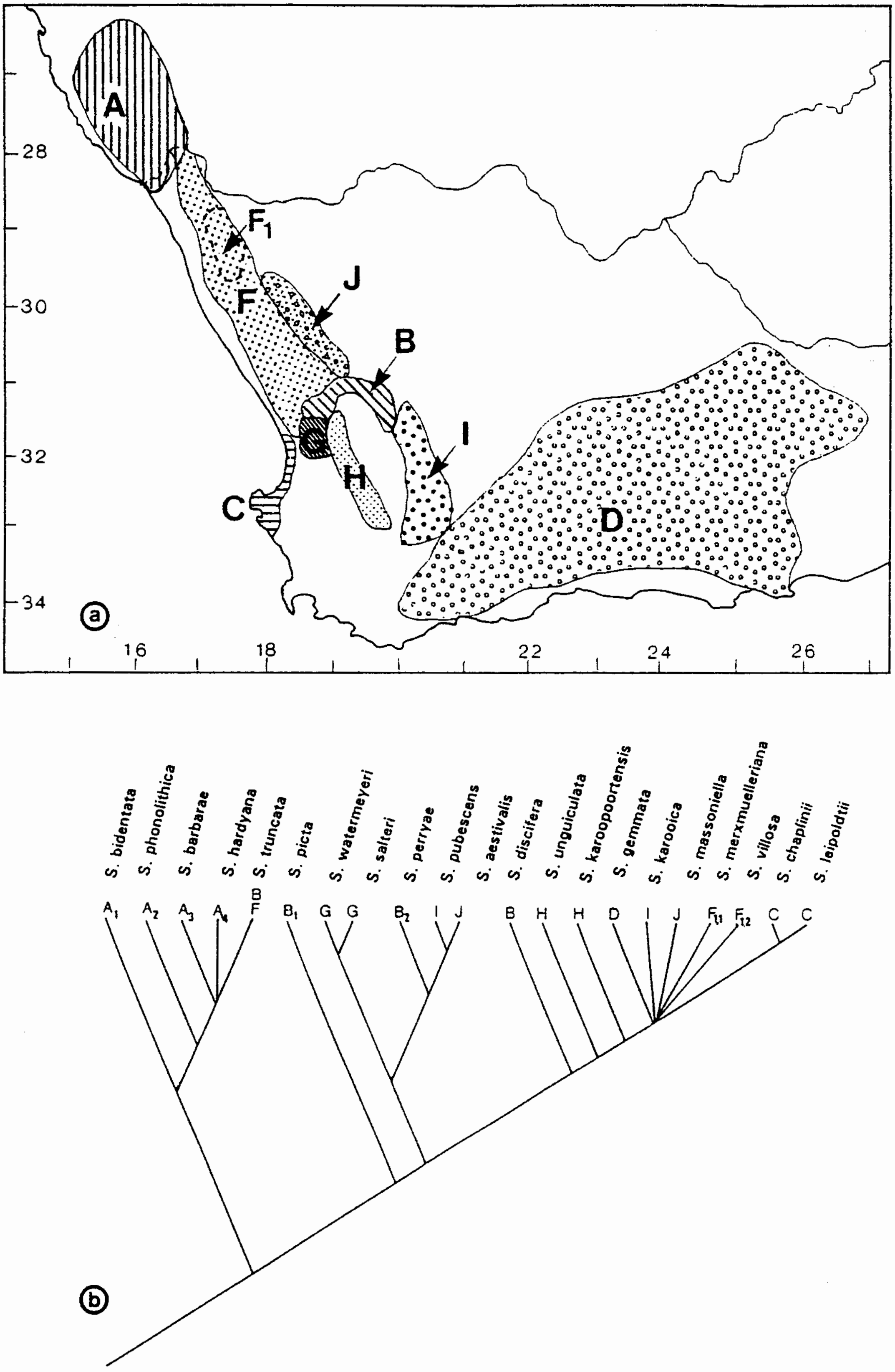


FIGURE 5.6-- Areas and area cladogram defined by *Strumaria* species. **A**, Areas defined by species listed in Table 5.2; **B**, area cladogram based on the strict consensus tree in Figure 4.20.

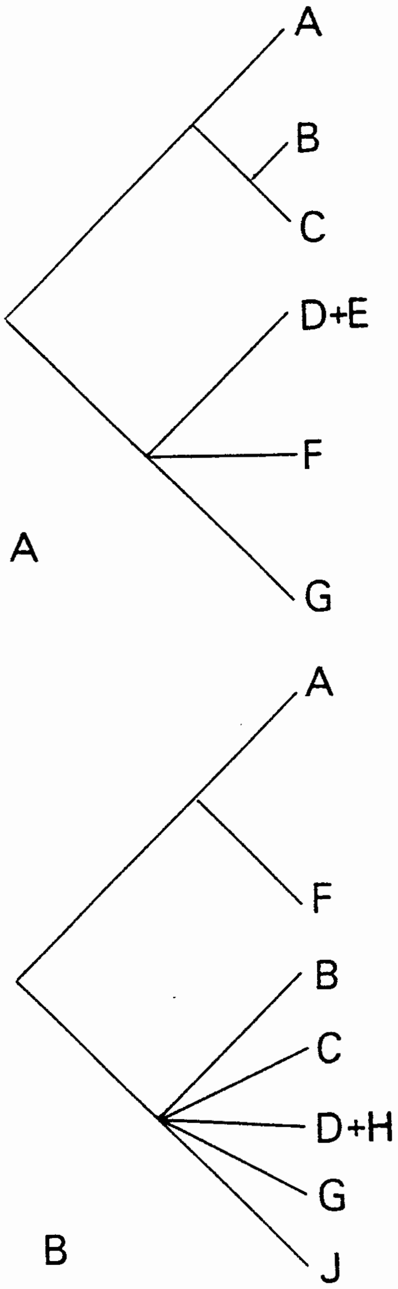


FIGURE 5.7-- Results of the biogeographic component analysis. a, Consensus tree defined by *Namaquanula* and *Hessea* data; b, consensus tree defined by ***Strumaria*** data.

Using the program COMPONENT (Page 1989), the cladogram for *Hessea*, in which six areas were recognised, resolved into three possibilities under Assumption 2. Using the same assumption, six possible trees were generated by the *Strumaria* data set, in which seven areas were recognised. The resultant consensus trees, which are shown in Figure 5.7, revealed no degree of intersection.

5.4 Discussion and conclusions

Biogeographic patterns within continental biotas are produced by cycles of vicariance of widespread species, followed by narrow endemism, followed thereafter by population expansion of descendant species to produce more widespread forms, in turn followed by new cycles of vicariance (Cracraft 1988). The hope of biogeographers is that traces of areas of endemism will persist in the histories of different biotic elements.

South western Africa, the region under consideration here, bears sufficient fossil evidence from a number of sources (Carrington & Kensley 1969, Coetzee 1978a, 1978b, 1983, 1986, Scholtz 1985) to show that the area enjoyed moist conditions throughout most of its pre-Pliocene history.

The earliest evidence of the modern semi-arid environment and winter-rainfall in the south-western Cape dates to the Pliocene (Hendey 1976, 1983, Tankard & Rogers 1978), after a marked cold upwelling on the west coast in the early Late Miocene (Siesser 1978). Whereas early Pleistocene marine deposits on the Saldanha coastline in the south-western Cape reflect oceonographic conditions which were similar to those of the present cold Benguela Current (Tankard 1975), mollusc fossils from contemporaneous deposits on the Namaqualand coast, to the north, indicate that early Pleistocene coastal waters there were considerably warmer (Carrington & Kensley 1969). Thus, when semi-arid conditions with winter rainfall were achieved in the south west, the Namaqualand coast was still north of the upwelling zone by the earliest Pleistocene (Tankard & Rogers 1978).

Aridity in southern Africa was fully established in the Quaternary (Tankard & Rogers 1978) but the climatic patterns were affected by a series of globally synchronous glacials and interglacials. The interpretation of the seasonality of Pleistocene climates is conflicting (Cockcroft *et al.* 1987, Deacon 1983, Tyson 1986, Van Zinderen Bakker 1976) but from the presence of extensive hyperthermal evaporite deposits on the west coast, Flemming (1977) inferred arid conditions and less frequent winter rainfall during the interglacial, as a result of a southerly shift of the westerlies.

Conversely, during the last Glacial Maximum, 18,000 years ago, the climatic model of Tyson (1986) predicts that the winter/summer-rainfall interface moved northwards and eastwards of its present position, to 25°S in the west and 30°S in the east. Cryoclastic debris in caves on the south coast, at present a frost-free area, indicate a significant lowering of temperature (Tankard 1976). The southern part of South Africa also experienced greater precipitation with a winter maximum (Cockcroft *et al.* 1987). These coincided with a northward shift of the arid zone (Lancaster 1984). The pattern was subsequently reversed by an expansion southward of the climate 12000 - 9000 years ago (Klein 1974), when the sea level recovered (Hendey 1981) and the mouths of the ephemeral rivers of Namaqualand approximately assumed their present positions (Tankard & Rogers 1978).

Thus, whereas arid conditions have had a profound effect on south western Africa, aridity was not a constant factor throughout the area. The evidence shows considerable expansions of the area of aridity in southern Africa, but at intervals, of which the precise chronology is unreliable (Lancaster 1984).

Cracraft (1988) argues that many barriers within continental biotas are ecological in nature and might be expected to be relatively ephemeral and susceptible to minor changes in climate. Following this argument, the variable climatic history of southern Africa would strongly imply that the region may have comprised a series of transient biotas, particularly in zones where the seasonality of rainfall fluctuated greatly. The conflicting area cladograms generated by the *Namaquanula, Hessea* and *Strumaria* data may thus be taken as evidence of the complexity of the biogeographic history; and each pattern may be taken to represent real aspects of the biota.

Alternatively, it may also be assumed that despite the conflicting area cladograms, the inability to extract a singular history of the areas of endemism is due to the inadequacy of current methods. Just one aspect of this problem is the difficulty encountered in comparing different areas occupied by species. Thus in south western Africa the areas identified by *Microloma* (Bruyns & Linder 1991) are not easily comparable to those identified by *Namaquanula, Hessea* or *Strumaria*. Likewise, the areas identified by the different genera in the study group are not readily comparable. This weakness consequently limits the information potentially available from biogeographic distributions (Henderson 1991).

Lastly, Page (1988) notes that certain modes of speciation may imply that certain spatial arrangements of phylogenetic relationships are more probable than others. Thus if lineage divergence in *Hessea* was caused predominantly by vicariance whereas allopatric speciation by peripheral isolation was most frequent in *Strumaria*, the derived area cladograms may be skewed and the possibility of obtaining intersection may be excluded.

In conclusion, although the results of the above analysis proved to be uninformative, the use of the closely related south western African genera, *Namaquanula, Hessea* and *Strumaria*, has to some extent also proved to be a valuable exploratory study for component analysis at regional level. Clearly, many more comparative biogeographic studies in the semi-arid, winter-rainfall region of southern Africa are required before this tangle of methodological problems and historical events can be resolved.

Chapter 6.
COMPARATIVE VEGETATIVE AND FLORAL BIOLOGY

6.1 Introduction

The life form of the taxa within Amaryllideae is remarkably simple. The perennial part of the plant is a bulb which encloses underground buds; the aerial unbranched parts consist of distichous or rosulate, basally concentrated leaves and an inflorescence-bearing, leafless scape; the seeds are fleshy and recalcitrant. If this constancy of growth form reflects developmental constraints due to the structure of the developmental system or canalising selection, the implication is that it can lead to complete fixation and extinction of systems when these are no longer able to meet the adaptive requirements of the external environment (Riedl 1978). Thus an examination of the evolutionary sequence of structure-function transformation in the tribe should allow an assessment of the limitations and possibilities of the strategies available to the taxa which occupy south-western Africa, the semi-arid area of particular interest in this study.

This investigation is limited to the study of the reproductive strategies within Amaryllideae: firstly, by an analysis of resource allocation, as determined by the morphological properties exhibited among the genera; and secondly, the floral features effective in pollination, particularly in the actinomorphic-flowered Amaryllidinae.

6.2 Method

The usefulness of phylogenetic trees for documenting patterns of structural and functional diversification has been well established (see Donoghue 1989, Funk & Brooks 1990, Linder 1991b, Schaefer & Lauder 1986, Wake & Larson 1987). Cladograms can help identify the context in which features evolved, the number of times a feature evolved and the character assembly in the lineage (Donoghue 1989).

For this investigation the phylogenetic comparative method was used as modified by Linder (1991b) and Schrire (1991). The characters selected for the analyses were plotted on the terminal taxa of the cladograms. All taxa and nodes were numbered on the cladogram and the most parsimonious interpretation of the binary character states at each inner node was obtained using Farris optimisation (Farris 1970). For a description of resolving the condition at each inner node refer to Mickevich (1982). The sequence in which various character states arose is then read from the base of the cladogram through the axes of the internal nodes to the terminal taxa.

A noncircular approach to this analysis is not yet possible since the phylogenetic hypothesis which serves as the basis for these analyses is the only one available at present. Thus with the exception of a few characters (bulb size, patterns of leaf growth, leaf number and leaf phenology), the features examined here were also used to generate the phylogenetic hypothesis. Confirmation of the sequencing therefore awaits the availability of an independently generated phylogeny.

Experimental data on energy allocation and pollination mechanisms of taxa within Amaryllideae are almost entirely lacking, hence the functions have been inferred from the morphology of the plants. A phylogenetic base greatly strengthens both problem formulation and analysis (Wanntorp *et al.* 1990), therefore, despite the explicit weakness of the paucity of data, it is hoped that future ecological and physiological studies in the tribe will nevertheless benefit from this preliminary approach.

6.3 Resource allocation

The structural features selected for the analysis of resource allocation strategies in Amaryllideae are shown in Figure 6.1 on a cladogram modified from the tribal cladogram in Figure 4.18. For this analysis *Boophane pulchra* is treated as a species of *Brunsvigia.* Noteworthy is the structural plasticity shown in terminal taxon 13 (*Strumaria*); a pattern which suggests that *Strumaria* may still be in a phase of radiation, making it ideal for the study of character evolution (see Vrba & Eldredge 1984).

6.3.1 Bulb size (b = large; B = small)

Although large and small-sized bulbs do not fall into two discrete categories, on a relative scale, small bulbs are more prevalent in Amaryllidinae than in Crininae. Reduced bulb size is particularly characteristic of the actinomorphic-flowered Amaryllidinae at node 17.

6.3.2 Leaf growth (g = successive; G = simultaneous)

Two vegetative growth patterns are evident. Extended sequential leaf growth is found at the basal nodes of the cladogram but this shifts to a pattern of rapid, simultaneous leaf growth at node 15. A single reversal to sequential vegetative growth is found at node 18 (in *Carpolyza* and *Strumaria* subgenus Tedingea). Both these switches are hypothesised as having arisen through heterochronic changes: acceleration to simultaneous growth, then reversal to sequential growth by neotony, following the system proposed by Alberch *et al.* (1979). Most of the taxa with rapid, synchronous vegetative growth at the beginning of the season are distributed in the winter-rainfall area, where the photosynthetic period is short (see Van Rooyen *et al.* 1979). Similar strategies have been recorded for several sub-alpine species of the northern hemisphere (Ogden 1974), and are considered to be adaptations to habitats with a short growing season and cold winters.

6.3.3 Leaf number (n = many; N = few)

Few-leaved plants (mostly less than three leaves) evolved twice from node 17, (the ancestral node to *Kamiesbergia, Hessea* and *Namaquanula*) and in *Strumaria* subgenus Gemmaria. Reduction in leaf number is also known in *Nerine* and *Brunsvigia* but this is restricted to one or two species only.

6.3.4 Flower senescence (f = withering; F = drying out)

Flowers of most taxa of Amaryllideae are retained at senescence, when they wither, collapse and the pigmentation becomes accentuated. At node 19 however, this pattern changes to rapid drying out and browning off of the flowers without the collapse of any parts. Although the collapse of floral parts may offer protection to the stigma and avoid pollen loss by preventing additional pollinator visits (Gori 1983), the novel drying off of the flowers in *Hessea*, *Namaquanula* and *Kamiesbergia* may be an adaptation, for the withdrawal and resorption of resources to other parts of the plant, particularly the developing seeds, under arid conditions.

6.3.5 Capsule dehiscence (c = indehiscent; C = dehiscent)

Indehiscent capsules occur at the basal node of the subtribe Crininae. The seeds are thus retained until the capsule walls slowly disintegrate or are broken by mechanical means (Markötter 1936, pers. obs.) At node 15 the capsules become dehiscent, opening by more or less well-developed slits. Accordingly the seeds are easily released.

6.3.6 Seed testa (s = without stomata; S = with stomata)

Throughout the tribe the seeds have no autonomous resting period. The significance of stomata on the seed, which occurs from node 16, has been assessed with reference to the detailed studies by Schlimbach (1924), on the seeds of *Crinum, Amaryllis* and *Nerine*. In *Crinum* extensive growth of the endosperm provides reserves for the embryo, which undergoes a period of after-ripening once the seed is fully developed. Chlorophyll is found in the peripheral region of the endosperm but is thought not to be involved with assimilation as the outer cork layer contains no stomata (Schlimbach 1924). A major ontogenetic shift is evident in *Nerine*. After fertilization the integument expands strongly and develops considerable amounts of chlorophyll; while stomata develop in the testa. Unlike *Crinum* the endosperm remains poorly developed and although not experimentally proven, photosynthesis appears to take place while the embryo undergoes a period of secondary ripening (Schlimbach 1924). In the absence of detailed studies in the rest of the subtribe, seeds with the structure of *Nerine* are assumed here to follow the same developmental and physiological pattern.

Although mineral nutrients and water must be gained by reproductive structures from the remainder of the plant, the energy and carbon needed for reproductive success has been shown to be obtained in several dicotyledonous species from photosynthesis in

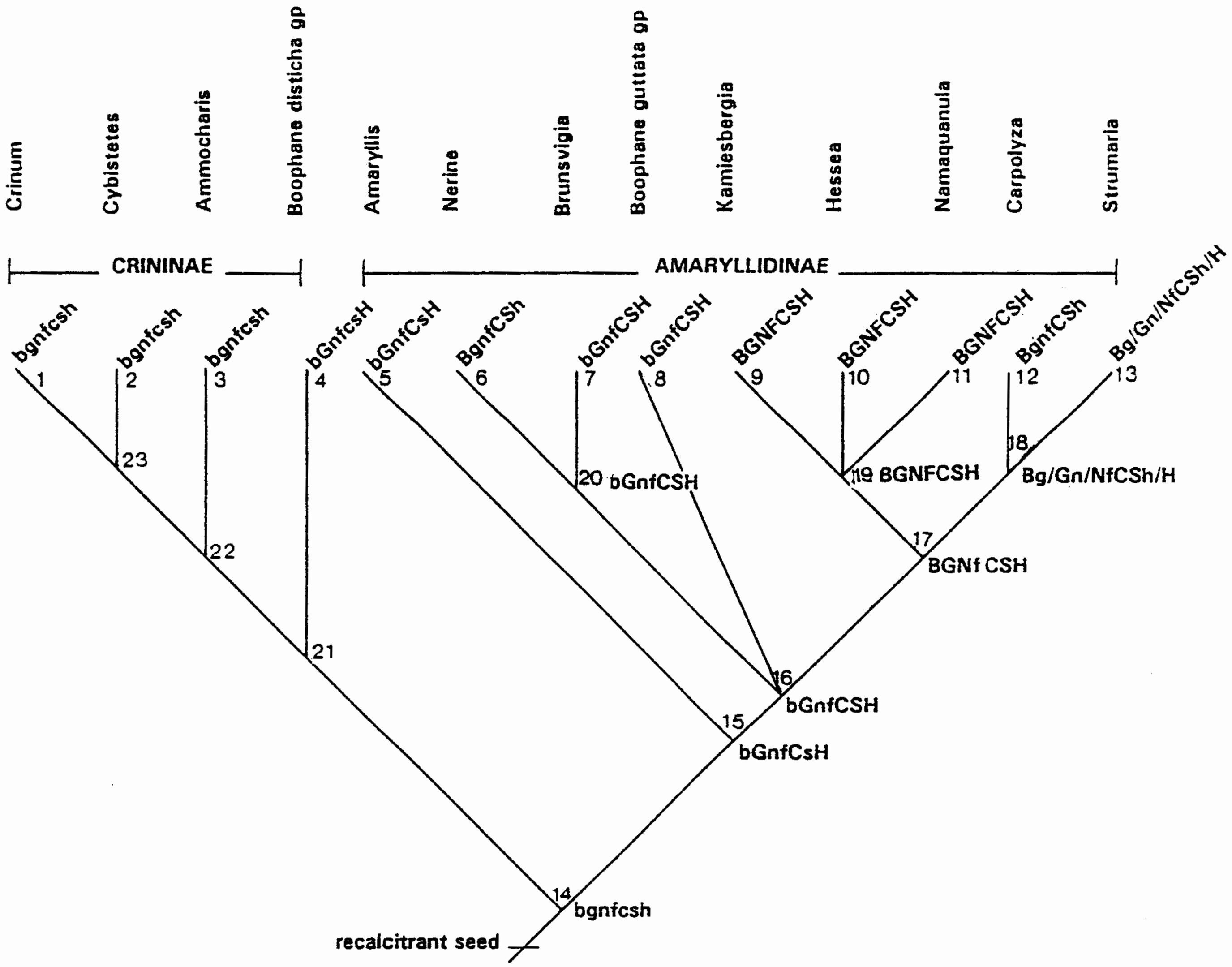


FIGURE 6.1-- Resource allocation mechanisms, mapped on the phylogeny of Amaryllideae in Figure 4.18. The symbols are explained in Part 6.3.

the reproductive structures themselves (Bazzaz *et al.* 1979). Thus the adaptive strategy of diminishing reproductive effort by photosynthesis of the seeds is assumed to operate in all Amaryllidinae from node 16.

6.3.7 Hysteranthous leaves (h = synanthous; H = hysteranthous)

Hysteranthous leaves are more prevalent in Amaryllidineae than in Crininae. This habit occurs from node 15 with two subsequent reversals to the synanthous leaf-habit above node 18 (*Carpolyza* and *Strumaria* subgenus Tedingea). A convergent pattern to the hysteranthous leaf-habit also occurs at taxon 4 in Crininae. Although the synanthous leaf-habit in Crininae has been treated as "the same" as that in *Carpolyza* and *Strumaria* subgenus Tedingea, they are not homologous. The leaves and flowers which mature synchronously in Crininae are from the same shoot. Whereas in *Carpolyza* and the species of *Strumaria* subgenus Tedingea, the leaves and flowers initiated in each annual shoot do not expand simultaneously: flowering is delayed to overlap with the leaf growth of the next year's shoot. The synanthous leaf-habit (although poorly developed) is thus secondarily derived in these taxa. Two sequences of post displacement in the onset of flowering (*sensu* Alberch *et al.* 1979) would appear to account for the sequential shift from the synanthous leaf-habit to the hysteranthous leaf-habit and the secondarily derived synanthous leaf-habit evident in Amaryllidinae.

The hysteranthous-leaved pattern, in which the reproductive and vegetative phases occur independently in autumn and winter respectively, is prevalent among the species of Amaryllidae from the winter-rainfall regions of the Cape; which supports the hypothesis that it is a strategy to ensure rapid and efficient flowering under seasonal Mediterranean-like climates, by allowing the reserves necessary for flowering to be accumulated in the previous year. Thus flowering can only be influenced to a limited extent by the immediate climatic conditions of autumn (Dafni *et al.* 1981a, 1981b). Inspection of the cladogram in Figure 6.1 indicates that the channeling sequence into the hysteranthous leaf-habit commences with the recalcitrant seed from the basal node. The switch to hysteranthy during the change to summer-aridity in south-western Africa therefore appears to have been promoted by this ancestral seed condition, which combines the competitive advantages of rapid germination at the onset of the growing season, with seedling vigour and aggressiveness.

6.4 Discussion of resource allocation

Comparison of the life histories shown by the subtribes of Amaryllideae reveals two major patterns. The life cycle among most genera of Crininae is one in which large-sized bulbs have steady and successive leaf growth and a protracted reproductive phase, which mostly overlaps the vegetative phase. Until the embryo reaches maturity the seed is retained in the capsule. In the absence of specialised structures for photosynthesis other than the vegetative structures, the cost of reproductive effort is borne fully by the leaves.

In contrast, the subtribe Amaryllidinae shows a wider amplitude of life cycle strategies. Taxa have large or small-sized bulbs, with many to few foliage leaves and sequential or synchronous growth. The onset of flowering and fruiting is delayed in several genera so that the leaves are hysteranthous. Constant throughout the subtribe (with the exception of *Amaryllis*) is the photosynthesising seed, which partitions the cost of reproductive effort between the vegetative parts and the integument. A comparison of the present distribution patterns in the subtribes indicates that Amaryllidinae occupies both the summer and winter-rainfall areas of southern Africa, whereas Crininae occurs predominantly in the summer-rainfall areas and only marginally in the winter-rainfall region of the Cape (Figures 5.1, 5.2 & 5.3). It has long been proven that new periods of evolutionary vigour and new diversification coincide with the conquest, by means of new features, of new ecological niches (Riedl 1978). Characters which permit a fairly rapid departure of a group of organisms from a preceding ecological sphere are referred to as "key innovations" (see Larson *et al.* 1981). Such innovations arise as preadaptations and promote the appearance of supportive adaptations during the ecological transition. Key innovations are stated to have two important results. They permit radiation by release from former ecological competitors and they tend to develop gaps between the new group and the ancestral group.

Examination of the sequence of character assembly in Amaryllidinae suggests that the stomatose seed is such a key innovation, since it initially freed the vegetative parts from the burden of providing the total assimilate enabling a new diversity of forms to develop under conditions of increasing summer aridity: firstly, small bulbs and, as the cost of maintenance of the bulb diminished, a reduced number of leaves. Other studies which support the importance of key innovations in evolutionary change are Bock (1965), Liem (1974) and Schrire (1991).

To highlight the critical limits of resource allocation strategies available within both subtribes, the life histories of certain species from the winter-rainfall area provide apposite examples.

Possibly as a result of physiological constraints, *Boophane haemanthoides*, one of the few species of Crininae known from the west coast, flowers during the summer drought (November), so that peak availability of the slowly maturing seeds may coincide with the onset of the rain period in autumn, when vegetative growth commences. This strategy, powered entirely by stored reserves, has led to the development of extremely large bulbs (± 300 mm diam); the largest in the tribe. The absence of juvenile plants in the known populations of *B. haemanthoides* (B. Liltved & E.J. van Jaarsveld pers. comm.) suggests that the reproductive output is low, and should the summer drought be prolonged, survival of the species would be further impaired. In accordance with the general hypothesis of Riedl (1978), the restricted number of species of the subtribe in this region and the appearance there of these extreme forms may be indicative of the dissolution of this lineage. The extinction of species as a slow process, leading from the survival of a few descendants, lingering in protected and isolated situations was also argued by Darwin (1859: 344). The ability of this species to resprout vegetatively may however make it resistant to extinction, although it appeas already to be in a period of contraction.

In contrast, the putative switch in energy allocation within Amaryllidinae is associated with reduced plant size among most genera from the semi-arid western regions (*Kamiesbergia, Hessea, Namaquanula, Strumaria*). The most diminutive species of all these autumn-flowering taxa is *Strumaria pygmaea.* As a result of the photosynthesis of the seeds, and in this species the green pedicels, the cost to the bulb of reproductive effort appears to be reduced to the minimum; and with the diminished need for stored reserves, the bulb is reduced to the smallest in the tribe (± 10 mm diam.) and possibly the entire family. This highly autapomorphous species is narrowly restricted to exposed quartzitic patches in the wind-swept Knersvlakte, thus constituting an ecologically highly specialised endemic.

As summarised in Figure 6.1 *Crinum* and *Strumaria* represent the extremes, in terms of morphological specialisation, of two trends. *Crinum*, the largest genus in the clade defining the subtribe Crininae, comprises species mostly restricted to seasonal streams and vleis. *Strumaria*, the second largest genus in Amaryllidinae, is almost entirely restricted to the semi-arid winter-rainfall region of southern Africa and comprises a high percentage (78%) of species known only from one or two populations in seasonally moist, open, rocky sites.

Under the effect hypothesis of macroevolution, trends may be the effects of any factors which incidentally result in differential speciation rates (Vrba 1980). Thus some long-term directional tendencies may result as nonadaptive consequences (Vrba & Eldredge 1984).

Reduced generation time is considered to be a key to diversification because it effectively increases a population's potential growth rate (Cole 1954); and rapid turnover of individuals in the population can lead to rapid evolution (Stanley 1979). The reduced plant size in *Strumaria* as well as its close allies (*Hessea, Namaquanula, Kamiesbergia* and *Carpolyza*) is a juvenile phase of up to four years, a reduction in comparison to the seven to eight years in the large bulbous genera of Crininae (as well as *Boophane* and *Brunsvigia* in Amaryllidinae), (G. Duncan & P.L. Perry pers. comm.). Thus the increased number of sexual generations in the small-bulbed species of the actinomorphic-flowered Amaryllidinae may be viewed as having effected a rapid evolutionary rate among these lineages. In contrast, the diversity in *Crinum* is interpreted here as the effect of overcoming the problems of resource availability and dispersability of its large seeds by adapting largely to an aquatic habitat.

Future studies may yet reveal the above combination of strategies (relatively short generation time and physiological capability of movement) in *Nerine,* a speciose genus which occupies the mesic, eastern, summer-rainfall region of southern Africa. Such data would thus add further support to current indications that these combined features are correlated with high taxonomic diversity (Marzluff & Dial 1991).

6.5 Floral features effective in pollination

For a summary of the floral features examined in this analysis, refer to Figure 6.2.

6.5.1 Flower form (f - actinomorphic; F = zygomorphic)

Both actinomorphic and zygomorphic flowers occur in the subtribe Crininae. The state of the flower form at the basal node is equivocal. The zygomorphic state is basal in Amaryllidinae at node 15 with a subsequent reversal to actinomorphy at node 17.

The only published data on the pollination ecology of Amaryllideae are those of Markötter (1936) on *Cybistetes longifolia* (= *Ammocharis falcata*) and *Strumaria tenella* (= *H. tenella*); and Marloth (1915) on *Amaryllis belladonna*. My own field observations on several species of Amaryllidinae with actinomorphic flowers indicate that the flowers are relatively unrestrictive of pollinator types (Table 6.1). The open stellate flowers appear to be pollinated by several short-tongued insects and the funnel-shaped flowers by several long-tongued insects. The specificity or not of pollinators to the zygomorphic-flowered representatives of the tribe is as yet unknown.

TABLE 6.1-- Insect visitors to species of the actinomorphic-flowered Amaryllidinae

Taxon	Flower depth	Visitors
Hessea		
H. stellaris	moderate (± 3,5 mm)	honey bees
H. breviflora	moderate (± 4 mm)	honey bees
H. incana	none	honey bees
H. monticola	shallow (± 2 mm)	short-tongued flies, butterflies (African Migrant, Painted Lady)
H. cinnamomea	shallow (± 2 mm)	honey bees, short-tongued flies
Namaquanula		
N. mathewsii	none	short-tongued flies
Strumaria		
S. tenella	none	small short-tongued flies
S. truncata	deep with narrow nectar wells (up to 9 mm)	honey bees, moths
S. karooica	none	honey bees, small butterflies
S. salteri	deep, wide (± 10 mm)	long-proboscid tabanid

Since the actinomorphic growth pattern is present in the very early bud of the zygomorphic flower (pers. obs.), it is not unreasonable to hypothesise that the secondary origin of the actinomorphic state from the ancestral zygomorphic condition resulted from neotony during the ontogeny of the flower. A notable secondary development towards asymmetry amongst the actinomorphic-flowered group occurs above node 19 in *Kamiesbergia,* through the elaboration of the stamens into distinctly unequal inner and outer whorls.

6.5.2 Flower position (d = spreading; D = pendulous)

Pendulous flowers occur only at taxa 1 and 13. The pendulous habit in *Strumaria* is due to lax pedicels and is associated with clustering of the flowers and the presence in the flowers of deep, narrow nectar wells: an interdependence of characters which may reflect the development of a specialised pollination mechanism.

6.5.3 Staminal tube (t = absent; T = present)

The basal node of subtribe Crininae is equivocal as regards the presence or absence of a staminal tube. This ambiguity is resolved by the presence of a staminal tube in Amaryllidinae at node 15, whereafter a reversal to its absence occurs at node 18. After its loss the secondary development of a staminal tube occurs at taxon 13, among most species of *Strumaria* subgenus Strumaria.

The marked extension in length of the staminal tube is a particular characteristic of some species of *Hessea* and *Strumaria* subgenus *Strumaria*; and may function to exclude pollinators with unspecialised foraging behaviour.

6.5.4 Nectar presentation (n = centrally pooled; N = partitioned into three sites)

Nectar is centrally pooled at the base of the perigone or staminal tube throughout most of the tribe, but the partitioning into three discrete sites as a result of the adnation of the inner filaments to the style occurs at node 18. The attainment in addition of an elaborate style in *Strumaria* appears to have effected a major switch in the floral pattern, which led to a greater diversity of floral forms in *Strumaria* than in any other genus of Amaryllideae. Specialisations which have evolved as a result of the enlargement of the style are the presentation of nectar as large, exposed droplets in the open, stellate flowers of subgenus Gemmaria (Figure 4.1L); or in deep wells formed by the extended fusion of the filaments to each other and to the winged style in the funnel-shaped flowers of subgenus Strumaria (Figure 4.4). Thus the enlarged or winged style appears to be an adaptation for specialised nectar presentation.

False nectar spots in the form of a shiny, solid, pellucid hemisphere on the proximal adaxial surface of each tepal is a novelty in *S. gemmata* (Figure 4.1L). Whether these spots play any role in food deception mimicry has not been tested, but may prove to be an interesting case study in mimicry.

6.5.5 Filament hooks (h = absent; H = present)

The presence of filament hooks is restricted to taxon 11. The hooks, which are particularly elaborate in *N. pulcherrima* and *N. mathewsii* (Figures 9.12 & 9.13), are associated in these species with a foetid odour, contrasting floral markings and papillae on the ovary dome: a combination of features which is regarded as important in myophily (Faegri & Van der Pijl 1976). The collection of five species of short-tongued flies from the flowers of *N. mathewsii* appears to support the effectiveness of the syndrome.

6.5.6 Positional changes in floral parts (p = position of tepals and stamens unchanged after anthesis; P = tepals and stamens close after anthesis)

Throughout the tribe, the position of the tepals and stamens does not alter substantially as the flowers age. However, a shift towards the loss of herkogamy (the spatial separation of anthers and stigma *sensu* Faegri & Van der Pijl 1976) through the closure of the flower after the stigma becomes receptive occurs at taxon 13 (for *Strumaria*). Thus, preliminary crosses to determine the breeding systems within Amaryllideae (Markötter 1936, Snijman unpubl. data) suggest that allogamy is obligate in all the genera examined (*Cybistetes, Amaryllis, Brunsvigia, Hessea, Namaquanula*), except in *Strumaria*, where the anthers and stigma of the same flower touch each other as the flowers close. Statistically testable data may alter this initial interpretation but the preliminary results suggest a trend towards greater dependence on outbreeding throughout the tribe than in *Strumaria.* Confirmation of this shift in breeding system would add to numerous studies which have already documented a change in mating system among related taxa through a corresponding change in floral structure (see Barrett 1989).

6.5.7 Pollen morphology (b = monosulculate; B = bisulculate)

A major autapomorphy for the tribe which is presumed to be effective in successful pollination and subsequent fertilization is the novel pollen grain morphology: bisulculate and covered with scattered large spinulae.

Pollen apertures serve to provide exit points for the tube at the time of germination as well as to regulate water movement in the period of dessication before release from the anther, during dispersal and at the time of rehydration on the stigma (Heslop-Harrison 1979a). In species with dry stigmas, Heslop-Harrison (1979b) has hypothesised that selection favours a pollen geometry that optimises the chance of direct contact between the aperture and the porous cuticle of the papillae, so that a continuous water film

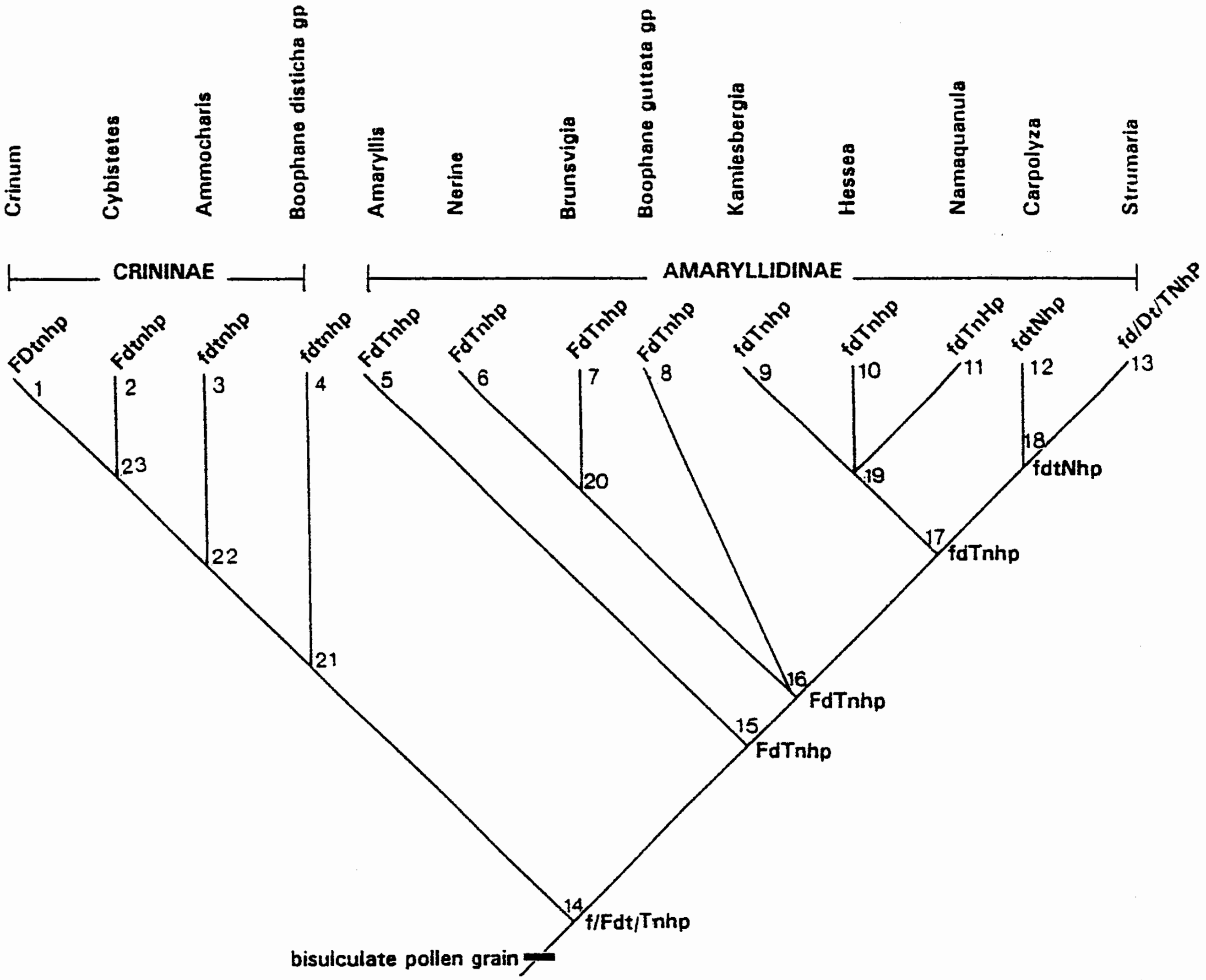


FIGURE 6.2-- Floral features effective in pollination, mapped on the phylogeny of Amaryllideae in Figure 4.18. The symbols are explained in Part 6.5.

between the apertural intine and stigma surface can be established. Although the same mechanism does not apply in taxa with wet stigmas, the geometry of the bisulculate pollen in Amaryllideae may also have adaptive significance, possibly for optimising the rate of pollen germination. Moreover, the large spinulae may be an adaptation for trapping the pollen on the stigmatic lobes.

6.6 Discussion of floral biology

Since data on floral biology were available at the species level in the actinomorphic-flowered Amaryllidinae only, the analysis revealed more detail in this group than elsewhere in the tribe. Despite this bias the study group is considered to show a real shift in pollination strategies though the channelling into several flower forms (in *Strumaria, Kamiesbergia* and *Namaquanula*) after a reversal from the zygomorphic state to the actinomorphic flower. In *Strumaria* a new sequence of features evolved: the loss of the staminal tube; the adnation of the filaments to the style; the elaboration of the style; and ultimately a secondarily-derived staminal tube, which in effect reflects a diversity of floral reward mechanisms.

Associated with these new developments among the actinomorphic genera of Amaryllidinae is a switch to autumn-flowering and fruiting. Dafni *et al.* (1981a) hypothesise that autumn-flowering by hysteranthous-leaved geophytes in Mediterranean-type climates is an adaptation for immediate germination before the rain period and better exploitation of pollinators during autumn. A comparison of the reproductive strategies shown in Figures 6.1 and 6.2 shows that delayed flowering (autumn-flowering) in the Amaryllideae developed after the recalcitrant seed. Future phylogenetic analyses may support the adaptational hypothesis of Dafni *et al.* (1981a) for pollination success in other taxa in Mediterranean-type climates. In Amaryllideae however, the phylogenetic pattern suggests that autumn-flowering and fruiting originated as an adaptation for optimising the time for germination success, rather than by any possible competitive interactions for pollination.

6.7 Conclusions

The patterns of vegetative and floral diversity of Amaryllideae indicate that the recalcitrant seed has been a key factor in the life histories of its taxa; and that the stomatose seed and actinomorphic flower have been key innovations in the evolution of the subtribe Amaryllidinae during the aridification of the western regions of southern Africa.

Firstly, I view seed recalcitrance as having directed the evolutionary development of taxa in the present-day winter-rainfall region towards autumn-flowering and the hysteranthous-leaved habit. These adaptations evolved synchronously thereby optimising the time of seed release and vegetative growth to coincide with the onset of the short growth period of the Mediterranean-type climate, which is inferred to have been attained in the south-western Cape after the Pliocene (Hendey 1976, 1983, Tankard & Rogers 1978).

The development thereafter of a smaller, more specialised seed with a photosynthetic integument and a stomatose cuticle, is interpreted as having led to a reduction in reproductive cost to the vegetative parent, which notably favoured the vegetative diversification through reduced plant size among Amaryllidinae in the semi-arid west, probably during the Pleistocene.

Finally, the shift to the actinomorphic flower from the ancestral zygomorphic condition among most autumn-flowering taxa of Amaryllidinae, appears to have evolved as a secondary adaptation for attracting pollinators under drought conditions, which are interpreted as being fully established in southern Africa in the Quaternary (Tankard & Rogers 1978). The origin of actinomorphy is probably attributable to the accessibility of this floral form to a wide range of pollinators; while its maintenance is probably due to the plasticity of the form, as seen among the lineages of *Strumaria.*

Chapter 7.
SPECIATION

7.1 Introduction

Lineage diversification (speciation) is one of the major processes underlying the patterns of descent, which constitute the phylogeny of living organisms (Wiley & Mayden 1985). Patterns of genealogy between clades may be similar or different. If the phylogeny has been correctly reconstructed, the similarities and differences observed in patterns of descent have a causal reason: different modes of speciation.

Allopatric speciation has been stated or implied as the dominant process in the Cape Flora (Bremer 1976, Goldblatt 1991, Karis 1989, Levyns 1954, Rourke 1972, Strid 1972) and the southern African flora (Goldblatt 1978). The concept of allopatric speciation attributes a central role to gene flow and genetic integrity of species (Mayr 1969). Consequently, speciation is only possible if spatial separation interrupts gene flow (Grant 1981, Wiley 1981). Divergence of the resulting daughter species, in the absence of novel characters, is dependent on the degree of geographic variation present in the ancestral species; the time to differentiation is dependent on the amount of migration between the demes within the smaller of the two incipient daughter species, as well as the magnitude of the selective differences operating between the incipient daughter species (Wiley 1981).

Linder (1985) has hypothesised that the rich diversity of the Cape Flora can be understood in terms of an ecological model of speciation, which holds that gene flow is spatially too restricted to be of significance in maintaining species integrity (see Ehrlich & Raven 1969) and that strong differential selection, derived from the steep ecological gradients which exist in this topographically complex region, plays a major role. Although few data are available on seed and pollen movement in the Cape Flora, preliminary evidence of the importance of the ecological component to species diversity is now available (Kurzweil *et al.* 1991, Linder 1980, Linder & Vlok 1991).

Lynch (1989) has explored a method of identifying putative cases of vicariant (allopatric model I, Wiley 1981), peripheral isolates (allopatric model II, Wiley 1981) and sympatric speciations using data for vertebrates. For vicariance, almost equal partitioning of the ancestral geographic range is envisioned, whereas in the peripheral isolation model the budding off of a very small part of the ancestral range is involved (Wiley & Mayden 1985). Thus the necessary information for such an analysis is reasonably accurate knowledge of the distribution areas of the taxa under study (sizes of distribution areas, distances separating them, amounts of geographic overlap between areas); and a knowledge of the sister elements separated by speciation.

Cracraft (1989) has reviewed the empirical consequences of alternative species concepts for understanding patterns and processes of diversification. The phylogenetic species, which is a basal taxonomic unit, is broadly comparable and thus provides a powerful framework for evolutionary biology (Cracraft 1989). As used in this study, the phylogenetic species is defined as the smallest aggregation of populations or lineages diagnosable by a unique combination of character states in comparable individuals (Nixon & Wheeler 1990).

7.2 Method

Three genera *Namaquanula, Hessea* and *Strumaria* were used for the analysis. Distribution areas were prepared from herbarium collections at B, BM, BOL, K, NBG, PRE, SAM & WIND which were plotted according to the degree reference system of Edwards & Leistner (1971). Distribution areas are expressed as the number of 30' x 30' grids occupied by species; distances separating sister elements are expressed in kilometers. The distribution maps for *Namaquanula, Hessea* and *Strumaria* are shown in Figures 9.40 - 9.51.

Sister components are either species sharing a terminal bifurcation or are equal to sister groups (one of which may be a single species or both may be sets of genealogically related species). All sister elements are strictly monophyletic as shown in Figures 7.1 & 7.2. However, not all species are monophyletic.

7.3 Analysis of geographic data between sister components in *Hessea, Namaquanula* and *Strumaria*

In general the distribution ranges of the sister components extend from north to south or from east to west in accordance with the ecological gradients which extend from the coastline to the inland plateau. None of the sister groups form rings. The distribution ranges of the three genera overlap. *Namaquanula* is the most restricted of the three genera whereas the speciose *Strumaria* is the most widespread.

In *Hessea* and *Namaquanula* only the widespread *H. breviflora* is sympatric with the more distantly related *H. pilosula* (grids 2917 BA, 2917 BB, 2917 BC), *H. monticola* (grid 3219 CA) and *H. incana* (grid 3018 AA). All the remaining species are allopatric, of which the sister species of *Namaquanula* are the most widely separated (Table 4.1).

Similarly, nearly all species of *Strumaria* are fully allopatric. The distances separating sister elements vary greatly, from approximately 150 to 10 km (Table 7.2). Only *S. merxmuelleriana* and *S. villosa* are partly sympatric near Kosies in the Richtersveld (grid 2917 BA), but each species occupies a discrete habitat. Furthermore the distributions of each of the subgenera overlap partly.

With few exceptions, the distribution sizes of sister species are approximately equal. The most widespread species are *Hessea stellaris,* which occupies 21 grids in the south eastern karroid regions, and *H. breviflora* which is recorded in 29 grids throughout

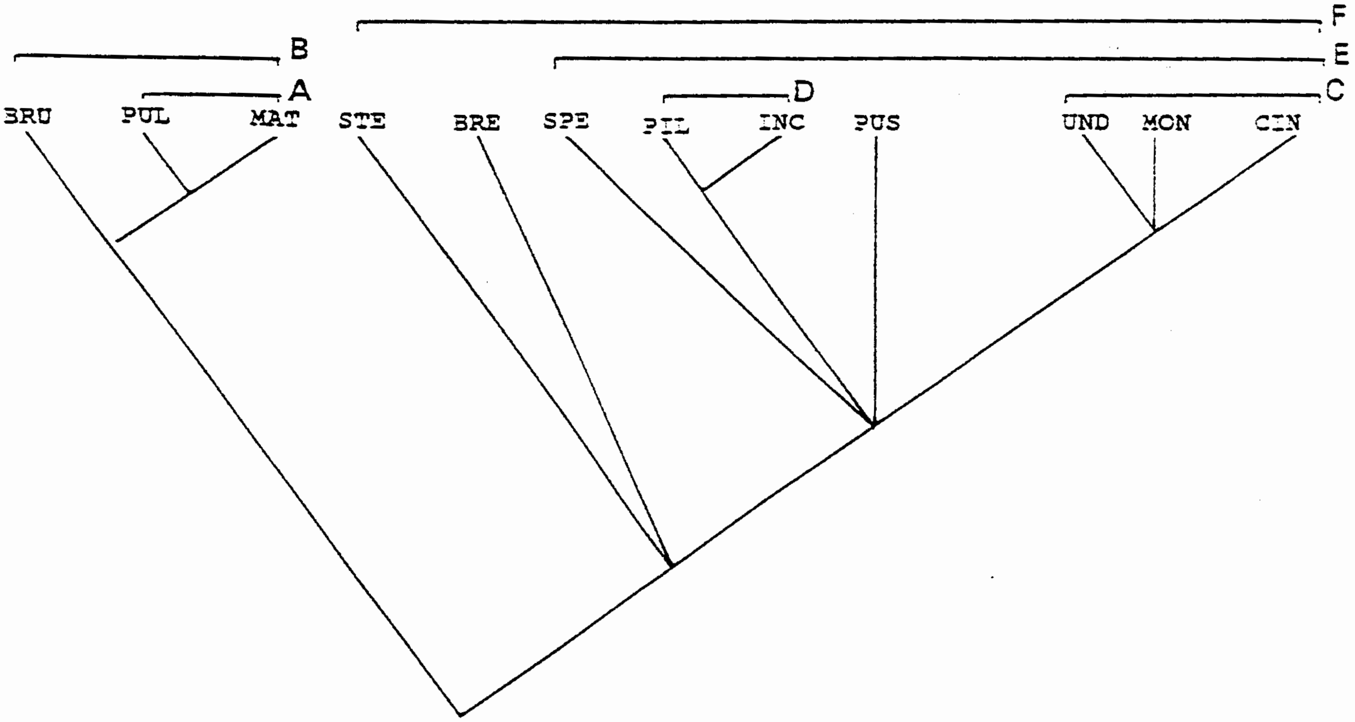


FIGURE 7.1-- Cladogram of *Namaquanula* and *Hessea* indicating sister elements used to gauge putative modes of speciation. The clades A - F are explained in Table 7.1.

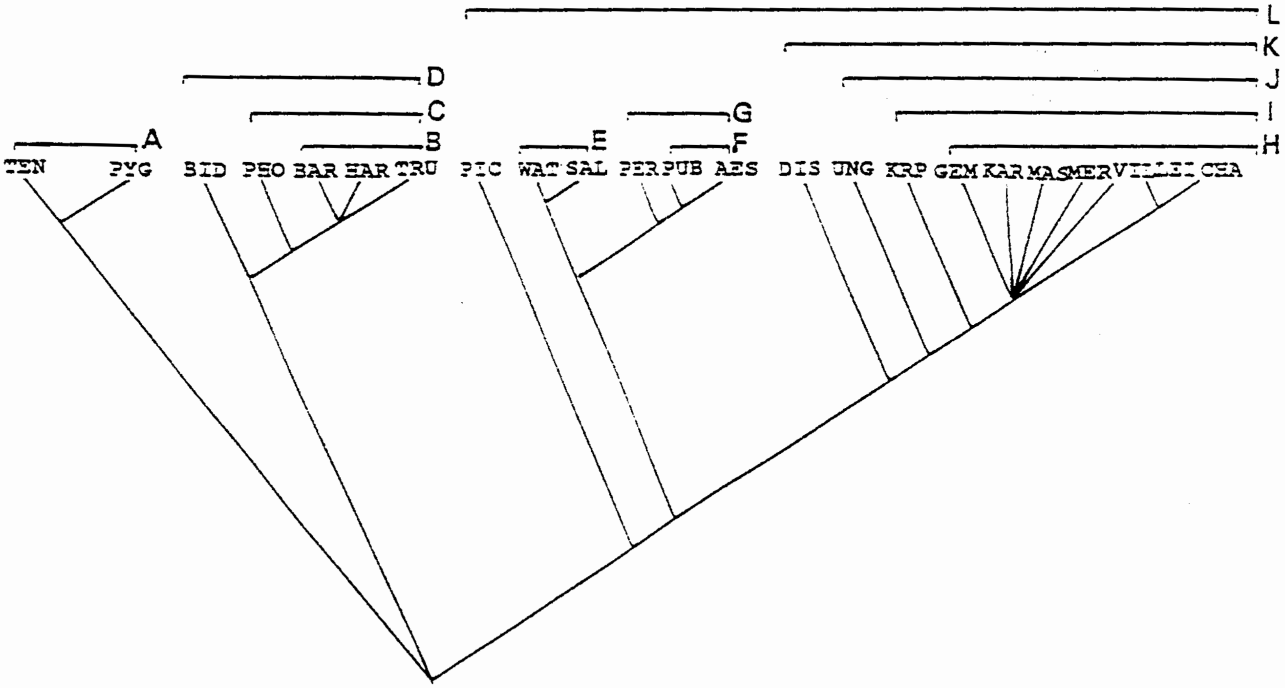


FIGURE 7.2-- Cladogram of *Strumaria* indicating sister elements used to gauge putative modes of speciation. The clades A - L are explained in Table 7.2.

Namaqualand and the south-western Cape. This pattern is repeated in each subgenus of *Strumaria*: *S. tenella* (in 28 grids) and *S. gemmata* (in 23 grids) occupy the south eastern karroid regions; and *S. truncata* (in 23 grids) is distributed throughout Namaqualand. In contrast to the presence of these widespread taxa in the somewhat uniformly weathered landforms of the eastern karroid regions and Namaqualand, the species with the smallest distribution ranges are confined to the rugged mountains, broken inland escarpment and adaphically variable coastline of the western Cape Province.

The gross ecological parameters evident in the habitats of sister species generally show differentiating factors. Sufficiently refined data however, are not available to characterise every species' habitat, particularly those of *S. watermeyeri* and *S. salteri* which extend along the Cape Fold Mountains between the Bokkeveld escarpment in the north and the Cedarberg in the south.

The most noteworthy feature is the difference in distribution size of the species belonging to the different genera (Table 7.3). The distribution sizes for the species of *Strumaria* are characteristically small: 56% of *Strumaria* species occupy two or less grids, whereas only 30% of *Hessea* and *Namaquanula* species are recorded in less than two grids.

TABLE 7.1-- Sizes of distribution areas, distances separating the sister groups and habitats of species of *Namaquanula* and *Hessea*. The clades correspond to those in Figure 7.1.

Clade	Sister element [a]	Distribution [b]	Separation [c]	Overlap	Diagnostic habitat parameters
A	(MAT) (PUL)	2:4	160	none	coastal limestone: elevated loamy flats
B	(BRU) (MAT/PUL)	3: as in A	400	none	alluvial gravel: as in A
C	(UND) (MON) (CIN)	2:5:5	60:100	none	dry fynbos without fire: montane fynbos with fire: coastal fynbos with fire
D	(INC) (PIL)	2:3	60	none	elevated sand-plains with snow: low-lying sand flats
E	(PUS) (SPE) (PIL-CIN)	1:9:as in C + D	90:20	none	deep white sands: wind-blown red sands: as in C+D
F	(STE) (BRE) (SPE-CIN)	29:21 as in C + E	20:5	partial	? : ? : as in C + E

[a] Species abbreviations: BRE, *H. breviflora*; BRU, *N. bruce-bayeri*; CIN, *H. cinnamomea*; INC, *H. incana*; MAT, *N. mathewsii*; MON, *H. monticola*; PIL, *H. pilosula*; PUL, *N. pulcherrima*, PUS, *H. pusilla*; SPE, *H. speciosa*; STE, *H. stellaris*; UND, *H. undosa*.

[b] Number of 30' x 30' grids occupied.

[c] Approximate distance in kilometers from nearest sister group.

TABLE 7.2-- Sizes of distribution areas, distances separating the sister groups and habitats of species of *Strumaria*. The clades correspond to those in Figure 7.2

Clade	Sister element [a]	Distribution [b]	Separation [c]	Overlap	Diagnostic habitat parameters
Subgenus Tedingea					
A	(PYG (TEN)	1:28	60	none	quartz field: loamy soils
Subgenus Strumaria					
B	(BAR) (HAR) (TRU)	3:3:23	60:40	none	limestone inselberg: limestone inselberg: variable
C	(PHO) (BAR-TRU)	2: as in B	20	none	isolated mountain block: as in B
D	(B+D) (PHO-TRU)	2: as in C	10	none	dry riverine flats: as in B + C
Subgenus Gemmaria					
E	(WAT) (SAL)	3:3	20	none	sandstone sheets in fynbos: sandstone sheet at fynbos margins
F	(AES) (PUB)	1:2	150	none	dry river bank: shale cliffs
G	(PER) (AES/PUB)	1: as in F	60	none	loamy flats: as in F
H	(LEI) (CHA)	2:2	120	none	sandstone outcrops: granitic outcrops
	(VIL) (MER) (MAS) (KAR) (GEM)	1:3:2:4:23	S:80:150:150	partial	quartz field: loamy flats: inland sandy flats: dolerite outcrops: variable
I	(KRP) (GEM-CHA)	1: as in H	120	none	inselberg: as in H
J	(UNG) (KRP-CHA)	1: as in I	80	none	in slate chips: as in I
K	(DIS) (UNG-CHA)	7: as in J	20	none	various: as in J
L	(PIC) (WAT-CHA)	1: as in E + G + K	20	none	loamy flats: as in E + G + K

[a] Species abbreviations: AES, *S. aestivalis*; BAR, *S. barbarae;* BID, *S. bidentata*; CHA, *S. chaplinii*; DIS, *S. discifera*; GEM, *S. gemmata*; HAR, *S. hardyana*; KAR, *S. karooica*; KRP, *S. karoopoortensis*; LEI, *S. leipoldtii*, MAS, *S. massoniella*; MER, *S. merxmuelleriana*; PER, *S. perryae*, PHO, *S. phonolithica*; PIC, *S. picta*; PUB, *S. pubescens*; PYG, *S. pygmaea*; SAL, *S. salteri*; TEN, *S. tenella*; TRU, *S. truncata*; UNG, *S. unguiculata*; VIL, *S. villosa*; WAT, *S. watermeyeri*.

[b] Number of 30' x 30' grids occupied.

[c] Approximate distance in kilometers from nearest sister group. S = sympatric.

TABLE 7.3-- Comparison of distribution sizes in terms of number of 30' x 30' grids occupied by species of *Namaquanula, Hessea* and *Strumaria.*

No. of grids	1	2	3	4	5	6	7	8	9	20+
No. of species										
Namaquanula		1	1	1						
Hessea	1	2	1		2				1	2
Strumaria	7	6	5	1			1			3

7.4 Discussion

Allopatric speciation requires extrinsic barriers which are external to the organism involved; either isolation by distance or some physical barrier. The strength of any particular extrinsic barrier varies widely among different taxa confronting the barrier and depends on inherent mobility (Diehl & Bush 1989). In the absence of extrinsic barriers Diehl & Bush (1989) regard populations utilising different habitats to be sympatric when all individuals can potentially move between habitats within the lifetime of an individual. Therefore to rigorously examine the concept of allopatric speciation and sympatric speciation, data concerning two aspects of the study group are required. Firstly, the pattern of gene flow due to pollen movement and seed dispersal should determine whether spatial distances between populations pose an extrinsic barrier or not. Secondly, the tolerance ranges of species should test whether intrinsic barriers such as habitat specialisation do exist. Thus, until such data become available the allopatric distribution patterns of the fairly closely situated sister species of *Hessea* and *Strumaria* cannot be assumed to reflect the corresponding process of allopatric speciation. They may be accounted for by sympatric or parapatric speciation.

Diehl & Bush (1989) have shown that parapatric and sympatric speciation can occur under genetically realistic conditions, if given sufficient time. Consequently, they suggest that the overall frequency of non-allopatric speciation, as well as allopatric speciation, may more often be limited by the stability of distinct habitats over time. This lack of knowledge of the distribution of habitats in time and space, as well as the lack pertaining to the knowledge of the extrinsic and intrinsic barriers to diversification, currently makes it impossible to evaluate definitely the relative likelihood of the alternative models of speciation. However, some informed speculations can be attempted, particularly for the speciose genus *Strumaria.*

The polychotomy of *Strumaria gemmata, S. karooica, S. massoniella, S. merxmuelleriana, S. villosa, S. leipoldtii* and *S. chaplinii* in clade L (Figure 7.2) is hypothesised to diagnose a group of sibling species. Basal to clade L is *S. discifera* which lacks an autapomorphy and is distributed over a fairly large area (seven grids), mostly on the Nieuwoudtville/Calvinia plateau. The remaining species in the clade are restricted mostly to one grid each and in two parallel "tracks": one along the edge of the inland escarpment and the other along the west coast. Only *S. gemmata* is widespread in the eastern karroid region. This phylogenetic pattern is one which might be expected from the peripheral isolates model of allopatric speciation (model II, Wiley 1981). The ancestral species, *S. discifera,* which originally may have been a single, geographically continuous species, may have given rise throughout the margins of its range to a series of closely related, narrowly distributed isolates. If peripheral isolation was followed by speciation, subsequent migration of the peripheral isolate, another peripheral isolation and so on, such that a progression in time and space is the result, then the pattern of descent as evidenced by synapomorphies is expected to be largely dichotomous (Wiley 1981). For the polychotomy the question remains as to whether it reflects simultaneous multiple splitting (a situation which cannot be conclusively demonstrated (Brundin 1972)), or successive dichotomous splitting that cannot be demonstrated at present because of insufficient knowledge of the character spectra.

With the exception of *S. gemmata* nearly all the species of the polychotomy in clade L (Figure 7.2) are distributed along the present-day interface of the winter/summer-rainfall regions, a zone which is postulated to have undergone great fluctuations in the Pleistocene (Cockcroft *et al.* 1987, Deacon 1983, Tyson 1986, Van Zinderen-Bakker 1976). During these postulated recurrent climatic fluctuations, plant populations in this transitional-rainfall zone would have experienced soil moisture stresses more than their sister populations in the adjacent regions, where established rainfall patterns were maintained. Consequently, rates of isolation, migration and extinction would have been highest in the transitional-rainfall zone and high rates of diversification would have resulted. A similar pattern of a high number of local endemics also characterises the transitional-rainfall zone of southwest Australia (Hopper 1979). Both these patterns of species diversity provide support for the concept that semi-arid transitional climatic zones are particularly favourable sites for lineage diversification (Axelrod 1967, 1972, Hopper 1979, Stebbins 1952). *Strumaria gemmata* is hypothesised as having expanded its range to coincide with the extreme eastern limit of the winter rainfall region, which is inferred to have moved eastwards of its present position to 30°S during the Last Glacial Maximum, 18 000 years ago (Tyson 1986, Cockroft *et al.* 1987).

The pattern shown by *S. tenella (28 grids) and S. pygmaea* (one grid) with a separation distance of 60 km probably also reflects the process of peripheral isolation. In addition, this is the only case among sister species which involves chromosomal repatterning: $x = 10$ in *S. tenella* and the derived bimodal $x = 11$ in *S. pygmaea,* thus Wiley's (1981) allopatric model III may apply. *Strumaria tenella* is one of just two species in which subspecies are recognised; subspecies *tenella* in the winter rainfall karroid regions and subspecies *orientalis* in the eastern Orange Free State. This phytogeographic pattern thus agrees with the assumption of model III that gene flow in the ancestral population is not a significant factor and that geographic variation is present if selection gradients are present (Wiley 1981). Like the peripheral isolates model, the allopatric speciation model III is a model of rapid lineage diversification. The karyotypic stability in the tribe contrasts with several South American genera of Amaryllidaceae (*Lycoris* Herbert and *Hymenocallis* Salisb.) where large chromosomal changes are evident (Meerow 1984). Thus gene mutation in Amaryllideae is perhaps of greater significance in generating diversity than is cytologically visible chromosomal repatterning (Meerow 1984).

The hypothesised phylogenies shown in Figures 7.1 & 7.2 also show a marked difference in species diversity between *Hessea* and *Strumaria*. Since both taxa occupy the same ecological region and have essentially the same means of seed dispersal, this difference strongly implies that diversity in *Hessea* and *Strumaria* is not regulated solely by extrinsic factors. Preliminary observations on the breeding system in the study group (Snijman unpublished data) suggest that *Hessea* species are outbreeders whereas *Strumaria* species are facultative selfers. With regard to the putative influence of the breeding system, it is noteworthy that the most northerly records for the study group are for species of *Strumaria* subgenus *Strumaria* in southern Namibia. Here *S. hardyana, S. barbarae* and *S. phonolithica* occupy isolated mountain blocks at the present-day northern limit of the winter/summer-rainfall interface. This corroborates frequent observations that in taxa with related outcrossers and selfers, the selfing taxa usually occupy the ecologically marginal sites within the ancestral species range (see Barrett 1989). Furthermore the close relationship shown by these species suggests that once these selfing populations became established, the geographic isolation, exposure to novel selection pressure and genetic drift probably enhanced genetic and phenotypic changes between these small populations, which led to their rapid reproductive isolation and evolution.

Unlike *Strumaria*, the species of *Hessea* do not display small, restricted distributions, possibly as a consequence of the obligate outbreeding system hypothesised for the genus. In particular the populations which make up the widespread species *H. breviflora* in the south-western Cape and Namaqualand, and *H. stellaris*, mainly in the Little Karoo, show quite a considerable degree of phenotypic differentiation, particularly at their distribution margins, but the pattern of variation remains continuous. This variation may reflect minor genetic variability as a result of natural selection, or random drift where the selective regimes are not very different, however, the outbreeding system in *Hessea* may account for incomplete reproductive isolation. The only major external barrier which is apparent between these two taxa is the Cape Fold Mountain belt which is characterised by extremely nutrient-poor soils.

Unlike the gradual microevolutionary differentiation which appears to be operative among the low density populations of *H. breviflora* and *H. stellaris*, the *Hessea* species confined to the edaphically isolated Cape Fold Mountains reflect another pattern. Populations of *H. monticola* and *H. cinnamomea* form extremely large, dense stands of thousands of individuals, narrowly confined to peaty, seasonally wet soils in association with fire-adapted fynbos. These species are typical fire opportunists, characterised by profuse post-fire flowering, followed thereafter by long sterile, fire-free intervals. It may be envisaged that a fire event temporarily released the natural selection operating in an ancestral population through the removal of local competition. Release from natural selection may have resulted in a population flush in which the population numbers increased rapidly. The combined effect of the recalcitrant seed, which characterises the subtribe and prohibits the development of stored seed banks, with a drought event may subsequently have led to a sudden reduction in the population size, thereby establishing a small genetically isolated population. As argued here, the conditions pertaining to *H. monticola* and *H. cinnamomea* may reflect a founder event, which according to Templeton's (1980) model is most likely to occur with a shift in population structure from a widespread ancestral population to an island situation; provided in this case by an "edaphic island" situation (see Wild 1964, 1968).

Like all other species of *Hessea, H. cinnamomea* and *H. stellaris* do not show an ecological shift from seasonally moist habitats. This agrees with one of the attributes which is hypothesised to be optimal for speciation via the founder effect. Thus following Templeton (1980) the ecological significance of the founder event is in placing the population into a relatively unexploited environment that presents the same basic niches, a condition that promotes rapid population growth soon after the initial founder event. Although *H. cinnamomea* and *H. monticola* do not have the same suite of characteristics as the fynbos shrubland species, the phylogeny and distribution of these species also supports Cowling's (1987) model of speciation in the south-western Cape, which invokes fire, edaphic conditions and short dispersal distances as its primary assumptions.

Lastly, I have also observed several examples in the study group in which the populations constituting the species are widely disjunct but show very little differentiation from one another. The two known populations of *Kamiesbergia stenosiphon* are separated by ± 160 km; those of *Strumaria massoniella* by ± 60 km; and those of *S. pubescens* by ± 120 km. The similarity of disjunct populations within species of *Crassula* distributed in Namaqualand has also evoked comment from Tölken (1977). These examples are similar to many other cases cited by Ehrlich & Raven (1969), which support their hypothesis that gene flow is not necessarily an important factor in keeping populations of the species undifferentiated.

7.5 Conclusion

This preliminary attempt to identify putative cases of speciation modes using phylogenetic and distribution data from the actinomorphic-flowered Amaryllideae indicates that lineage diversification in the group did not follow a common pattern. With one exception all species show an allopatric pattern, however, the separation distances between sister-species and the distribution sizes of sister-species varies greatly. Peripheral isolation (Wiley's (1981) allopatric model II), is hypothesised for species in *Strumaria* section Gemmaria and subgenus Tedingea. *Hessea breviflora* and *H. stellaris* suggest a pattern of large scale allopatry (Wiley's (1981) allopatric model I), whereas the phylogenetic patterns, distribution patterns and population characteristic of *H. monticola* and *H. cinnamomea* on the Cape Fold Mountains of the south-western Cape suggest speciation via the founder-effect model (Templeton 1980). The only evidence of putative sympatric or parapatric speciation is shown by sister-species *S. merxmuelleriana* and *S. villosa*, which occupy the same grid but different habitats.

The widespread occurence of putative peripheral isolation speciation in *Strumaria* implies that lineage diversification has been more rapid in this genus than in *Hessea.* A further implication is that groups of species arising from peripheral isolation do not comprise a biota in the sense discussed by vicariance biogeographers. Thus other clades will not necessarily be expected to show similar biogeographic patterns because peripheral isolation is expected to occur in different ways in different species (Funk & Brooks 1990). The result of the cladistic biogeographic analysis in which *Hessea* and *Namaquanula* were compared with *Strumaria* supports this.

Moreover, it is apparent that environmental factors alone have not been wholly responsible for patterns of diversification in the actinomorphic-flowered Amaryllidinae. Based on my hypotheses regarding the differences in reproductive strategies which have evolved in the group, it would appear that the properties of the breeding system in *Hessea* and *Strumaria* have also exserted a strong influence over the evolutionary possibilities of the genera, particularly in the transitional-rainfall zone.

In conclusion, the hypothesis of rapid diversification in *Strumaria* within the transitional climatic zone between the winter and summer-rainfall region allows the prediction that it is highly probable that several new *Strumaria* species will yet be discovered as botanical exploration is extended north westwards along the Great Escarpment beyond the Hantamsberg near Calvinia.

Chapter 8.
CONCLUSION

To date, a phylogeny of the nine tribes of Amaryllidaceae (*sensu* Dahlgren *et al.* 1985) is entirely absent; the phylogeny of the essentially African tribe Amaryllideae is in the early stages of resolution; whereas the phylogeny of the actinomorphic-flowered Amaryllidinae, (*Kamiesbergia, Namaquanula, Hessea, Carpolyza* and *Strumaria*), a group confined to the winter and autumn-rainfall regions of southern Africa, is more fully understood. Although further data are required to refine the phylogeny of the Amaryllideae the emended subtribal delimitation presented in this study, nevertheless establishes a monophyletic framework which facilitates a reconstruction of some of the events which may have influenced the recent evolution of the tribe.

If a sister-group relationship exists between Hippeastreae and Amaryllideae, then it can be hypothesised that the ancestral group arose in Gondwana. Thus, the first major phase of diversification may have occurred with the separation of West Gondwana during the Jurassic (see Truswell 1977), whereafter Hippeastreae diversified in South America and Amaryllideae in Africa.

The next wave of evolutionary activity is considered to be the diversification of the fleshy-seeded ancestral species of Amaryllideae widely throughout Africa, when seasonally moist subtropical/tropical conditions prevailed during the early Tertiary (see Axelrod & Raven 1978). During the subsequent evolutionary events, the data indicate that the ancestral recalcitrant seed, which favours seedling vigour and aggressiveness, remained advantageous and was maintained, while Crininae and Amaryllidinae underwent active evolution under the summer-rainfall conditions of Africa and the winter-rainfall conditions of south western Africa respectively. I hypothesise that the key innovation which permitted the fairly rapid divergence of Amaryllidinae from the preceding ecological sphere shared with Crininae was the evolution of small seeds, with a photosynthetic integument and stomatose cuticle. This key character promoted the appearance of several supportive adaptations which are inferred to coincide with the advent of aridity and winter-rainfall conditions in the south-western Cape; a climatic change which is dated to the Pliocene (Tankard & Rogers 1978).

Adaptations which appear to have evolved synchronously among ancestral taxa in all the south western African genera of Amaryllidinae are hysteranthous leaves and an autumn-flowering habit. Thus, seed release and vegetative growth were optimally timed to coincide with the onset of the short growth period which characterises the Mediterranean-type climate of the south western region. A further consequence of the small photosynthetic seed was a reduction in reproductive cost to the vegetative parent; an effect which promoted a reduction in plant size among ancestors of the allied genera *Kamiesbergia, Namaquanula, Hessea, Carpolyza* and *Strumaria*. The most active phase of evolution is currently discernable amongst this generic alliance. Xerophilous characters which evolved in the group are sheathing cataphylls, a reduced number of leaves, fan-shaped leaf arrangement and prostrate, pubescent leaves. Associated with this derived vegetative morphology was a secondary development of the actinomorphic flower from the ancestral zygomorphic condition present in Amaryllidinae; an adaptation which probably originated through the accessibility of its form to pollinators under stress conditions. Although actinomorphic flowers have been maintained throughout the generic group of *Kamiesbergia, Namaquanula, Hessea, Carpolyza* and *Strumaria*, the greatest diversity of floral morphology evolved in *Strumaria*, where an associated change from obligate outbreeding to facultative selfing is hypothesised. Consequently, of all the genera of Amaryllidinae, *Strumaria* appears to have undergone the most rapid lineage diversification, particularly in the climatic transition zone between the winter and summer-rainfall regions of southern Africa, where past climatic conditions fluctuated greatly (Tyson 1986).

With the advent of aridity in Africa, Crininae followed a different evolutionary strategy. The large, slowly developing seed of the subtribe is hypothesised as having been a constraint to the conquest of the new ecological niches offered by the Mediterranean-type climate of the south west. Thus Crininae evolved rapidly only in the summer-rainfall regions of Africa. The most speciose genus *Crinum*, in particular, evolved a strategy of drought avoidance through the evolution of a hydrophilic habit, which allowed species to survive at the margins of permanent or seasonal water bodies. The evolution of a great number of *Crinum* species in southern Africa is hypothesised to be a consequence of high rates of isolation, migration and extinction among ancestral taxa inhabiting the seasonal water systems in the increasingly arid regions of the west. Based on the evolutionary considerations of Nordal & Wahlstrøm (1980), the ancestors of the persistently subtropical taxa of *Crinum* from Central Africa are considered to have undergone long distance dispersal out of Africa to the subtropics of the Old and New Worlds.

From the evolutionary events hypothesised here it is apparent that environmental change has been just one causal agency of the evolution of Amaryllideae. Pending the experimental verification of the reproductive strategies proposed in this study, several intrinsic factors are also presumed to have influenced diversification. Thus, the reproductive strategies available within Crininae and Amaryllidinae are interpreted as having been influenced by developmental constraints or key innovations; the effects of which are expressed particularly as divergent resource allocation strategies.

In conclusion, the foregoing hypothesis yields certain falsifiable predictions for the focus of future studies. The predictions concern phytogeography and character evolution. In particular, I predict that when the phylogeny of the tribes of Amaryllidaceae becomes available the sister-group relationships should support my hypothesis that the early causal events in the evolution of Amaryllideae reflect, in part, the pattern of the Gondwanan break-up, thereby strengthening my interpretation of a Jurassic-Cretaceous age for the

Amaryllideae. Moreover, as regards the phylogeny of Amaryllideae, I finally predict that as new data become available, the independently generated cladograms will corroborate the same sequence of character evolution which forms the major part of the foregoing evolutionary hypothesis for Crininae and Amaryllidinae.

Chapter 9.
TAXONOMIC TREATMENT

Amaryllideae

Type: *Amaryllis* L., Species Plantarum: 292 (1753).
Synonym: Crineae Traub: 81 (1957).
Hesseae Traub: 51 (1962) nom. inval.
Strumarieae (Salisb.) Traub: 69 (1963).

Small to large-sized bulbous herbs. *Bulb* tunics producing extensible threads when torn. *Leaves* distichous or rosulate, deciduous or evergreen, few to many, glabrous or bearing trichomes. *Inflorescence* borne on a solid, leafless scape, subtended by 2, equitant, free spathe valves. *Flowers* few to many, zygomorphic or actinomorphic, with or without a perigone tube; perigone tube broad and funnel-shaped or campanulate to narrowly tubular; stamens free or connate into a tube; filaments sometimes toothed; anthers dorsifixed, subcentrifixed or centrifixed, rarely almost basifixed; pollen bisulculate; style mostly slender, sometimes enlarged and winged. *Fruit* usually dry, indehiscent or loculicidally dehiscent; ovules unitegmic or possibly rarely ategmic; seeds water-rich, greenish or rarely white to pink. Basic chromosome number $x = 11$, or rarely 10.

Genera 13, mainly African but *Crinum* L. pantropical.

Subtribe Crininae

Crininae Traub ex Snijman, subtribus nova, a subtribu Amaryllidinae foliis plerumque undulatis, perigonii tubo longitudine tepala plerumque aequantes, staminibus liberis, capsula indehiscenti, testa suberosa differt.

Type: *Crinum* L., Species Plantarum: 291 (1753).

Large-sized herbs. *Bulbs* covered with softly fibrous outer tunics. *Leaves* linear to lorate, usually more than 8, often arranged in a fan, usually with undulate edges, sometimes with truncate tips formed by abscission; margins usually with cartilagenous cilia. *Flowers* zygomorphic or actinomorphic, usually with a well-developed perigone tube equalling the tepals; stamens free; anthers dorsifixed. *Style* slender. *Fruit* indehiscent; seeds irregularly-shaped, green, covered with a thin, corky testa. *Basic chromosome number* $x = 11$.

Genera 4 (*Crinum* L., *Ammocharis* Herbert, *Cybistetes* Milne-Redhead & Schweickerdt, *Boophane* Herbert pro parte, as to *B. disticha* (L.f.) Herbert and *B. haemanthoides* Leighton), mainly in sub-Saharan Africa.

1. Kamiesbergia

Kamiesbergia Snijman in Bothalia 21: 125 (1991). Type: *Kamiesbergia stenosiphon* Snijman.

Description as for the species.

A monotypic genus; confined to the north-western Cape Province.

Autapomorphies for the genus are the dissimilar inner and outer filament whorls and the insertion of the filament in the proximal quarter of the anther, which is without a sheathing connective.

1. **Kamiesbergia stenosiphon** Snijman in Bothalia 21: 125 (1991). Type: Cape, Kamiesberg, granite domes near Karas on E slopes of Rooiberg, 28 April 1988, *Snijman 1175* (NBG, holo. K; PRE).

Bulbous perennial herb, up to 210 mm tall. *Bulb* solitary, deep-seated, subglobose, 12--30 mm across, with thin light brown parchment-like outer tunics, fleshy and whitish within, extended into a long slender neck up to 110 mm. *Leaves* absent at anthesis or rarely persisting to anthesis, 2 (-3), spreading, narrowly lorate, 60--300 x 1--3 mm, glabrous, with the adaxial surface shallowly canaliculate, subtended by a subterranean non-amplexicaul prophyll. *Inflorescence* slightly spreading, 40--80 mm across; scape stiffly erect, 50--140 mm long, 1--2 mm diam., greyish pink to leaden-grey, breaking off at the base in fruit; spathe valves linear-lanceolate, 15--30 x 1--2 mm; bracteoles filiform, up to 5 mm long. *Flowers* 5--9, ascending, hypocrateriform, pale lemon-yellow, usually with a greenish to reddish brown tube, flushed dorsally with reddish brown on the outer tepals, ageing to light brown, scentless; pedicels straight to upwardly curved, 35--60 mm long, green. *Tepals* recurving from a narrow 8--12 mm long tube, narrowly lanceolate, 6--8 x 2--3 mm, slightly channelled. *Stamens* in 2 unequal whorls, epitepalous, filaments basally connate into a greenish yellow tube extending to 0,5--1,0 mm above the perigone throat, free above, reduced to a 0,25 mm long filiform free tip in the outer whorl, prominent and spreading in the inner whorl; the inner filaments free for 3--4 mm, clavate in the distal half with a subulate tip; anthers dorsifixed near the base, ± 2,5 mm long and maroon before opening; the outer anthers occluding the perigone throat after dehiscence; pollen cream-coloured. *Ovary* subglobose, 2--3 mm across, with up to 4--6 ovules per locule. *Style* erect, slender throughout, up to 5--11 mm long, remaining included in the perigone tube; stigma shortly trifid, shortly penicillate on the inner surfaces. *Fruit* a subglobose, papery, loculicidal capsule, 7,5 mm across. *Seeds* fleshy, ovoid, up to 2,5 mm across, reddish brown when ripe. *Chromosome number* $2n = 22$. Figure 9.1.

Flowering time: Late April to May.

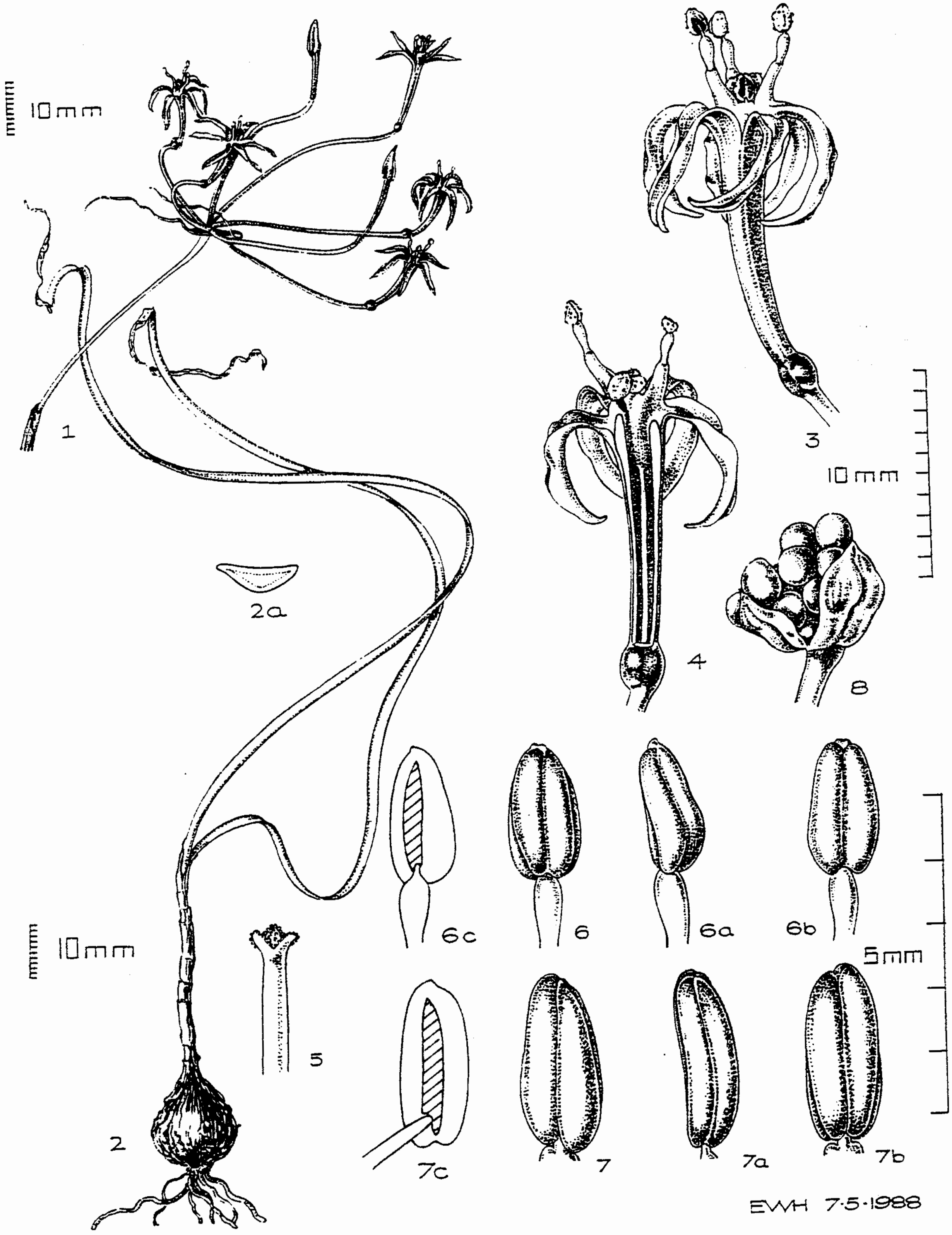


FIGURE 9.1-- *Kamiesbergia stenosiphon*: 1, inflorescence, life size; 2, bulb and leaves, life size; 2A, transverse section of leaf; 3, whole flower; 4, section of flower; 5, stigma; 6, anther attachment of inner stamens, ventral view, 6A, lateral view, 6B, dorsal view; 7, anther attachment of outer stamens, ventral view, 7A, lateral view, 7B, dorsal view; 8, capsule and seeds. Drawn from *Snijman 1175*.

Diagnostic features and affinities: This species is easily distinguished by its long-tubed, yellow flowers and markedly dissimilar stamens. The inner filaments are uniquely club-shaped; the outer stamens occlude the perigone throat and the style remains included in the upper third of the perigone tube. Character states which indicate an alliance between *K. stenosiphon* and the genus *Hessea* and *Namaquanula* are the staminal tube and the actinomorphic flowers, which remain open and turn brown with age.

Distribution and habitat: This apparently rare species has a disjunct distribution range in the eastern Kamiesberg and at Namies, west of Pofadder (Figure 9.40) On the massive granite domes of the Kamiesberg, the deep-seated bulbs are restricted to small pockets of loam in seasonally moist rock crevices and shallow water-worn gullies, at elevations of approximately 610 m. The associated plant community consists of dwarf succulent shrubs and the fern species *Cheilanthes multifida* (Swartz) Swartz. At Namies to the north east, the species occupies similar habitats on isolated granite outcrops, which rise above the sandy plains of Bushmanland (J.J. Lavranos pers. comm.).

Specimens examined

--2919 (Pofadder): Numis [Namies] near Pofadder (-AC), *Lavranos 20311* (PRE).

--3018 (Kamiesberg): Kamiesberg, near Karas on E slopes of Rooiberg (-AC), fl 28 Apr 1988, *Snijman 1175* (K, NBG, PRE); *Snijman 1179* (NBG).

2. Hessea

Hessea Herbert, Amaryllidaceae: 289 (1837); Kunth: 630 (1850); Bentham & Hooker: 720 (1883) pro parte, as to *Periphanes* Salisb.; Baker: 21 (1888) pro parte, as to subgenus Hessea; Baker: 189 (1896) pro parte, as to subgenus Hessea; nom. cons., non Berg. ex Schlecht.: 252 (1826) (= *Carpolyza* Salisb.). Type: *Hessea stellaris* (Jacq.) Herbert, typ. cons.

Imhofia sensu Herbert: 290 (1837) pro parte; sensu Roemer: 27 (1847), as to *I. crispa* (Jacq.) Herbert and *I. cinnamomea* (L'Hérit.) Roemer, non Heist.: 29 (1755), non Herbert: 18 (1821).

Periphanes Salisb.: 118 (1866). Type: *Periphanes cinnamomea* (L'Hérit.) Leighton (= *Hessea cinnamomea* (L'Hérit.) Durand & Schinz), lecto., designated by Müller-Doblies (1985)).

Perennial deciduous bulbous herbs, ranging from 50--250 mm high. *Bulb* solitary or rarely clumped, globose to depressed globose, with thin fibrous or thick felt-like outer tunics, fleshy and whitish within. *Leaves* distichous, absent or incipient at anthesis; with the lowermost prophyll bladeless, adaxial and non-amplexicaul, rarely absent; cataphyll mostly hidden, rarely exserted; foliage leaves 2 or rarely 3, sheathing at the base, with the innermost non-sheathing; blades spreading, narrowly lorate, plane or slightly channelled, mostly glabrous, rarely shortly pilose. *Inflorescence* held erect by a glabrous scape, with 2 membranous spathe valves each subtending a helicoid cyme; pedicels stiff, distinctly longer than the flowers; bracteoles subtending individual flowers filiform. *Flowers* actimorphic, spreading, stellate, pink or occasionally white, usually with darker central markings, remaining open and turning brown with age; tepals either shortly connate into a tube or free to the base, oblong-lanceolate, spreading to recurved, plane or with cripsed edges. *Stamens* 6, free from the style; filaments connate proximally into a long or very short tube, usually confluent with the tepals, spreading; anthers oblong, centrifixed, latrorse, opening by longitudinal slits; pollen bisulculate, covered with scattered large spinulae. *Ovary* somewhat sphaeroidal, glabrous, mostly with up to 4 ovules per locule, rarely 7; ovules subglobose, anatropous, with axile placentation; septal nectaries egressing on the ovary dome into a central pool around the style. *Style* slender or rarely stout proximally; stigma papillose, trifid. *Infructescence* rapidly drying and detaching at ground level; fruit a papery, subglobose, trilocular capsule; seeds fleshy, ovoidal, reddish green when ripe, covered with stomata. *Basic chromosome number* $x = 11$; diploid number $2n = 22 + 1 - 3B$.

Species 9; exclusively southern African where it is restricted to southern Namibia and the Cape Province, predominantly in the winter-rainfall region.

The only autapomorphy for the genus is the centrifixed anther insertion, where the filaments are inserted into a connective sheath with almost equal dorsal and ventral walls. A synapomorphy for *Hessea*, *Kamiesbergia* and *Namaquanula* is the characteristic ageing of the flowers, which rapidly turn brown and remain open.

Key to the species of Hessea

1a Tepals with distinctly crisped edges: 2

2a Flowers secund; outer tepals mucronulate; style somewhat stout proximally .... **9. H. cinnamomea**

2b Flowers equally spreading; tepals not mucronulate; style slender proximally: 3

3a Tepals 6--8 mm long; stamens equalling or as little as two-thirds the length of the tepals .. **7. H. undosa**

3b Tepals 10--25 mm long; stamens less than two-thirds the length of the tepals .... **8. H. monticola**

1b Tepals with plane edges: 4

4a Leaf blades minutely pilose: 5

5a Spathe valves up to 2.5 mm wide at anthesis; leaf blades 1--5 mm wide, shallowly canaliculate, shiny green ....**4. H. pilosula**

5b Spathe valves 8--20 mm wide at anthesis; leaf blades 3--8 mm wide, plane, hoary .... **5. H. incana**

4b Leaf blades entirely glabrous: 6

6a Leaf blades at most 1 mm across. If 1 mm across, then bulbs less than 15 mm diam., and perigone tube equalling or less than length to which filament tube is exserted beyond throat............ **6. H. pusilla**

6b Leaf blades more than 1 mm across, or rarely 1 mm: 7

7a Cataphyll exserted above ground, initially reddened, later turning brown and dying back . **2. H. breviflora**

7b Cataphyll subterranean, remaining hidden within the bulb: 8

8a Perigone tube longer than length to which filament tube is exserted beyond the throat..... 1. **H. stellaris**

8b Perigone tube absent or at most equalling the extent to which filament tube is exserted beyond the throat: 9

9a Filament tube exserted by less than 1,5 mm beyond the throat; stamens shorter than tepals by 3 mm or more...4. **H. pilosula**

9b Filament tube exserted by 1,5 mm or more beyond the throat; stamens equalling or up to 2 mm longer than the tepals...3. **H. speciosa**

1. **Hessea stellaris** (Jacq.) Herbert, Amaryllidaceae: 289 (1837); Kunth: 630 (1850) Baker: 21 (1888), 189 (1896). Type: figure in Jacq., Plantarum rariorum horti caesarei schoenbrunnensis 1: t.71 (1797), lecto.!, designated by Müller-Doblies (1985).

Amaryllis stellaris Jacq.: 37 t. 71 (1797); Willd.: 61 (1799); Aiton: 229 (1811). *Strumaria stellaris* (Jacq.) Ker-Gawl.: t. 1363 (1811). *Periphanes stellaris* (Jacq.) Salisb. ex Leighton: 81 (1948).

Hessea weberlingiorum D. & U. Müller-Doblies: 38 (1985). Type: Cape, Ghaapkop, near Matjiesfontein, 23 July 1980, *Müller-Doblies 80022s* (PRE, holo.!; B, Herb. M-D.).

Hessea cinnabarina D. & U. Müller-Doblies: 40 (1985). Type: Cape, E of Gifkop, 5 km E of Kromrivier on Loeriesfontein/Kliprand road, 10 August 1980, *Müller-Doblies 80077b* (PRE, holo.!; B, K!, Herb. M-D.).

Bulb solitary, subglobose, 15--25 mm diam., with thinly fibrous light brown outer tunics, extended into a slender neck 35--170 mm long. *Leaves* absent or incipient at anthesis, 2, initially erect, later recurved, narrowly lorate, 100--210 x 1--7 mm, shiny green, often reddened proximally, glabrous, subtended by a subterranean amplexicaul cataphyll and non-amplexicaul prophyll. *Inflorescence* ranging from somewhat clustered to widely spreading, 35--120 mm across; scape more or less straight, deflexed laterally, 50--150 mm long, 1--2mm diam., light green, reddened basally, breaking off at the base in fruit; spathe valves narrowly lanceolate, 20--30 x 2--4 mm; bracteoles up to 10 mm long. *Flowers* 6--30, spreading, stellate, pale to dark pink, with a darker pink or occasionally wine-red star-shaped central pattern, ageing to light brown, scented or not; pedicels straight, 12--55 mm long, light green. *Tepals* adnate to the staminal tube for (0,5-) 1,0--3,5 mm, outspread above, oblong-lanceolate, 6,0--9,5 x 1,75--3,0 mm, somewhat channelled, with plane edges or occasionally somewhat undulate towards the perigone throat. *Stamens* ranging from 4 mm shorter to equalling the tepals, rarely exceeding the tepals by 2 mm, spreading; filaments connate basally into an upwardly widened tube reaching up to 1,0 (-1,5) mm beyond the perigone throat and always remaining shorter than the perigone tube, subulate above; anthers centrifixed, 2 mm long and wine-red before opening; pollen cream-coloured. *Ovary* with up to 4 ovules per locule. *Style* ultimately up to 5--9 mm long, subtriquetrous, slender throughout, with nectar collecting in a well around the base. *Seeds* 3,0--4,5 mm diam. *Chromosome number* $2n = 22$. Figure 9.2.

Flowering time: Flowering usually commences in April in the eastern regions (Matjiesfontein to Oudtshoorn) but May and June and occasionally July in the northern and western areas of the distribution range.

Diagnostic features: Hessea stellaris is most closely related to *H. breviflora*. Both species have flowers with a distinct perigone tube but of diagnostically different proportions. *Hessea stellaris* has flowers in which the perigone tube (0,5--2,5 mm long) always exceeds the length to which the filament tube is exserted beyond the throat (up to 1,5 mm). In contrast to *H. breviflora*, the leaves are typically narrow (1--7 mm wide) and the sheathing cataphyll is not exserted above ground.

Distribution and habitat: Hessea stellaris occurs in widely differing soil types but always on flats or gently sloping gradients in the succulent Karoo of the western and southern Cape. Soils vary from loose sand, loam, sandy gravel to broken weathered shale. The species extends from near Loeriesfontein in the north and the Vanrhynsdorp district in the west, south eastwards along the Doorn River Valley to Karoo Poort and to Oudtshoorn in the Little Karoo (Figure 9.42).

Discussion: D. & U. Müller-Doblies (1985) described *Hessea weberlingiorum* and *H. cinnabarina* as closely related to *H. stellaris*. *Hessea weberlingiorum* is recorded as differing by the hemispehrical not clustered umbel, by the longer perigone tube (1,5--3,5 mm instead of only 1,0 mm long) and the stamens as long, not half as long as the tepals. These features are considered insufficient to separate *H. weberlingiorum* since additional specimens from the Matjiesfontein district have been found to link the type of *H. weberlingiorum* with the Worcester populations, cited by D. & U. Müller-Doblies (1985) as constituting *H. stellaris*. In *Marloth 11083* & *3935*, *Bayer 503*, *Snijman 547* and *Goldblatt 6089*, all from the Matjiesfontein district, the perigone tubes show a continuous range from 1,0--2,5 mm long; likewise the stamens vary from 2--3 mm shorter than the tepals to equalling the tepals in length.

Hessea cinnabarina described from near Loeriesfontein is also no longer upheld. Intermediates occur from north west of Calvinia, the Tanqua Karoo and Karoo Poort which link the type of *H. cinnabarina* with specimens from the Worcester district. The colouring of the stamens throughout this region varies from vermillion to dark wine-red, whereas specimens from elsewhere in the distribution range have flowers with paler pink central markings. However this character alone is considered insufficient to separate the collections into specific taxa. Indeed it is an intermediate specimen from the Tanqua Karoo (*Bayer 3535*) which best matches the lectotype of *H. stellaris*.

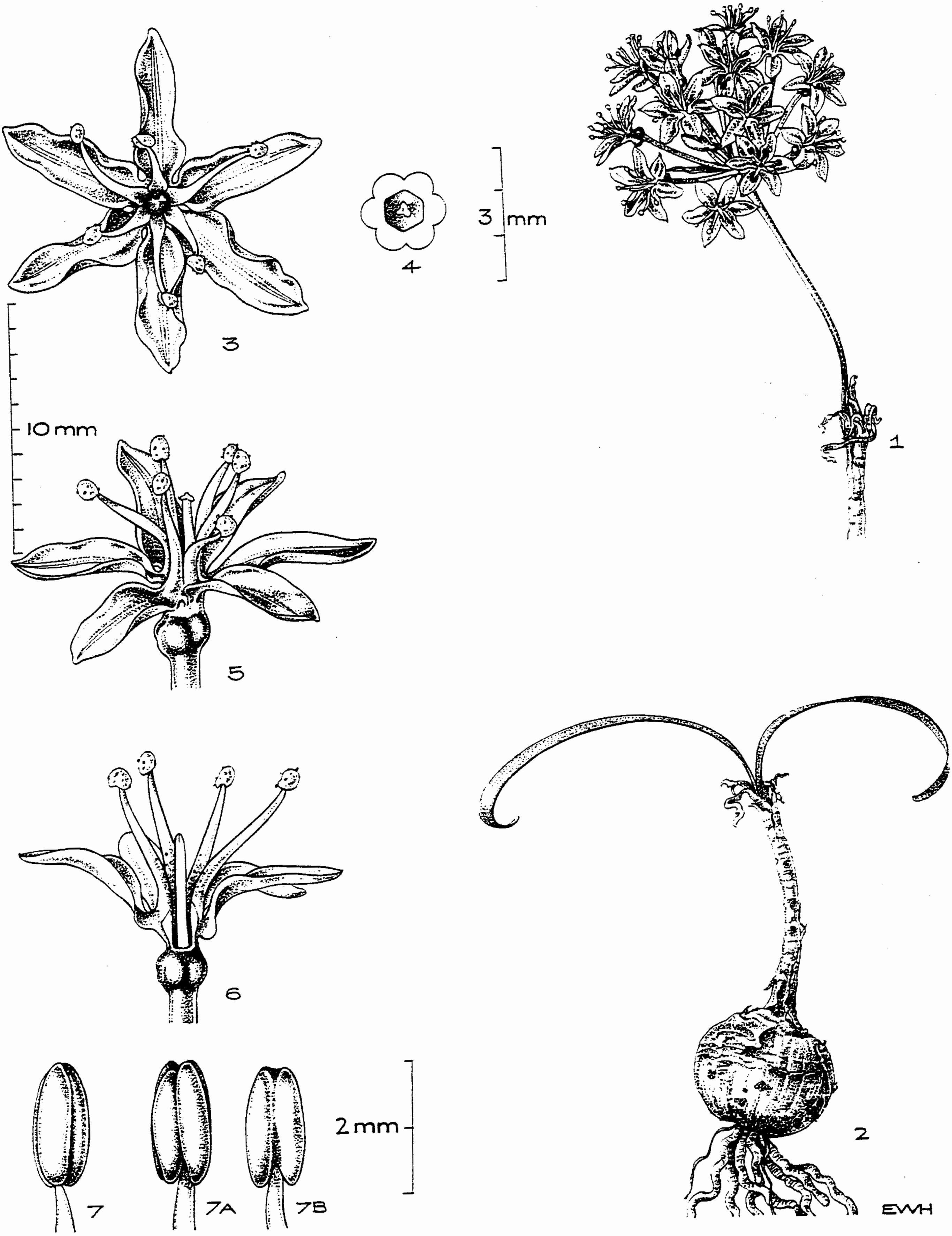


FIGURE 9.2-- *Hessea stellaris*: **1**, inflorescence, life size; **2**, bulb and leaves, life size; **3&5**, whole flowers; **4**, transverse section through perigone tube; **6**, portion of flower; **7**, anther attachment, lateral view, **7A**, ventral view, **7B**, dorsal view. Drawn from *Snijman 547* 1-2, and *van Zijl 13* 3-7,.

Specimens examined

--3019 (Loeriesfontein): E of Gifkop, 5 km E of Kromrivier on Kliprand road (-CC), *Müller-Doblies 80077b* (K, PRE).

--3118 (Vanrhynsdorp): 6 miles S of Vanrhynsdorp (-DA), fl 15 May 1935, *Salter 5308* (BOL, K); 37 miles N of Clanwilliam (-DA), *Salter & Creasey* sub *NBG 874/37* (BOL); farm Sandkraal at foot of Matzikamma (-DB), fl 16 Jun 1983, *Snijman 713* (NBG); fl 11 Jun 1989, *Snijman 1177* (NBG).

--3119 (Calvinia): farm Rietfontein between Calvinia and Loeriesfontein (-BC), *Perry 990* (MO, NBG, PRE).

--3219 (Wuppertal): Gemsbokkloof near the confluence of the Doringrivier and Tratrarivier (-AD), *Snijman 1213* (K, NBG, PRE); Tertia, NW of Elandsvlei, Tanqua Karoo (-BC), *Bayer 3535* (NBG, PRE); Varkkloof on N banks of Grootrivier drift between Clanwilliam and Ceres (-CB), fl 23 Apr 1989, *Snijman 1202* (K, MO, NBG, PRE); Zuurvlakte between Bokkeveld Sneeuwkop and Winkelhaaks (-CD/DC), fl 20 Apr 1946, *Esterhuysen 1270* (BOL); near farm Groenfontein, Katbakkies Pass (-DC), fl 19 May 1988, *Viviers s.n.* (NBG); 3,2 km towards Bakovenkloof from Karoopoort/Sutherland road (-DD), *Snijman 509* (NBG).

--3319 (Worcester): Karoopoort (-BA), fl 21 May 1941, *Leipoldt 4051* (BOL); farm Bloedrivier, N of Karoopoort towards Calvinia (-BB), *Van Zijl 13* (NBG); Hex River valley between Orchard station and De Doorns (-BC), fl 18 May 1932, *Salter 2185* (BOL, K); farm Nuwerus, Worcester district (-CB), fl 4 May 1965, *Van Breda & Joubert 1836* (PRE); Aan de Doorns, near Wynkelder (-CB), *Perry 1896* (NBG, PRE); Aan de Doorns, Sandberg koppie (-DA), fl 8 Jun 1977, *Walters 1722* (NBG); Kanetvlei, Sandhills (-DA), fl 23 May 1977, *Walters 779* (NBG); Naudesia farm, Sandhills (-DA), fl 20 May 1977, *Walters 799* (NBG); Robertson (-DD), fl May 1925, *Hurling & Neil* sub *Marloth 6470* (PRE).

--3320 (Montagu): farm Hillandale near Matjiesfontein (-BA), fl Mar 1922, *Austin* sub *Marloth 11083* (PRE); Whitehill Ridge (-BA), fr Jul 1944, *Compton 15727* (NBG); Dwarsindeweg, Matjiesfontein district (-BA), fl Apr 1905, *Marloth 3935* (PRE), 14 km N of Matjiesfontein (-BA), fl 19 Apr 1977, *Bayer 503* (NBG); Ghaapkop near Matjiesfontein (-BA), *Müller-Doblies 80022s* (PRE); *Snijman 547* (NBG); 8 Km N of Matjiesfontein (-BA), *Goldblatt 6089* (NBG, PRE); Dobbelaars Kloof (-CB), fl 25 Apr 1954, *Hall 879* (NBG).

--3321 (Ladismith): 18 miles W of Prince Albert (-AB), fl 24 Apr 1933, *Salter 3123* (BOL, K); Nooitgedacht, Calitzdorp (-DB), fl 17 May 1990, *Van Jaarsveld 10865* (NBG).

--3322 (Oudtshoorn): Farm Klein Sleutelfontein, northern foothills of Swartberg (-AB), Fl 8 Apr 1990, *Marincowitz s.n.* (NBG); Oudtshoorn (-CA), *A. Taylor s.n.* (GRA); 3 miles WNW of Wynandsrivier (-CA), fl 21 May 1959, *Acocks 20480* (K, PRE).

2. **Hessea breviflora** Herbert, Amaryllidaceae: 289 t. 29,6 t. 45,4 (1837). Type: ex hort. Kew, 1800, [probably one of Masson's collections] (BM, holo.!).

Hessea dregeana Kunth: 633 (1850); Baker: 22 (1888); Baker: 190 (1896). Type: Cape, between Bergvallei and Langevallei, Clanwilliam, July 1834 and 1840, *Drege 252b* (B, holo.; BM, E!, K!, S). *Periphanes dregeana* (Kunth) Leighton: 82 (1948).

Hessea zeyheri Baker: 22 (1888), 191 (1896); Phillips: t. 43 (1922). Type: Little Namaqualand, Hardeveld, Lieslap, [neither Province of Uitenhage as in original description nor Clanwilliam as in Müller-Doblies (1985) but Lieslap according to Zeyher's original label in SAM], May, *Zeyher 1661* (K, holo.!; BOL!, E!, S, SAM!, Z). The specimens at S and Z are mixed gatherings (Müller-Doblies 1985). *Periphanes zeyheri* (Baker) Leighton: 82 (1948).

Hessea brachyscypha Baker: 191 (1896). Type: Cape, Schaapplaats near Hopefield, Malmesbury division, June, *Bachmann s.n.* (K, holo.!; BOL!, Z). *Periphanes brachyscypha* (Baker) Leighton: 82 (1948).

Hessea bachmanniana Schinz: 812 (1896). Type: Cape, Division Malmesbury, umgegend von Hopefield, June 1886, *Bachmann 1141* (Z, lecto.!), designated by Müller-Doblies (1985).

Hessea longituba D. & U. Müller-Doblies: 42 (1985). Type: Cape, Eenrietsberg, 10 km N of Steinkopf, 800 m, 14 August 1980, *Müller-Doblies 80096v* (PRE, holo.!; B, K!, M, NBG, Herb. M-D.).

Bulb solitary, subglobose, 20--40 mm diam., thickly covered with felt-like tunics, extended into a stout neck up to 140 mm long. *Leaves* absent or emergent at anthesis, 2 (-3), lorate, erect to spreading, up to 70--220 x (4-) 5--13 (-16) mm, canaliculate towards the base, shiny green to somewhat glaucous, becoming flushed with red proximally, glabrous, subtended by an amplexicaul cataphyll and subterranean non-amplexicaul prophyll; cataphyll initially reddened and exserted to 25 mm above ground, later turning brown and dying down. *Inflorescence* usually dense and widely spreading, 25--130 mm across; scape straight or flexuose, deflexed laterally, 50--200 mm long, 2--3 mm diam. green to leaden-grey, reddened towards the base, breaking off at the base in fruit; spathe valves lanceolate, 10--30 x 3--5 mm; bracteoles up to 10 mm long. *Flowers* 10--55, spreading, stellate, rarely somewhat hypocrateriform, pale to deep pink, sometimes flushed with deeper pink towards the centre, ageing to light brown, sometimes scented; pedicels straight, 20--55 mm long, green to glaucous. *Tepals* adnate to the filament tube for 0,5--3,5 (-4,0) mm, outspread above, oblong-lanceolate, 5,5--12,0 x 1,5--4,0 mm, with plane edges. *Stamens* ranging from 2(-3) mm shorter to 2 mm longer than the tepals, becoming outspread; filaments connate basally into a tube reaching 1,0--4,0 (-4,5) mm beyond the perigone throat thereby either equalling or exceeding the length of the perigone tube, subulate above; anthers centrifixed, 2,0--2,5 mm long and dark wine-red before opening;

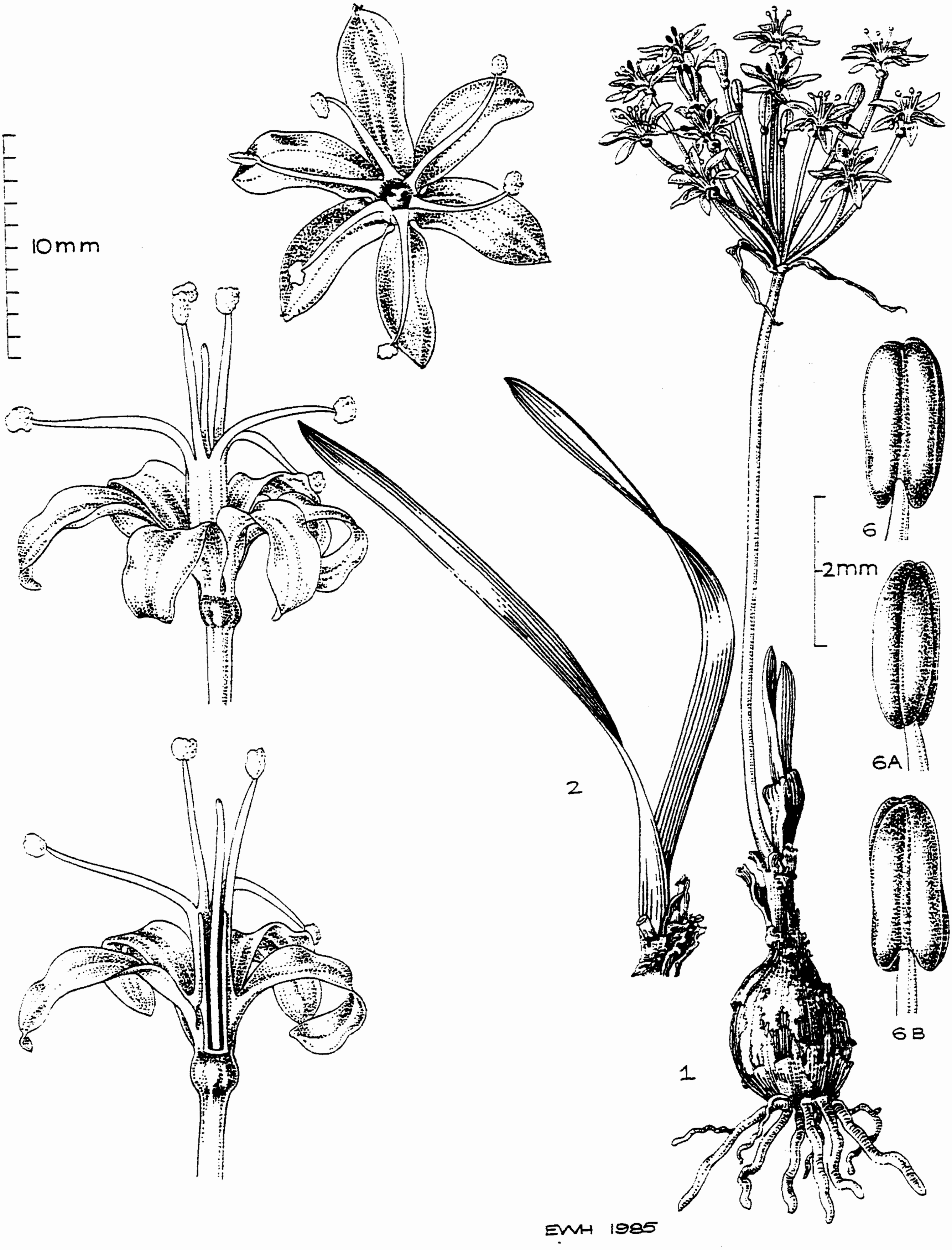


FIGURE 9.3-- *Hessea breviflora*: 1, bulb, inflorescence and new foliage with sheathing cataphyll, life size; 3-4, whole flowers; 5, section of flower; 6, anther attachment, dorsal view, **6A**, lateral view, **6B**, ventral view. Drawn from *Hall* sub *NBG 1162/82* 1-2, and *Snijman 853* 3-6,.

pollen cream-coloured. *Ovary* with up to 3 ovules per locule. *Style* up to 5--16 mm long, narrowly subtriquetrous throughout, with nectar collecting in a well around the base. *Seed* 3--4 mm diam. *Chromosome number* 2*n* = 22 or occasionally 22 + 1B, 22 + 1--3B. Figure 9.3.

Flowering time: Mostly during May but occasionally commencing in April and extending into the first half of June. Cultivated bulbs are known to flower as early as March.

Diagnostic features: The bulbs typically have thick, felt-like outer tunics and are usually the largest in the genus (up to 40 mm diam.). The mature leaves are broad (4--16 mm) and when they first emerge above ground are sheathed by a conspicuous reddened cataphyll. The flowers are similar to those of *H. stellaris* but are distinguished by the length of the perigone tube, which equals or is less than the length to which the filament tube is exserted beyond the throat.

Distribution and habitat: Hessea brevifolia occupies rocky sites in a range of substrates, either sandy soil at the base of exposed granite boulders, sandy pockets overlying sandstone sheets or loamy soils. The species ranges from near Steinkopf in the north, southwards through Namaqualand, the Olifants River Valley and the low lying areas of the Cedarberg to near Malmesbury (Figure 9.42).

Discussion: Two centres where the perigone tube is longer than elsewhere are the Steinkopf area in the extreme north (*Hugo 1221, Müller-Doblies 80096v* and *Meyer 6474*) and the area east of the Pakhuis Pass, near the Brandewyn River, on the easternmost limit of the distribution range (*Barker 7317, Lewis 2377, Snijman 255* and *Snijman 850*). In *Meyer 6474* the perigone tube varies from 2--4 mm in length, and in *Hugo 1221* and *Müller-Doblies 80096v* from 3--4 mm long. Specimens from the Brandewyn River area have perigone tubes ranging from 1,5--3,5 mm long. Elsewhere in the distribution range the perigone tube varies from 0,5--1,5 mm long. As no other feature distinguishes the specimens with long perigone tubes, the continuity in the length of the perigone tube from within the known populations has led to the decision here to amplify the former concept of *H. brevifolia* to include *H. longituba*. The inflorescences of the types of *H. brachyscypha* and *H. bachmanniana* from the Malmesbury division, match those of *H. breviflora* but have immature leaves which are unusually narrow (3--4 mm). However other collections (*Middelmost* sub *NBG 1415/36*) from this southern extreme of the distribution range, have wider mature leaves (7 mm across) which match those from the central and northern areas.

Specimens examined

--2917 (Springbok): about 12 km W of Umdaus (-BA), fl 20 May 1988, *Williamson 3873* (NBG); towards Kosies from Steinkopf/Port Nolloth road (-BA), *Perry 1053* (NBG); near Arabies (-BB), fl 6 Apr 1985, *Williamson 3431* (NBG); Eenrietsberg, 10--12 km N of Steinkopf (-BB), *Müller-Doblies 80096v* (K, PRE); Steinkopf (-BC), *Meyer*

6474 (PRE); Varswater, NW of Springbok (-BC), *Oliver s.n.* (NBG); near Paddagat, 22 miles NW of Springbok (-BD), fl 28 May 1961, *Leistner 2558* (PRE); Kommagas Reserve (-CB), fl 30 Apr 1981, *Van Berkel 330* (NBG); Klein Komaggas (-CD), *Lavranos s.n.* (PRE); Spektakel Pass, W of Springbok (-DA), fl 30 May 1974, *Goldblatt 2018* (NBG); Nababiep (-DB), fl 18 May 1916, *Ridgell* sub *NBG 1157/16* (BOL); O'Kiep, outskirts of town (-DB), fl 13 May 1978, *Hugo 1221* (PRE); Wildepaardehoek Pass towards Messelpad (-DC), fl 3 Jun 1980, *Van Jaarsveld & Drijfhout 5305* (NBG, PRE); farm Sannagas (-DC), *Van Jaarsveld 5371* (NBG); about 5 km from Bokkeveld towards Kommagas (-DC), fl 5 Jun 1980, *Van Jaarsveld & Drijfhout 5377* (NBG, PRE).

--3017 (Hondeklipbaai): Riethuis (-AB), *Bruyns 3852* (NBG); Kharkams, 2 miles S of Darters Grave (-BD), fl 4 May 1963, *Barker 9868* (NBG); just N of Kharkams (-BD), *Snijman 1121* (NBG); 24,5 miles W of Garies (-DA), *Creasey* sub *894/37* (NBG); Grootbrakfontein ESE of Waterklip (-DB), fl 29 Apr 1981, *Van Berkel 326* (NBG).

--3018 (Kamiesberg): 4 km SW of Rooifontein on the Kamieskroon/Gamoep road (-AA), *Lavranos & Bleck 24211* (NBG); 5,8 km SW of Draaiklip towards Brakputs, Kamiesberg (-AC), *Snijman 1123* (NBG); Garies (-CA), *Caporn* sub *NBG 729/15* (BOL); Hardeveld, Lieslap (-DA), fl May, *Zeyher 1661* (BOL, E, K, SAM).

--3118 (Vanrhynsdorp): farm Kliphoek, 67 km NW of Klawer towards Nuwerus (-AD), *Perry 2026* (NBG); 6 miles N of Koekenaap (-CB), fl 13 May 1962, *Hall 2359* (NBG); farm Liebendal, Vredendal district (-CB), *Hall* sub *NBG 1162/82* (NBG, PRE); 29 km N of Clanwilliam along old Klawer road (-DD), fl 25 Apr 1978, *Perry 690* (NBG); N of Bulshoek barrage (-DD), fl 4 May 1951, *Barker 7302* (NBG, PRE); 27 miles S of Vanrhynsdorp (-DD), *Barker 7302* (NBG); 27 miles S of Vanrhynsdorp (-DD), fl 15 Apr 1958, *Thomas s.n.* (NBG); farm Bulshoek, Olifants River valley (-DD), fl 14 Apr 1986, *Simpson s.n.* (NBG).

--3218 (Clanwilliam): Ratelfontein (-BA), *Herre* sub *SUG 3704* (BOL); W end of Pakhuis Pass (-BB), *Barker 10462* (NBG); 15 miles N of Clanwilliam (-BB), fl 2 May 1966, *Thomas s.n.* (NBG); Clanwilliam (-BB), *Creasey* sub *NBG 873/37* (NBG); fl May, *Leipoldt 823* (BOL, K); *Leipoldt 923* (NBG, SAM); *Leipoldt s.n.* (SAM); fl May, *Putterill* sub *Marloth 11618* (PRE); near Clanwilliam (-BB), fl 24 May 1931, *Salter 669* (K); *Salter* sub *375/12* (K); *Leipoldt 823* (BOL, K); Olifants River valley, Clanwilliam district (-BB), *Salter* sub *NBG 1148/35* (NBG); Kransvlei, 7 miles S of Clanwilliam (-BB), fl 16 Jun 1945, *Leipoldt 4114* (BOL); Paleisheuwel (-BC), fl 4 Jun 1954, *Hall 887* (NBG); 5km N of Hex River, N of Citrusdal (-BD), *Pretorius 11* (NBG, PRE); Olifants River Valley, 13 miles N of Citrusdal (-BD), fl 10 May 1934, *Galpin 12941* (K, PRE); *Galpin 14025* (PRE); 15,6 km from Algeria Forest Station towards Clanwilliam (-BD), fl 20 May 1980, *Snijman 251* (NBG); 14 miles N of

Citrusdal (-BD), fl 19 May 1935, *Salter 5402* (BOL); 12 miles N of Citrusdal (-BD), fl 10 May 1934, *Salter 4435* (BOL, K).

--3219 (Wuppertal): foot of Pakhuis Pass near Brandewyn River (-AA), fl 19 May 1974, *Goldblatt 1849* (K, MO, NBG, PRE); near Brandewyn River (-AA), fl 29 Apr 1947, *Barker 4512* (NBG); Brandewyn River rocks (-AA), fl 7 May 1951, *Barker 7317* (NBG); between Brandewyn River and Doornbosch (-AA), *Lewis 2377* (SAM); Kliprandfontein (-AA), fl 22 Apr 1948, *Compton* sub *NBG 629/48* (NBG); 30,2 km from Clanwilliam along Pakhuis road (-AA), fl 21 May 1980, *Snijman 255* (NBG); farm Kleinfontein, E of Pakhuis Pass (-AA), fl 6 May 1985, *Snijman 850* (NBG, PRE, K); Boontjieskloof, NE of Waterfall (-AA), fl 6 May 1971, *Oliver 3382* (K, PRE); farm Boontjieskloof, E of Pakhuis Pass (-AA), fl 6 May 1985, *Snijman 853* (NBG, MO, K); 19 km E of farm Mertenhof along Biedou Valley near Mietjiesfontein (-AB), fl 5 May 1989, *Snijman 1206* (K, NBG, PRE); between Clanwilliam and Algeria (-CA), fl 2 Jun 1980, *Goldblatt 5509* (PRE).

--3318 (Cape Town): Schaapplaats near Hopefield (-AB), fl Jun, *Bachmann s.n.* (BOL, K); Oudepost, Malmesbury (-BC), *Middelmost* sub *NBG 1415/36* (NBG).

--Imprecise localities: Between Clanwilliam and Klawer, fl 5 May 1965, *Barker 10369* (NBG); 9 miles from Doorn River Bridge, fl 30 Apr 1946, *Smith 6487* (NBG); 6 miles from Doorn River Bridge, *Smith 6488* (NBG); along Oliphants River between Citrusdal and Clanwilliam, fl 4 May 1951, *Hodge A148* (K); N of Citrusdal, fl 5 May 1951, *Barker 7298* (NBG); between Bergvallei and Langevallei, Clanwilliam, *Drege 2526* (E, K); Piquetberg, *Compton* sub *NBG 617/38* (NBG); between Citrusdal and Clanwilliam, fl 25 Apr 1960, *Runkel* sub *NBG 359/60* (NBG); Malmesbury division, umgegend von Hopefield, fl Jun 1886, *Bachmann 1141* (Z).

3. **Hessea speciosa** Snijman in Bothalia 22 (in press). Type: Namibia, Warmbad district, farm Witpütz, 15 May 1963, *Giess, Volk* & *B. Bleissner 6960* (WIND, holo.; PRE).

Hessea zeyheri sensu Sölch & Roessler 150: 11 (1970) pro parte, as to *Bleissner 268, Giess, Volk & Bleissner 6960.*

Bulb solitary, deep-seated, subglobose, 25--60 mm diam., covered with several layers of cream-coloured cottony fibrous tunics, extended into a stout neck 100--170 mm long. *Leaves* absent at anthesis, 2, recurved, lorate, up to 120 x 4--6 mm, plane, glabrous, dark green and flushed with red towards the base; amplexicaul cataphyll remaining subterranean; prophyll unknown. *Inflorescence* dense, hemispherical to spherical, 70--120 mm across; scape erect to somewhat flexuose, 60--160 mm long, 3--5 mm diam., initially green, breaking off at the base in fruit; spathe valves linear-lanceolate, 20--40 x 3--7 mm; bracteoles up to 25 mm long. *Flowers* (20-) 30--65, spreading, stellate, white to delicate pink with deep pink or greenish median stripes on the

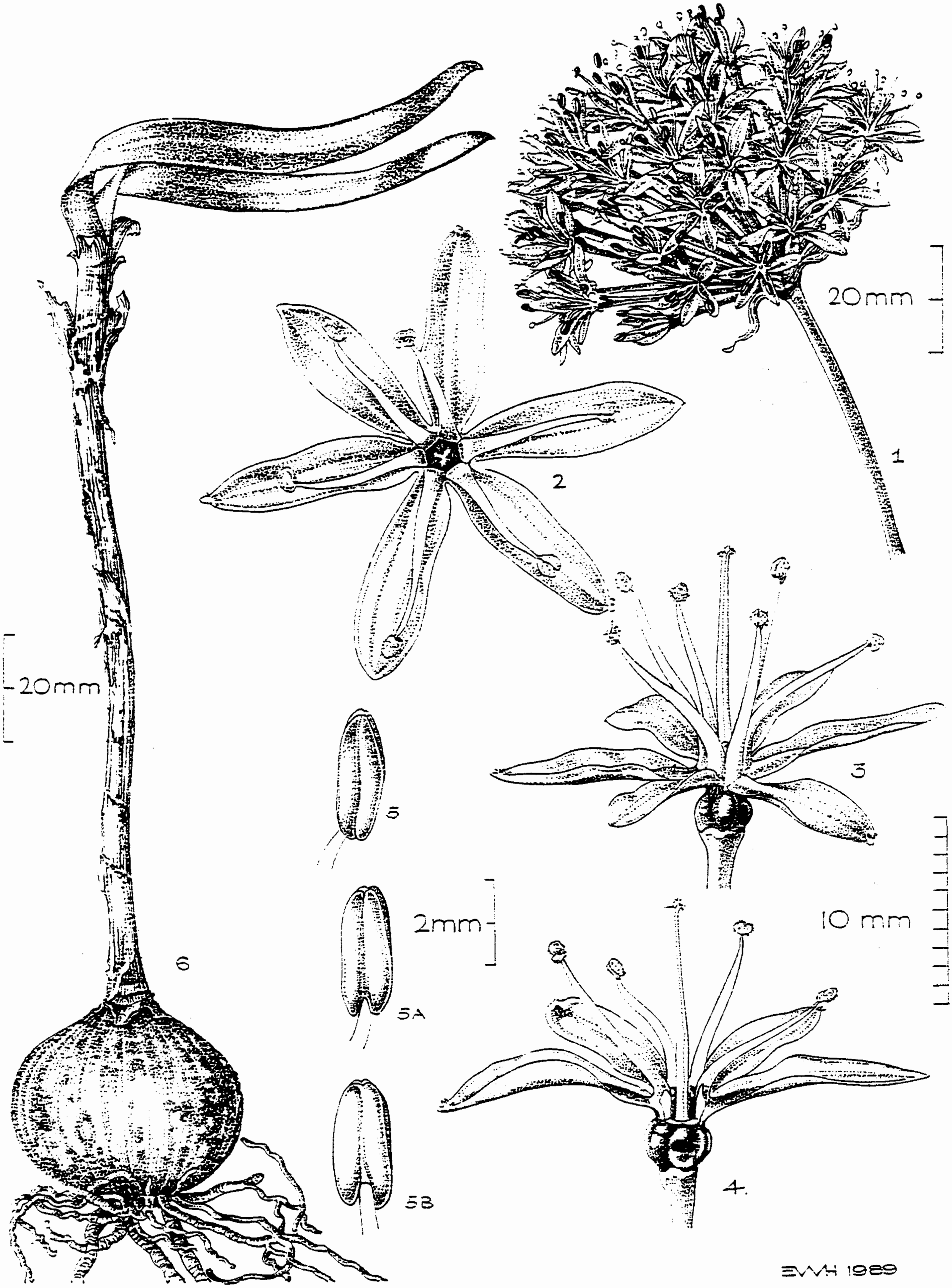


FIGURE 9.4– *Hessea speciosa*: **1**, inflorescence, life size; **2-3**, whole flowers; **4**, section of flower; **5**, anther attachment, lateral view, **5A**, ventral view, **5B**, dorsal view; **6**, bulb and leaves, life size. Drawn from *Snijman 1163*.

undersurface, ageing to light brown, with a heavy coconut-like scent; pedicels straight, 20--50 mm long, becoming straw-coloured. *Tepals* almost free to the base or very shortly adnate to the staminal tube for up to 0,25 mm, otherwise outspread, oblong-lanceolate, 8--15 x 2--4 mm, with plane edges. *Stamens* equalling or up to 2 mm longer than the tepals, becoming outspread; filaments connate proximally into a tube protruding (1,0-) 1,5--4,0 mm above the perigone throat, subulate above, occasionally shortly toothed in the axils between adjacent filaments; anthers centrifixed, 3 mm long and dark wine-red before opening; pollen cream-coloured. *Style* up to 15 mm long, narrow throughout, with nectar collecting in a well around the base. *Seeds* unknown. *Chromosome number* $2n = 22$. Figure 9.4.

Flowering time: From late March into May.

Diagnostic features are are the deep-seated bulb with a long neck (up to 170 mm); the somewhat spherical inflorescence and the very short perigone tube (0,25 mm or less). *Hessea speciosa* is most closely allied to *H. pilosula* and *H. incana*, with which it shares the very short perigone tube and plane tepals. It is distinguished from these species by its glabrous leaves and the relative length of the stamens to the tepals. The stamens equal or extend up to 2 mm longer than the tepals in *H. speciosa*, whereas they are distinctly shorter than the tepals (by 3 mm or more) in *H. pilosula* and *H. incana.*

Distribution and habitat: Recorded from red sand dunes and friable loams found along the extensive drainage system of seasonal rivers, from Warmbad in southern Namibia to Fraserburg in the central Cape (Figure 9.43). The associated vegetation is most commonly grassland.

Variation: Often the northerly populations have a distinct staminal tube (1,5--3,5 mm), whereas in the south of the range specimens have only a shortly developed tube (less than 1,5 mm). It is one of the few *Hessea* species recorded with white flowers. However, flower colour is not constant and pink forms also occur. A further novelty is the occasional presence of small teeth in the axils between adjoining filaments.

Specimens examined

--2818 (Warmbad) Warmbad district, farm Witpütz (-CA), fl 15 May 1963, *Giess, Volk & B. Bleissner 6960* (PRE, WIND); fl 15 May 1963, *S. Bleissner 268* (PRE).

--2918 (Gamoep): farm Eendop, SW of Klipvlei (-AC), fl 1 May 1981, *Van Berkel 331* (NBG): Aggenys Mine (-BB), fl 23 May 1989, *S. Dean 655* (NBG); Banke, Pofadder (-DB), fl 3 May 1988, *S. Dean s.n.* (NBG).

--2919 (Pofadder): farm Kykgate, along road between Springbok and Pofadder (-AC), fl 13 May 1969, *Van Breda 4147* (PRE).

--2921 (Kenhardt): Kenhardt (-AC), fl 9 May 1927, *Long* sub *NBG 947/27* (BOL); fl 14 May 1936, *Martin* sub *NBG 1188/36* (BOL).

--3120 (Williston): 40 miles N of Calvinia (-AA/AB), fl 30 Mar 1953, *Hall 684* (NBG); 36 km N of Downes towards Brandvlei (-AC), fl 3 Apr 1988, *Snijman 1163* (NBG, PRE).

--3121 (Fraserburg): 49 miles from Fraserburg towards Williston (-AC), *Smith 6491* (NBG).

4. **Hessea pilosula** D. & U. Müller-Doblies in Botanische Jahrbücher für Systematik 107 : 38 (1985). Type: Cape, 7 km W of Steinkopf on Port Nolloth road, 19 August 1979, *Müller-Doblies 79216a* (PRE, holo.!; B, Herb. M-D., BM, K!, M, MO, NBG, S, STE, Z).

Bulb solitary, deep-seated, subglobose, 17--30 mm diam., with thinly fibrous light brown outer tunics, extended into a slender neck up to 120 mm long. *Leaves* absent or when cultivated sometimes incipient at anthesis, 2 (-3), spreading, narrowly lorate, 70--170 x 1--5 mm, shallowly canaliculate to hemiterete, shiny green, often reddened proximally, with short patent trichomes covering both surfaces or the abaxial surface only, occasionally glabrous, subtended by a subterranean amplexicaul cataphyll and non-amplexicaul prophyll. *Inflorescence* dense and widely spreading, 50--90 mm across; scape flexuose, woody and slender at anthesis 25--65 (-80) mm long, 0,5--2,0 mm diam., leaden-grey, flushed with pink proximally, breaking off at the base in fruit; spathe valves linear-lanceolate, 15--30 x 1,5--2,5 mm; bracteoles up to 3 mm long. *Flowers* 10--27, spreading, stellate, pale pink with a white or deeper pink centre, ageing to light brown, scentless; pedicels straight, 15--45 mm long, glaucous. *Tepals* almost free to the base or shortly adnate to the staminal tube for up to 1 mm, outspread above, oblong-lanceolate, 7,5--11,0 x 2--4 mm, slightly channelled towards the base with plane or occasionally somewhat undulate edges. *Stamens* shorter than the tepals by 3 mm or more, becoming outspread; filaments connate basally to form a short tube extending to 1,5 mm above the perigone throat and either equalling or exceeding the length of the perigone tube, subulate above; anthers centrifixed, 2 mm long and dark wine-red before opening; pollen cream-coloured. *Ovary* with up to 3 ovules per locule. *Style* up to 6 mm long, narrowly subtriquetrous throughout, with nectar collecting in a central well around the base. *Seeds* ± 2,5 mm diam. *Chromosome number* $2n = 22$. Figure 9.5.

Flowering time: Usually May but extending to late June when cultivated.

Diagnostic features: Hessea pilosula is distinguished vegetatively by the deep seated bulb with a long, slender neck; narrow (1--5 mm) leaves, which are usually more or less pilose; short stamens (less than 3 mm shorter than tepals); and short to absent perigone tube (less than 1 mm). The most closely allied species is *H. incana*, the only

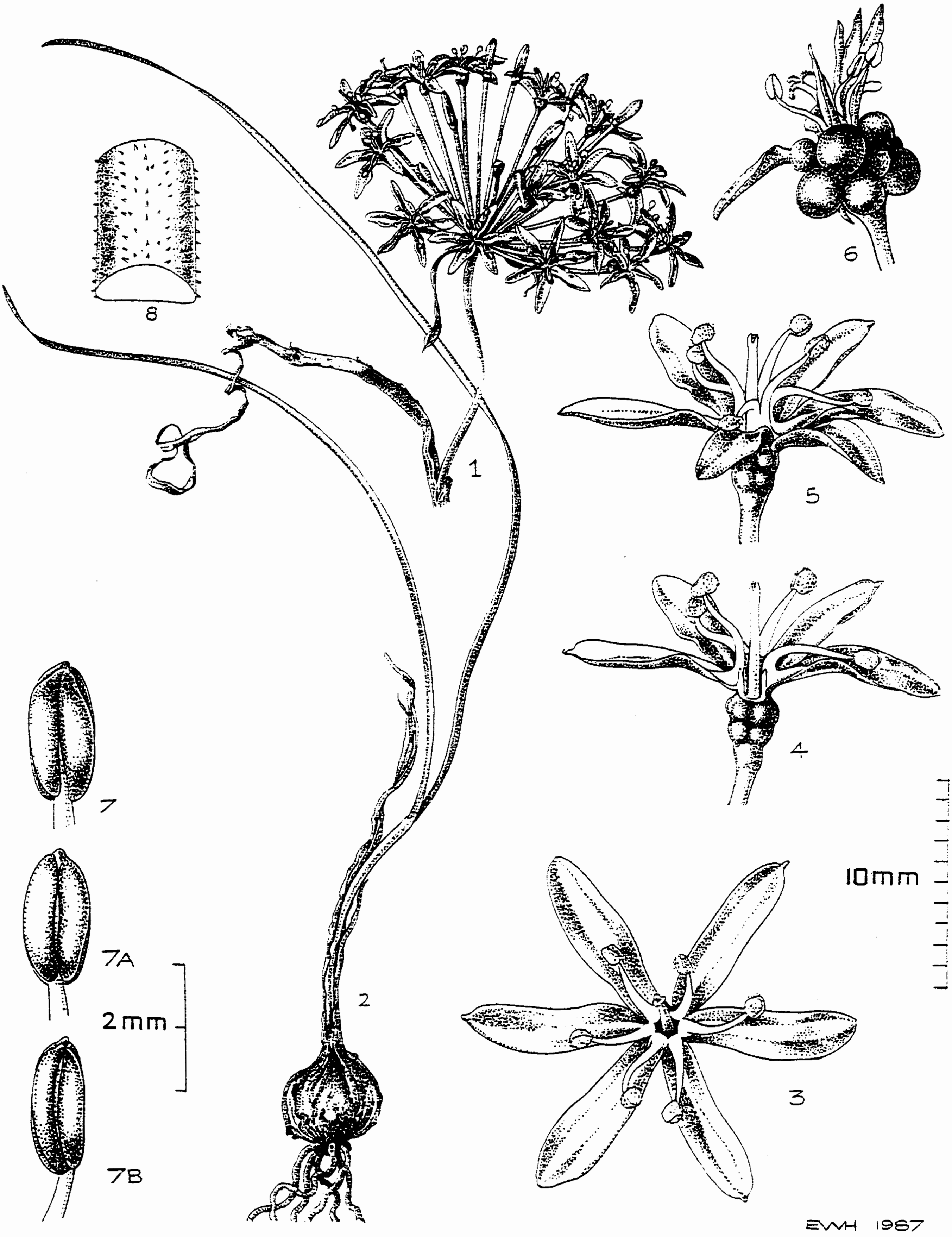


FIGURE 9.5– *Hessea pilosula*: 1, inflorescence, life size; 2, bulb and leaves, life size; 3&5, whole flowers; 4, section of flower; 6, seeds emerging from dehiscent capsule; 7, anther attachment, dorsal view, 7A, ventral view, 7B, lateral view; 8, portion of adaxial leaf surface. Drawn from *Snijman 1134.*

other species with shortly pilose leaves. *Hessea pilosula* is vegetatively and florally less robust than *H. incana* and flowers one to two months earlier. For detailed differences between the two species refer to *H. incana*.

Distribution and habitat: The species grows in coarse, deep sand on disturbed, heavily grazed flat plains in the Springbok area, as well as deep red sands along the north-western coast (Figure 9.43). In the Springbok region the species is locally abundant, with populations of many scattered individuals, but on the west coast individuals are less frequent and widely scattered.

Specimens examined

--2917 (Springbok): 7 km W of Steinkopf on Port Nolloth road (-BA), *Müller-Doblies 79216a* (K, PRE); fl 31 May 1981, *Van Berkel 339* (NBG); 6,5 km W of Steinkopf at turnoff to Rabas (-BA), *Snijman 1134* (NBG); near northern base of Eenriet, N of Steinkopf (-BB), fl 6 May 1985, *Williamson 3444* (NBG); Steinkopf (-BC), *M. Schlechter 71* (BOL, GRA, PRE); fl 7 May 1897, *M. Schlechter s.n.* (E, K); 5 km SSW of Steinkopf (-BC), *Müller-Doblies 80099a* (K); 7,5 km SSW of Steinkopf near Besondermeid (-BC), *Snijman 1133* (NBG); between Koufontein and Tweerivier (-BC), *Snijman 1131* (NBG, PRE).

--3017 (Hondeklipbaai): Halfway between Hondeklipbaai and Wallekraal (-AD), *Lavranos & Bleck 22109* (NBG).

5. **Hessea incana** Snijman in South African Journal of Botany 55,3: 355 (1989). Type: Cape, Kamiesberg, farm De Kuilen, 18 July 1988, *Snijman 1180* (NBG, holo.; K, MO, PRE, S).

Bulb solitary, subglobose, 25--35 mm diam., with a dark brown parchment-like outer covering, extended into a stout neck up to 100 mm long. *Leaves* absent or when cultivated sometimes incipient at anthesis, (1-) 2 (-3), suberect or spreading, lorate, 80--200 x 3--8 mm, flattened, with minute retrorse hairs covering the abaxial surface and occasionally the adaxial surface, flushed with pink basally, subtended by a subterranean amplexicaul cataphyll and non-amplexicaul prophyll. *Inflorescence* usually densely hemispherical, 70--120 mm across; scape deflexed northwards, stout and fleshy, 60--90 mm long, 2--7 mm diam., wine-red to greenish, becoming dry and breaking off at the base in fruit; spathe valves broadly lanceolate, 20--40 x 8--20 mm; bracteoles up to 3 mm long. *Flowers* 20--70, spreading, stellate, pink with a deeper pink centre and median dorsal banding, ageing to light brown, faintly scented; pedicels straight, 30--55 mm long, stout, green to reddish brown. *Tepals* free to the base, outspread or sometimes slightly deflexed,

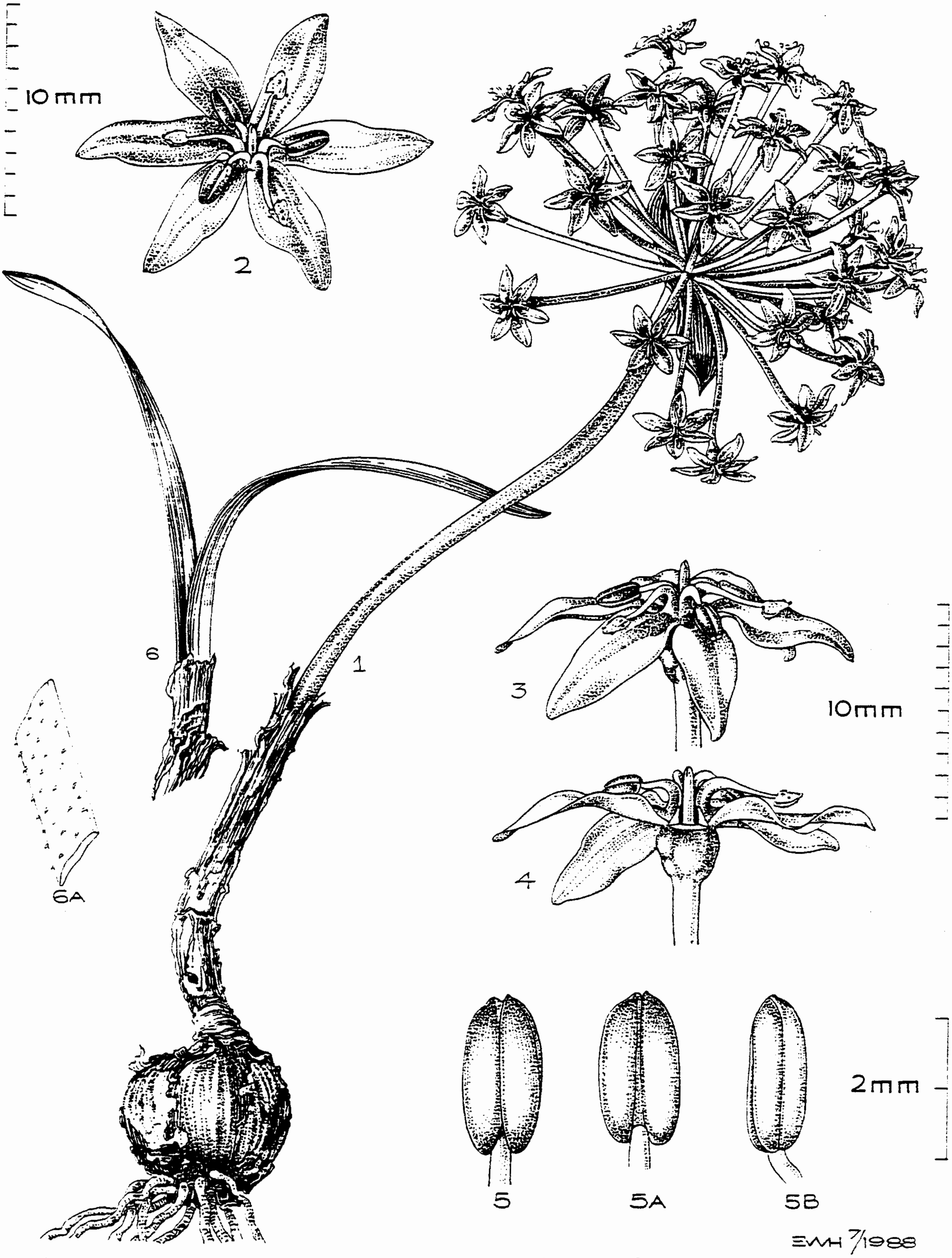


FIGURE 9.6-- *Hessea incana*: 1, bulb and inflorescence, life size; 2-3, whole flowers; 4, section of flowers; 5, anther attachment, ventral view, 5A, dorsal view; 5B, lateral view; 6, leaves, life size, 6A, portion of abaxial leaf surface. Drawn from *Snijman 1180.*

ovate-lanceolate, 6--11 x 3--4 mm, plane. *Stamens* shorter than the tepals by 4--5 mm; filaments connate basally into a short tube up to 1,5 mm long, outspread and subulate above; anthers centrifixed, 2 mm long and dark wine-red before opening; pollen cream-coloured. *Ovary* with 3 or 4 ovules per locule. *Style* slender, up to 7 mm long with nectar collecting in a well around the base. *Seeds* ± 3 mm diam. *Chromosome number* $2n$ = 22. Figure 9.6.

Flowering time: In comparison to all other species of *Hessea,* which flower between March and June, *H. incana* is typically late-flowering; from July to the beginning of August.

Diagnostic features: Hessea incana is most closely allied to *H. pilosula*, a species from approximately 80 km to the north in the Springbok area. Together they constitute the only species pair with the apomorphy of vestiture on the leaves. The covering of minute retrorse hairs in *H. incana* is dense, giving a hoary appearance to the abaxial surface of the leaf. Furthermore the leaf blades are flattened and broad (3--8 mm). Despite the covering of short hairs or papillae in *H.pilosula,* the leaves appear shiny green; the blades are shallowly canaliculate and thickened abaxially in cross section and narrow (1--5 mm). The inflorescence of *H. incana* is also distinct in having broadly lanceolate spathe valves (8--20 mm wide at anthesis), whereas *H. pilosula* has linear-lanceolate spathe valves at anthesis, at most 2,5 mm wide.

Distribution and habitat: Hessea incana inhabits elevated sandy plains (1035 m) bounded by huge granite domes on the Kamiesberg in Namaqualand (Figure 9.43). Populations are localised and comprise a hundred or more fairly closely aggregated bulbs. The associated vegetation of the only known populations is disturbed and sparse so that the sites remain open during the flowering period. When flowering the scapes incline northwards to face the sun. Unlike the remaining high-lying areas of Namaqualand, the Kamiesberg has periodic snowfalls in winter and occasionally *H. incana* has been seen flowering in the snow (W. van Niekerk pers. comm.).

Specimens examined

--3017 (Hondeklipbaai): Kamiesberg Pass (-BB), *Goldblatt 5762* (NBG, PRE).

--3018 (Kamiesberg): 1,5 km W of De Kuilen (-AA), fl 8 Aug 1980, *Van Berkel 161* (NBG); farm De Kuilen (-AA), fl 18 Jul 1988, *Snijman 1180* (K, MO, NBG, PRE, S).

6. Hessea pusilla Snijman in South African Journal of Botany 55(3): 353 (1989). Type: Cape, Northern Bokkeveldberge, Perdekraal, approximately 12 km NW of Grasberg, near Tweevlei, 27 April 1988, *Snijman 1174* (NBG, holo.; K, PRE).

Bulb solitary, subglobose, 10--15 mm diam., thinly covered with brown parchment-

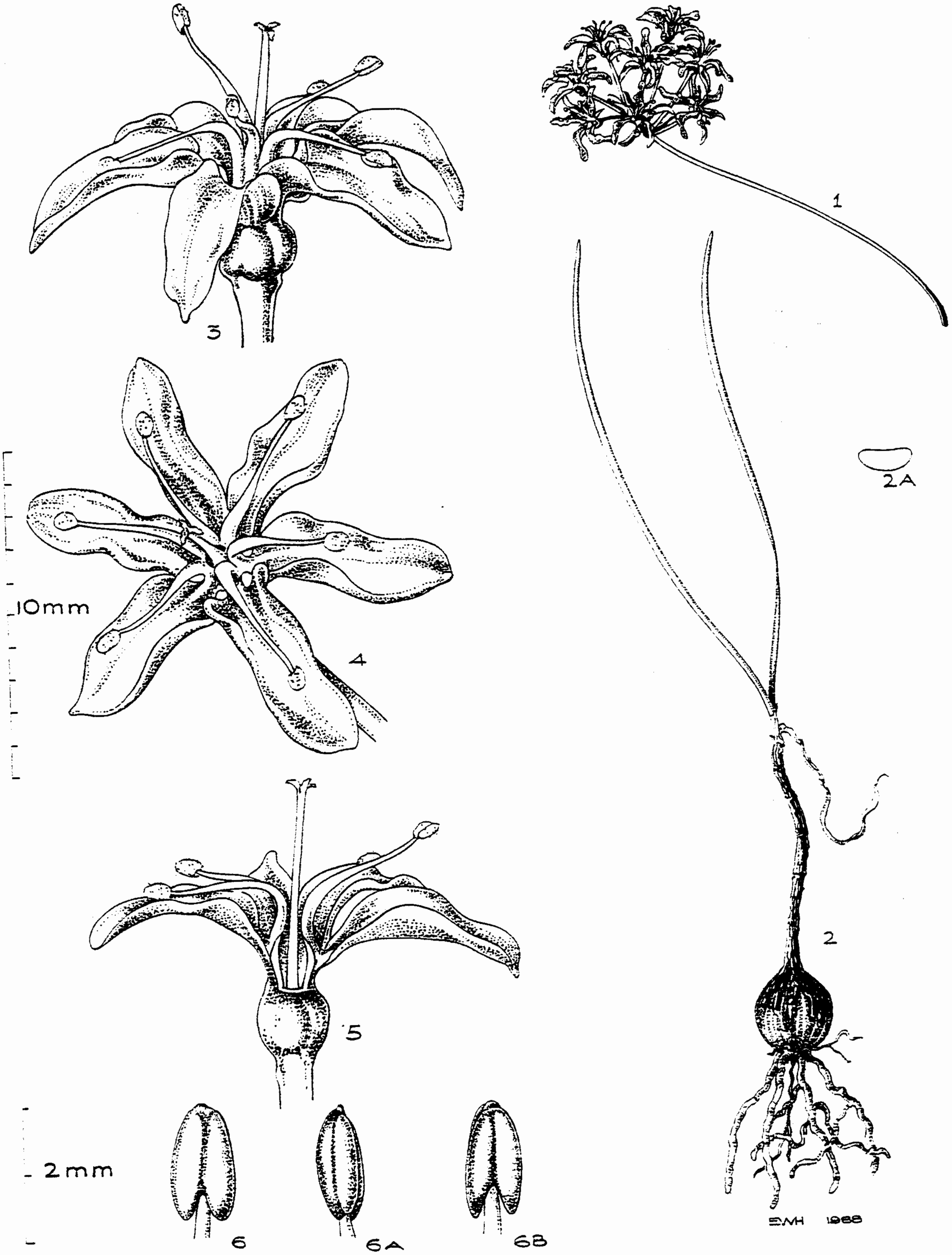


FIGURE 9.7-- *Hessea pusilla*: 1, inflorescence, life size; 2, habit of bulb and leaves, life size, 2A, leaf in transverse section; 3-4, whole flowers; 5, section of flower; 6, anther attachment, ventral view, 6A, lateral view, 6B, dorsal view. Drawn from *Snijman 1072*.

like fibrous tunics, extended into a slender neck 10--80 mm long. *Leaves* absent at anthesis (1-) 2, spreading, narrowly lorate, 70--190 x 0,5--1,0 mm, glabrous, sometimes flushed with red basally, subtended by a subterranean amplexicaul cataphyll and non-amplexicaul prophyll. *Inflorescence* somewhat clustered, 15--40 (-50) mm across; scape flexuose, 20--110 mm long, 0,5--1,0 mm diam., green to reddish brown, habit during seed dispersal unknown; spathe valves linear-lanceolate, 10--20 mm x 1 mm; bracteoles up to 4 mm long. *Flowers* 4--11, spreading, widely funnel-shaped, glistening, pale pink with a central deeper pink star-shaped pattern, occasionally flushed with deeper pink towards the base of the undersurface, ageing to light brown, scentless; pedicels straight, 10--25 mm long, green to reddish brown. *Tepals* adnate proximally to the staminal tube for 0,5--1,5 mm, somewhat recurved above, oblong-lanceolate, 6--8 x 1--2 mm, channelled, sometimes with slightly undulate edges. *Stamens* equalling or up to 1,5 mm shorter than the tepals; filaments connate basally into a distally narrowed tube extending to 2 mm above the perigone throat, abruptly outspread and subulate above; anthers centrifixed, 1,5 mm long and wine-red before opening; pollen cream-coloured. *Ovary* with 2 or 3 ovules per locule. *Style* slender, up to 6,5 mm long with nectar collecting in a well around the base. *Seeds* unknown. *Chromosome number* $2n = 22$. Figure 9.7.

Flowering time: Flowering commences during April and extends to mid May.

Diagnostic features: Hessea pusilla is the most diminutive species of the genus. Distinguishing features are the narrowly lorate, glabrous leaves (less than 1 mm wide); the widely funnel-shaped, glistening flowers, with slightly recurved uncrisped tepals; and filaments connate basally into a distally narrowed tube reaching to 2 mm above the perigone throat, which then become abruptly outspread above. Although sometimes approaching *H. stellaris* in size, it nevertheless remains distinguishable by androecial characters. In *H. stellaris* the filament tube is shorter (up to 1,5 mm above the perigone throat) and distally widened, while the free portion of the filament remains erecto-patent at anthesis. Only when withering do the filaments become outspread.

Distribution and habitat: Hessea pusilla is known from only one population on the plateau of the northern Bokkeveldberge at Perdekraal, north-west of Nieuwoudtville (Figure 9.44). It occupies an open flat habitat, at an elevation of 800 m, in a community dominated by the asteraceous shrub *Elytropappus rhinocerotis* (L.f.) Less. The widely scattered bulbs grow in deep white sand, derived from sandstone at the northwestern-most extension of the Cape Supergroup.

Specimens examined

--3119 (Calvinia): Perdekraal, approximately 12 km NW of Grasberg, near Tweevlei (-AA), *Snijman 870* (NBG, PRE); *Snijman 1072* (NBG); fl 27 Apr 1988, *Snijman 1174* (K, NBG, PRE).

7. **Hessea undosa** Snijman in South African Journal of Botany 55(3): 351 (1989). Type: Cape, Gifberg, along the road from the summit of the Gifberg Pass towards the Matsikammaberg, 11 June 1988, *Snijman 1178* (NBG, holo.; K, MO, PRE).

Bulb solitary or rarely forming bulblets, depressed-globose, 10--20 mm diam., with light brown parchment-like outer tunics, extended into a slender neck up to 120 mm long. *Leaves* absent at anthesis, 2, suberect to spreading, narrowly lorate, 60--220 x 1--2 mm, shallowly canaliculate, glabrous, subtended by a subterranean amplexicaul cataphyll and a non-amplexicaul prophyll. *Inflorescence* spreading to somewhat less than a hemisphere, 40--80 mm across; scape flexuose, more or less deflexed laterally, 55--90 mm long, 1--2 mm diam., leaden-grey to reddish brown, habit during fruit dispersal unknown; spathe valves narrowly lanceolate, 20--25 x 2--5 mm; bracteoles up to 5 mm long. *Flowers* (7-) 12--20, spreading, stellate, glistening, ranging from pale to deep pink, with reddish centre and reverse, sometimes outlined with delicate pink, fading to magenta, scentless; pedicels straight to slightly upwardly curved, 25--37 mm long, green. *Tepals* free to the base or adnate proximally to the staminal tube for up to 1mm, outspread above, oblong-lanceolate, 6,5--8,0 x 2--3 mm, with crisped edges. *Stamens* equalling or at most 2 mm shorter than the tepals, filaments thickened and connate basally into a tube 0,5--1,0 mm long, becoming outspread and subulate above; anthers centrifixed, 2 mm long and dark wine-red before opening; pollen cream-coloured. *Ovary* with 3--7 ovules per locule. *Style* up to 5mm long, slender, with nectar collecting in a well around the base. *Seeds* ± 3 mm across. *Chromosome number* $2n = 22$. Figure 9.8.

Flowering time: During the latter half of June, probably extending into July.

Diagnostic features: Hessea undosa is one of just three species in the genus with markedly crisped tepals. Of these, it shows closest affinity with *H. monticola* which it resembles in the orientation and shape of the flowers (wide-open, stellate and equally spreading). *Hessea undosa* usually attains approximately half the size of *H. monticola* in most of its parts and although some overlap may occur, discontinuity in flower size is diagnostic. *Hessea undosa* has tepals 6--8 mm long with stamens two thirds as long or equalling the tepals, whereas the tepals in *H. monticola* are 10--25 mm long with the stamens less than two thirds the length of the tepals.

Distribution and habitat: Confined to the upper plateau of the Gifberg and Matsikammaberg near Vanrhynsdorp in the western Cape (Figure 9.44), where the species occupies seasonally waterlogged sand on exposed flat sandstone rocks, in relatively open mountain fynbos, at elevations of 600 m.

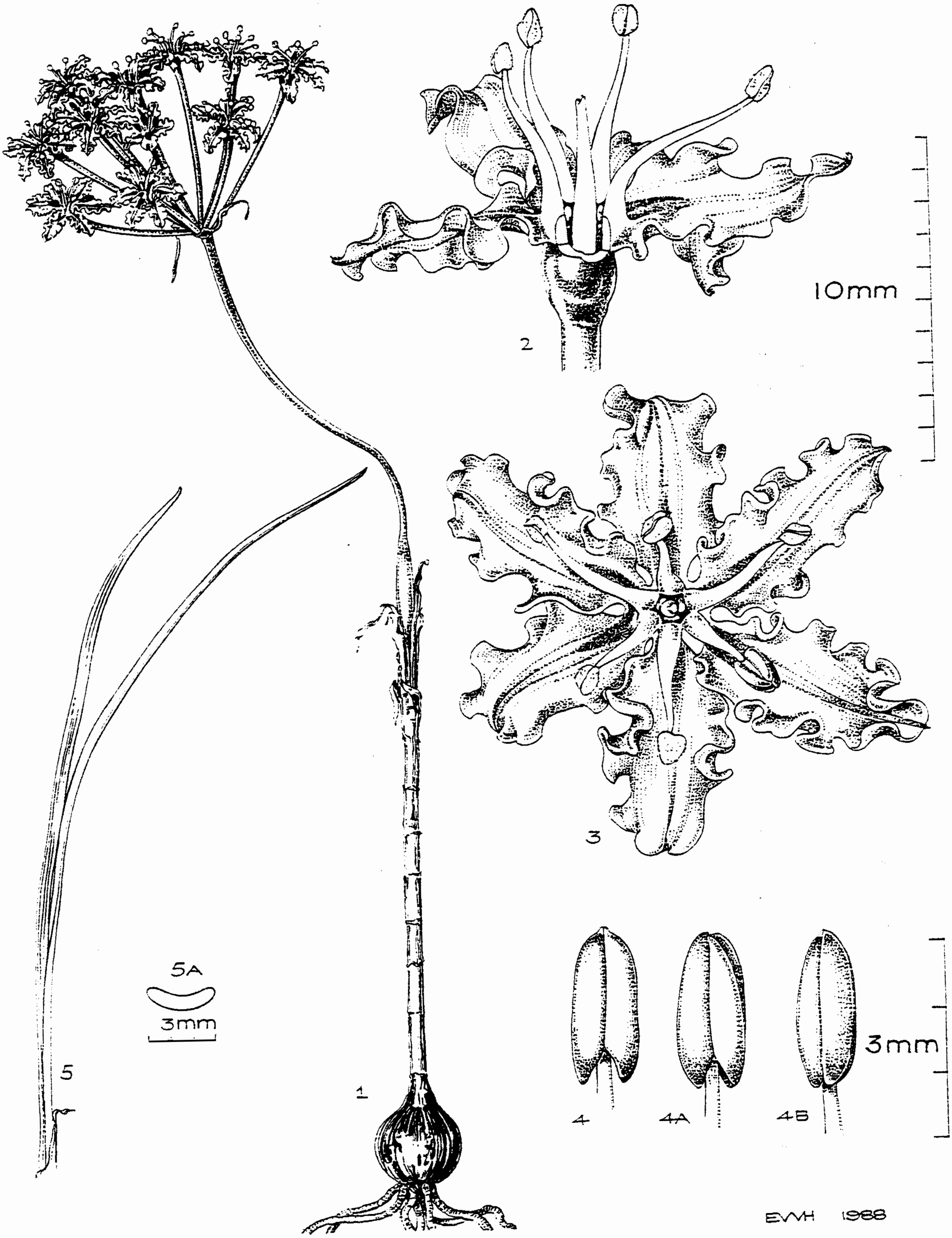


FIGURE 9.8-- *Hessea undosa*: 1, habit, life size; 2, section of flower; 3, whole flower; 4, anther attachment, ventral view, 4A, dorsal view, 4B, lateral view; 5, habit of leaves, life size, 5A, transverse section of leaf. Drawn from *Snijman 1178*.

Specimens examined

--3118 (Vanrhynsdorp): Matsikammaberg, W of Sewefontein (-DB), fl 12 Jul 1974, *E. Oliver 4904* (PRE); Gifberg plateau (-DC), fl 25 Jun 1985, *Kotze 721* (NBG); top of Gifberg Pass (-DD), fl 11 Jun 1965, *E. Oliver s.n.* (NBG 83650); along road from the summit of the Gifberg Pass towards the Matsikammaberg (-DD), fl 11 Jun 1988, *Snijman 1178* (K, MO, NBG, PRE).

8. Hessea monticola Snijman in South African Journal of Botany 55(3): 349 (1989). Type: Cape, Cedarberg, between the top of Uitkyk Pass and farm Dwarsrivier, 11 April 1986, *Perry 3435* (NBG, holo.; PRE).

Bulb solitary or occasionally producing bulblets, deep-seated, globose to depressed-globose, 20--40 mm diam., thinly covered with light brown parchment-like fibrous tunics, extended into a neck 60--120 mm long. *Leaves* absent at anthesis, (1-) 2 (-3), erect to spreading, narrowly lorate, 50--250 x 1,5--3,0 mm, hemiterete to somewhat canaliculate, glabrous, flushed with red basally, subtended by a subterranean amplexicaul cataphyll and non-amplexicaul prophyll. *Inflorescence* clustered to hemispherical, 80--220 mm across; scape somewhat flexuose, 50--150 (-220) mm long, 2--5 mm diam., green, breaking loose at ground level during fruiting; spathe valves linear-lanceolate, 25--40 x 4--7 mm; bracteoles up to 15 mm long. *Flowers* (7-) 10--30 (-40), spreading, stellate, white to pink with deeper pink to reddish pink stripes leading into the throat as well as towards the base of the undersurface, ageing to light brown, with a strong acrid scent; pedicels straight, 35--60 (-95) mm long, green. *Tepals* adnate proximally to the staminal tube for 0,5--1,5 (-3,0) mm, outspread above, oblong-lanceolate, 10--18 (-25) x 2,5--5,0 (-6,0) mm, with crisped edges. *Stamens* shorter than the tepals by 3,5--8,0 (-14,0) mm; filaments shortly connate basally into a tube extending to 1 mm above the perigone throat, becoming outspread and subulate above; anthers centrifixed, up to 3 mm long and wine-red before opening; pollen cream-coloured. *Ovary* with 2--6 ovules per locule. *Style* up to 7(-9) mm long, slender throughout, with nectar accumulating in a well around the base. *Seeds* 3--4 mm diam. *Chromosome number* $2n = 22$. Figure 9.9.

Flowering time: From the end of March until late May, usually after recent veld fires. Bulbs do not flower readily in cultivation.

Diagnostic features: In the past, herbarium collections of *H. monticola* were assigned most often to *H. cinnamomea*, since both species have flowers with crisped tepals and narrowly lorate leaves. However, living material clearly shows the discontinuities between the two species. *Hessea monticola* is distinguished by wide-open stellate flowers; the absence of a short mucro on the tip of each outer tepal; short filaments (8--14 mm shorter than the tepals); slender style; and straight pedicels.

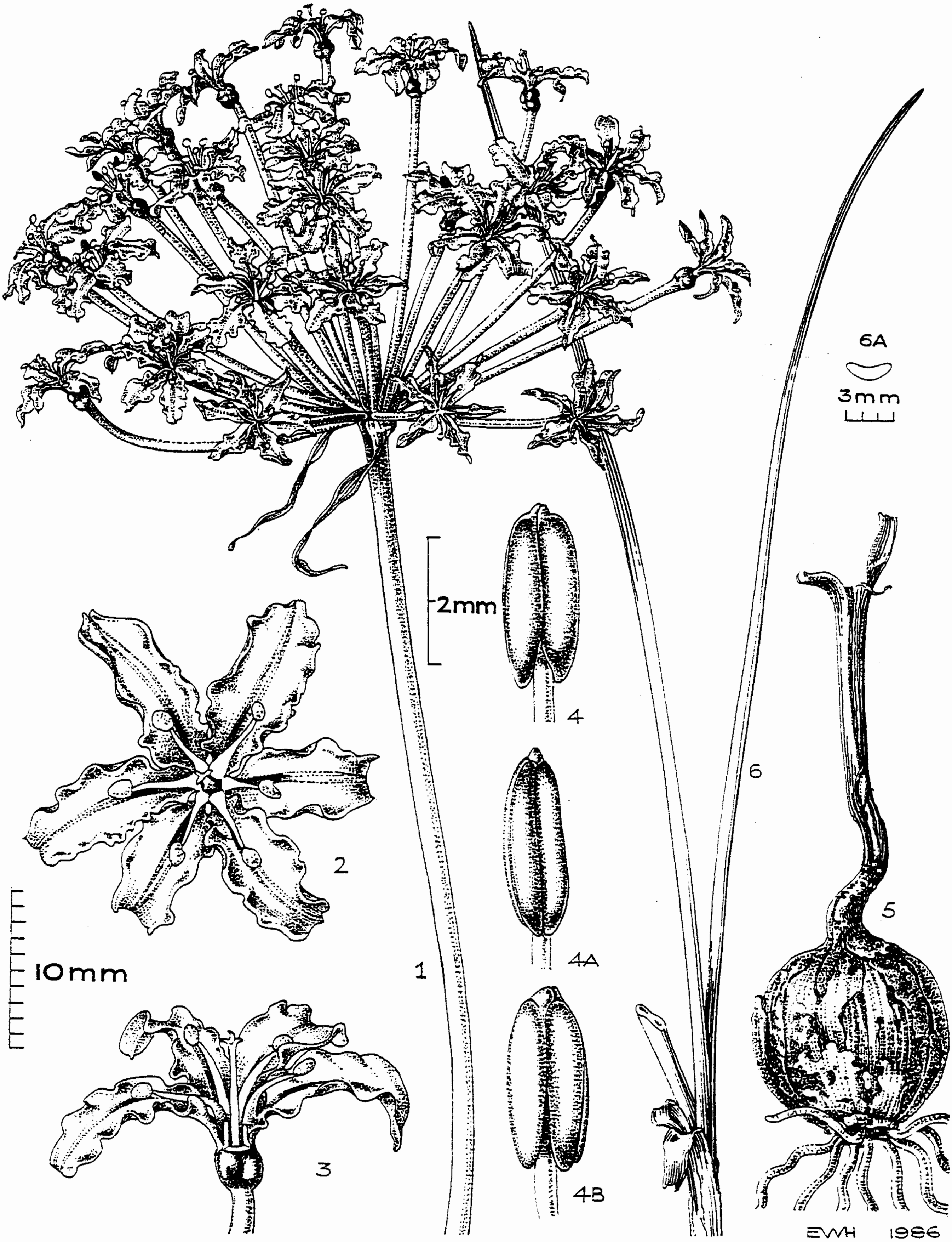


FIGURE 9.9-- *Hessea monticola*: 1, inflorescence, life size; 2, whole flower; 3, section of flower; 4, anther attachment, dorsal view, 4A, lateral view, 4B, ventral view; 5, bulb, life size; 6, habit of paired leaves with dry remains of scape, life size, 6A, transverse section of leaves. Drawn from *Perry 3435*.

Furthermore the flowers are not secund. In contrast *H. cinnamomea* has widely funnel-shaped, secund flowers with mucronulate tips in the outer tepals; filaments shorter than the tepals by 3--6 mm; and a proximally stout style.

Distribution and habitat: Hessea monticola occurs in the mountains of the south-western Cape (at elevations of 750--900 m), from the Piketberg and Cedarberg in the north, along the mountain chain east of the Olifants River to the Groot Winterhoekberge near Tulbagh in the south (Figure 9.44). Populations are localised in mountain fynbos, in sandy or peaty soil, either on rocky slopes or flat seasonally wet plains, where recurrent fires are a major disturbance.

Specimens examined

--3218 (Clanwilliam): Piketberg Mountain (-DC), fl 4 May 1948, *Brink s.n.* (NBG 65869); fl 25 May 1952, *Brink s.n.* (NBG 65871); fl 25 Apr 1948, *Esterhuysen 14472* (BOL, PRE); fl 26 Apr 1957, *Mackenzie* sub *NBG 184/57* (NBG).

--3219 (Wuppertal): Cedarberg, top of Uitkyk Pass (-AC), fl 22 Apr 1946, *Esterhuysen 12758* (BOL, PRE); Driehoek Valley, top of Uitkyk Pass (-AC), fl 11 Apr 1952, *Esterhuysen 20039* (BOL); between the top of Uitkyk Pass and farm Dwarsrivier (-AC), fl 11 Apr 1986, *Perry 3435* (NBG, PRE); fl 25 Mar 1989, *Snijman 1197* (NBG, PRE); 34 km towards Algeria from old road to Clanwilliam (-AC), fl 26 Apr 1978, *Perry 689* (NBG); Kleinjongenskraal, Citrusdal (-AC), fl 2 Apr 1989, *Abrahams 294* (NBG); Buffelspas, E of Citrusdal (-CA), fl 26 Apr 1984, *Viviers 1307* (NBG); Elandskloof, Cold Bokkeveld (-CA), fl 24 Mar 1951, *Barker 7275* (NBG); fl 22 May 1984, *Bayer 4045* (NBG); fl 25 Mar 1951, *Esterhuysen 18462* (BOL, PRE); fl 20 Apr 1935, *Levyns s.n.* (BOL 34354); top of Hexberg, Clanwilliam division (-CA), fl Mar 1951, *Stokoe s.n.* (SAM 63767); farm Grootfontein, Dasklip Pass (-CC), *L. Hugo s.n.* (NBG 132589); Olifants River Dome above Thee River Kloof (-CC), fl 12 May 1963, *Esterhuysen 30185* (BOL).

--3319 (Worcester): Groot Winterhoek farm (-AA), fl 15 Apr 1979, *Low 858* (NBG).

--Imprecise localities: Dwarsrivier between Disselfontein and Elandskloof, Clanwilliam division, fl Apr 1933, *Leipoldt s.n.* (BOL 34332); north of Olifants River, Clanwilliam Division, fl 30 Mar 1932, *Leipoldt s.n.* (BOL 34333); Porterville mountain, fl 17 Mar 1969, *Jackson s.n.* (NBG 88251); fl 16 May 1950, *Stanford s.n.* (BOL 34329); Cape, *sine legit.*, Herb. hort. Kew 108.85 (K).

--Doubtful locality: Swellendam race course, fl 20 May 1930, *N. J. S. van der Merwe s.n.* (BOL 34329).

9. Hessea cinnamomea (L'Hérit.) Durand & Schinz, Conspectus florae africae 5: 242 (1894). Type: figure in L'Hérit., Sertum anglicum: t. 17 (1792), lecto!, designated by Müller-Doblies (1985).

Amaryllis cinnamomea L'Hérit.: 16 (1789), t. 17 (1792). *Imhofia cinnamomea* (L'Hérit.) Roemer: 28 (1847). *Periphanes cinnamomea* (L'Hérit.) Leighton: 82 (1948).

Amaryllis crispa Jacq.: 37 t. 72 (1797); Willd.: 61 (1799); Aiton: 229 (1811). Type: figure in Jacq., Plantarum rariorum horti caesarei schoenbrunnensis 1: t. 72 (1797), lecto.!, designated by Müller-Doblies (1985). *Strumaria crispa* (Jacq.) Ker-Gawl.: t. 1363 (1811); Schultes & Schultes: 790 (1830). *Imhofia crispa* (Jacq.) Herbert: 290 (1837). *Hessea crispa* (Jacq.) Kunth: 632 (1850); Baker: 22 (1888), 190 (1896). *Periphanes crispa* (Jacq.) Salisb. ex Baker: 190 (1896).

Bulbs solitary or occasionally clumped, deep-seated, depressed-globose, 20--30 mm diam., with lightly fibrous and dark-brown to tan outer tunics; neck long and slender, extending up to 150 mm. *Leaves* absent or occasionally incipient at anthesis, 1--2, suberect to spreading, narrowly lorate, hemiterete, 100--200 x 1,0--2,5 mm, dark shiny green, reddened basally, glabrous, sheathed by a subterranean amplexicaul cataphyll. *Inflorescence* spreading, more or less secund, 30 --130 mm across; scape erecto-patent, 40--80 mm long, 2--3 mm diam., wine-red proximally otherwise dark green, breaking off at the base in fruit; spathe valves lanceolate, 15--35 x 3--4 mm; bracteoles up to 5 mm long. *Flowers* 5--27, somewhat secund, widely funnel-shaped, glistening white to pink with a deep pink to claret or brownish red centre, becoming light brown with age, heavily scented like spice; pedicels more or less unilaterally curved below the flowers, 20--65 mm long, green. *Tepals* adnate basally to the staminal tube for up to 1,0 (-2,5) mm, spreading above, oblong-lanceolate, 7,5--13,0 x 3--5 mm, with crisped edges; apices of the outer whorl conspicuously mucronulate. *Stamens* shorter than the tepals by 3--6 mm, spreading abruptly from the base; filaments shortly connate at the base forming a tube up to 0,5 mm above the perigone throat, stout proximally, otherwise subulate; anthers centrifixed, 2,5 mm long and dark wine-red before opening; pollen cream-coloured. *Ovary* with up to 2 (-4) ovules per locule. *Style* up to 9 mm long, stout proximally, triquetrous, with nectar collecting in a well around the base. *Seeds* 2,5--3,0 mm diam. *Chromosome number* $2n = 22$. Figure 9.10.

Flowering time: Occasionally commencing in April but mostly flowering in May and June. Characteristically, the species flowers profusely after veld fires but fails to flower in cultivation.

Diagnostic features: The characteristic crisped tepals place *H. cinnamomea* close to *H. monticola* and *H. undosa* but it is readily distinguished by its widely funnel-shaped, secund flowers with a claret centre; mucronulate outer tepals and stout style.

Distribution and habitat: Hessea cinnamomea favours seasonally waterlogged peaty lowlands at elevations of less than 60 m. Early records indicate that the species

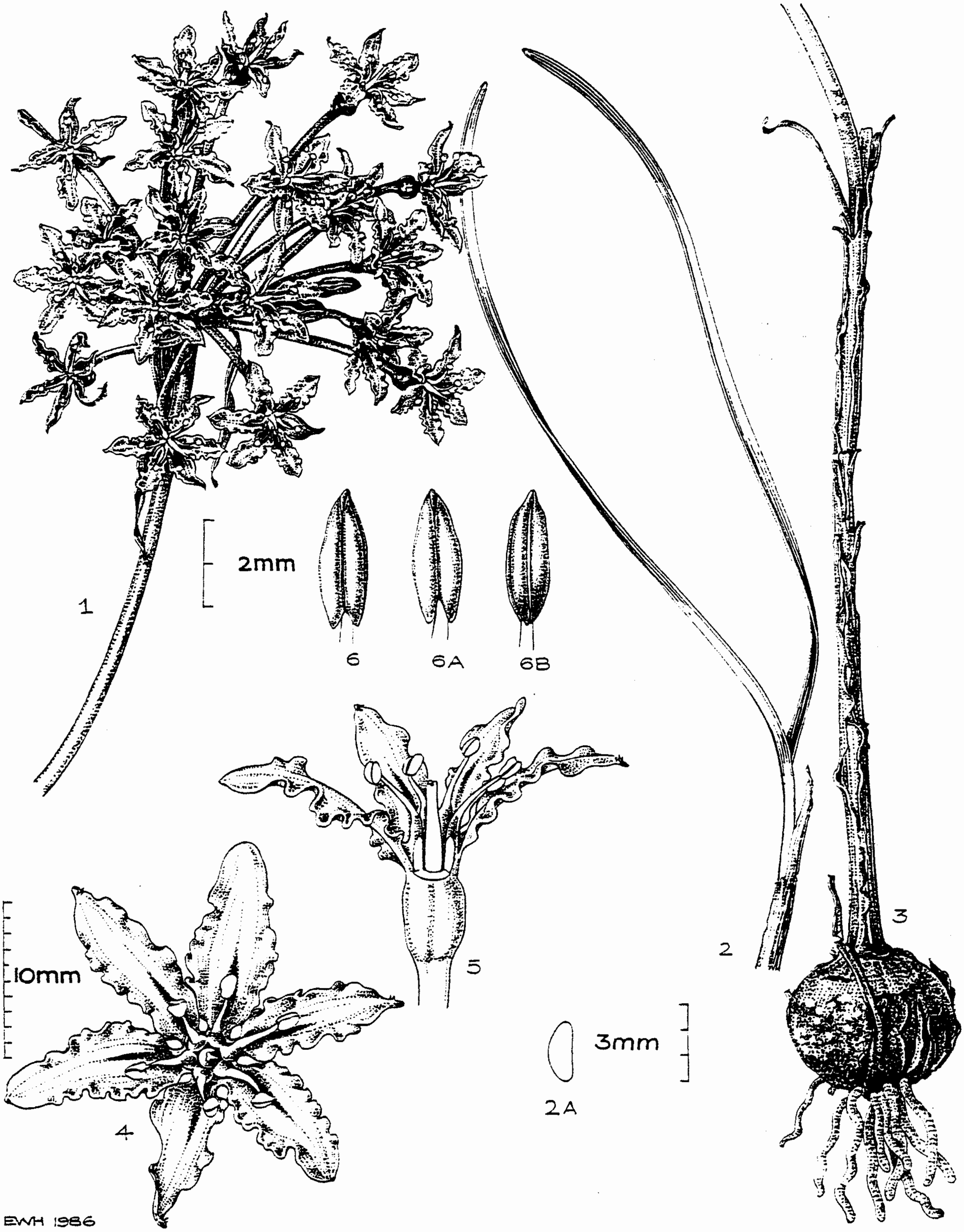


FIGURE 9.10-- *Hessea cinnamomea*: **1**, inflorescence, life size; **2**, leaf habit, life size; **2A**, transverse section of leaf; **3**, bulb, life size; **4**, whole flower; **5**, section of flower; **6**, anther attachment, ventral view, **6A**, dorsal view, **6B**, lateral view. Drawn from *Snijman 1029*.

was locally abundant in such habitats on the Cape Peninsula and around Stellenbosch (Figure 9.44), but current records indicate that the species is now restricted to the Cape of Good Hope Nature Reserve and its immediate environs. Flowering is stimulated by fire. Thousands of bulbs flowered in June 1986 after a wild fire cleared large areas of lowland fynbos within the Reserve the preceding summer, and several hundred bulbs flowered at Modderdam adjacent to the Reserve after a similar fire in 1989. Flowering in these populations declines rapidly for one to three years after each fire as the density of the shrubby fynbos increases (pers. obs). Ultimately only the vegetative phase is evident for the remaining interfire period.

Specimens examined

--3318 (Cape Town): Sandown Road, Rondebosch (-CD), fl Apr 1896, *Wolley Dod 1076* (BOL); fl 17 May 1897, *Wolley Dod 2481* (K); near Claremont (-CD), fl Jun 1884, *MacOwan 2567* (K); Campground (-CD), fl Jun, *Zeyher 416* (BOL, SAM); Kenilworth (-CD), fl May 1892, *Bolus s.n.* (BOL 34327); fl 28 May 1931, *Salter 771* (K); Kenilworth Race Course (-CD), fl 6 Jun 1941, *Isaac s.n.* (BOL 34295, PRE); fl 10 May 1936, *Salter s.n.* (BOL 34296); fl 14 May 1929, *Salter* sub *337/16* (K); Lions Rump, near Cape Town (-CD), fl 18 Jun 1815, *Burchell 8444* (K); Doornhoogde, Cape Flats (-DC), *Zeyher s.n.* (PRE 23157); near Mulders Vlei (-DD), fl 26 Jun 1934, *Acocks s.n.* (BOL 34294).

--3418 (Simonstown): between Modderdam and road junction to Red Hill (-AB), fl 24 Jun 1965, *Barker 10242* (NBG); *Barker 10362* (NBG, PRE); Bergvliet farm (-AB), fl Jun 1917, *Purcell 124--129* (SAM); fl 1 Jun 1918, *Purcell 234--238* (SAM); fl Jun 1918, *Purcell 241--248* (SAM); *Purcell 250* (SAM); near Wynberg (-AB), *MacOwan & Bolus* in *Herb. Norm 297* (BOL, K, SAM); Pollsmoor (-AB), fl 12 Jun 1947, *Barker 4582* (NBG); near Fish Hoek (-AB), fl 29 Jun 1924, *Andreae 576* (PRE); near Royal Cape Golf Club (-AB), fl 6 Jun 1942, *Eaton s.n.* (NBG); West Lake Mountain (-AB), fl 27 May 1964, *Thomas s.n.* (NBG); Cape of Good Hope Nature Reserve (-AD), fl 13 Jun 1986, *Snijman 1038* (K, MO, NBG, PRE); Wynberg flats (-BA), fl 14 Jun 1847, *Alexander s.n.* (PRE); ex legato *Alexander Prior s.n.* (K).

--Imprecise localities: Cape flats, fl May--Jun 1877, *Bolus 4012* (BOL; K); fl Jun 1907, *Logeman* sub *Marloth 12036* (PRE); fl Jun, *Zeyher 4112* (SAM); Cape Peninsula beyond Simon's Town, fl May 1914, *Duthie 630* (K).

3. Namaquanula

Namaquanula D. & U. Müller-Doblies in Botanische Jahrbucher für Systematik 107: 20 (1985) emend. Snijman. Type: *Namaquanula bruce-bayeri* D. & U. Müller-Doblies.

Perennial, deciduous, glabrous bulbous herbs, ranging from 50--200 mm high. *Bulb* usually solitary, occasionally forming bulblets, ovoidal to depressed globose, covered by soft, fibrous or brittle, cartilagenous outer tunics, ranging from tawny to tan-coloured, fleshy and whitish within. *Leaves* distichous, hysteranthous, lacking a bladeless non-amplexicaul prophyll, with or without a sheathing cataphyll; foliage leaves usually 2, rarely solitary or 3--4, sheathing at the base, with the innermost leaf non-sheathing; blades suberect to spreading, narrowly lorate, sometimes sticky. *Inflorescence* held erect with 2 membranous spathe valves each subtending a helicoid cyme; pedicels stiff or wiry, distinctly longer than the flowers; bracteoles subtending individual flowers filiform. *Flowers* actimorphic, widely spreading, funnel-shaped or stellate, pink or white, unmarked with contrasting central markings, remaining open and browning with age; tepals shortly connate into a tube or free to the base, oblanceolate to ovate-lanceolate, plane-edged. *Stamens* 6, free from the style; filaments connate proximally into a short tube, rarely separate, confluent with perigone tube when present, each bearing a short or prominent adaxial hook shortly above the base, ventral surface papillose proximally; anthers oblong, dorsifixed to subcentrifixed, latrorse, opening by longitudinal slits; pollen morphology unknown. *Ovary* irregularly sphaeroidal, with up to 4 ovules per locule; ovules subglobose, anatropous, with axile placentation; septal nectaries egressing on the ovary dome into a central pool around the style, or into 3 green, papillose pulvini. *Style* slender or rarely stout proximally; stigma papillose, trifid. *Infructescence* rapidly drying and detaching at ground level; fruit a papery, subglobose, trilocular capsule; seeds fleshy, ovoidal, reddish green when ripe, covered with stomata. *Basic chromosome number* $x = 11$; diploid number $2n = 22$.

Species 3; confined to the western region of southern Africa, ranging from southern Namibia through the north-western Cape to the south-western Cape.

Namaquanula is defined by the novel characteristics of the stamens: the adaxial filament hooks and the papillose ventral surface towards the base of the filaments.

Key to the species of Namaquanula

1a Bulb tunics brittle and cartilagenous; flowers funnel-shaped; perigone tube 0,5--1,8 mm long; stamens exserted beyond tepals by 4 mm or more .... 1. **N. bruce-bayeri**

1b Bulb tunics fibrous; flowers stellate; perigone tube absent; stamens equalling or shorter than tepals: 2

2a Bulb 20--25 mm diam.; pedicels 40--80 mm long, rigid; tepals 6--8 mm long; leaf blades 2--5 mm across, straight .... **2. N. mathewsii**

2b Bulb 10--20 mm diam.; pedicels 20--50 mm long, wiry; tepals 4--6 mm long; leaf blades 1--2 mm across, spirally twisted apically .... **3. N. pulcherrima**

3.1 Subgenus Namaquanula

Bulb covered with cartilagenous tunics; lacking a bladeless, adaxial prophyll and amplexicaul cataphyll. *Flowers* funnel-shaped, with suberect stamens; anthers dorsifixed.

Species 1.

1. **Namaquanula bruce-bayeri** D.& U. Müller-Doblies in Botanische Jahrbücher für Systematik 107: 20 (1985). Type: Cape, Richtersveld, Perdemonde, N of Kuboos/Oranjemund road on road to Koeskop, 10 March 1979, *Müller-Doblies 79112a* (PRE, holo.!; B, K!, M, MO, NBG).

Hessea zeyheri sensu Sölch & Roessler: 150: 11 (1970) pro parte, as to *Pearson 4170.*

Bulb solitary or occasionally forming bulblets, ovoidal, 15--40 mm diam., covered by several thick dry tan-coloured, cartilagenous tunics; neck up to 80 mm long. *Leaves* absent at anthesis, (1-) 2--3 (-4), suberect to spreading, lorate, up to 150 x 2,5--5,0 mm, firm, fleshy, compressed-terete in cross section, glabrous, occasionally somewhat sticky, shiny green, curved or twisted distally; subterranean cataphyll and prophyll lacking. *Inflorescence* laxly or densely hemisherical, 25--60 mm across; scape 25--70 mm long, 1,5--3,0 mm diam., more or less sticky, green to wine red, breaking off at the base in fruit; spathe valves lanceolate, 13--32 x 3--6 mm; bracteoles up to 3 mm long. *Flowers* 6--17, spreading, funnel-shaped, pale pink and somewhat hyaline, turning light brown with age, scentless; pedicels straight, 19--22 mm long, trigonous, green to pink, ultimately wine-red. *Tepals* adnate to the stamens and extended into a distinct tube 0,5--1,8 mm long, slightly spreading above, oblanceolate, 4,5--6,5 x 1--1,5 mm. *Stamens* well exserted, proximally adpressed to the style for up to 2 mm, otherwise slightly spreading; filaments 7--11 mm long, basally connate forming a tube up to 0,5 mm above the perigone throat, otherwise free, papillose adaxially for approximately 2 mm above the throat and raised to form a short inwardly-curved hook, smooth and subulate above; anthers dorsifixed, ± 1,5 mm long before opening, dark maroon; pollen cream-coloured. *Ovary* usually with 1 ovule per locule. *Style* up to 15 mm long, equalling the stamens, slender throughout, with nectar collecting in a pool around the base; stigma very shortly trifid. *Seeds* ± 2,5 mm diam. *Chromosome number* $2n = 22$. Figure 9.11.

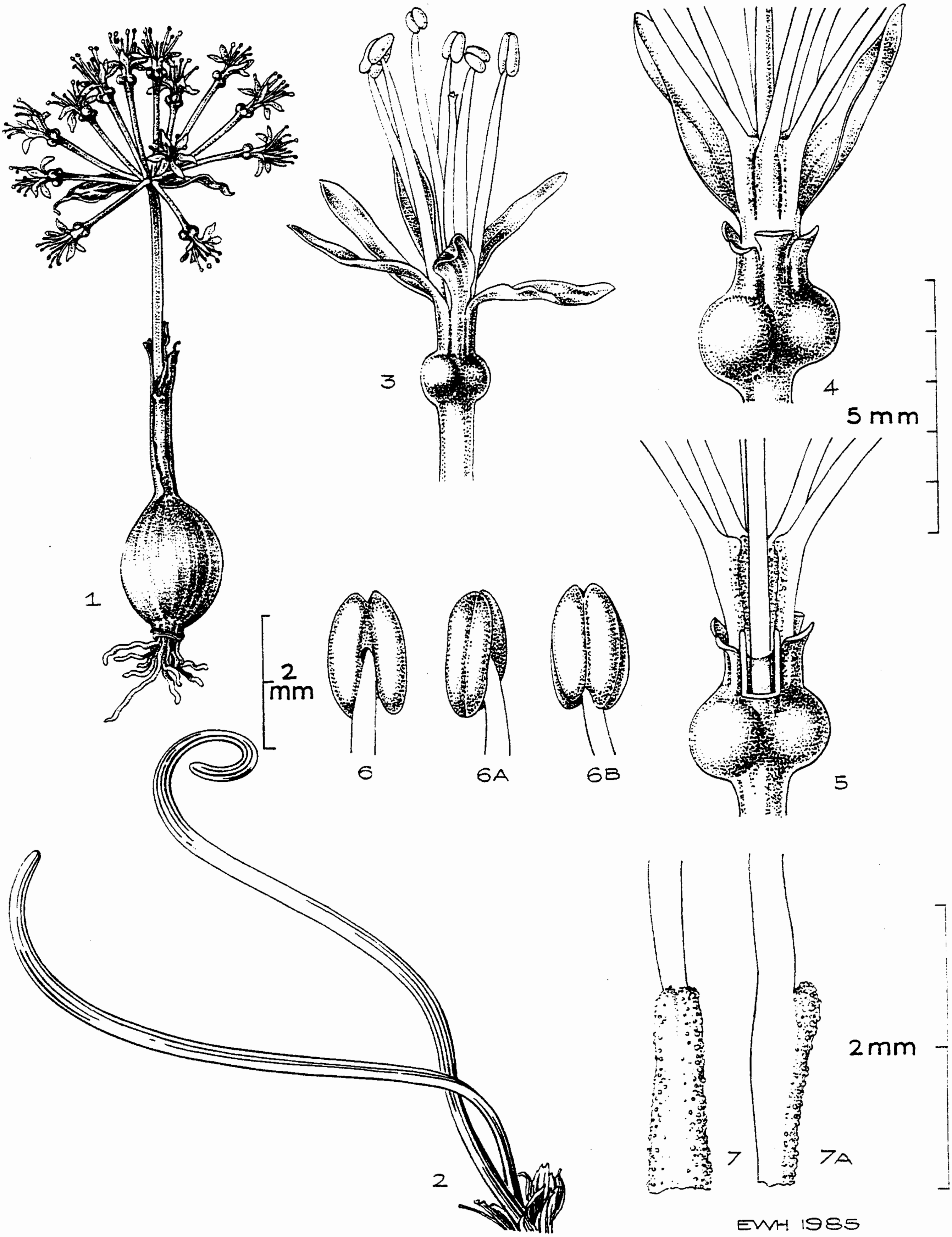


FIGURE 9.11-- *Namaquanula bruce-bayeri*: 1, bulb and inflorescence, life size; 2, leaves, life size; 3, whole flower; 4, portion of flower showing short perigone tube and filament tube; 5, portion of flower showing proximal portion of style; **6**, anther attachment, dorsal view, **6A**, lateral view, **6B**, ventral view; 7, filament base, ventral view, 7A, lateral view. Drawn from *Williamson 3405.*

Flowering time: Late February until the end of March.

Diagnostic features: Namaquanula bruce-bayeri is easily distinguished both vegetatively and florally. The bulb is coverd by brittle, tan-coloured tunics, and the cataphyll and non-amplexicaul prophyll are absent. The leaves are typically fleshy, somewhat sticky and spirally curved. The funnel-shaped flowers are thinly-textured and almost hyaline, with well-exserted stamens. These specialisations set *N. bruce-bayeri* somewhat apart from the remaining two species in the genus, with the exception of the spiralled leaves, which also characterise *N. pulcherrima.*

Distribution and habitat: This diminutive species is limited to the extreme southern region of Namibia and the northern Richtersveld (Figure 9.41). All records indicate a habitat preference for flats or low hills in alluvial gravel. The associated vegetation is low succulent shrubland, in which species of *Cheiridopsis* N.E.Br. and *Dracophilus dealbatus* (N.E. Br.) Walg. are locally dominant (G. Williamson, pers. comm.).

Specimens examined

--2716 (Witputz): Lat. 27°50' Long.16°36' (-DC), fl 30 Mar 1986, *Van Berkel 549* (NBG, PRE).

--2816 (Oranjemund): 1 mile N of Sendlings Drift (-BB), fl Mar 1960, *Hall 1901* (NBG); Perdemonde, E of Arrisdrif (-BC), fl 10 Mar 1977, *Bayer 350* (NBG); Perdemonde, N of Kuboos/Oranjemund road on road to Koeskop (-BC), fl 10 Mar 1979, *Müller-Doblies 79112a* (K, PRE); 4 km NE of Beesbank (-BC), fl 10 Mar 1985, *Williamson 3405* (K, NBG, PRE).

--Inexact locality: Great Namaqualand, between Gariep and Aus, fl 20 Feb 1909, *Pearson 4170* (BOL, K).

3.2 Subgenus Myophila

Myophila Snijman, subgen. nov., a subgenere Namaquanula bulbo vestimento brunneo byssaceo obtecto, floribus stellatis, antheris subcentrifixis, disco papilloso 3-gibboso differt. Type: *Namaquanula mathewsii* (W.F. Barker) Snijman.

Bulb with softly fibrous outer tunics. *Foliage leaves* sheathed by a cataphyll. *Flowers* stellate, with outspread stamens; anthers subcentrifixed. *Ovary* dome raised, with 3 green, trichome-covered pulvini between the style and inner filament whorl.

Species 2.

2. **Namaquanula mathewsii** (W.F. Barker) Snijman, comb. nov. Type: Cape, Malmesbury division, Vredenburg, 9 May 1930, *Mathews* sub *NBG 690/30* (BOL, holo.!; K!).

Hessea mathewsii W.F. Barker: t. 404 (1931). *Gemmaria mathewsii* (W.F. Barker) D.& U. Müller-Doblies: 35 (1985).

Bulb solitary or occasionally forming bulblets, depressed-globose, 20--25 mm diam., with lightly fibrous and rusty-brown outer tunics; neck slender, up to 55 mm long. *Leaves* absent or rarely incipient at anthesis, 2 (--3), suberect to recurved, narrowly lorate, up to 185 x 2--5 mm, adaxially shallowly canaliculate, glabrous, reddened abaxially towards the base, sheathed by a cataphyll; cataphyll initially shortly exserted above ground, green or red, soon withering back. *Inflorescence* widely spreading, 50--140 mm across; scape straight to somewhat flexuose, 45--120 mm long, 2--5 mm diam., wine-red proximally, otherwise light greyish brown, breaking off at the base in fruit; spathe valves narrowly lanceolate, 20--25 x 3--5 mm; bracteoles up to 2 mm long. *Flowers* 5--18, spreading, stellate, white to delicate pink, marked with rose-pink to crimson around the centre, on the median dorsal line as well as the tips of the outer tepals, turning light brown with age, strongly and unpleasantly scented; pedicels straight to somewhat upwardly curved, 40--80 mm long, green. *Tepals* free to the base, outspread and obliquely twisted at the base, ovate-lanceolate, 6,0--8,5 x 2--3 mm. *Stamens* shorter than the tepals, erect in the proximal third, otherwise outspread; filaments shortly connate at the base for 0,2 mm, otherwise free; the proximal third laterally broadened, with the adaxial surface densely covered with papillae and bearing a 1 mm long inwardly curved, rounded hook ± 1 mm from the base which overarches the disc, rose-pink to crimson; the distal two thirds subulate, smooth, white; anthers subcentrifixed, 2 mm long before opening, dark maroon; pollen cream-coloured. *Ovary* with up to 4 ovules per locule, with the dome elevated into 3 green trichome-covered pulvini between the style and the inner filament whorl. *Style* up to 5 mm long, distinctly triquetrous and deep pink proximally, tapering slightly and becoming paler distally, with nectar collecting in a pool around the style base as well as amongst the trichomes on the filaments. *Seeds* 3--5 mm diam. *Chromosome number* $2n = 22$. Figure 9.12.

Flowering time: May.

Diagnostic features: Namaquanula mathewsii is immediately distinguished by the conspicuous filament hooks which overarch the disc. This well-developed feature is most often shared with its close ally *N. pulcherrima* and contrasts with the smaller, less developed filament hooks present in the more distantly related *N. bruce-bayeri*. *Namaquanula mathewsii* and *N. pulcherrima* also share contrasting central floral markings and bulbs which possess an amplexicaul cataphyll but lack a subterranean prophyll.

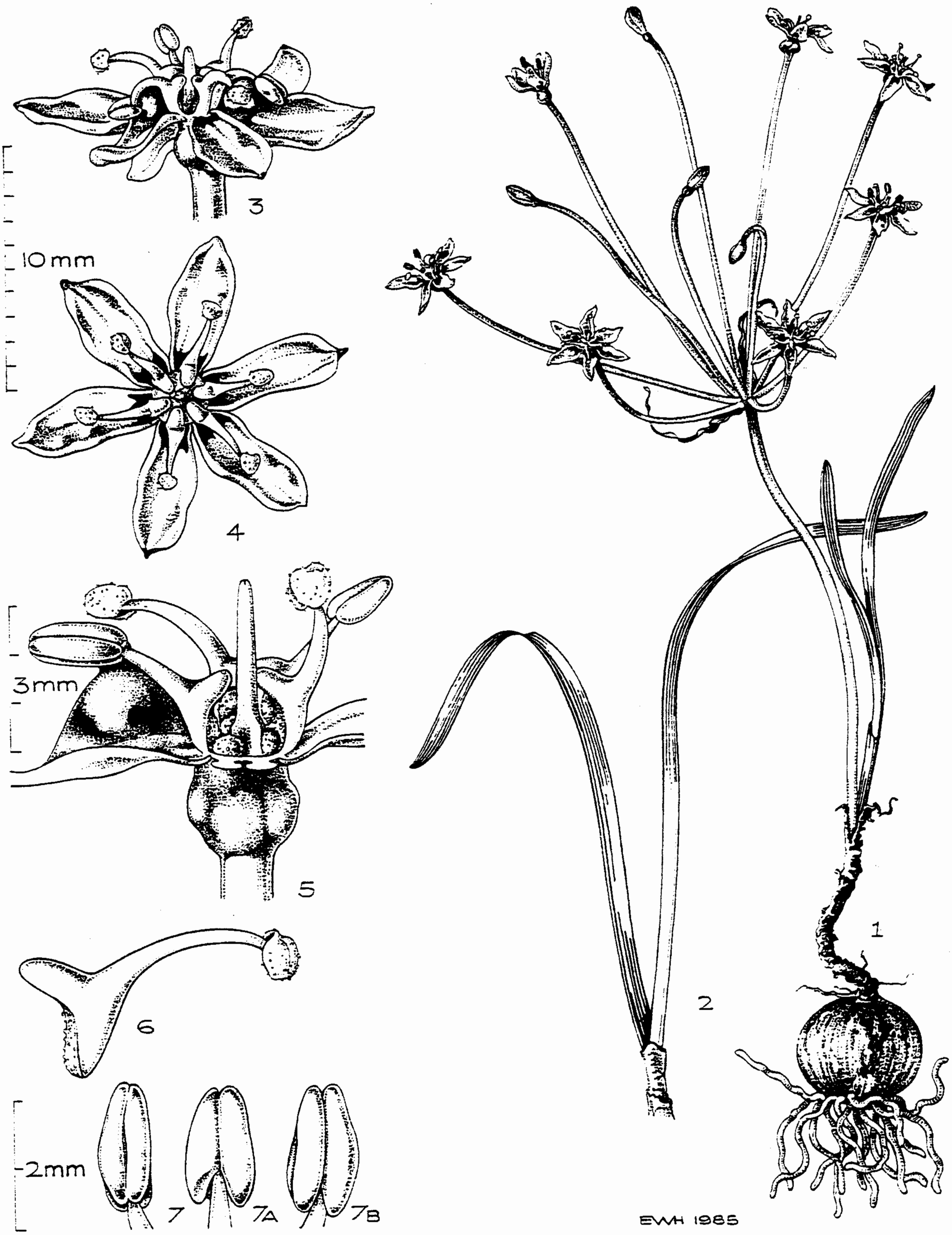


FIGURE 9.12-- *Namaquanula mathewsii*: 1, habit, life size; 2, leaf habit, life size; 3-4, whole flowers; 5, portion of flower; 6, stamen; 7, anther attachment, lateral view, 7A, dorsal view, 7B, ventral view. Drawn from *Snijman 847* 1-2, and *Snijman 840* 3-7.

Namaquanula mathewsii is separated from *N. pulcherrima* on overall size, namely larger bulbs (20--25 mm diam.), broader recurved leaves (2--5 mm wide) and a rigid, broader scape (2,0--2,5 mm diam.). Furthermore the central green floral disc is flat or sometimes sunken, in contrast to the slightly raised disc in *N. pulcherrima*.

Distribution and habitat: This species is narrowly confined to low-lying limestone flats in the vicinity of Vredenburg and Langebaanweg in the south-western Cape (Figure 9.41), where the only known populations are surrounded by cultivated lands. At present, the survival of *N. mathewsii* is dependent upon the stony nature of their habitat but the extension of cultivation into these marginal areas would render the species endangered. The flowers are notably attractive to flies.

Discussion: Originally placed in the genus *Hessea*, the species was subsequently transferred to *Gemmaria* (Müller-Doblies 1985) due to the apparent absence of a filament tube and the somewhat enlarged floral disc. In the present study these character states were re-evaluated and found to be lacking or non-homologous. Serial transverse sections through the flowers of *N.mathewsii (Snijman 840)* firstly confirmed the presence of an extremely short filament tube, reaching up to 0,2 mm and secondly indicated that the floral disc differs from those of other species previously placed by D. & U. Müller-Doblies (1985) in *Gemmaria*. Thus in both *N. mathewsii* and *N. pulcherrima* the disc is green and papillose, as opposed to those found in *Strumaria* subsection *Gemmaria* which are smooth or crystalline, white to pink and concolorous with the style.

Specimens examined

--3217 (Vredenburg): Malmesbury division, Vredenburg (-DD), fl 9 May 1930, *Mathews* sub *NBG 690/30* (BOL, K); *Mathews* sub *NBG 1272/30* (BOL); farm Witteklip, SW of Vredenburg (-DD), fl 2 May 1985, *Snijman 847* (B, K, MO, NBG, PRE, S).

--3318 (Cape Town); farm Soutkuil, approximately 5 km S of Langebaanweg (-AA), fl 2 May 1985, *Snijman 840* (K, MO, NBG, PRE); farm Skaapplaas, approximately 5 km S of Langebaanweg (-AA), fl 2 May 1985, *Snijman 842* (K, MO, NBG, PRE).

3. **Namaquanula pulcherrima** (D.& U. Müller-Doblies) Snijman, comb. nov. Type: Cape, Kareeboomfontein S of Calvinia, 13 October 1978, *Müller-Doblies 78042e* (PRE, holo.!; B, GRA, GZU, K! M, MO, NBG, S, STE, Z).

Gemmaria pulcherrima D.& U. Müller-Doblies: 35 (1985).

Bulb usually solitary, deep-seated, depressed-globose, 10--20 mm diam., with outer tunics lightly fibrous and tawny-brown; neck slender, up to 85 mm long. *Leaves* absent at anthesis, 2, suberect to spreading, narrowly lorate, up to 150 x 1--2 mm, more or less spirally twisted towards the apex, glabrous, with adaxial surface shallowly grooved, sheathed by a subterranean cataphyll. *Inflorescence* widely spreading, 30--90 mm across;.

scape stiff and wiry, 35--90 mm long, 0,5 mm diam., wine-red basally, light greyish brown above, breaking off at the base in fruit; spathe valves linear-lanceolate, 15--30 x 0,2--2,0 mm; bracteoles up to 3 mm long. *Flowers* 4--20, spreading, stellate, white, marked with crimson centrally as well as on the tips of the outer tepals, rarely unmarked, turning light brown with age, faintly scented; pedicels wiry, upwardly curved, 20--50 mm long, deep wine-red, occasionally green. *Tepals* free to the base, outspread or deflexed, sometimes slightly obliquely twisted, oblanceolate, 4,5--6,0 x 1,0--2,5 mm, the adaxial surface covered with minute papillae proximally. *Stamens* equalling the tepals or shorter than the tepals, suberect proximally and outspread distally; filaments varying from shortly connate to free at the base, dark crimson or white; the proximal half broadened laterally, with the ventral surface densely covered with papillae and bearing a 1 mm long inwardly-curved blunt or irregalarly raised hook 1,0--1,5 mm from the base which overarches the disc; the distal half subulate; anthers subcentrifixed, 1--2 mm long before opening, red to dark crimson; pollen pale yellow to cream-coloured. *Ovary* with up to 3 ovules per locule, with the dome elevated into 3 green trichome-covered pulvini between the style and inner filament whorl. *Style* up to 6 mm long, somewhat trigonous proximally but slender throughout, dark crimson or white, with nectar collecting in a pool around the base and spreading up the filament bases where it is held by the trichomes on the ventral surface. *Seeds* 2--4 mm diam. *Chromosome number* 2*n* = 22. Figure 9.13.

Flowering time: May. Cultivated bulbs flower in April.

Diagnostic features: This delicate species has a wiry scape and pedicels, which give it a somewhat quivering habit in flower. Together with its close ally *N. mathewsii,* it is characterised by slightly rotate tepals and a central disc which bears three raised green pulvini between the style and inner filaments. *Namaquanula pulcherrima* is the more diminutive of the two species, with a typically small bulb (10--20 mm diam.), slender scape (0,5 mm diam.) and narrowly lorate leaves, which are spirally twisted distally.

Distribution and habitat: Namaquanula pulcherrima inhabits the foothills of the Bokkeveld escarpment and the high-lying plateau between Nieuwoudtville and Calvinia in the north-western Cape (Figure 9.41). Small populations are found on flat or gently sloping terrain, amongst low succulent of small-leaved shrubs, in heavy loamy soils.

Variation: The most westerly known populations from below the Bokkeveld escarpment differ slightly from the more elevated easterly populations in flower colour and stamen morphology. Collections from below the Vanrhyns Pass (*Salter 2146* and *Snijman 1022*) have white or delicate pink flowers, which lack the central red markings characteristic of the other known populations. Eastern populations (*Bayer 2746* and *Snijman 855*) have large, irregularly-shaped hooks, whereas elsewhere the hooks are smaller and smooth. In the western-most collection (*Snijman 1022*) the hooks are comparable in shape and size to those of *N. bruce-bayeri.* Also variable is the extent to

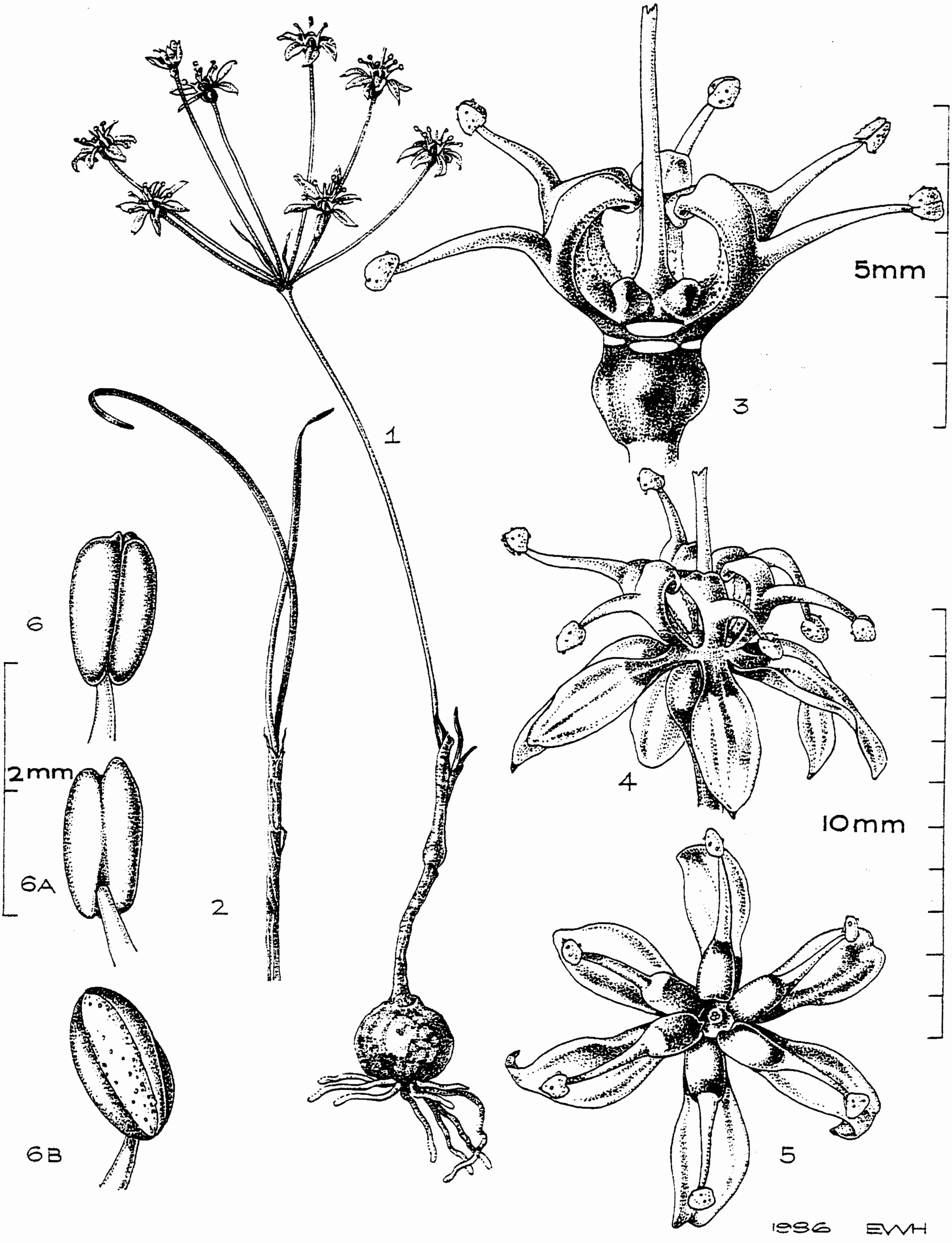


FIGURE 9.13-- *Namaquanula pulcherrima*: 1, bulb and inflorescence, life size; 2, leaf habit, leaf size; 3, flower with tepals and one stamen removed; 4-5, whole flowers; 6, anther attachment, ventral view, **6A**, dorsal view, **6B**, lateral view. Drawn from *Snijman 871*.

which the filaments are basally connate into a tube, which either reaches up to 0,25 mm (*Snijman 1022*) or is absent (*Bayer 2746* and *Snijman 855*). Thus since the original description, new material has provided confirmation of the presence of a filament tube and the possession of filament hooks which are considered to be homologous with those of *N. bruce-bayeri.*

Specimens examined

--3118 (Vanrhynsdorp): SW of Grootdrif between Vanrhyns Pass and Vanrhynsdorp (-BD), fl 6 May 1986, *Snijman 1022* (NBG, PRE).

--3119 (Calvinia): 4 miles E of Nieuwoudtville (-AC), fl 13 May 1934, *Salter 4484* (BOL); Glen Lyon, E of Nieuwoudtville (-AC), fl 8 May 1985, *Snijman 865* (K, NBG, PRE); Buffelsvley 628, approximately 11,5 km E of Nieuwoudtville (-AC), fl 9 May 1985, *Snijman 871* (K, NBG, PRE); 5 km SW of Oorlogskloof River bridge towards Botterkloof (-CB), fl 6 May 1982, *Bayer 2746* (MO, NBG, PRE); farm Soetwater, between Nieuwoudtville and Calvinia (-CB), fl 6 May 1985, *Snijman 855* (K, NBG, PRE); Kareeboomfontein, S of Calvinia (-DA), *Müller-Doblies 78042e* (K, PRE).

--Inexact localities: between Vanrhynsdorp and Vanrhyns Pass, fl 5 May 1932, *Salter 2146* (BOL); 15 miles NE of Calvinia, *Lewis 5026* (SAM).

4. Carpolyza

Carpolyza Salisb., The paradisus londinensis 1: t. 63 (1807). Type: *Carpolyza spiralis* (L'Hérit.) Salisb.

Hessea Bergius ex Schlechtend.: 252 (1826) nom. rej.

A monotypic genus, restricted to the south-western Cape and southern Cape.

Defined by the autapomorphy of the inner filament whorl proximally adnate to the style. Shared with *Strumaria* is the derived character state of $x = 10$.

1. **Carpolyza spiralis** (L'Hérit.) Salisb., The paradisus londinensis 1: t. 63 (1807); Kunth: 629 (1850); Baker: 23 (1888), 192 (1896). Type: figure in L'Hérit., Sertum anglicum t. 13 (1792), lecto!, designated by Müller-Doblies (1985). *Amaryllis spiralis* L'Hérit.: 10 ('1788' Jan. 1789) t. 13 (1792). *Crinum spirale* (L'Hérit.) Andr.: t. 92 (1800). *Strumaria spiralis* (L'Hérit.) Aiton: 213 (1811); D. Dietr.,: 1188 (1840). *Hessea spiralis* (L'Hérit.) Bergius ex Schlechtend.: 252 (1826), non Baker (1888).

Haemanthus spiralis Aiton, Hortus Kewensis 1: 405 (Aug. 1789); Willd: 28 (1799), non Thunb. (1794). Type: Cape of Good Hope, *Masson* (K, holo.!).

Crinum tenellum Jacq.: 14 t. 363 (1795); Jacq.: 43 ('1796' 1797) nom. illeg., non L.f. (1781).

Bulb solitary, subglobose, 5--14 mm diam., with thinly fibrous greyish-brown outer tunics, whitish and fleshy within; neck slender, up to 75 mm long. *Leaves* well developed or rarely absent at anthesis, 4--6, with only 1--4 exserted at a time, spreading, straight or curled, filiform, hemiterete, 30--150 x 1 mm, glabrous, shiny green, subtended by a non-amplexicaul prophyll; cataphyll lacking; seedling glabrous. *Inflorescence* sparse, up to 65 mm across; scape slender, 25--210 mm long, 0,5--1,0 mm diam., spirally twisted and reddish brown basally, otherwise suberect stiff and green; persisting and remaining green for several months after seed-release; spathe valves linear-lanceolate, 5--20 x 1--2 mm; bracteoles not visible. *Flowers* 1--5, slightly spreading, funnel-shaped, pure white or flushed with pink abaxially, occasionally greenish yellow in the throat, buff-coloured when withered, sometimes scented; with the innermost flowers of the cymes often aborting; pedicels ascending, filiform, 5--50 mm long, green. *Tepals* connate basally into a tube 3--4 mm long, expanding gradually upwards to 2,5--3,0 mm across at the throat, spreading, oblong-lanceolate, 7--14 x 2,0--3,5 mm. *Stamens* 6, suberect, only shortly exserted from the perigone tube; filaments separate, 3--5 mm long, adnate to the perigone tube for ± 2--3 mm, with the inner whorl basally adnate to the style for up to 1 mm, subulate; anthers subcentrifixed, 2 mm long and pale yellow before opening; pollen cream-coloured. *Ovary* 1,5--2,0 mm diam., green, with 1--6 ovules per locule. *Style* up to 5 mm long, only shortly exserted beyond the perigone tube, triquetrous, stout, with nectar collecting in the sinuses between the style and inner filaments; stigma trifid. *Seeds* 3--4 mm diam., more or less ovoidal, obtusely hooked. *Chromosome number* $2n = 20$ (Goldblatt 1976) Figure 9.14.

Flowering time: Usually June to July but occasionally commencing in May and extending to August.

Diagnostic features: Carpolyza spiralis is distinguished by the funnel-shaped flowers, with well-developed perigone tube and inner stamens which are adnate to the somewhat stout style for approximately 1 mm. The seeds are comma-shaped in outline due to the presence of a short curved hook. Species of *Strumaria* also have stamens which are adnate to the style, but never only the inner whorl. Thus as first proposed by Müller-Doblies (1985), the characteristics of the filaments and the style in *Carpolyza* and *Strumaria* are regarded as non-homologous.

Distribution and habitat: This slender species is limited to the south-western Cape, southern Cape and margins of the Little Karoo (Figure 9.45), where it occupies a range of habitats: flats, slopes or rock crevices; either in loam, sand or limestone; but always in areas which remain seasonally moist in winter. The associated vegetation varies from fynbos, renosterbos to marginal succulent veld of the Little Karoo. The populations are localised, either small when confined to rocky sites or forming large patches on open flats.

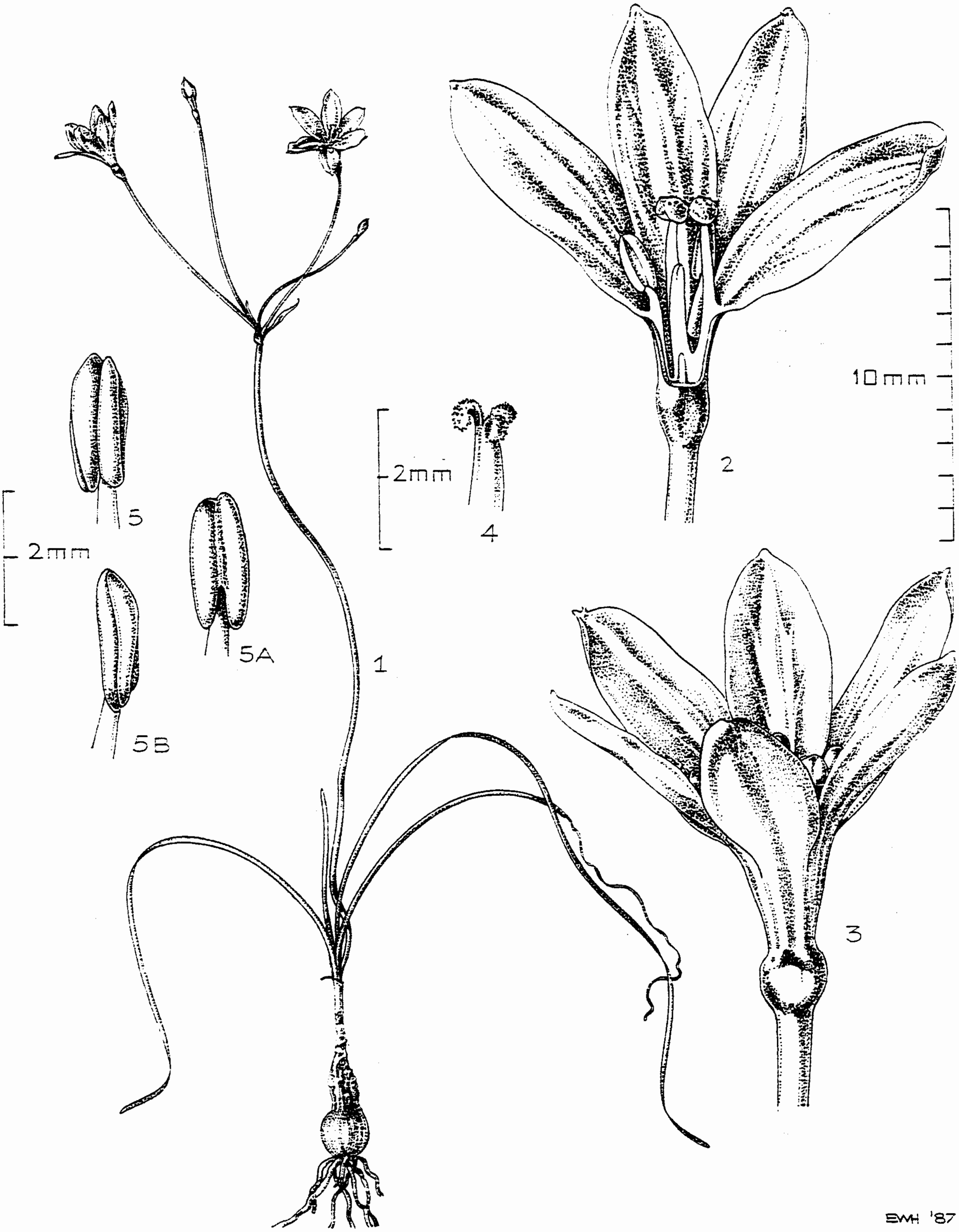


FIGURE 9.14-- *Carpolyza spiralis*: 1, habit, life size; 2, section of flower; 3, whole flower; 4, stigma; 5, anther attachment, ventral view, 5A, dorsal view, 5B, lateral view. Drawn from *Van Zijl s.n. ex hort.*

Specimens examined

--3318 (Cape Town): Lion Mountain (-CD), *Burchell 837-2* (K); *Drége 1840* (K); Jun 1883 *MacOwan* in *Herb. Norm. Austr. Afr. 295* (K, SAM); Jun 1892, *Schlechter* in *Herb. Norm. Austr. Afr. 1385* (BOL, K, SAM); 11 Jun 1892, *Schlechter 812* (BOL, GRA); Table Mountain (-CD), Jun 1884, *MacOwan 2572* (SAM); 1 Jul 1917, *Moss s.n.* (K); Green Point (-CD), 6 Jul 1846, *Alexander s.n.* (K, PRE); May 1918, *Marloth 8096* (PRE); Camps Bay (-CD), Jun 1847, *Alexander s.n.* (K); Sea Point (-CD), Jun 1877, *H. Bolus 3730* (BOL, K, PRE); Clifton (-CD), 9 Jul 1942, *Barker 1798* (NBG); Cape flats near Doornhoogte (-DC), *Ecklon & Zeyher 12* (K); Stellenbosch (-DD), Jul 1912, *Worsdell s.n.* (K); 20 Jun 1913, *Garside 456* (K); 11 Jul 1918, *Garside 1070* (K).

--3319 (Worcester): Lemoenpoort (-CD), *Snijman 1051* (NBG).

--3320 (Montagu): Keur Kloof, Montagu (-BC), 11 Jul 1954, *Barker 8267* (NBG); Cogmanskloof (-CC), 10 Jul 1931, *Salter 1093* (K); 24 May 1941, *Barker 1451* (NBG); 19 Jun 1974, *Goldblatt 2102* (K, NBG, PRE); 9 Jul 1956, *Van Niekerk 752* (BOL).

--3321 (Ladismith): Ladismith on lower slopes of Rooiberg near entrance to farm Opsoek (-CB), 21 May 1988, *Vlok 1938* (NBG, PRE); foot of Sandberg near Calitzdorp (-DA), 3 Jun 1959, *Wurts 1668* (NBG).

--3322 (Oudtshoorn): Rosselerf, S foothills of Swartberg (-AD), 13 May 1985, *Vlok 1010* (NBG).

--3418 (Simonstown): Brakkloof near Kommetjie (-AB), 8 Jun 1945, *Compton 18027* (NBG); 8 Jun 1942, *Leighton s.n.* (NBG); Llandudno (-AB), 10 Jul 1938, *Barker 463* (NBG); Fish Hoek flats (-AB), 18 Jun 1940, *Isaac s.n.* (NBG); west of Fish Hoek (-AB), 25 May 1896, *Wolley Dod 1129* (K); Sir Lowrys Pass (-BB), Jul 1942, *Solly s.n.*(SAM); Aug 1946, *Stokoe s.n.* (SAM); 27 Jul 1955, *Van Niekerk 392* (BOL); 4 Aug 1951, *Martin 1018* (NBG).

--3419 (Caledon): W of Caledon Baths (-AB), 3 Jul 1918, *Purcell 229* (SAM); Caledon (-AB), 24 Jun 1963, *Taylor 4892* (K, NBG, PRE); Jul 1936, *Levyns 3057* (BOL); 7 Jul 1930, *Marloth 14125* (PRE) Paardeberg Mountains, Kleinmond (-AC), Jun 1950, *Stokoe s.n.* (SAM); Havengas farm near Strandkloof (-CB), 12 Jun 1950, *Martin 351* (NBG); Viljoenshof, Bredasdorp (-DA), 7 Jul 1970, *Barker 10692* (K, NBG); Hagelkraal (-DA), Jun 1950, *Lewis s.n.* (SAM); farm Mierkraal, Bredasdorp district (-DB), 30 Jul 1981, *Goldblatt 6112* (NBG); farm Hangnes, Soetanysberg (-DD), 1 Aug 1985, *Rourke 1831* (NBG); Brandfontein, 9 Aug 1983, *Esterhuysen 35967* (BOL).

--3420 (Bredasdorp); Swellendam, between aerodrome and Bandietskop (-AB), 21 Jul 1963, *E. Oliver 4301* (K); De Hoop Nature Reserve (-AD), 28 Jul 1970, *Van der*

Merwe 126 (PRE); 15 Jun 1979, *Burgers 1882* (PRE); Bredasdorp, National Bontebok Park (-CA); 25 Jun 1953, *Brynard 224* (PRE).

--3421 (Riversdale): Riversdale (-AB), Jul 1927, *E. Ferguson s.n.* (BOL).

--Imprecise localities: Highlands estate, Elgin, *Lewis s.n.* (SAM); Riviersonderend Mountains, Jun 1949, *Stokoe s.n.* (SAM); near Elim, Bredasdorp, 10 Aug 1949, *Barker 5580* (NBG); Wittkamp, 26 Jun 1849, *Zeyher s.n.* (GRA); Cap.bon Spei, *Villette s.n.* (K); bonae Spei, *Masson s.n.* (K).

5. Strumaria

Strumaria Jacq., Collectanea 5: 49 ('1796' 1797); Willd.: 31 (1799); Aiton: 212 (1811); Herbert: 287 (1837); Kunth: 622 (1850); Bentham & Hooker: 728 (1883); Baker: 103 (1888), 215 (1896); Müller-Doblies: 22 (1985). Type: *Strumaria truncata* Jacq., designated by Phillips: 201 (1951).

Imhofia sensu Herbert: 290 (1837) pro parte, excluding *I. crispa* (Jacq.) Herbert, non Heist.: 29 (1755), non Herbert: 18 (1821).

Nesynstylis Raf.: 123 ('1836' 1838) pro parte, as to *N. filifolia* (Jacq. ex Willd.) Baker (= *Strumaria tenella* (L.f.) Snijman).

Pugionella Salisb.: 128 (1866). Type: *Pugionella angustifolia* (Jacq.) Salisb. ex Baker (= *Strumaria truncata* Jacq.).

Hymenetron Salisb.: 128 (1866). Type: *Hymenetron truncata* (Jacq.) Salisb. ex Baker (= *Strumaria truncata* Jacq.), designated by Müller-Doblies (1985).

Stylago Salisb.: 127 (1866). Type: *Stylago rubella* (Jacq.) Salisb. ex Baker (= *Strumaria truncata* Jacq.).

Gemmaria Salisb.: 127 (1866); Müller-Doblies: 29 (1985). Type: *G. gemmata* (Ker-Gawl.) Salisb. ex D. & U. Müller-Doblies (= *Strumaria gemmata* Ker-Gawl.).

Hessea sensu Bentham & Hooker: 720 (1883) pro parte; sensu Baker: 21 (188) pro parte, as to subgenus Imhofia; sensu Baker: 189 (1896) pro parte, as to subgenus Imhofia; non Herbert: 289 (1837).

Periphanes sensu Leighton (1948) pro parte, non Salisb.: 118 (1866).

Bokkeveldia D. & U. Müller-Doblies: 27 (1985). Type: *B. watermeyeri* (L. Bolus) D. & U. Müller-Doblies (= *Strumaria watermeyeri* L. Bolus).

Tedingea D. & U. Müller-Doblies: 45 (1985). Type: *T. tenella* (L.f.) D. & U. Müller-Doblies (= *Strumaria tenella* (L.f.) Snijman).

Perennial deciduous bulbous herbs, ranging from 50--450 mm high. *Bulbs* solitary or rarely clumped, globose to subglobose with parchment to felt-like outer fibrous tunics and fleshy whitish to yellowish or rarely mauve inner tunics, usually extended into a slender or stout neck. *Leaves* distichous, sometimes arranged as in a fan, with the lowermost prophyll and cataphyll remaining hidden within the bulb; prophyll adaxial and non-amplexicaul; cataphyll when present amplexicaul, sometimes exserted; foliage leaves 2--6, with only the uppermost leaf not sheathing at the base, ranging from filiform to lorate or elliptical, absent or incipient and only rarely fully developed at anthesis, erect or appressed to the ground, glabrous or pubescent, sometimes sticky. *Inflorescence* held erect by a somewhat flexuose, glabrous or sometimes shortly pubescent scape, with 2 membranous spathe valves each subtending a helicoid cyme; pedicels as long as or distinctly longer than the flowers, lax or stiff; bracteoles subtending individual flowers filiform, often inconspicuous. *Flowers* actinomorphic, clustered and pendulous or widely spreading, varying from funnel-shaped to stellate, white to pink, rarely lemon-yellow, often marked with a constrasting darker pink or green median band on the abaxial surface, closing and usually turning deeper pink with age; tepals free to the base, oblanceolate to elliptical, plane or channelled, rarely crisped, sometimes adnate to the filaments proximally. *Stamens* 6, variously adnate to the style, at the base only, or reaching up to the proximal third; filaments separate from each other or fused into a tube reaching up to half their length, sometimes variously thickened and toothed; anthers oblong, dorsifixed to subcentrifixed, latrorse, dehiscing by longitudinal slits; pollen bisulculate, covered with scattered large spinulae. *Ovary* somewhat sphaeroidal, glabrous or rarely minutely pubescent, with up to 9 ovules per locule, usually less; ovules subglobose, anatropous with axile placentation, septal nectaries egress by short or long efferent canals into shallow sinuses or deep wells formed between the inner filaments and style. *Style* variously thickened proximally, ranging from three-winged to ovoidal or discoid and depressed conoidal, slender distally; stigma papillose, trifid. *Infructescence* either persisting and remaining flexuose or rapidly drying and detaching at ground level; fruit a papery, subglobose, trilocular capsule; seeds fleshy, ovoidal, reddish green when ripe, covered with stomata. *Basic chromosome number* $x = 10$ except for *S. pygmaea:* $x = 11$; diploid number $2n = 20 + 1$--3B.

Species 23; restricted to southern Africa, extending from the mountains of southern Namibia through the winter-rainfall region of the Cape Province through the Great Karoo to the eastern Orange Free State and Lesotho.

Synapomorphies for the genus are the choritepalous flowers; both filament whorls or at least the outer filament whorl adnate to the style. The conspicuously thickened, inflated or three-winged style is autapomorphic. With the exception of *S. pygmaea* ($x = 11$), the basic chromosome number: $x = 10$, is a derived condition shared with *Carpolyza.*

Key to the subgenera and sections of Strumaria

1a Leaf blades filiform, at most 1,5 mm across, glabrous; anthers dorsifixed .... **1. subgen. Tedingea**

1b Leaf blades lorate to ovate, plane, at least 2,5 mm across; anthers dorsifixed or subcentrifixed: 2

2a Foliage leaves arranged in a fan, usually more than 3, occasionally only 2, glabrous; juveniles glabrous; anthers dorsifixed .... **2. subgen. Strumaria**

2b Foliage leaves spreading to prostrate, more or less pubescent or pustulate, sometimes only microscopically so and sometimes only in the juveniles; anthers subcentrifixed ..... **3. subgen. Gemmaria**

3a Foliage leaves usually more than 3; with only 2 exserted above ground; cataphyll absent .... **3.1 sect. Cryptomeria**

3b Foliage leaves 2 or rarely 3; cataphyll present: 4

4a Flowers stellate .... **3.2 sect. Gemmaria**

4b Flowers funnel-shaped .... **3.3 sect. Bokkeveldia**

Key to the species of Strumaria

1a Leaf blades filiform or hemiterete, at most 1,5 mm across: 2

2a Foliage leaves 3-6, developing sequentially, with only 1-4 exserted at a time; scape straight or flexuose proximally; pedicels slender in comparison to the scape .... **1. S. tenella**

2b Foliage leaves 2, rarely 3, present simultaneously; scape spirally twisted; pedicels fleshy in comparison to the scape .... **2. S. pygmaea**

1b Leaf blades lorate to ovate, plane, at least 2,5 mm across: 3

3a Foliage leaves arranged in a flat fan, glabrous, usually more than 3, occasionally only 2: 4

4a Flowers ascending; tepals less than 8 mm long; filaments free from each other .... **3. S. bidentata**

4b Flowers spreading to pendulous, rarely ascending; tepals longer than 8 mm; filaments fused to each other to form a tube: 5

5a Tepals 25 mm or more long: 6

6a Flowers spreading, narrowly funnelform; tepals less than 4 mm across .... **4. S. phonolithica**

6b Flowers pendulous, trumpet-shaped; tepals more than 4 mm across .... **5. S. barbarae**

5b Tepals 20 mm or less long: 7

7a Leaves plane or slightly undulate, without an exserted cataphyll; margins hyaline; apex emarginate .... **6. S. hardyana**

7b Leaves twisted or rarely plane; with an exserted reddened cataphyll; apex entire .... **7. S. truncata**

3b Foliage leaves spreading to prostrate, more or less pubescent or pustulate although sometimes only microscopically so and sometimes only in juveniles, apparently 2, occasionally 3: 8

8a Foliage leaves not sheathed by a cataphyll; flowers campanulate, white marked with broad contrasting reddish-brown dorsal bands .... **8. S. picta**

8b Foliage leaves sheathed by a cataphyll which remains hidden in the bulb; flowers stellate to funnelform, white or pink marked with narrow greenish, reddish or deeper pink dorsal stripes. 9

9a Flowers stellate; pedicels at least twice as long as the perigone at anthesis; style distinctly broadest at the base (except in *S. discifera*): 10

10a Flowers large with tepals longer than 10 mm, if 10 mm then tepals distinctly clawed: 11

11a Inner bulb tunics white; tepals clawed, with conspicuous windows between adjacent claws; flowers becoming translucent with age .... **10. S. unguiculata**

11b Inner bulb tunics yellow; tepals with small windows between adjacent tepal bases; flowers darkening with age .... **11. S. karoopoortensis**

10b Flowers small, with tepals less than 10 mm long, if 10 mm then tepals not clawed: 12

12a Flowers lemon-yellow; tepals crisped .... **16. S. gemmata**

12b Flowers white or pink; tepals ± undulate but not crisped: 13

13a Foliage leaves minutely pubescent: 14

14a Leaves "hump-backed" .... **14. S. massoniella**

14b Leaves with plane surfaces: 15

15a Tepals plane and outspread; flowers appearing flat and wide-open; leaf margin minutely ciliate .... **15. S. karooica**

15b Tepals slightly spreading; flowers appearing somewhat closed; leaf edges scabrid adaxially .... **13. S. merxmuelleriana**

13b Foliage leaves with long soft hairs (2 mm or more) on the adaxial surface or margins: 16

16a Inner bulb tunics white (or rarely mauve in *S. discifera*): 17

17a Foliage leaves densely fringed with long soft hairs, both surfaces glabrous .... **17. S. leipoldtii**

17b Foliage leaves with adaxial and occasionally abaxial surface hairy: 18

18a Tepals flat; style broadest at base .... **18. S. chaplinii**

18b Tepals channelled; style distinctly swollen proximally for at least a third of its length .... **9. S. discifera**

16b Inner bulb tunics yellow: 19

19a Foliage leaves with adaxial surface densely covered with long soft patent hairs, glaucous; tepals distinctly channelled .... **12. S. villosa**

19b Foliage leaves sparsely covered with long soft hairs, green; tepals plane-surfaced .... **15. S. karooica**

9b Flowers distinctly funnel-shaped; pedicels slightly longer or shorter than the perigone at anthesis; style more or less equally thickened in the lower half: 20

20a Foliage leaves appressed to the ground, with pustulate or minutely ciliate edges: 21

21a Leaf blades with pustulate edges; tepals less than 3,5 mm across .... **22. S. watermeyeri**

21b Leaf blades with minutely ciliate margins; tepals more than 4 mm across .... **23. S. salteri**

20b Foliage leaves spreading, densely covered with long soft hairs: 22

22a Leaf blades at most 5 mm across; inner bulb tunics white .... **19. S. perryae**

22b Leaf blades at least 10 mm across; inner bulb tunics yellow: 23

23a Stamens much shorter than the tepals, at least half as long; style not conspicuously winged .... **20. pubescens**

23b Stamens equalling the tepals; style conspicuously winged .... **21. S. aestivalis**

5.1 Subgenus Tedingea

Subgenus **Tedingea** (D. & U. Müller-Doblies) Snijman, stat. nov. Type: *Tedingea tenella* (L.f.) D. & U. Müller-Doblies (= *Strumaria tenella* (L.f.) Snijman).

Tedingea D. & U. Müller-Doblies: 45 (1985).

Bulb with whitish inner tunics. *Foliage leaves* spreading, filiform, varying from 2 to 6, when several then only 1--4 exserted at a time. *Scape* often flexed proximally or spirally twisted, usually persisting during seed release or sometimes breaking loose. *Flowers* stellate, rarely somewhat campanulate, borne on pedicels much exceeding the length of the perigone; anthers dorsifixed.

Species 2.

1. **Strumaria tenella** (L. f.) Snijman, comb nov. Type: Cape, Simonstown, June or July 1772, *Sparrman 77* in Herb. Linn. 416.9; 416.10 (LINN, photo.!), syntypes.

Basionym: *Crinum tenellum* L.f.: 194 (1781); non Jacq. : 14 t. 363 (1795); non Jacq.: 43 ('1796' 1797) (= *Carpolyza spiralis* (L'Herit.) Salisb.). *Hessea tenella* (L.f.) Oberm.: t. 1413 (1964). *Tedingea tenella* (L. f.) D. & U. Müller-Doblies: 45 (1985).

Leucojum strumosum Sol. ex Aiton: 407 t. 5 (1789); Jacq.: 222 ('1789' 1790) nom. superfl. Type: as for *Crinum tenellum* L.f. *Periphanes strumosa* (Sol. ex Aiton) Leighton: 83 (1948). *Strumaria strumosa* (Sol. ex Aiton) Salisb. ex Oberm.: t. 1413 (1964).

Haemanthus spiralis Thunb.: 58 (1794); Willd.: 28 (1799), nom. illeg., non Aiton (1789). Type: as for *Crinum tenellum* L.f.

Strumaria filifolia Jacq. ex Willd.: 32 (1799); Ker-Gawl.: t. 440 (1820); Schultes & Schultes: 788 (1830). Type: figure in Jacq., Icones plantarum rariorum 2: t. 361 (1790). *Nesynstylis filifolia* (Jacq. ex Willd.) Raf.: 123 ('1836' 1838). *Imhofia filifolia* (Jacq. ex Willd.) Herbert: 290 (1837); Kunth: 626 (1850). *Hessea filifolia* (Jacq. ex Willd.) Benth. & Hook.: 721 (1883); Baker: 22 (1888), 191 (1896).

Strumaria liliifolia D. Dietr.: 1187 (1840) nom. superfl. Type: as for *S. filifolia* Jacq. ex Willd.

Bulb solitary, globose, 7--20 mm diam., thinly covered with light greyish brown to cream-coloured fibrous outer tunics, whitish within; neck slender, up to 30 (-80) mm long. *Leaves* usually well developed at anthesis, 3--6, but with only 1--4 exserted at a time, erect to recurved, linear, up to 200--380 x 0,75--1,5 mm, hemiterete, with the adaxial surface shallowly channelled, glabrous, shiny green, flushed with reddish brown at the base, subtended by a non-amplexicaul prophyll; cataphyll absent; seedling glabrous.

Inflorescence widely to somewhat spreading, 10--50 (-180) mm across; scape slender, somewhat flexuose, 15--150 (-250) mm long, 0,5--2,0 mm diam., reddish brown proximally, otherwise green, persisting or sometimes breaking loose in fruit; spathe valves linear-lanceolate, 7--30 x 0,25--3,0 mm; bracteoles up to 10 mm long, often not visible. *Flowers* 2--21, spreading, stellate, rarely somewhat campanulate, white to delicate pink, occasionally marked with several deep pink median dorsal lines, turning deep pink with age, scented; the innermost of the cymes often aborting; pedicels straight to upwardly curved, ultimately 10--35 (-95) mm long, green. *Tepals* free to the base, outspread, oblanceolate, (3,0-) 3,5--6,0 x 1,5--3,0 mm. *Stamens* equalling the tepals, spreading, obliquely twisted before the anthers dehisce; filaments separate, up to 4 mm long, adnate to the base of the swollen style, laterally broadened and slightly raised ventrally forming a longitudinal ridge in the proximal third, tapering evenly upwards; anthers dorsifixed, 2 mm long before opening, dark wine-red or green; pollen cream-coloured. *Ovary* with 1--4 ovules per locule. *Style* up to 5 mm long, dilated from the base into an irregular hexahedron, slender in the distal half, with 3 droplets of nectar held between the inner filaments and stylar swelling. *Seeds* 2--3 mm diam. *Chromosome number* $2n = 20$.

Diagnostic features: Strumaria tenella is easily distinguished by its slender habit. The leaves are filiform and develop sequentially, so that the bulbs appear to have only one to four leaves at any particular time during the growth period, but usually up to six leaves will emerge during the year. The flowers are characteristically small (tepals 4,5--7,0 mm long) and the style is conspicuously swollen in the proximal half. The most closely related species is *S. pygmaea*, which is even more diminutive than *S. tenella* and shows characteristic specialisation of the leaves, scape and pedicels.

Distribution and habitat: This species has a disjunct distribution in the winter and summer rainfall areas of southern Africa. It has been widely recorded in the south-western Cape, with recent collections extending its range along the Roggeveld escarpment to near Nieuwoudtville in the north western Cape. Populations from the summer rainfall region in the south-eastern Orange Free State and Lesotho have been recorded since 1917, however no intermediates in the Great Karoo are known (Figure 9.46).

Discussion: The populations in the different rainfall regimes exhibit small morphological differences which led Obermeyer (1964) to suggest that the eastern populations from the Orange Free State may constitute a new species, closely allied to *S. tenella sensu stricto* from the winter rainfall region of the Cape. Unlike all other species of *Strumaria*, the flowering of *S. tenella* is usually synchronous with the leaves, which develop sequentially over several months. Thus the growth cycle is sufficiently extended to adapt to either summer or winter rainfall conditions. My preference is to attribute these populations to the rank of subspecies. *Strumaria tenella* subsp. *tenella* is usually smaller

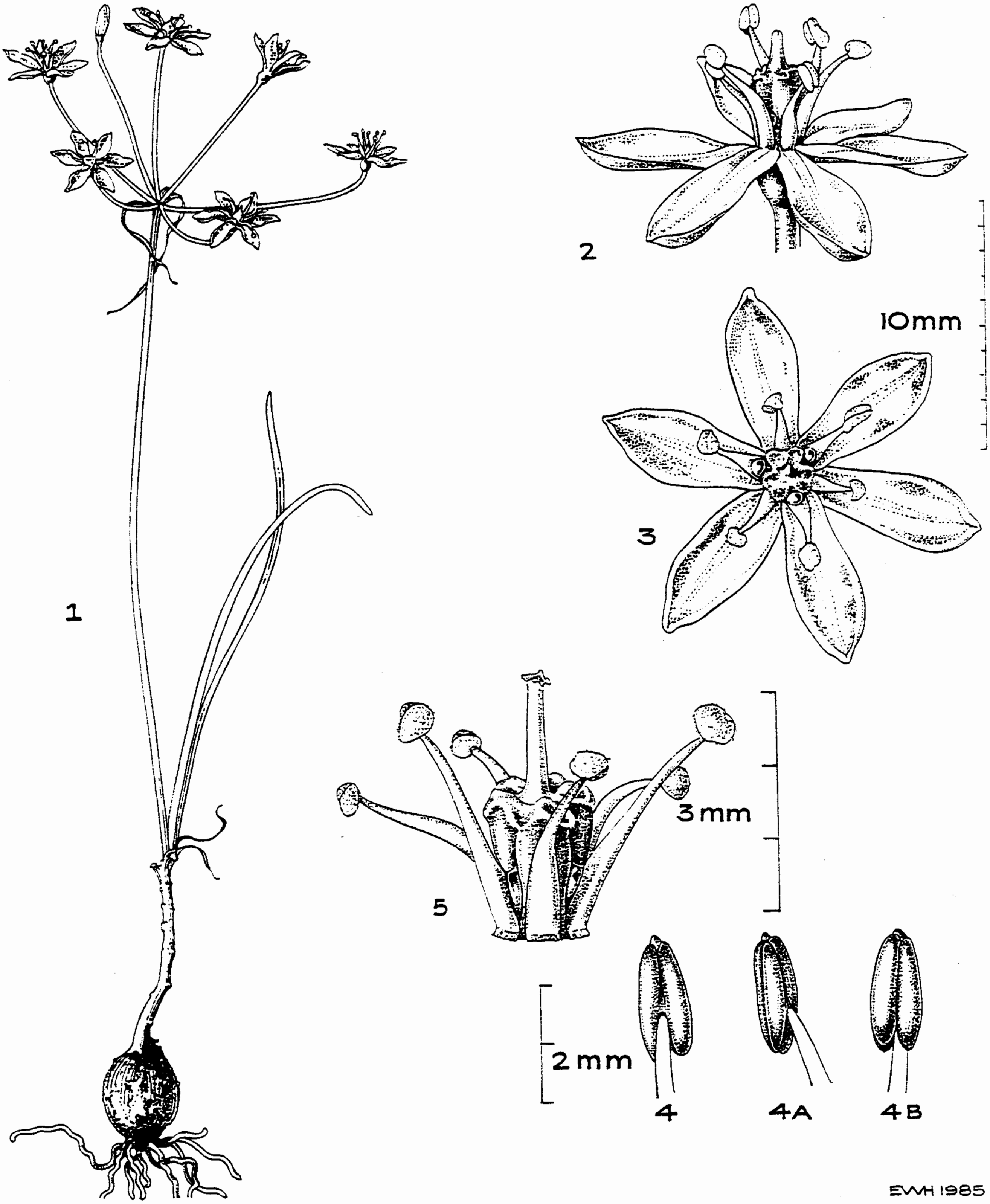


FIGURE 9.15-- *Strumaria tenella* subsp. *tenella*: 1, habit, life size; 2-3, whole flowers; 4, anther attachment, dorsal view, 4A, lateral view, 4B, ventral view; 5, detail of androecium and style. Drawn from *Perry & Snijman 2065*.

than *S. tenella* subsp. *orientalis*, particularly in the diameter of the stylar swelling. Furthermore the stylar swelling is typically indented above, whereas in *S. tenella* subsp. *orientalis* it is consistently dome-shaped.

1a. S. tenella (L.f.) Snijman subsp. **tenella**

Bulb 7--18 mm diam., extended into a neck up to 30-(-60) mm long. *Leaves* usually well developed at anthesis, with 1--3 exserted at a time, filiform, 200--300 x 0,75 mm. *Inflorescence* somewhat spreading, 10--50 mm across; scape flexuose, 15--150 mm long, 0,5--1,0 mm diam.; spathe valves 7--20 x 0,25--2,0 mm, pink before turning brown; bracteoles not visible. *Flowers* 2--14, white to delicate pink, occasionally marked with several pink median dorsal lines; pedicels 10--35 mm long. *Tepals* 1,5--2,0 mm wide. *Anthers* dark wine-red. *Style* up to 5 mm long, dilated above the filaments into an irregular hexahedron with rounded corners (1--2 mm diam.) and an irregularly indented apical surface, slender in the distal half. Figure 9.15.

Flowering time: From the end of April until the end of July and rarely as late as August.

Distribution and habitat: Strumaria tenella subsp. *tenella* is widespread in the south-western Cape and extends through the Worcester Karoo to the Roggeveld escarpment, north to Calvinia and Nieuwoudtville. The populations are often dense and encompass large numbers of individuals, which favour seasonally moist habitats, mostly in loamy soils or rarely sand.

Specimens examined

--3119 (Calvinia): Glen Lyon, E of Nieuwoudtville (-AC), fl 7 May 1985, *Snijman 856* (K, MO, NBG, PRE); Nieuwoudtville Wildflower Reserve (-AC), fl 20 Apr 1983, *Perry & Snijman 2065* (NBG); Holdrif, between Nieuwoudtville and Grasburg (-AC), fl 8 May 1985, *Snijman 866* (NBG, PRE); summit of Hantamsberg, Calvinia (-BD), fl 27 Apr 1986, *Viviers s.n.*(NBG 133798); farm Botterkloof, between Clanwilliam and Calvinia (-CD), fl 15 May 1989, *Snijman 1207* (K, NBG, PRE).

--3217 (Vredenburg): near farm Noodhulp, between Vredenburg and Paternoster (-DD), fl 2 May 1985, *Snijman 846* (K, MO, NBG, PRE).

--3220 (Sutherland): Voëlfontein farm, N of Sutherland (-AD), fl 10 May 1969, *Hall 229* (NBG, PRE); *Rourke 1741* (NBG); *Snijman 517* (K, NBG).

--3318 (Cape Town): Langebaan (-AA), fl 29 May 1944, *Chaplin s.n.* (NBG); Darling (-AD), fl 14 May 1945, *Middelmost* sub *NBG 295a/44* (NBG); fl 20 May 1934, *Adamson 485* (BOL); Darling Flora Reserve (-AD), fl 8 Jun, 1956, *Winkler 89* (NBG); fl 4 Jun 1971, *Axelson s.n.* (NBG); between Mamre and Darling (-AD), fl 22 Apr 1940, *Bolus s.n.* (BOL, PRE); 2 km E of Mamre Road station (-BC), *Goldblatt 3567* (K, PRE); banks of Berg River, near Hermon (-BD), fl 29 May 1952, *Esterhuysen 20163* (BOL, K, NBG, PRE); Mamre (-CB), *Middelmost* sub *NBG 333/46* (NBG); rocks near Mamre (-CB), fl 26 May 1934, *Adamson 485A* (BOL); Campground (-CD), fl 21 Jun 1896, *Wolley-Dod 1186* (K); fl 28 May 1897, *Wolley-Dod 2559* (BOL); fl Jun *Zeyher s.n.* (SAM); Rondebosch Common (-CD), fl 18 Jun 1949, *Steyn 192* (NBG); Rosebank (-CD), fl May 1899, *Bolus 4013* (BOL, K, SAM); Table Mountain (-CD), *Schlechter 84* (BOL); Green Point (-CD), fl May 1847, *Alexander s.n.* (K, PRE); Green Point Common (-CD), fl May 1944, *Stokoe s.n.* (BOL, SAM); farm Groenrivier, between Dassenberg and Kalabaskraal (-DA), fl 20 Jun 1983, *Rourke 1805* (NBG); Kersefontein, on banks of Berg River (-DB), fl 28 May 1952, *Esterhuysen 20121* (BOL); Paardeberg (-DB), fl 15 Jun 1866, *Pamphlett 37* (NBG); *Salter 1038* (K); Tigerberg and Greenpoint (-DC/-CD), fl Jun, *Zeyher 4108* (SAM); Langverwacht above Kuils River (-DC), fl 20 Jun 1974, *E. Oliver 4882* (PRE); Stellenbosch flats (-DD), *Garside 460* (K); Stellenbosch (-DD), fl Jun 1920, *Garside 1499* (K); fl Jun 1917, *Duthie 504* (BOL).

--3319 (Worcester): between Tulbagh and the Drostdy (-AC), fl 1 Jul 1811, *Burchell 1030* (K); above Tulbagh Waterfall (-AC), fl 25 May 1966, *Rycroft 2961* (NBG); Gouda (-AC), fl 15 May 1939, *Leipoldt s.n.* (BOL); Therons Pass (-BC), *Esterhuysen 3502* (BOL); Theronsberg (-BC), fl 2 May 1940, *Compton 8778* (NBG); Hex River Kloof (-BD), *Drege s.n.* (K); beside the Breede River, near Goudini (-CB), fl 3 May 1980, *Perry 1294* (NBG, PRE); near Worcester (-CB), fl 4 Aug 1949, *Steyn 225* (NBG); Keerom, NE base of Keeromsberg (-DA), fl 30 May 1976, *Esterhuysen 34309* (BOL, K).

--3320 (Montagu): Pienaars Kloof, near Touws River (-AA), fl Jun 1940, *Esterhuysen 3867* (BOL); Tweedside (-AB), fl Jun 1925, *Marloth 12074* (PRE).

--3418 (Simonstown): near Wynberg (-AB),fl May 1884, *Macowan & Bolus* in *Herb. Norm. 294* (BOL, K, SAM); Strand to Gordons Bay (-BB), fl 24 Jul 1942, *Parker 3689* (BOL, K, NBG); Sir Lowrys Pass (-BB), fl 5 Jul 1894, *Schlechter 4815* (BOL).

--3419 (Caledon): 2 miles S of Villiersdorp (-AB), fl Jun 1939, *Leipoldt s.n.* (BOL); 5 miles NW of Riviersonderend (-BB), fl 26 May 1949, *Heginbotham 15* (NBG).

--Imprecise localities: Ceres division, fl 1 Jun 1931, *Leipoldt* in Herb. Bol. *19848* (BOL); South Western Region, fl 22 May 1932, *Salter 2204* (K).

1b. **S. tenella** (L.f.) Snijman subsp. **orientalis** Snijman, subsp. nov., a subspecie typica statura majore, styli basi strumosa, struma tholiformi distincta. Type: Orange Free State, Orange Free State National Botanic Garden, Bloemfontein, fl. ex Kirstenbosch Naional Botanic Garden, 1 April 1985, *I. B. Oliver 313* (NBG holo; K, MO, PRE).

Bulb 10--20 mm diam., produced into a narrow neck up to 80 mm long. *Leaves*

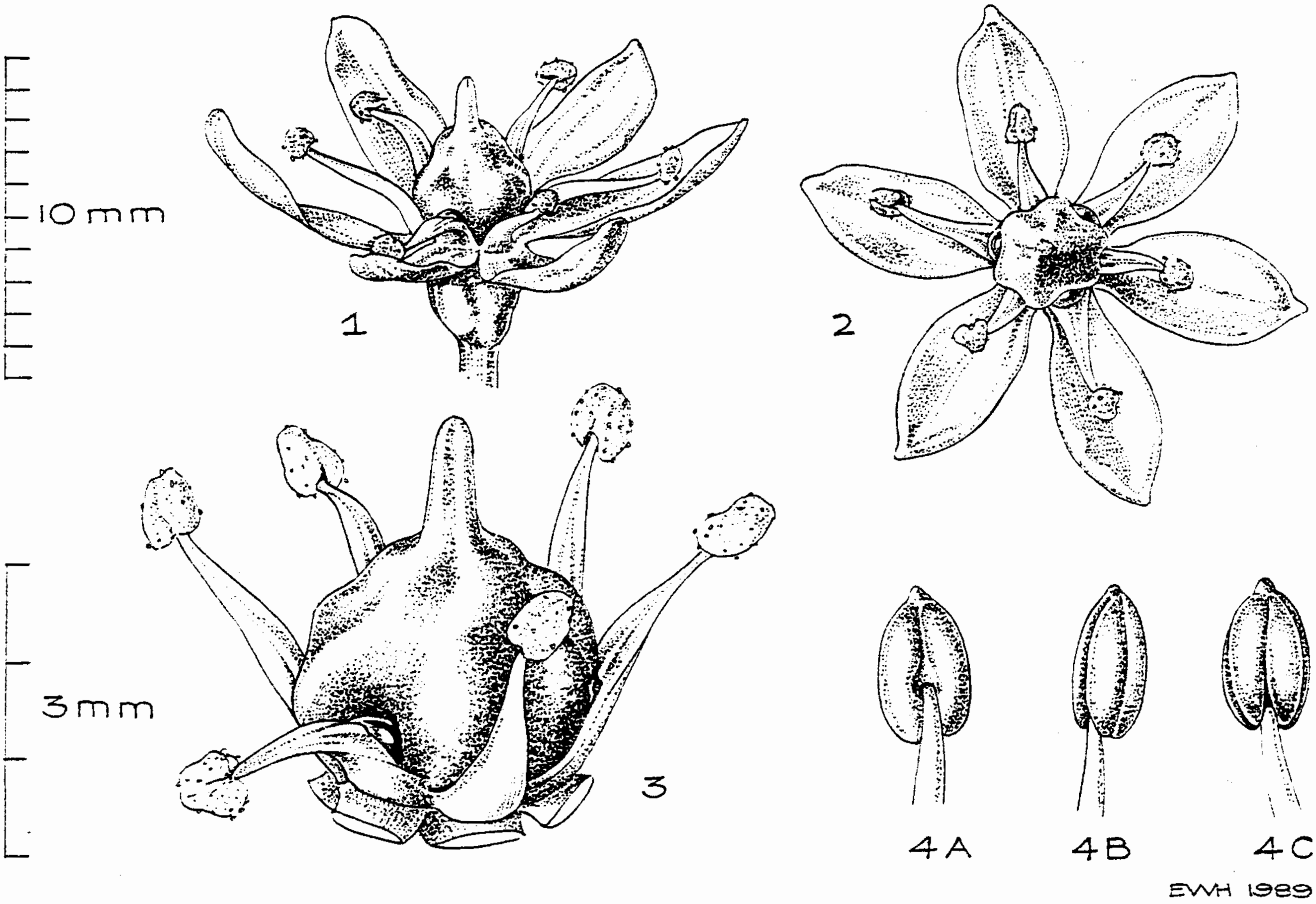


FIGURE 9.16-- *Strumaria tenella* subsp. *orientalis*: 1-2, whole flowers; 3, detail of androecium and style; 4, anther attachment, 4A, dorsal view, 4B, lateral view, 4C, ventral view. Drawn from *I. Oliver 313*.

well developed or incipient at anthesis, 6, with 1--3 present at a time, 70--380 x 1,0--1,5 mm. *Inflorescence* spreading widely, 25--180 mm across; scape straight, suberect, 120--250 mm long; spathe valves linear-lanceolate, 12--30 x 2--3 mm, green, ultimately turning pale brown; bracteoles up to 10 mm long. *Flowers* 8--21, pure white; pedicels (15-) 30--85 (-95) mm long. *Tepals* 2--3 mm wide. *Anthers* green. *Style* up to 4 mm long, enlarged in the proximal two thirds into a hexahedron (up to 3 mm diam.), with rounded angles and a dome-shaped apex, tapering apically. Figure 9.16.

Distribution and habitat: Strumaria tenella subsp. *orientalis* is currently known only from the Orange Free State and Lesotho, where it is recorded as locally abundant in shallow soil amongst dolerite rocks, usually on karroid koppies.

Specimens examined

--2827 (Senekal): 3 miles SW of Winburg (-CA), fl 22 Feb 1946, *Acocks 12504* (PRE).

--2925 (Jagersfontein): Zamekomst (-CB), fr 7 Mar 1940, *Henrici 3242* (PRE), fl 27 Jan 1954, *Henrici 4734A* (PRE).

--2926 (Bloemfontein): Bloemfontein (-AA), fl Feb 1923, *Irving 23159* (PRE); fl 6 Mar 1953, *Mostert 807* (PRE); Bloemfontein, Eagles Nest (-AA). fr Mar 1917, *Potts 2876* (PRE); Bloemfontein, Orange Free State National Botanic Garden (-AA), fl 12 Mar 1969, *Müller 519* (NBG); *I. B. Oliver 313* (K, MO, NBG, PRE); Winter Valley (-AA), fl 23 Mar 1968, *Müller 218* (PRE).

--2927 (Maseru); Hillandale (-AD), fl 27 Feb 1944, *Wasserfall 852* (NBG).

2. **Strumaria pygmaea** Snijman, nom. nov. Type: Little Namaqualand, Hardeveld, Elandsfontein, May, *Zeyher 1662* (K, holo.!; BOL!, E!, SAM!).

Hessea spiralis Baker: 22 (1888), 191 (1896); Müller-Doblies: 46 (1985) nom. illeg., non *Hessea spiralis* (L'Hérit.) Bergius ex Schlechtend.: 252 (1826) (= *Carpolyza spiralis* (L'Hérit.) Salisb.); non *Strumaria spiralis* (L'Hérit.) Aiton: 213 (1811) (= *Carpolyza spiralis* (L'Hérit.) Salisb.). *Periphanes spiralis* (Baker) Leighton: 82 (1948).

Bulb solitary, small, globose, ± 10 mm diam., with thinly fibrous light brown outer tunics, whitish within; neck slender, up to 60 mm long. *Leaves* absent at anthesis, 2 (--3), suberect to spreading, filiform, up to 80 x 1 mm, hemiterete, glabrous, bright green, subtended by a subterranean amplexicaul cataphyll; seedling glabrous. *Inflorescence* spreading widely, 25--50 mm across; scape extremely slender and wiry, spirally twisted throughout its length or basally, reaching up to 30--60 mm, 0,25 mm diam., reddish brown, persisting until the leaves die down; spathe valves linear-lanceolate, 5--13 x 0,75--1,0 mm; bracteoles not visible. *Flowers* 3--8, stellate, pure white, turning cream with age or occasionally with a pale pink blush towards the base of the dorsal surface, slightly

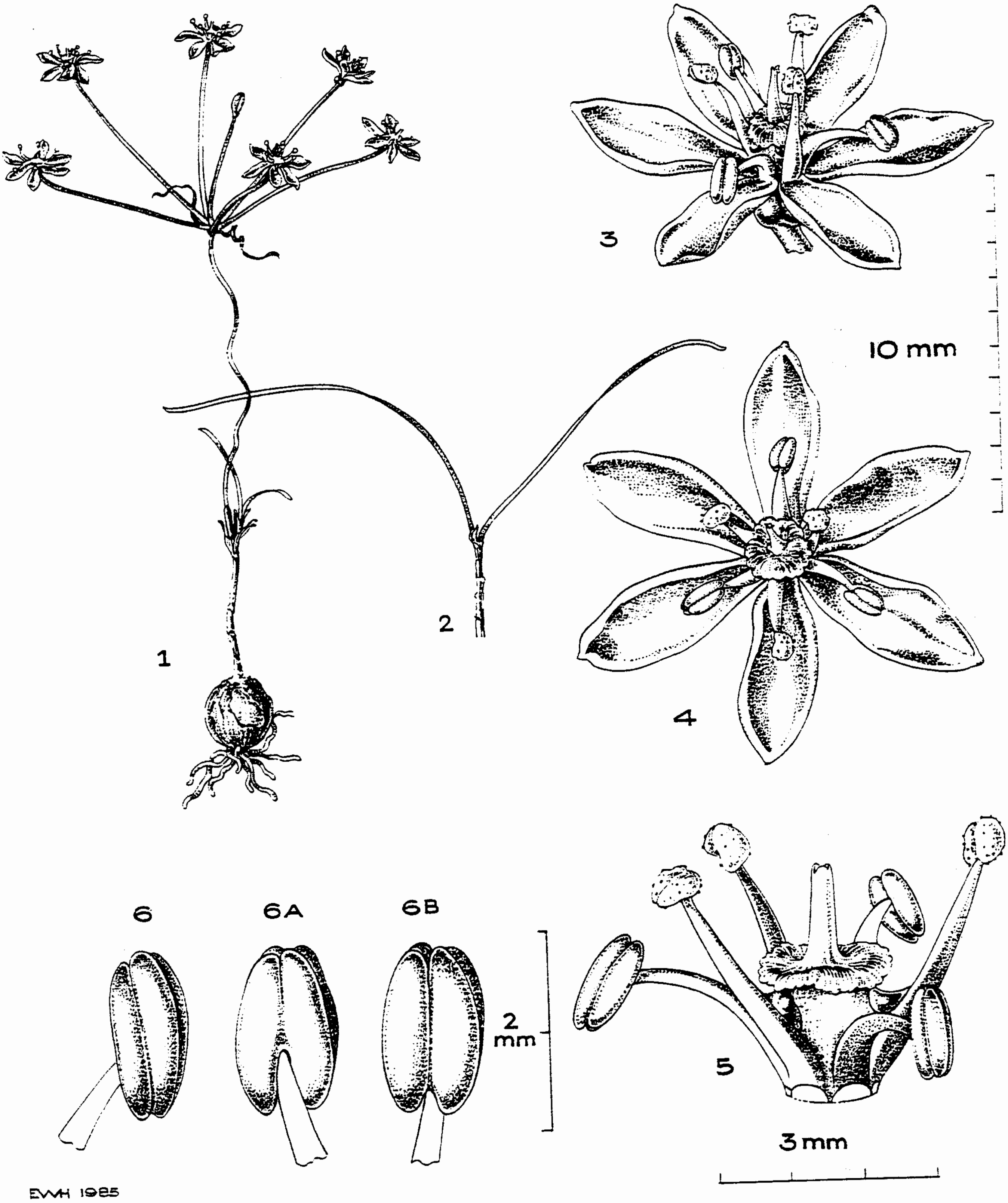


FIGURE 9.17-- *Strumaria pygmaea*: **1**, habit, life size; **2**, leaf habit, life size; **3-4**, whole flowers; **5**, detail of androecium and style; **6**, anther attachment, lateral view, **6A**, dorsal view, **6B**, ventral view. Drawn from *Snijman 862*.

scented; the innermost of the cymes often aborting; pedicels upwardly curved to straight, 20--60 mm long, green and stout, contrasting strongly with the slender wiry scape; remaining green until the leaves die down. *Tepals* free to the base, outspread, ovate-lanceolate, 4,5--5,0 x 1,5--2,0 mm. *Stamens* equalling the tepals, ascending to widely spreading; filaments separate, adnate to the base of the swollen style, laterally broadened and with a slight longitudinal ventral ridge in the proximal half, tapering gradually upwards; anthers dorsifixed, 1,5 mm long before opening, dark maroon; pollen cream-coloured. *Ovary* with (0-) 1--2 ovules per locule. *Style* up to 3,5 mm long, stout and cylindric in the proximal half, with an overhanging scalloped upper margin, abruptly narrowed into a slender, terete column distally, with nectar collecting in 3 droplets between the inner filaments and the style base. *Seeds* 2--3 mm diam. *Chromosome number* $2n = 22$. Figure 9.17.

Flowering time: May.

Diagnostic features: The delicate habit of *S. pygmaea* places it close to *S. tenella*. Both species have filiform leaves and the smallest flowers in the genus, however, *S. pygmaea* has only two to three leaves (up to 80 mm long) and a sheathing cataphyll, whereas *S. tenella* has up to six leaves per annum (70--380 mm long) and lacks a cataphyll. A novelty is the extremely slender, wiry and spirally twisted scape which bears contrasting stout, green pedicels. The infructescence persists throughout the vegetative phase, with the green pedicels apparently functioning as assimilatory structures.

Distribution and habitat: This rarely collected species is known from only two localities, approximately 20 km south of Bitterfontein in the Knersvlakte (Figure 9.46). Almost one hundred and fifty years lapsed before the species was rediscovered in the vicinity of Zeyher's original locality. The species appears to be localised in quartz outcrops, in low succulent vegetation.

Specimens examined

--3118 (Vanrhynsdorp): Little Namaqualand, Hardeveld, Elandsfontein (- AD), fl May, *Zeyher 1662* (BOL, E, K, SAM); farm Kersbosvlei II, between Nuwerus and Koekenaap (-AD), fl 7 May 1985, *Snijman 862* (K, NBG, PRE).

5.2 Subgenus Strumaria

Bulbs with whitish inner tunics. *Foliage leaves* erect, arranged in a fan, usually more than 3 or rarely 2, glabrous, sometimes basally sheathed by a cataphyll. *Scape* persisting during seed release. *Flowers* funnel-shaped, rarely somewhat campanulate, borne on pedicels ± equalling the length of the perigone; filaments usually connate to form a tube; anthers dorsifixed.

Species 5.

3. **Strumaria bidentata** Schinz in Bulletin De L'Herbier Boissier 4, App. 3: 46 (1896); Baker: 532 (1897); Müller-Doblies: 27 (1985). Type: Gross Namaland, Unterer Oranjefluss, *1885, Schenck 232* (Z, holo.!).

Bulb solitary, globose to ovoid, 20,0--27,5 mm diam., with outer tunics felt-like and light brown, whitish within; neck stout, up to 50 mm long. *Leaves* absent at anthesis, (2-) 3--4, arranged in a fan, erect, more or less falcate, broadening towards an obtuse to truncate apex, 45--100 x 9--20 mm, leathery, somewhat sticky when young, glabrous, bright green on both surfaces, usually flushed with red towards the base, subtended by a subterranean amplexicaul cataphyll; seedling glabrous. *Inflorescence* clustered, 10--30 mm across; scape straight to slightly flexuose, 80--150 mm long, 1--2 mm diam., green to wine-red, persisting throughout fruiting then collapsing; spathe valves lanceolate, 15--18 x 2--4 mm; bracteoles up to 12 mm long. *Flowers* 5--8, ascending, campanulate, glistening white, sometimes faintly flushed with pink along the median dorsal surface, remaining unchanged or becoming completely flushed with pink with age, scented; pedicels straight, 8--25 mm long, green. *Tepals* free to the base, spreading slightly, ovate-lanceolate, 5--8 x 3--4 mm, somewhat channelled. *Stamens* longer than the tepals, spreading slightly; filaments separate, up to 9 mm long, shortly adnate to the swollen style base, expanding upwards in the proximal half and terminating midway in a prominent irregularly toothed transverse ridge, abruptly narrowed and subulate distally; anthers dorsifixed, ± 2,5 mm long and deep pink before opening; pollen cream-coloured. *Ovary* with up to 2--4 ovules per locule. *Style* up to 7,5 mm long, with the proximal half enlarged into a 2,5 mm broad, slightly fluted disc with a raised irregularly toothed upper rim, abruptly narrowed into a slender terete column in the distal half, with nectar collecting in three droplets between the base and inner filaments. *Seeds* 3 mm diam. *Chromosome number* $2n = 20$. Figure 9.18.

Flowering time: From March to April.

Diagnostic features: A diminutive species, distinguished by the erect, clustered habit of the inflorescence; the proximally thickened filaments with a ridge of irregular teeth midway along their length; and the style in the shape of a fluted disc for half its length. The leaves are typically broader towards the apex, firm and somewhat sticky. Vegetatively the species may be confused with the broad, blunt leaves of *S. hardyana* which also occurs in southern Namibia, but these have hyaline margins and slightly emarginate apices.

Distribution and habitat: Known only from the Orange River mouth in southern Namibia and the Richtersveld (Figure 9.47) where the bulbs are recorded growing in sand on exposed flats and amongst rocks, in association with sparse succulent vegetation.

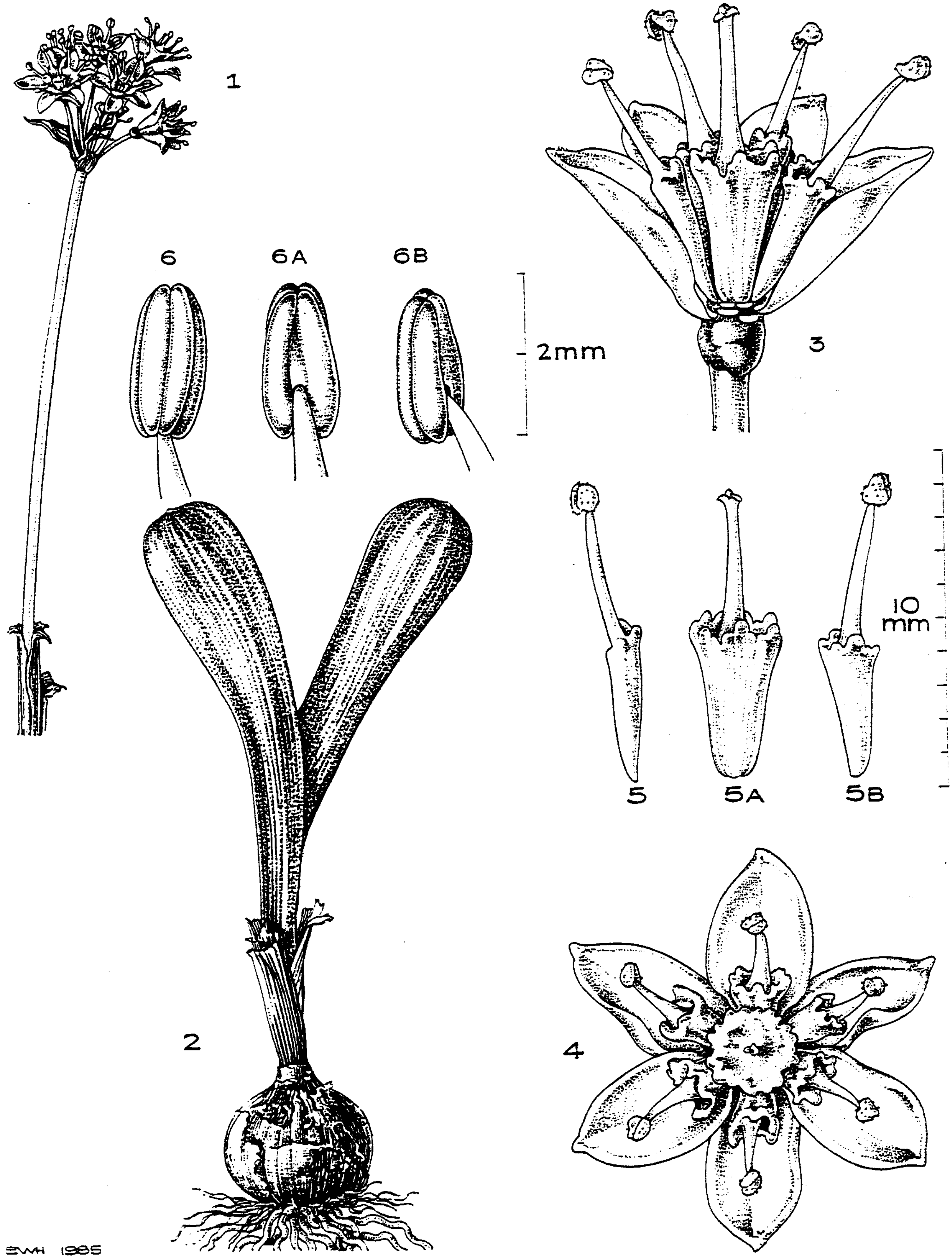


FIGURE 9.18-- *Strumaria bidentata*: 1, inflorescence, life size; 2, vegetative habit, life size; 3, flower with two tepals and stamens removed; 4, whole flower; 5, lateral view of stamen, 5A, style, 5B, ventral view of stamen; 6, anther attachment, ventral view, 6A, dorsal view, 6B, lateral view. Drawn from *Viviers s.n.*

Specimens examined

--2816 (Oranjemund): Oranjemund (-CB), *Wilhelm 2* (NBG, PRE); Oranjemund area (-CB), *Viviers s.n.* (NBG); Orange River, 2 km E of Beauvallon (-DA), *Bayer 1027* (NBG); Richtersveld, Beauvallon (-DA), fl 1 Apr 1982, *Williamson 2927* (BOL); Alexander Bay (-DA), *Woolley s.n.* (NBG); Kortdoring, Alexander Bay (-DA), *Van Jaarsveld & Kuhn 8221* (NBG).

--Imprecise locality: Richtersveld, Little Namaqualand, *Pillans 5779* (BOL); Diamond Area No. 1, Luderitz-Süd, *T. Polland* sub *Giess 4337* (WIND); South West Africa, *E. Erni* sub *NBG 1293/28* (BOL); unterer Oranjefluss, *Schenck 232* (Z).

4. **Strumaria phonolithica** Dinter in Repertorium specierum novarum regni vegetabilis 19: 178 (1923); Müller-Doblies: 24 (1985). Type: Grossnamaland [Namibia], Klinghardtgebirge, zahlreich zwischen Phonolithtrümmern auf dem an den Pietab I anstossenden Berge, September 1922, blühend in Lichtenstein 15 Mei 1923, *K. Dinter 4735* (lost); *Dinter s.n.* (B, lecto.!), designated by Müller-Doblies (1985).

Bulb forming clumps, subglobose, ± 30 mm across, covered by softly fibrous, parchment-like outer tunics; neck stout, up to 160 mm long, exposed for more than half its length. *Leaves* incipient at anthesis, 3--4, arranged in a fan, suberect, narrowly to broadly lorate, 60--130 x 7--25 mm, plane-surfaced, glabrous, obtuse apically; cataphyll and prophyll unknown. *Inflorescence* somewhat spreading, up to 80 mm across; scape straight, 130--200 mm long, ± 3 mm across, brownish green or pale green with a grey bloom, persisting throughout fruiting then collapsing; spathe-valves lanceolate, 25--30 x 4--6 mm; bracteoles up to 15 mm long. *Flowers* 3--7, somewhat secund, narrowly funnelform, white to pink, scented; pedicels straight to slightly curved, 10--12 mm long, concolorous with the scape. *Tepals* cut to the base but adnate to the stamens for 1 mm, closely imbricate for ± three quarters of their entire length, spreading and reflexed distally, narrowly oblanceolate, 30--38 x 3--4 mm, channelled distally. *Stamens* somewhat shorter than the tepals, slightly spreading, exserted; filaments 27--35 mm long, connate proximally into a tube 2--5 mm long; the outer whorl adnate to the 3-winged style base for ± the same length as the filament tube; the inner whorl with the inner face free from the style thus forming 3 tubular nectar wells; anthers dorsifixed, ± 4 mm long and dirty-red before opening; pollen cream-coloured. *Ovary* with up to 7--8 ovules per locule. *Style* 18--35 mm long, equalling the stamens, slender, with the proximal quarter narrowly 3-winged. *Seeds* unknown. *Chromosome number* unknown. Figure 9.19.

Flowering time: Cultivation records indicate that the species flowers in May.

Diagnostic features: Together with *S. barbarae*, *S. phonolithica* has the largest

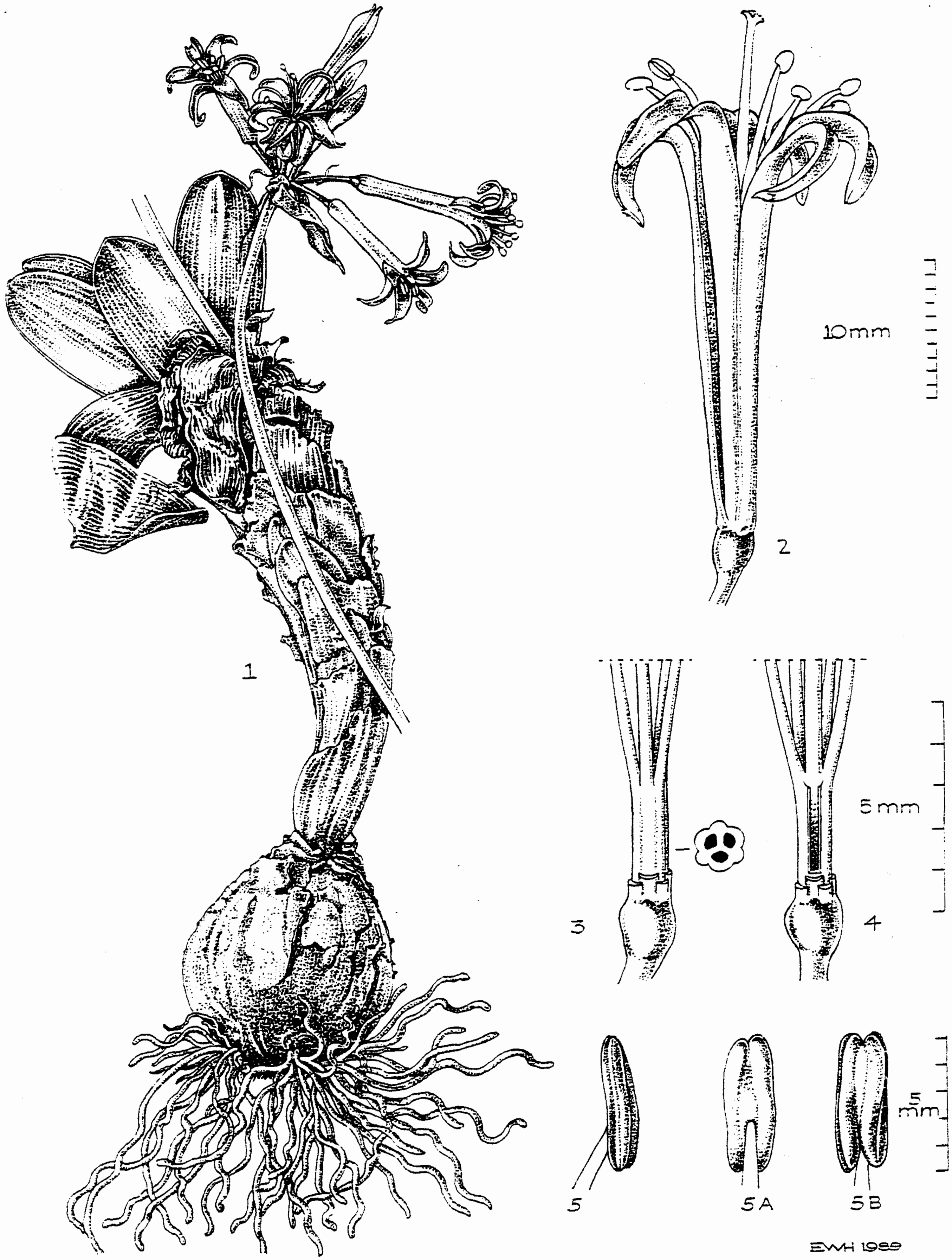


FIGURE 9.19-- *Strumaria phonolithica*: 1, habit, life size; 2, whole flower; 3-4, portion of flowers with tepals removed to show deep nectar wells formed by partial fusion of stamens to the style; 5, anther attachment, lateral view, **5A**, dorsal view, **5B**, ventral view. Drawn from *Bruyns 3081*.

flowers in the genus (longer than 30 mm). *Strumaria phonolithica* is easily distinguished by the stout bulb neck (up to 160 mm long), which extends well above ground level and the slender funnel-shaped flowers, in which the narrow tepals (at most 4 mm across) spread weakly upwards for approximately three quarters of the perigone length and then become distinctly recurved.

Distribution and habitat: Currently the species is known only from the Klinghardt and Aurus mountains in southern Namibia (Figure 9.47). In the Aurus Mountains the species forms large clumps, on wide ledges of steep south-facing slopes, in association with low, winter-growing succulent shrubland. The populations appear to benefit from fog which is borne inland towards the mountains across the coastal plain (P. Bruyns pers. comm.). The specific epithet refers to the bulbs' habitat preference for sites among fragments of phonolite.

Specimens examined

--2715 (Bogenfels): Pietab II, Klinghardtberge (-BC), *Merxmüller & Giess 28384* (WIND); *Merxmüller & Giess 29023* (WIND, photo.); Pietab I, Klinghardgebirge, (-BC/BD), *Dinter s.n.* (B).

--2716 (Witputz): Aurus Mountains (-CB), *Bruyns 3081* (NBG).

5. **Strumaria barbarae** Oberm. in Bothalia 13 : 435 (1981) sphalm. *S. barbariae*; Müller-Doblies: 24 (1985). Type: South West Africa [Namibia], farm De Aar, about 30 km ESE of Aus, fl. ex hort. Feb. 1980, *Lavranos & Pehlemann 17153* (PRE, holo.!).

Bulb solitary, ovoid, ± 25--30 mm diam, with softly fibrous dark to pale brown outer tunics, cream-coloured within; neck up to 90 mm long or sometimes absent. *Leaves* incipient at anthesis, 2--4, arranged in a fan, erect to recurved, lorate, up to 200 x 5--8 mm, glabrous, shiny green; cataphyll and prophyll unknown; seedling unknown. *Inflorescence* somewhat clustered, up to 80 mm across; scape erect, 215--250 (-400) mm long, 2--4 mm diam., green with a grey bloom; spathe valves lanceolate, 25--60 x 5--6 mm, bracteoles up to 50 mm long. *Flowers* (3-) 4--12, pendulous, funnel-shaped, white, becoming flushed with pink towards the base with age, strongly scented; pedicels declinate at anthesis, later becoming erect, 18--35 mm long, lengthening to 45 mm in fruit, green. *Tepals* cut to the base, with the outer and inner whorls adnate to the base of the staminal tube for up to 6 mm and 7 mm respectively, oblanceolate, 30--38 x 4,5--9,0 mm, imbricate in the lower two thirds, spreading to recurved above. *Stamens* slightly shorter than the tepals, somewhat spreading; filaments up to 30 mm long, connate proximally into a tube ± 4 mm long, adnate proximally to the sharp edges of the 3-angled style for 4--7 mm, with the inner surface or the inner filaments free from the style thus forming 3

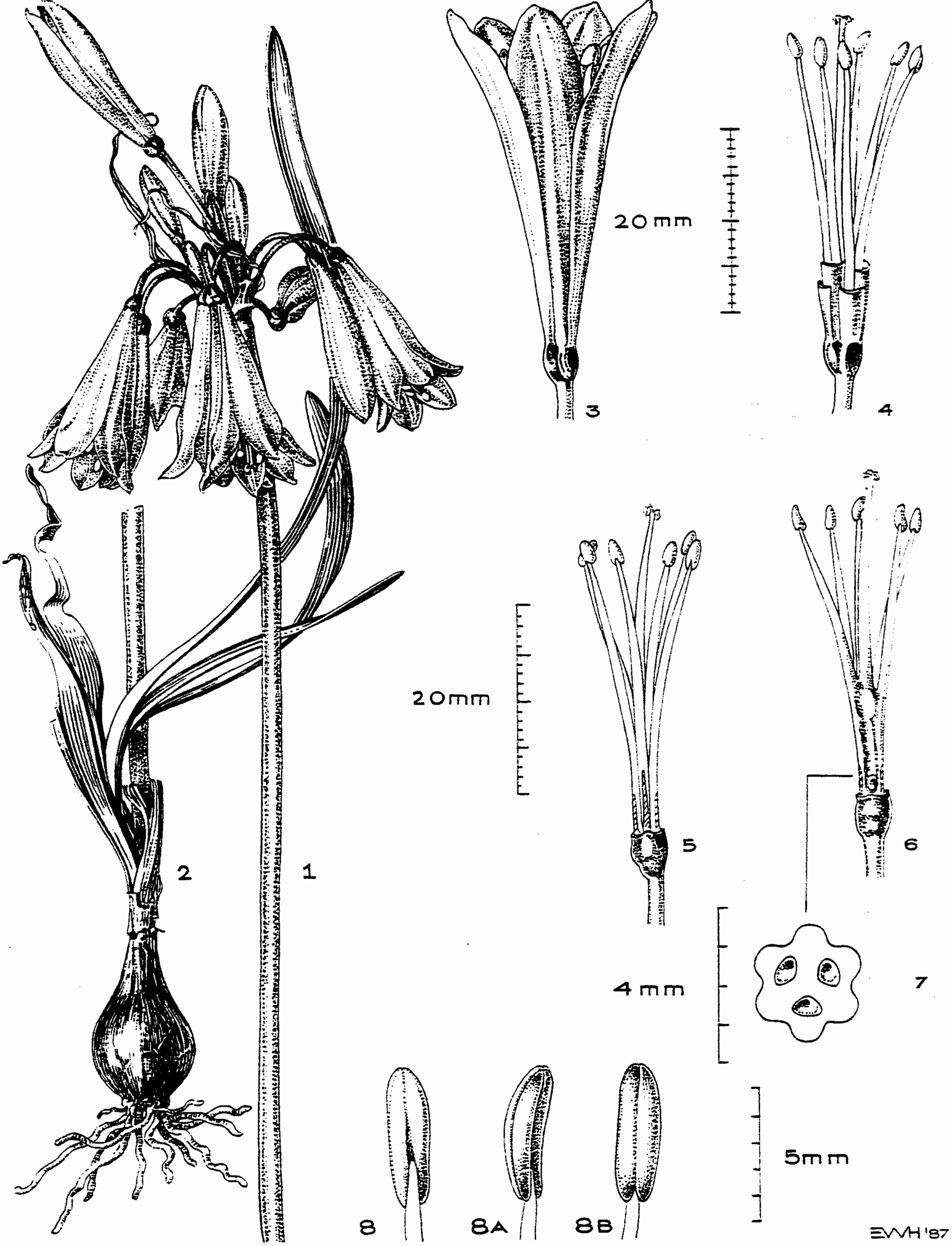


FIGURE 9.20– *Strumaria barbarae*: 1, inflorescence, life size; 2, vegetative habit, life size; 3, whole flower; 4, flower with tepals partially removed; 5, flower with tepals entirely removed; 6, androecium and gynoecium with nectar well dissected open; 7, transverse section through androecium and style to show three nectar wells; 8, anther attachment, dorsal view, 8A, lateral view, 8B, ventral view. Drawn from *Lavranos s.n.*

tubular nectar wells ± 4 mm deep; anthers dorsifixed, ± 4 mm long before opening, pale yellow; pollen cream-coloured. *Ovary* usually with 6 or 7 ovules per locule. *Style* up to 35 mm long, slender, 3-angled in the proximal third. *Seeds* unknown. *Chromosome number* unknown. Figure 9.20.

Flowering time: April, but only following autumn rains. (J.J. Lavranos pers. comm.). January to February in cultivation.

Diagnostic features: Strumaria barbarae, together with its close ally *S. phonolithica*, has the largest flowers in the genus, with tepals 30--40 mm long. *Strumaria barbarae* is additionally distinguished by its pendulous, clustered flowers.

Distribution and habitat: This little known species is recorded from only two areas in southern Namibia and the Richtersveld, where it is locally abundant on exposed limestone screes (Figure 9.47). The limestone, known as schwarzkalk, is typically blackish, intercalated with some green shale.

Specimens examined

--2616 (Aus): farm De Aar, approx. 30 km ESE of Aus (-CB), *Lavranos & Pehlemann 17153* (PRE); farm Plateau (-CB), *W. Rauh s.n.* (PRE 649443, WIND 3370); farm Aar, LU16 (-DA/CD), *H. Erni 1038* (WIND); farm Aar, LU16 (-DA), *Giess 13683* (WIND).

--2817 (Vioolsdrif): Richtersveld, De Hoop (-AA), *Oliver, Tölken & Venter 387* (PRE).

6. **Strumaria hardyana** D. & U. Müller-Doblies in Botanische Jahrbucher für Systematik 107 : 24 (1985). Type: Namibia, Witputz, 4 km along road to Konkiep, 2 October 1978, *Hardy 4877* (PRE, holo.!; B, K, M, Herb. M-D.).

Bulb solitary, ovoid to subglobose, 15--35 mm diam, with densely fibrous and light brown outer tunics, whitish within; neck somewhat stout, up to 65 mm long. *Leaves* absent at anthesis, 3 or 4, arranged in a fan, erect, varying from lorate to obovate and falcate, 30--100 x 5--19 mm, plane or occasionally undulate, glabrous, sometimes flushed with red towards the base; margin hyaline; apex shallowly emarginate but becoming less evident with age; usually subtended by a subterranean amplexicaul cataphyll; prophyll absent; seedling glabrous. *Inflorescence* unilaterally clustered, 15--40 mm across; scape more or less straight, 170--350 mm long, 1,5--2,5 mm diam., glaucous-green to pink, withering after seed-release; spathe valves narrowly lanceolate, ± 18 x 1,5--4,0 mm; bracteoles up to 10 mm long. *Flowers* 4--16, secund, more or less pendulous, narrowly funnel-shaped, ranging from cream to pure white, occasionally flushed with pink, becoming buff-coloured with age, sometimes with a coconut-like scent; pedicels declinate at anthesis, 10--18 mm long, lengthening and becoming erect in fruit, green. *Tepals*

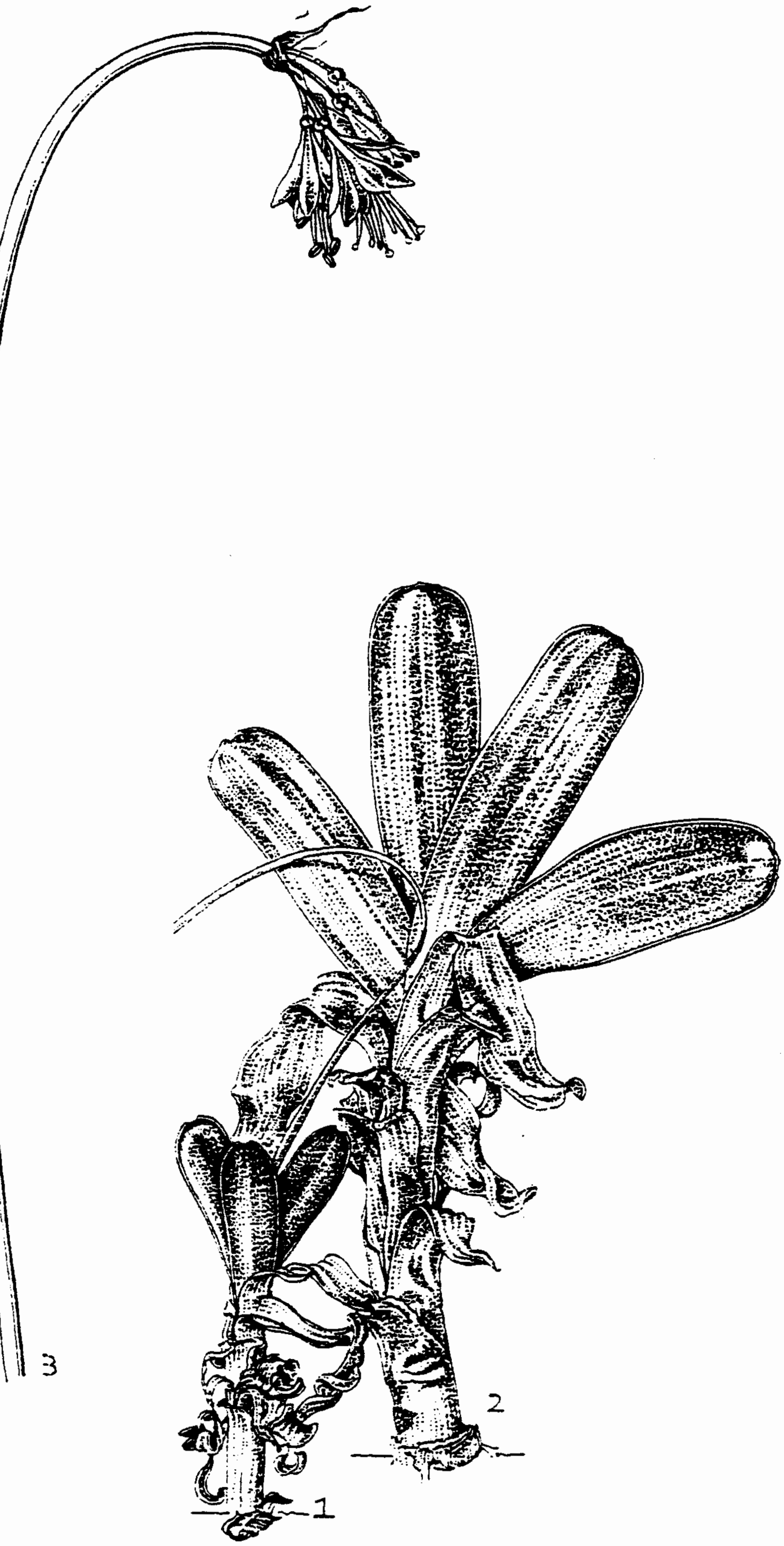


FIGURE 9.21-- *Strumaria hardyana*: 1-2, vegetative habit, life size; 3, inflorescence, life size. Drawn from *Hardy 5014* 1&3, and *Van Berkel 490* 2.

separate, with the outer and inner whorls adnate to the base of the staminal tube up to 0,5 mm and 2,5 mm respectively, spreading slightly, oblanceolate, 9--15 x 2,0--3,5 mm. *Stamens* slightly longer than the tepals, somewhat spreading distally; filaments 12--18 mm long, connate proximally into a tube 5--9 mm long; the outer filaments adnate proximally to the angles of the 3-winged style for 2--10 mm; the inner surface of the inner whorl free from the style thus forming 3 tubular nectar wells 3--5 mm deep; anthers dorsifixed, ± 3 mm long before opening, wine-red; pollen cream-coloured. *Ovary* with 2--4 ovules per locule. *Style* up to 20 mm long, slender, 3-winged proximally for 2--10 mm. *Seeds* 2,0--3,5 mm diam. *Chromosome number* $2n = 20$ (Goldblatt 1976, as *S.* cf *bidentata*). Figure 9.21.

Flowering time: March to April.

Diagnostic features: Strumaria hardyana is most closely allied to *S. truncata*, both of which have clustered, secund flowers; and in the absence of leaves both species are indistinguishable. The leaves of *S. hardyana* which are diagnostic, are plane or occasionally slightly undulate, with a hyaline margin and emarginate apex, a feature which is particularly evident in young leaves. Unlike *S. truncata* the blades are never twisted. *Strumaria hardyana* is one of four *Strumaria* species which occur in southern Namibia. Of these it can be most easily confused in the vegetative state with *S. bidentata.* The differences between the two species are given under *S. bidentata.*

Distribution and habitat: The species is scattered but fairly abundant in crevices amongst schizts and black limestone along the mountain ranges between Witputz and Rosh Pinah in southern Namibia (Figure 9.47).

Specimens examined

--2716 (Witputz): Witputz, 4 km along road to Konkiep (-DA), *Hardy 4877* (PRE); near Witputz (-DA), *Van Berkel 493* (NBG); 27 km N of Rosh Pinah (-DA), *Hardy 5014* (K, MO, NBG); 10 miles E of Witputz (-DB), fl 15 Apr 1971, *Tölken 3989* (BOL); southern Nasepberg, 2,4 km NW of Kolke (-DB), *Van Berkel 490* (NBG); farm Aub, Huib Plateau (-DB), *Lavranos & Pehlemann 21197* (NBG, PRE); Spitskop, Rosh Pinah (-DC), fl Mar 1983, *Van Berkel 485* (NBG); *Van Berkel 550* (NBG); Lat. 27° 51,5' Long. 16° 37' (-DC), fl 16 Apr 1985, *Van Berkel 548* (NBG); 8 km NNW of Rosh Pinah (-DC), *Lavranos & Pehlemann 21246* (NBG).

7. **Strumaria truncata** Jacq., Collectanea 5: 47 (1797); Willd.: 31 (1799); Aiton: 212 (1811); Schultes & Schultes: 792 (1830); Herbert: 288 t. 29, 11 (1837); D. Dietr.: 1188 (1840); Kunth: 623 (1850); Baker: 104 (1888), 216 (1896); Phillips: t. 127 (1924); Müller-Doblies: 23 (1985). Type: figure in Jacq., Icones plantarum rariorum, 2 : t. 357 (1795), lecto.!, designated by Müller-Doblies (1985).

Hymenetron truncata (Jacq.) Salisb. ex Baker: 216 (1896).

Strumaria linguaefolia Jacq.: 45 (1797). Willd.: 31 (1799); Schultes & Schultes: 791 (1830); Herbert: 288 t. 29, 10 (1837); D. Dietr.; 1188 (1840); Kunth: 624 (1850); Baker: 216 (1896); Müller-Doblies: 23 (1985). Type: figure in Jacq., Icones plantarum rariorum 2: t. 355 (1795), lecto!, designated by Müller-Doblies (1985). *Hymenetron linguaefolia* (Jacq.) Salisb. ex Baker: 216 (1896).

Strumaria angustifolia Jacq: 48 (1797); Willd.: 32 (1799); Aiton: 212 (1811); Schultes & Schultes: 789 (1830); Herbert: 287 t. 29, 14 (1837); D. Dietr.: 1187 (1840); Kunth: 623 (1850); Baker: 104 (1888), 216 (1896); Müller-Doblies: 23 (1985). Type: figure in Jacq., Icones plantarum rariorum 2: t. 359 (1795), lecto.!, designated by Müller-Doblies (1985). *Pugionella angustifolia* (Jacq.) Salisb.ex Baker: 217 (1896).

Strumaria rubella Jacq.: 46 (1797); Willd.: 31 (1799); Aiton: 212 (1811); Schultes & Schultes: 790 (1830); Herbert: 288 t. 29, 12 (1837); D. Dietr.: 1187 (1840); Kunth: 624 (1850); Baker: 104 (1888), 217 (1896); Müller-Doblies: 23 (1985). Type: figure in Jacq., Icones plantarum rariorum 2: t. 358 (1795), lecto!, designated by Müller-Doblies (1985). *Stylago rubella* (Jacq.) Salisb. ex Baker: 217 (1896).

Haemanthus vaginatus Thunb.: 188 (1800), 254 (1820) sphalm. *H. vaginans*; Thunb.: 297 (1823). Type: sheet no. 7937 in Herb. Thunberg (UPS, holo., microfiche!). *Hessea vaginata* (Thunb.) Herbert: 289 (1837).

Strumaria baueriana Herbert ex Kunth: 625 (1850). Type: drawing by Bauer in Botany library (BM, holo.!)

Bulb globose to ovoid, 20--50 mm diam., occasionally forming bulblets, covered with densely fibrous pale brown to cream-coloured outer tunics, whitish within; neck usually stout, up to 70 mm long. *Leaves* absent or incipient at anthesis, 2--6, arranged in a fan, suberect or rarely recurved, narrowly to broadly lorate or somewhat falcate, 80--250 x (3-) 7--16 (-20) mm, twisted 1--3 times or rarely plane, varying from green to somewhat glaucous, glabrous, subtended by 1 or 2 amplexicaul cataphylls reaching up to 40 mm above ground; cataphyll initially inflated and liver-coloured, soon withering and turning brown; seedling glabrous. *Inflorescence* unilaterally clustered, 15--60 mm across; scape straight to somewhat flexuose, usually recurved near the apex, 90--480 mm long, 2--5 mm diam., pale green often suffused with pink or brown, covered with a grey bloom, collapsing after seed-release; spathe valves lanceolate, 15--28 x 3--8 mm, bracteoles up to 15 mm long. *Flowers* (3-) 4--26, secund, more or less pendulous, varying from somewhat narrowly to broadly funnel-shaped, ranging from pure white to pink, turning deeper pink with age, scented; pedicels straight to recurved, 10--40 mm long, lengthening slightly and becoming upright in fruit, shiny green. *Tepals* free or with the outer and inner whorls adnate to the base of the staminal tube for ± 1 mm and 2 mm respectively, spreading slightly, narrowly to broadly oblanceolate or occasionally narrowly elliptical, (7-) 8--13 (-16) x 2--5 mm. *Stamens* longer than the tepals, more or less spreading distally; filaments

(9-) 12--20 mm long, connate proximally into a tube 1,5--7,0 (-10,0) mm long; the outer filaments adnate proximally to the sharp angles of the 3-winged style for (1,5-) 3,5--9,0 mm; the inner surface of the inner filaments free from the style thus forming 3 tubular nectar wells 2--8 mm deep; anthers dorsifixed, 2--4 mm long before opening, cream to pink; pollen cream-coloured. *Ovary* with (2-) 4--5 (-7) ovules per locule. *Style* up to 25 mm long, slender, 3-winged proximally for 1,5--9,0 mm; the wings often protracted into teeth distally. *Seeds* 2--4 mm diam. *Chromosome number* $2n = 20, 20+1B, 22$. Figure 9.22.

Flowering time: April until June, occasionally commencing in March when cultivated.

Diagnostic features: Strumaria truncata is the only member of the genus with an exserted, reddened cataphyll which sheathes the mostly twisted foliage leaves. With respect to the size, shape and position of the flowers it is extremely similar to *S. hardyana* which lies to the north of its range. No distinguishing floral characters are known.

Distribution and habitat: Strumaria truncata is the most commonly found *Strumaria* species in the north western Cape. It extends from the southern parts of the Richtersveld, through Namaqualand to the Vanrhynsdorp district in the south, as well as from the lowlands in the west, eastwards to the western foothills of the Hantamsberg (Figure 9.47). The species occupies a variety of soils, always in fairly open sites.

Variation: Geographic variation is evident throughout the distribution range. Populations from the Steinkopf and Kosies areas of northern Namaqualand have stiff firm scapes which remain upright at anthesis. Similarly the pedicels are stiff, thus the flowers are ascending to spreading. Combined with this feature is the shorter length of the stamens (equalling the tepals) and the absence of a filament tube in some specimens (*Duncan 257*). Generally the leaves are broad, long and not twisted. These specimens match the type of *S. linguifolia.*

Elsewhere, in populations south of this centre, the scapes are usually distally curved, the pedicels are lax, the flowers are secund and pendulous, and the filaments extend beyond the tepals. The scape and pedicels subsequently stiffen after anthesis, thereby developing a suberect habit. Populations bordering on the quartzitic plains of the Knersvlakte in the Vanrhynsdorp district comprise bulbs with a noticeably stunted habit, sometimes with only two foliage leaves (*Snijman 1119*), which match the type of *S. angustifolia.*

Flowers vary considerably in colour and range from deep pink to white colour forms before subsequently ageing to a deeper pink after anthesis. Other variables are the extent to which the filaments are adnate to the style, the length of the filament tube and the dentition on the confluence between the outer filaments and the style. The plasticity of these floral features is such that they may vary between flowers of a single inflorescence.

Of all the names available for this variable species, *S. truncata* has been chosen because of its long standing usage in South African herbaria.

Specimens examined

--2816 (Oranjemund): Cornells Kop, Richtersveld (-BD), *Lavranos 27701* (NBG).

--2917 (Springbok): 6 Km W of Steinkopf (-BA), *Perry 1057* (K, MO, NBG, PRE); Varswater, NW of Springbok (-BD), fl May 1983, *Olivier s.n.* (NBG); Komaggas, approximately 30 miles SW of Springbok (-CD), fl 4 May 1972, *Van der Westhuizen 222* (PRE); 3 miles W of foot of Spektakel Pass (- DA), fl 13 Jun 1956, *Hall* sub *NBG 252/56* (NBG); at Nigramoep turnoff between Springbok and Steinkopf, 12,8 km from Bulletrap (-DA), *Duncan 257* (NBG); 'Ookiep (-DB), fl May 1931, *Good* sub *NBG 470/31* (BOL, NBG); Komaggas (-DC), *Herre* sub *SUG 1060* (BOL); fl Apr 1925, *Meyer* sub *Marloth 6447* (PRE); Sandberge near Komaggas (-DC), *Lavranos 8828* (PRE); 4 km from Sanaggas towards Komaggas (-DC), fl May 1980, *Van Jaarsveld & Drijfhout 5371a* (NBG); Drie Riviere (-DC), fl May 1980, *Van Berkel 122* (NBG); SW of Wildepaardehoek Pass (-DC), *Hiemstra 493* (K, MO, NBG, PRE).

--3017 (Hondeklipbaai): 1 Km N of Kamieskroon (-BB), fl 20 May 1974, *Goldblatt 1850* (NBG); 9 miles N of Bowesdorp (-BB), fl 5 May 1960, *Middlemost 2079* (NBG, PRE); Arkoep turnoff from N7, N bank of Arkoep River (-BB), fl 10 May 1981, *Van Berkel 338* (NBG); 3 miles NW of Garies (-DB), fl Jun 1937, *Salter & Creasey* sub *NBG 889/37* (BOL, NBG).

--3018 (Kamiesberg): Garies (-CA), *Caporn* sub *NBG 1070/15* (BOL); 12,5 km S of Garies (-CA), fl 4 Jun 1980, *Snijman 282* (NBG); Arondegas, SE of Garies (-CB), fl 7 May 1982, *Bayer 2796* (NBG); 16,5 miles S of Garies (-CC), *Creasey* sub *NBG 906/37* (NBG); Kammapuss (-DA), *Zeyher 4103* (BOL).

--3019 (Loeriesfontein): 16 km SW of Loeriesfontein towards Kliprand (-CD), *Bayer 2759* (NBG).

--3118 (Vanrhynsdorp): Meerhofskasteel (-AA), fl May, *Zeyher 1660* (K, SAM); *Perry 3142* (NBG); Mieren Kasteel (-AA), *Pappe s.n.* (SAM 22396); Bitterfontein (-AB), fl 6 Jun 1956, *Hall* sub *NBG 251/56* (NBG); 15 miles E of Bitterfontein (AB), fl 27 Apr 1971, *Hall 3961* (NBG); farm Kersbosvlei, SW of Nuwerus (-AD), fl 7 May 1985, *Snijman 858* (K, NBG, PRE); 4,1 km NE towards Douse-the-Glim from the national road (-BC), *Snijman 1119* (NBG); farm Grootdrif, W of Vanrhyns Pass (-BD), fl 15 Jun 1983, *Snijman 712* (NBG); 6 miles N of Koekenaap (-CB), fl 13 May 1962, *Hall 2358* (NBG); between Vredendal and Lutzville (-CB), fl 9 Jun 1980, *Hall 4956* (NBG); Strandfontein (-CC), fl 15 May 1970, *Hall 3538* (NBG); Strandfontein, Doornbaai (-CC), *Smith* sub *NBG 250/46* (NBG); Vanrhynsdorp (-DA), *Mostert* sub

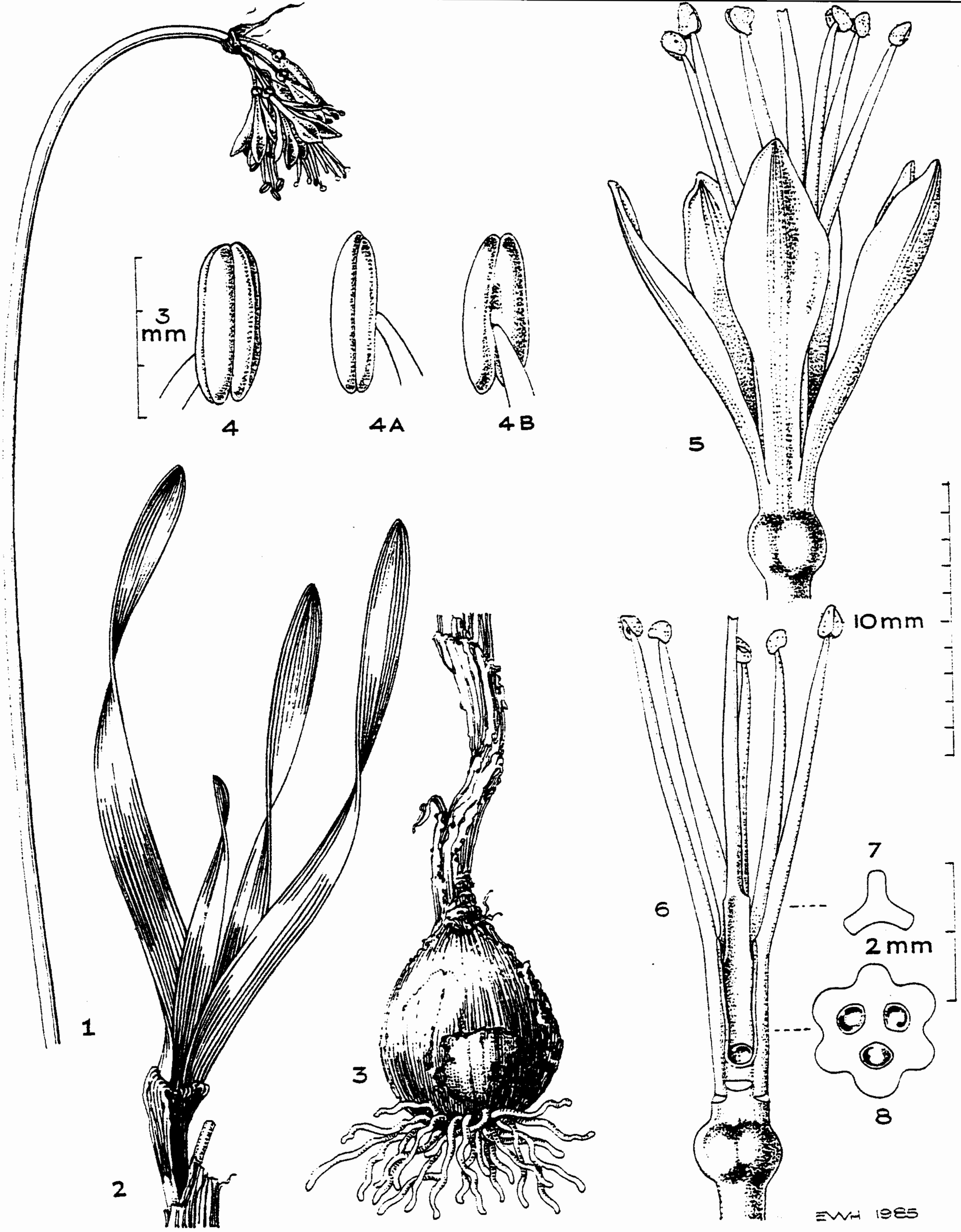


FIGURE 9.22– *Strumaria truncata*: 1, inflorescence, life size; 2, vegetative habit, showing sheathing cataphyll, life size; 3, bulb, life size; 4, whole flower; 5, anther attachment, ventral view, 5A, lateral view, 5B, dorsal view; 6, androecium and gynoecium with inner stamen cut away to show nectar well; 7, transverse section through androecium and style to show three nectar wells; 8, transverse section through style midway along its length. Drawn from *Snijman 712*.

NBG 1405/20 (BOL); *Herre* sub *SUG 7030* (BOL); fl May 1917, *Marloth 7716* (PRE); *Herre s.n.* (BOL 34289); 3 miles N of Vanrhynsdorp (-DA), fl 6 May 1965, *Barker 10192* (NBG); about 3 miles SW of Vanrhynsdorp (-DA), *Pillans s.n.* (BOL 34286); 8 km W of Vredendal (-DA), fl 27 May 1972, *Hall 4200* (NBG); farm Aties, Vanrhynsdorp (-DA), *Hall 4211* (NBG); Sandkraal near Vanrhynsdorp (-DA), fl 30 Apr 1946, *Smith 6485* (NBG); *Smith* sub *NBG 96/46* (NBG); 0,25 miles from Doorn River bridge towards Klawer (-DC), fl 30 Apr 1946, *Smith 6484* (NBG).

--3119 (Calvinia): 12 km from Grasberg towards Perdekraal, Bokkeveld Plateau (-AA), fl 8 May 1985, *Snijman 868* (NBG); Vanrhyns Pass (-AC), *Martin* sub *NBG 1569/37* (NBG); along Groot Toring road, NW of Calvinia (-BC), fl 27 May 1984, *Goldblatt 6062a* (NBG); farm Klein Toring, NW of Calvinia (-BC), fl 9 May 1985, *Snijman 872* (NBG).

--Imprecise localities: Doorn River bridge, *Lewis* sub *NBG 1823/32* (K); fl 4 May 1971, *Barker 7307* (NBG, PRE); Bitterfontein to Kliprand, fl 12 Apr 1971, *Hartmann 1513* (BOL); between Vanrhynsdorp and Bitterfontein, *Ross-Frames s.n.* (BOL 34283); N of Clanwilliam, fl May 1941, *Van der Merwe X22* (PRE); Namaqualand, *Caporn* sub *NBG 899/15* (BOL); NW of Calvinia, *Goldblatt* sub *NBG 1085/82* (NBG, PRE).

--Doubtful locality: Carnarvon District, *De Villiers* sub *NBG 432/33* (BOL);

--Without locality: *Drege s.n.* (SAM 22397).

5.3 Subgenus Gemmaria

Subgenus **Gemmaria** (Salisb.) Snijman stat. nov. Type: *Strumaria gemmata* Ker-Gawl.

Gemmaria Salisb.: 127 (1866).

Bulbs with whitish or yellowish inner tunics. *Foliage leaves* spreading to prostrate, plane, lorate or ovate, at least 2,5 mm across, more or less pubescent or pustulate, at least in the juveniles. *Scape* mostly detaching at ground level at seed set. *Flowers* stellate to funnel-shaped; anthers subcentrifixed.

Species 16.

5.3.1 Section Cryptomeria

Cryptomeria Snijman, sect. nov., sectio foliis ciliatis plus quam 3 sed solis 2 exsertis, cataphyllo nullo diversa. Type: *Strumaria picta* W.F. Barker.

Bulb with whitish inner tunics. *Foliage leaves* spreading to prostrate, ciliate, usually more than 3, with only 2 exserted above ground, without a sheathing cataphyll. *Flowers* widely campanulate.

Species 1.

8. Strumaria picta W.F. Barker in Journal of South African Botany 9:145 (1943). Type: Cape, Calvinia division, Lokenberg, 12 May 1943, *Compton & party* sub *NBG 466/41* (NBG, holo.!; BOL!).

Bokkeveldia picta (W.F. Barker) D. & U. Müller-Doblies: 28 (1985).

Bulb solitary, ovoid, 25--45 mm diam., densely covered with felt-like greyish brown outer tunics, cream-coloured within; neck stout, up to 30 mm long. *Leaves* absent or incipient at anthesis, (2-) 3--4 (-5), appearing to be only 2 through reduction of the blades in other leaves, spreading, lorate, 40--150 x 12--30 mm, somewhat leathery, glaucous, with the edges plane or slightly revolute; abaxial surface flushed with pink at the base; margin densely ciliate with minute hairs; apex obtuse; subtended by a non-amplexicaul prophyll; cataphyll lacking; seedling more or less pubescent or rarely glabrous. *Inflorescence* somewhat clustered, 30--70 mm across; scape somewhat flexuose, 65--135 mm long, 2--3 mm diam., minutely pubescent, pale green to wine-red, persistent throughout fruiting then collapsing; spathe valves ovate-lanceolate, 13--15 x 3--5 mm; bracteoles up to 10 mm long. *Flowers* 5--11, more or less ascending, widely campanulate, white, broadly banded with reddish brown dorsally, becoming reddish brown with age, with a spicy scent; pedicels straight to somewhat upwardly curved, 10--30 mm long, minutely pubescent, red to green. *Tepals* free to the base, spreading, oblanceolate, 12,0--18,5 x 4,5--5,0 mm. *Stamens* shorter than the tepals, spreading slightly; filaments separate, up to 9 mm long, adnate to the style base, laterally expanded and with a longitudinal ventral ridge in the proximal half, tapering gradually distally; inner filaments broader than the outer; anthers subcentrifixed, ± 3 mm long before opening, dark red; pollen cream-coloured. *Ovary* with 3--5 ovules per locule, sometimes minutely pubescent. *Style* up to 12 mm long, narrowly ovoidal and shallowly 6-grooved in the proximal two thirds, tapering gradually distally, with 3 nectar droplets collecting between the base and inner filaments. *Seeds* 4--5 mm diam. *Chromosome number* $2n = 20$. Figure 9.23.

Flowering time: May to June. Cultivated bulbs flower from April.

Diagnostic features: Florally *S. picta* is recognised by its widely campanulate flowers; the broad brownish red median band on the abaxial surface of each tepal; the broadened filaments and ovoidal style. Vegetatively the species is differentiated by its spreading, lorate, glaucous leaves with the margins densely fringed with minute cilia.

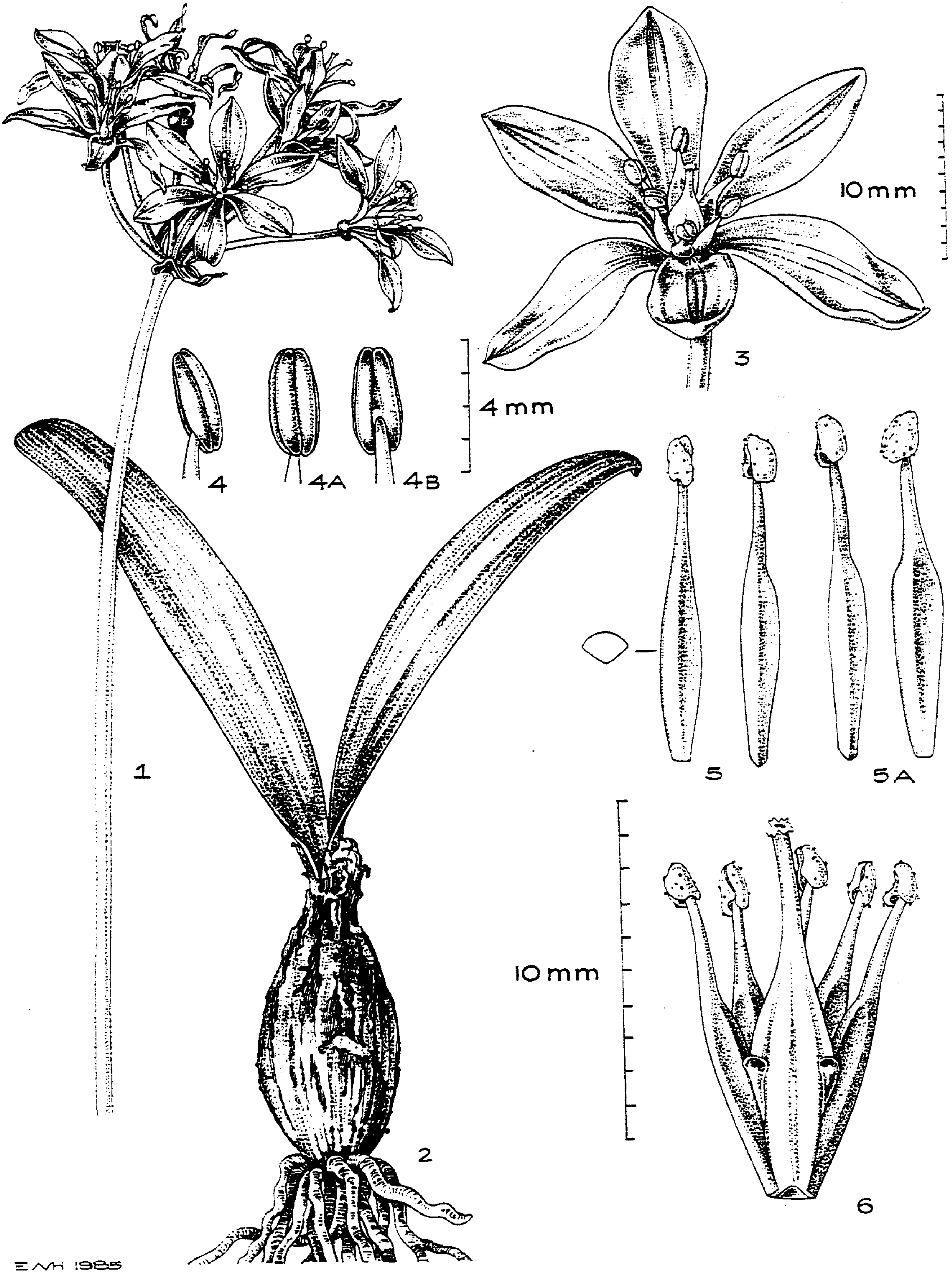


FIGURE 9.23-- *Strumaria picta*: 1, inflorescence, life size; **2**, vegetative habit, life size; **3**, whole flower; **4**, anther attachment, lateral view, **4A**, ventral view, **4B**, dorsal view; **5**, outer filaments, ventral view left,, lateral right,, **5A**, inner filaments, lateral view left,, ventral view right,; **6**, androecium and style with one stamen removed to show nectar droplets. Drawn from *Snijman 257*.

Strumaria picta is the only species in the genus in which one to three leaves with reduced leaf blades, remain hidden in the bulb. These are not comparable to the cataphylls of other species as they do not occur in a regular sequence from year to year.

Microscopic studies of the floral morphology show that the filaments are fused to the style. D. & U. Müller-Doblies' (1985) comment that they are free is based on inaccurate observation.

Distribution and habitat: Strumaria picta is localised in the Nieuwoudtville district in the north-western Cape, where it inhabits flats or gentle slopes, in greyish clayey soils, derived from shales of the Karoo Sequence (Figure 9.48). Although recorded from only three adjacent farms, the populations span several kilometers in extent.

Specimens examined

--3119 (Calvinia): Lokenberg (-CA), *Compton & party* sub *NBG 466/41* (BOL, NBG); farm Mensieskraal along the road to Lokenburg, fl 22 May 1980, *Snijman 257* (NBG); *Perry 1337* (NBG); farm Papkuilsfontein, fl 2 Jun 1989, *Snijman 1227* (MO, NBG, PRE).

--Imprecise locality: near Nieuwoudtville, *Leipoldt 4211* (BOL).

5.3.2 Section Gemmaria

Bulb with whitish or yellowish inner tunics. *Foliage leaves* 2 or rarely 3, exserted simultaneously above ground, sheathed basally by a cataphyll. *Flowers* stellate, borne on pedicels at least twice as long as the perigone or mostly well exceeding the perigone.

Species 10.

9. Strumaria discifera Marloth ex Snijman in Bothalia 22 (in press). Type: Cape, Bokkeveld Mountains, top of Koebee Pass, 18 April 1981, *Snijman 443* (NBG, holo.; K, PRE).

Bulbs solitary or forming large clumps, ovoid to subglobose, 10--20 mm diam., with outer tunics light brown and softly fibrous, white or occasionally pale mauve within; neck (10-) 20--60 mm long. *Leaves* absent or incipient at anthesis, 2 (-3), suberect to prostrate, narrowly lanceolate, 20--160 x 3--10 mm, pubescence variable, with long soft hairs or short hairs covering both surfaces or the adaxial surface only, rarely glabrous, sometimes flushed with red towards the base of the abaxial surface, with subacute tips, subtended by a subterranean amplexicaul cataphyll and non-amplexicaul prophyll. *Inflorescence* spreading, 25--130 mm across; scape somewhat flexuose, 50--140 mm long, ± 2 mm diam., green to reddish brown, variably pubescent to glabrous; usually breaking off at ground level while fruiting; spathe valves linear-lanceolate, up to 30 x 3 mm; bracteoles up to 5 mm long. *Flowers* (2-) 5--16, spreading, stellate, glistening white, with an olive-green to pink median dorsal stripe on each tepal, scented or scentless; pedicels straight to upwardly curved, 20--75 mm long, concolorous with the scape. *Tepals* free to base, outspread, with the outer whorl often deflexed, oblong-lanceolate, 4--7 x 1,5--3,0 mm, channelled, sometimes abruptly conduplicate in the proximal third. *Stamens* equalling or slightly shorter than the tepals, spreading; filaments separate, adnate proximally to the swollen style, with the inner whorl usually attached slightly higher up than the outer; anthers subcentrifixed, ± 2 mm long and wine-red before opening; pollen cream-coloured. *Ovary* with up to 1--3 ovules per locule. *Style* up to 7 mm long, equalling or shortly exceeding the stamens, variably dilated in the proximal half, either bulbiform or solidly cylindrical with a prominent irregular distal rim, narrowly terete in the distal half, with nectar collecting in 3 droplets between the base and inner filaments. *Seeds* 2,5--4,0 mm diam. *Chromosome number* $2n = 20$.

Flowering time: March to May.

Diagnostic features: In comparison to the closely allied pubescent-leaved species with white-fleshed bulbs and stellate flowers (*S. chaplinii* & *S. leipoldtii*), *S. discifera* has consistently long, narrow lanceolate leaves, distinctly channelled tepals and a bulbiform to discoid swelling at the base of the style.

Distribution and habitat: Strumaria discifera is distributed between Vanrhynsdorp and Nieuwoudtville eastwards to Calvinia in the north-western Cape (Figure 9.50).

Discussion: The species includes a polymorphic range of populations. From the dolerite koppies on the outskirts of Nieuwoudtville the bulbs are densely clump-forming, whereas other known populations comprise scattered aggregations of solitary bulbs. The shape of the swelling at the base of the style is also variable. The clump-forming bulbs have pronounced discoid stylar swelling with an irregular frilly rim. This character state is fairly consistent within the population and is probably maintained through recurrent vegetative propagation. Collections east of Nieuwoudtville to the Hantamsberg and Bloukranz Pass near Calvinia (*Perry 1014*, *Barker 9344*, *Bayer 1853*) also have a disc-like stylar swelling, but these are not as broad as those in the Nieuwoudtville populations and lack a prominent rim. Elsewhere in the distribution range the stylar swelling tends to be bulbiform in shape. Since the specimens from the clonal population from the doleritic koppies at Nieuwoudtville can be adequately diagnosed these are recognised as a separate subspecies.

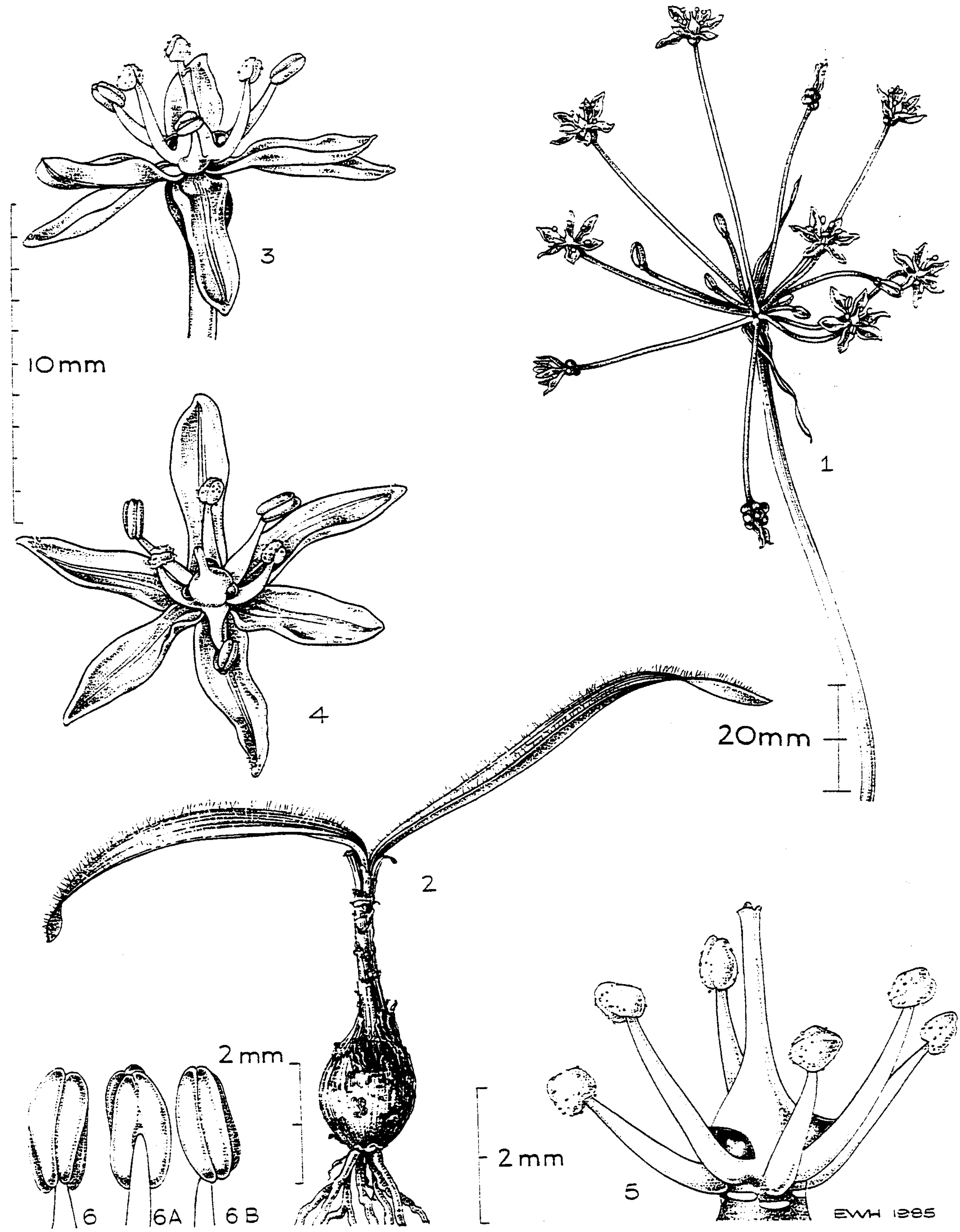


FIGURE 9.24-- *Strumaria discifera* subsp. *discifera*: **1**, inflorescence, life size; **2**, vegetative habit, life size; **3-4**, whole flowers; **5**, androecium and style; **6**, anther attachment, ventral view, **6A**, dorsal view, **6B**, lateral view. Drawn from *Snijman 261*.

9a. Strumaria discifera subsp. discifera

Bulbs solitary. *Leaves* 20--120 x 4--10 mm, with 1--3 mm long, soft patent white hairs, occasionally both surfaces glabrous but then juveniles pubescent. *Scape* glabrous. *Tepals* 5--6 x 1,5--3,0 mm, channelled evenly throughout. *Style* smoothly bulbiform or irregularly thickened and longitudinally ridged in the proximal quarter. Figure 9.24.

Distribution and habitat: The known distribution extends from near Vanrhynsdorp, eastwards onto the Bokkeveld escarpment, across the high-lying plateau to Calvinia, then south along the Roggeveld escarpment to near Middelpos.

Specimens examined

--3019 (Loeriesfontein): Kafferdam, about 6 km NW of Loeriesfontein on road to Kubiskouw Mountain (-CD), *Lavranos 27602* (NBG).

--3118 (Vanrhynsdorp): N banks of Wiedourivier, near bridge between Klawer and Vanrhynsdorp (-DA), *Snijman 261* (K, MO, NBG, PRE); top of Koebee Pass, Bokkeveld Mountains (-DB), fl 26 Apr 1988, *Snijman 1172* (NBG, PRE); *Snijman 443* (K, NBG, PRE).

--3119 (Calvinia): Glenridge (-AC), *Barker 4672* (NBG); Glen Lyon (-AC), fl 3 Apr 1982, *Perry 1824* (K, MO, NBG, PRE); *Mauve & Oliver* sub *G.N. 19699* (PRE); 5 miles E of Nieuwoudtville towards Calvinia (-AC), fl 18 Apr 1969, *Barker 10613* (NBG); 11 km E of Nieuwoudtville towards Calvinia (-AC), *Perry 1014* (MO, NBG, PRE); Akkerdam, lower slopes of Hantam Mountains (-BD), *Barker 9344* (NBG); Bloukranz Pass (-DA/DB), *Bayer 1853* (NBG); farm Blomfontein, Roggeveld escarpment (-DD), fr 10 May 1985, *Snijman 876* (NBG).

9b. Strumaria discifera subsp. bulbifera *Snijman* in Bothalia 22 (in press). Type: Cape, Nieuwoudtville Wildflower Reserve, 19 April 1983, *Perry & Snijman 2042* (NBG, holo.; K, MO, PRE, S).

Bulb producing bulblets and forming dense clumps. *Leaves* 6,5--150,0 x 3--10 mm, both surfaces covered with 2 mm long, white, patent hairs; adaxial surface flushed with red proximally. *Scape* minutely pubescent or glabrous. *Tepals* 5--7 x 2--3 mm, abruptly conduplicate at a point almost a third from the base, otherwise channelled; outer whorl slightly deflexed. *Style* discoid proximally, with a prominent irregular rim on the disc distally, abruptly narrowed into a slender column above. Figure 9.25.

Distribution and habitat: The subspecies inhabits slopes and hollows of low exposed dolerite ridges on the Bokkeveld escarpment near Nieuwoudtville. The population is composed of dense aggregations of clumped bulbs in deep, red loamy soils, in

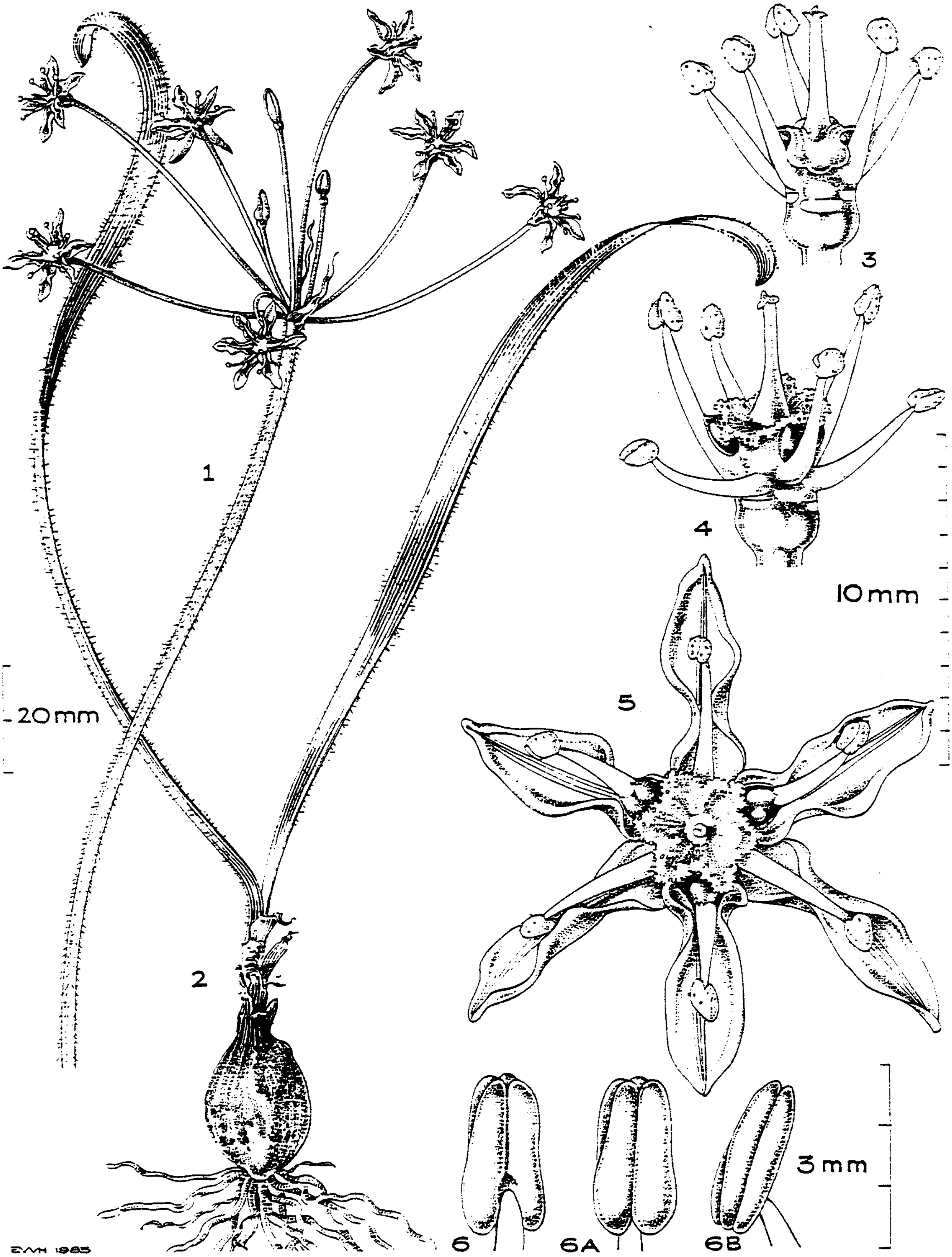


FIGURE 9.25– *Strumaria discifera* subsp. *bulbifera*: 1, inflorescence life size; 2, vegetative habit, life size; 3-4, flowers with tepals removed to show varied style sculpturing; 5, whole flower; 6, anther attachment, dorsal view, 6A, ventral view, 6B, lateral view. Drawn from *Perry & Snijman 2042*.

association with open low, succulent shrubland.

Cape.--3119 (Calvinia): Meulsteen Vley (-AC), fl May 1927, *Watermeyer* in *Herb. Afr. Bol. 18648* (BOL); top of Vanrhyns Pass (-AC), fl 30 Apr 1946, *Smith 6490* (NBG); farm Glen Lyon (-AC), fl May 1985, *Snijman 863* (NBG, PRE); Nieuwoudtville Wildflower Reserve (-AC), fl 19 Apr 1983, *Perry & Snijman 2042* (K, MO, NBG, PRE, S).

10. Strumaria unguiculata (W.F. Barker) Snijman, comb. nov. Type: Cape, Clanwilliam division, 1--2 miles S of Doorn River Bridge, near Doornbosch, 11 May 1934, *Salter 4441* (SAM, holo.!; BOL!, K!): [holotype not in NBG as indicated by Müller-Doblies (1985) but in SAM].

Hessea unguiculata W.F. Barker: 33 (1935). *Periphanes unguiculata* (W.F. Barker) Leighton: 82 (1948). *Gemmaria unguiculata* (W.F. Barker) D. & U. Müller-Doblies: 30 (1985).

Bulb solitary, large, ovoid, 25--40 mm diam., with densely fibrous, light brown to cream-coloured outer tunics, whitish within; neck stout, up to 100 mm long. *Leaves* absent or incipient at anthesis, 2 (-3), suberect to recurved, elliptical-lanceolate to broadly elliptical, 70--200 x (15-) 30--60 mm, usually distinctly narrowed at the base to 5--10 mm across, light green, occasionally flushed with red towards the base of the abaxial surface, thin-textured with the edges often more or less undulate or conduplicate; margin smooth or minutely ciliate; apex subacute; amplexicaul cataphyll shortly exserted, green, soon dying back; non-amplexicaul prophyll subterranean. *Inflorescence* spreading widely, 60--100 mm across; scape stout, somewhat flexuose, 80--350 mm long, 2--5 mm diam., green to deep wine-red with a slight grey bloom, persisting throughout fruiting and breaking loose thereafter; spathe valves lanceolate, 23--30 x 3--6 mm; bracteoles up to 5 mm long. *Flowers* (7-) 11--24, spreading, shallowly campanulate, glistening, white with a wine-red median dorsal stripe on each tepal, turning translucent with age, with a strong spicey scent; pedicels straight to upwardly curved, 20--66 mm long, varying from reddish green to pink or deep wine-red. *Tepals* free to the base, upwardly curved in the proximal half, outspread in the distal half, ovate-lanceolate, 8--13 x 4,0--6,5 mm, distinctly clawed at the base forming conspicuous windows between adjacent tepals, usually conduplicate towards the apex of the inner whorl. *Stamens* equalling the tepals, spreading; filaments separate, subulate, up to 8 mm long, adnate to the broadened style base, somewhat bulbous proximally, subulate towards the apex; anthers subcentrifixed, ± 4 mm long before opening, wine-red; pollen cream-coloured. *Ovary* with up to 3--5 (-6) ovules per locule. *Style* up to 10 mm long, more or less equalling the stamens, broad and depressed-conoidal basally, elongated into an evenly tapered terete column distally. *Seeds* 2,5--3,0 mm diam. *Chromosome number* $2n = 20$. Figure 9.26.

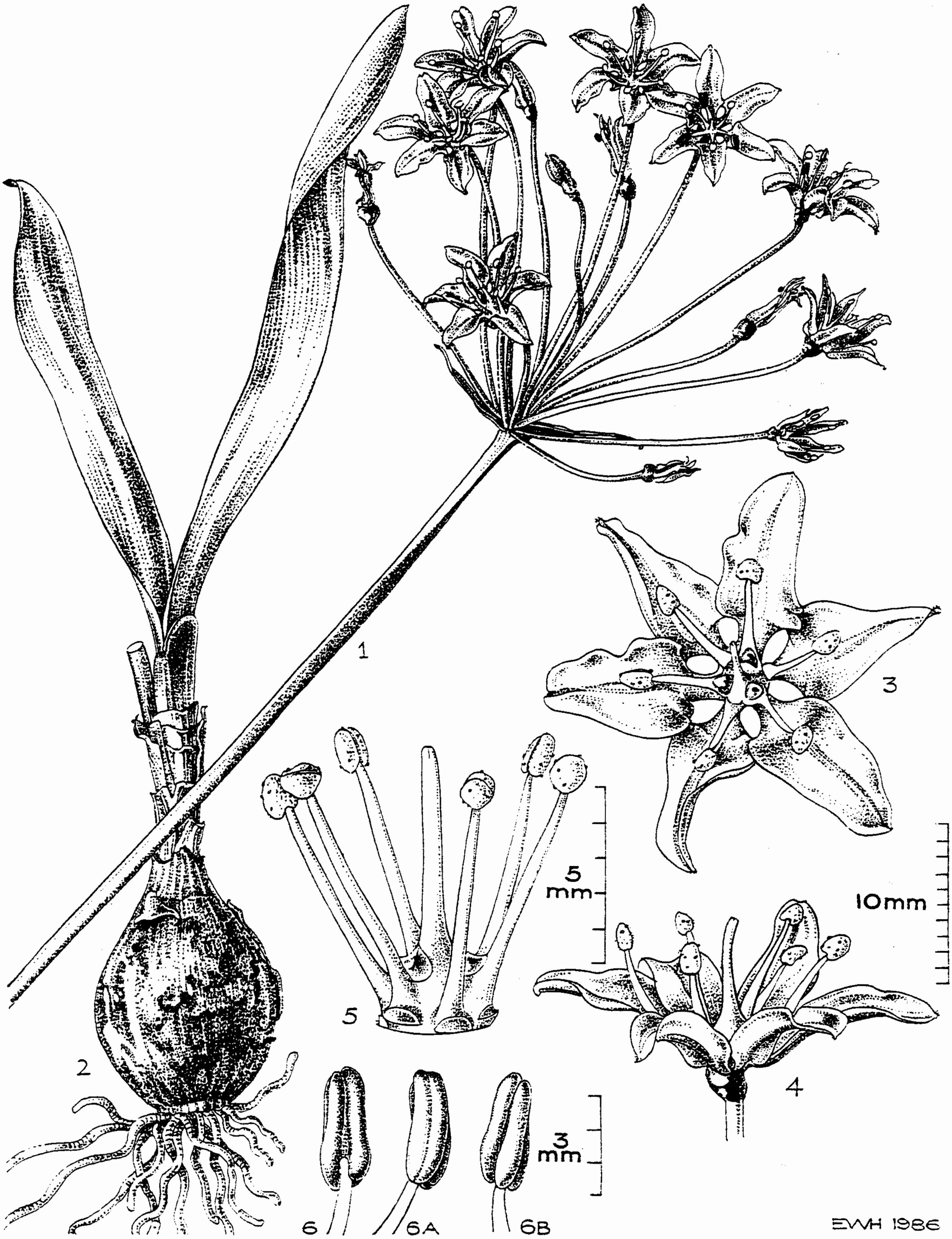


FIGURE 9.26-- *Strumaria unguiculata*: 1, inflorescence, life size; **2**, vegetative habit, life size; **3-4**, whole flowers; **5**, androecium and style; **6**, anther attachment, dorsal view, **6A**, lateral view, **6B**, ventral view. Drawn from *Lavranos 18977*.

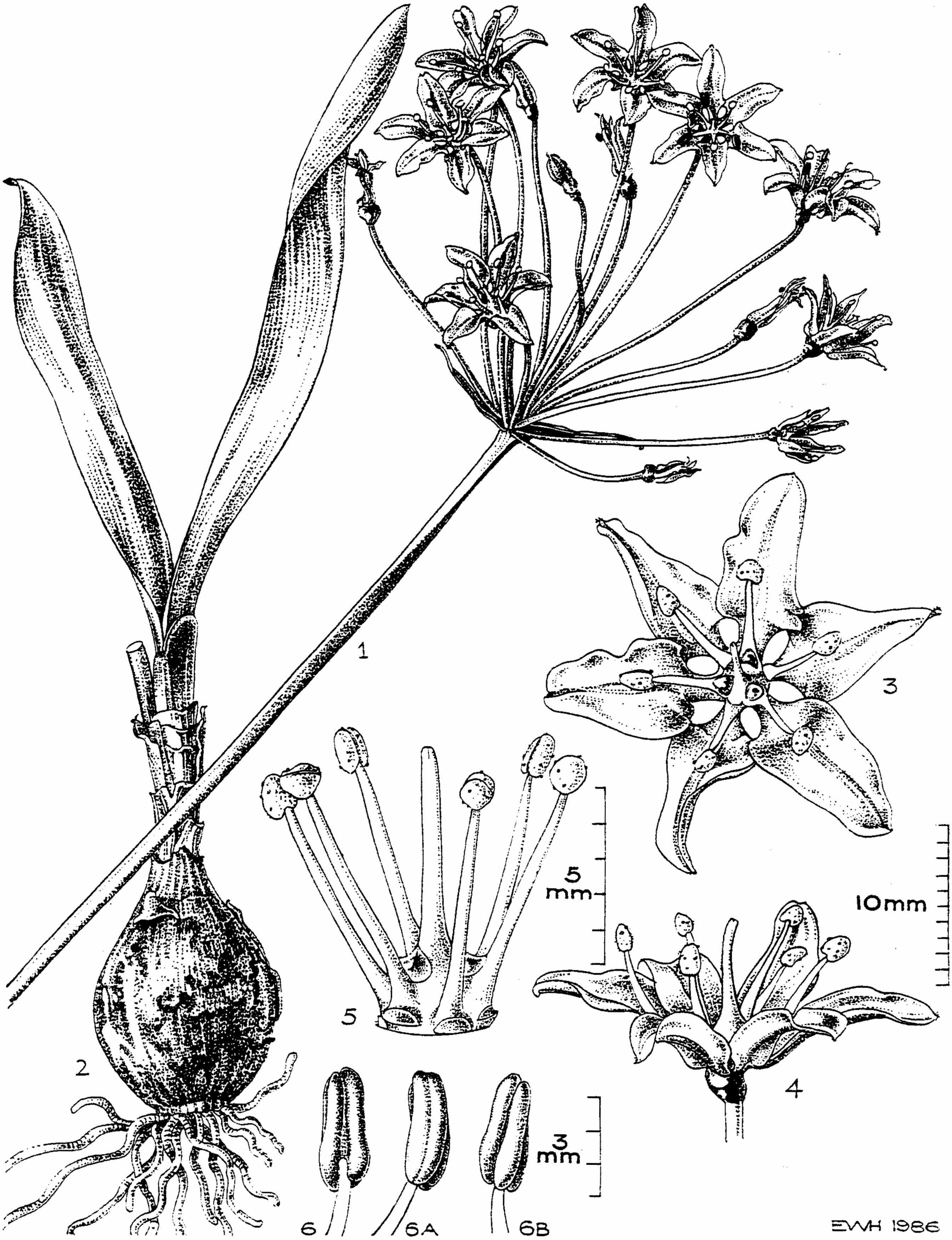


FIGURE 9.26-- *Strumaria unguiculata*: 1, inflorescence, life size; 2, vegetative habit, life size; 3-4, whole flowers; 5, androecium and style; 6, anther attachment, dorsal view, 6A, lateral view, 6B, ventral view. Drawn from *Lavranos 18977*.

Flowering time: May but shifting to April when cultivated.

Diagnostic features: As the specific epithet suggests, the distinctly clawed tepals are diagnostic for the species. In addition, the abrupt broadening of the tepals above the proximal claw creates characteristic "windows" between adjacent tepals at the base of the flower. The leaves also readily distinguish the species and are charateristically broad (usually 30--60 mm across), thin-textured, with the edges somewhat undulate or conduplicate. The closest ally is *S. karoopoortensis*, which occurs as an isolated population in the more arid Tanqua Karoo to the south east. Both species share a great likeness with respect to size in all their parts. See discussion of *S. karoopoortensis* for distinguishing characteristics.

Distribution and habitat: Strumaria unguiculata is recorded only from near Doornbosch on the lower northern slopes of the Anysberg, north east of Clanwilliam, at approximately 180 m (Figure 9.48). Situated a few kilometers to the east of the locality is the Doringrivier, which forms a deep divide between the mountain ranges on either side of its course. The bulbs grow in heavy loamy soil covered with slate chips and rocks. The predominant cover is provided by *Atriplex lindleyi* Moq. subsp *inflata* (Muell.) P.G. Wilson and succulent species of *Euphorbia*.

Specimens examined

--3119 (Calvinia): Doornbosch (-CC), fl 17 May 1958, *Hall 1402* (NBG); fl 17 May 1947, *Barker* sub *NBG 223/47* (NBG); *Lewis* sub *NBG 1824/37* (NBG); 1--2 miles S of Doorn River bridge, near Doornbosch (-CC), fl 11 May 1934, *Salter 4441* (BOL, K, SAM), *Barker 6555* (NBG); fl 11 May 1934, *Galpin 12939* (K, PRE); 1 km W of Doringrivier towards Pakhuis Pass (-CC), *Lavranos* & *Pehlemann 18977* (NBG, PRE); approximately 3 km S of Doring River bridge (-CC), fl 6 May 1985, *Snijman 854* (K, MO, NBG, PRE); near Doornbosch (-CC), *Lewis 2381* (SAM).

11. **Strumaria karoopoortensis** (D. & U. Müller-Doblies) Snijman, comb. nov. Type: Cape, near Karoopoort, S facing slope, ca. 800 m, 30 July 1982, *Müller-Doblies 8218a* (PRE, holo.!; B, K, M, MO, NBG, Herb. M-D.).

Gemmaria karoopoortensis D. & U. Müller-Doblies: 30 (1985).

Bulb solitary, subglobose, 27--40 mm diam., with outer tunics usually densely fibrous and light brown, yellowish within, neck (30-) 50--100 mm long. *Leaves* absent at anthesis, 2 (-3), recurved to procumbent, ovate to broadly lorate 75--250 x 20--53 mm, glabrous or sparsely ciliate with hairs up to 2 mm long, flaccid, glaucous-green; apex subacute to obtuse; subtended by a subterranean amplexicaul cataphyll and non-amplexicaul prophyll; seedlings more or less pubescent. *Inflorescence* spreading widely,

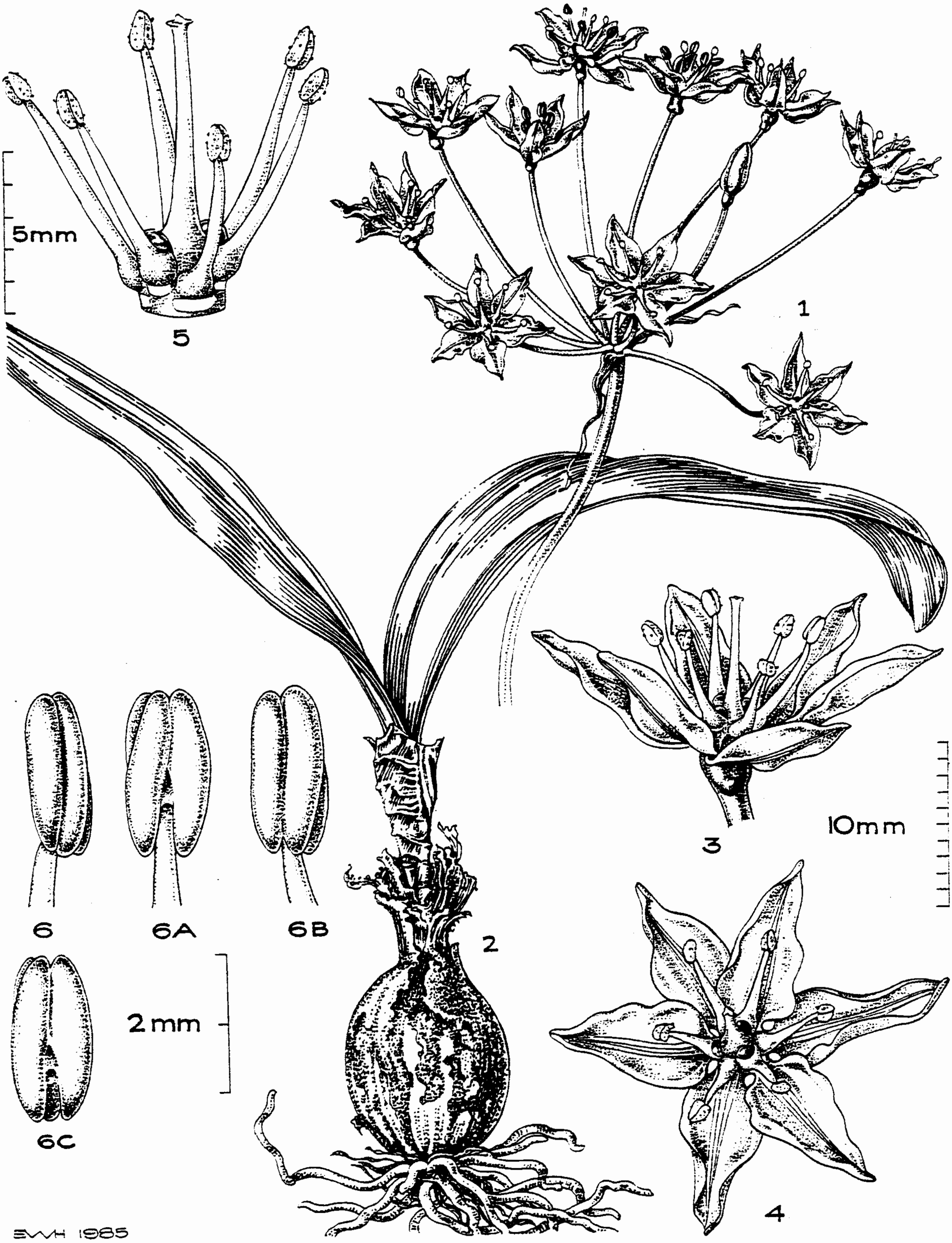


FIGURE 9.27-- *Strumaria karoopoortensis*: 1, inflorescence, life size; 2, vegetative habit, life size; 3-4, whole flowers; 6, anther attachment, lateral view, 6A, dorsal view, 6B, ventral view, 6C, anther showing subcentrifixed insertion. Drawn from *Snijman 854*.

80--110 mm across; scape stout and erect, 135--180 mm long, 2--3 mm diam., glaucous-green, breaking off at the base in fruit; spathe valves lanceolate, 20--30 x 2--5 mm; bracteoles up to 7 mm long. *Flowers* 11--16, spreading, stellate, white, marked with a deep pink median stripe on each tepal, sometimes suffused with green apically, becoming increasingly flushed with deep pink with age, scentless; pedicels straight to upwardly curved, glaucous-green, 40--65 mm long. *Tepals* free to the base, spreading, ovate-lanceolate, 10--14 x 3,5--6,0 mm, shortly clawed at the base, sometimes forming small windows between adjacent tepals, conduplicate apically. *Stamens* equalling the tepals, spreading; filaments separate, adnate to the broadened style base, distinctly bulbous at the base, subulate above, up to 8 mm long; anthers subcentrifixed, ± 3 mm long before opening, deep pink; pollen cream-coloured. *Ovary* with up to 2--5 ovules per locule. *Style* up to 10 mm long, equalling the stamens, broad and depressed-conoidal basally, elongated into an upwardly tapered terete column distally, with nectar collecting in 3 droplets between the base and inner filaments. *Seeds* 3--5 mm diam. *Chromosome number* 2*n* = 20. Figure 9.27.

Flowering time: March, both in the wild and in cultivation.

Diagnostic features: Strumaria karoopoortensis is most closely related to *S. unguiculata*. Both species have the broadest leaves (up to 50 mm or more across) and the longest (10--14 mm) and broadest tepals (3,5--6,5 mm wide) of all the stellate-flowered species of *Strumaria*. Several differences separate *S. karoopoortensis* from *S. unguiculata*, namely the yellowish inner tunics of the bulb and the flaccid leaves. Furthermore the flowers are scentless and the tepals, which are slightly undulate along the edges, become conduplicate apically. With age the pigmentation of the tepals is accentuated, whereas in *S. unguiculata* the ageing flowers become translucent.

Distribution and habitat: This rare species is only known from an isolated elevated outcrop, which rises approximately 100 m above the otherwise flat, wind-eroded Tanqua Karoo, just north east of Karoopoort (Figure 9.48). The bulbs cling to the southern and eastern slopes of this inselberg between shale slabs, amongst extremely sparse succulent vegetation.

Specimens examined

--3319 (Worcester): Fonteinskop, NE of Karoopoort towards Sutherland (-BB), *Perry 194* (NBG); *Perry 1278* (NBG); near Karoopoort (-BB), *Müller-Doblies 8218a* (PRE).

12. Strumaria villosa Snijman in Bothalia 22 (in press). Type: Cape, Richtersveld, latitude 29° 10,05', longitude 17° 41, 49', E of Kosies, 3200 ft, 29 Mar 1981, *Van Berkel 311* (NBG, holo.; K, PRE).

Bulb solitary, subglobose, 15--25 mm diam., with light brown lightly fibrous outer tunics, yellowish within; neck up to 35 mm. *Leaves* absent at anthesis, 2, prostrate, narrowly elliptical to lorate, 30--85 x 10--15 mm; adaxial surface glaucous, covered with 2,5 mm long, soft white patent hairs; abaxial surface glabrous, shiny green, subtended by a subterranean amplexicaul cataphyll and non-amplexicaul prophyll. *Inflorescence* spreading, 30--100 mm across; scape slightly flexuose, 60--140 mm long, 2--3 mm diam., pale green to pink with a grey bloom, breaking loose at the base in fruit; spathe valves linear-lanceolate, 15--20 x 4 mm; bracteoles up to 5 mm long. *Flowers* 8--14, spreading, stellate, pure white or white to pink with a pale pink median dorsal stripe on each tepal, scentless; pedicels straight to upwardly curved, 35--80 mm long, concolorous with the scape. *Tepals* free to the base, outspread to slightly deflexed, oblong-lanceolate, 6,5--8,5 x 2--3 mm, distinctly channelled with undulate margins proximally. *Stamens* equalling or slightly shorter than the tepals, spreading; filaments separate, adnate to the broadened style base, with the inner whorl attached higher up than the outer, broad but not bulbous basally, tapering slightly upwards; anthers subcentrifixed, 1,5 mm long and wine-red before dehiscing; pollen whitish. *Ovary* with up to 4 ovules per locule. *Style* up to 5 mm long, more or less equalling the stamens, tapering smoothly upwards from a broad obscurely conoidal base, with nectar collecting in 3 droplets between the base and inner filaments. *Seeds* ± 2 mm diam. *Chromosome number* $2n = 20 + 2\text{--}3B$. Figure 9.28.

Flowering time: March to April.

Diagnostic features: Like *S. chaplinii, S. discifera* and *S. leipoldtii*, this species has the plesiomorphic character state of retaining the long soft pubescence on the leaves into maturity. The leaves of *S. villosa* are softly villous on only the adaxial surface and characteristically glaucous. Unlike the other pubescent-leaved species of subsection Gemmaria, *S. villosa* has the derived character state of yellow inner bulb tunics, which suggests a close affinity to *S. merxmuelleriana*: a species which becomes hairless at maturity and co-occurs with *S. villosa* near Kosies in the grid square 2917BA. Although close morphologically, *S. villosa* and *S. merxmuelleriana* occupy distinct habitats and they retain their vegetative differences in cultivation.

Distribution and habitat: This rare species is known from only one locality in the southern Richtersveld near Kosies, north of Springbok. Bulbs are locally abundant on open, exposed, east-facing slopes amongst quartz pebbles, overlying weathered granite soil (Figure 9.49).

Specimens examined

--2917 (Springbok): Latitude 29° 10,05', longitude 17° 41,49' east of Kosies (-BA), 2 Aug 1980, *Van Berkel 156* (NBG); 29 Mar 1981 *Van Berkel 311* (K, NBG, PRE); *Perry 1544* (K, MO, NBG, PRE, S).

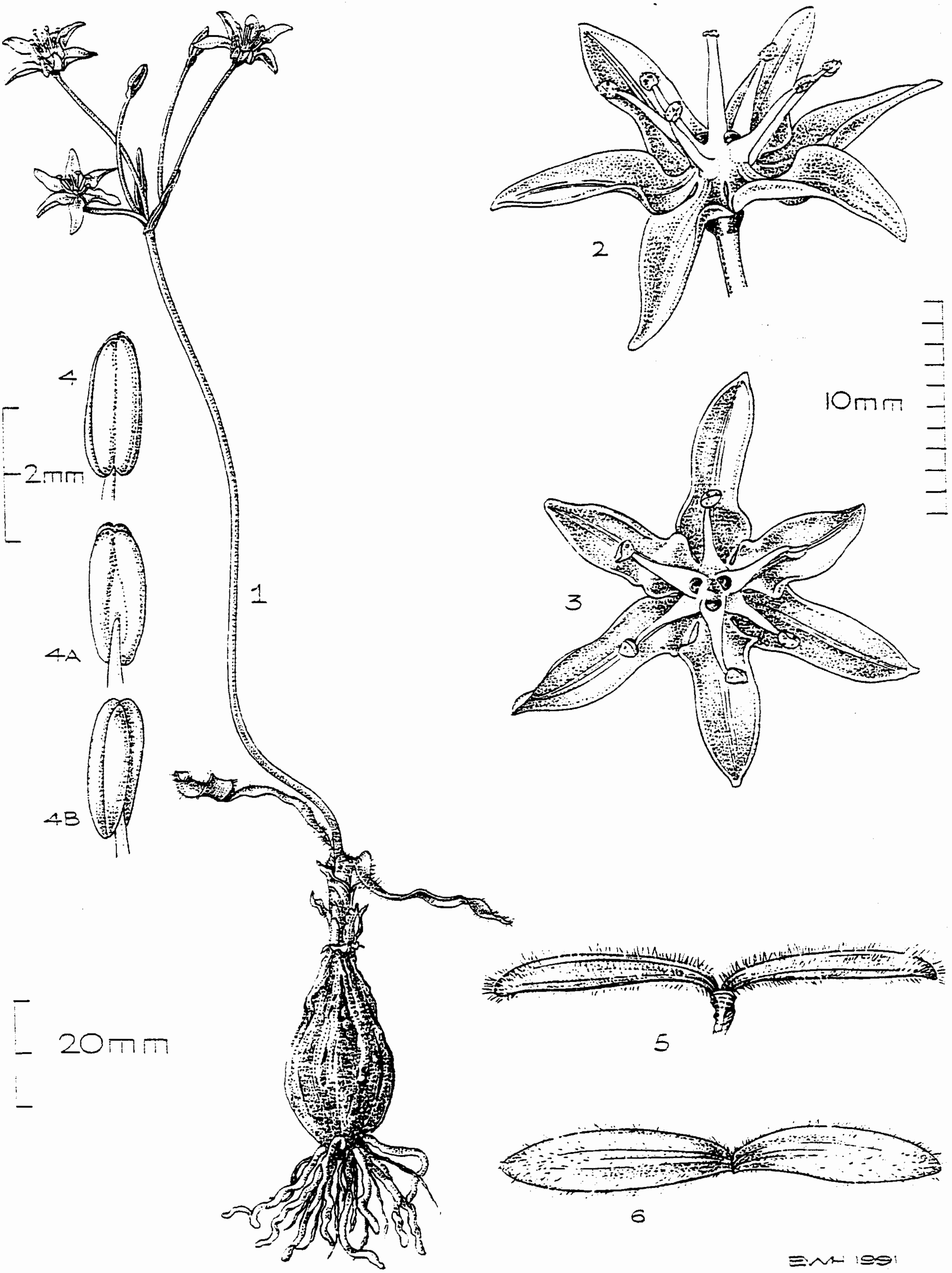


FIGURE 9.28-- *Strumaria villosa*: 1, inflorescence; 2-3, flowers indicating the attachment of the filaments to the style base and nectar droplets between the inner filaments and style; 4, anther attachment, dorsal view; **4A**, ventral view; **4B**, lateral view; **5-6**, vegetative habit. Drawn from *Van Berkel 156.*

13. Strumaria merxmuelleriana (D. & U. Müller-Doblies) Snijman, comb. nov. Type: Cape, Klipdam Golf Course, 3,5 km W of Okiep, 11 March 1979, *Müller-Doblies 79113c* (PRE, holo.!; B, GRA, K!, M, MO, NBG, S, STE, Z, Herb. M-D.).

Gemmaria merxmuelleriana D. & U. Müller-Doblies: 34 (1985).

Bulb solitary, ovoid, 15--19 mm diam., covered with lightly fibrous light brown outer tunics, yellowish within; neck up to 50 mm long. *Leaves* absent at anthesis, 2, usually appressed to the ground, occasionally ascending, ovate, 15--20 (-50) x 7--18 mm; adaxial surface dark shiny green, minutely scabrid around the edges and on the margin; abaxial surface light green, smooth; subtended by an amplexicaul cataphyll and non-amplexicaul prophyll. *Inflorescence* slightly spreading, 20--40 mm across; scape straight to flexuose, 40--100 mm long, 1--2 mm diam., green becoming reddened proximally; spathe valves narrowly lanceolate, 10--20 x 2 mm; bracteoles up to 3 mm long. *Flowers* 5--12, very widely funnel-shaped, pale pink, flushed with pink medianly, ageing to reddish pink, scentless; pedicels straight, 15--40 mm long, rosy-green. *Tepals* free to the base, spreading, oblong-lanceolate, 6,5--7,5 x 1,8--2,5 mm, with involute edges. *Stamens* more or less equalling the tepals, closely surrounding the style; filaments separate, up to 6 mm long, adnate to the slightly thickened style base, both whorls only slightly thickened basally, tapering smoothly distally; anthers subcentrifixed, ± 1,5 mm long and deep pink before opening; pollen cream-coloured. *Style* up to 8 mm long, equalling the stamens, narrowly conoidal proximally, tapering gradually distally, with nectar collecting between the base and the inner filaments. *Seeds* unknown. *Chromosome number* 2*n* = 20. Figure 9.29.

Flowering time: April.

Diagnostic features: Apart from its relationship with *S. villosa*, *S. merxmuelleriana* also forms a close alliance with *S. massoniella* and *S. karooica*, which occur to the south east in Bushmanland and on the Roggeveld escarpment. *Strumaria merxmuelleriana* and the latter two species have yellow-fleshed bulbs and more or less ovate leaves, which are appressed to the ground. The minute scabrid papillae are more prominently developed around the leaf edges in *S. merxmuelleriana* than in *S. massoniella* or *S. karooica*. The flowers of *S. merxmuelleriana* have a distinctly narrower style base than those in related species; the base of the filaments are not as broad and the stamens remain close to the style. Neither filament whorl is conspicuously broader than the other. This contrasts strongly with the flowers of *S. karooica* which have a flat, wide-open appearance and plane tepals, but less so with the flowers in *S. massoniella*, which differs vegetatively by the typically "hump-backed" leaves. The marked difference in length between the filaments and style noted by D. & U. Müller-Doblies (1985), was not apparent in the more

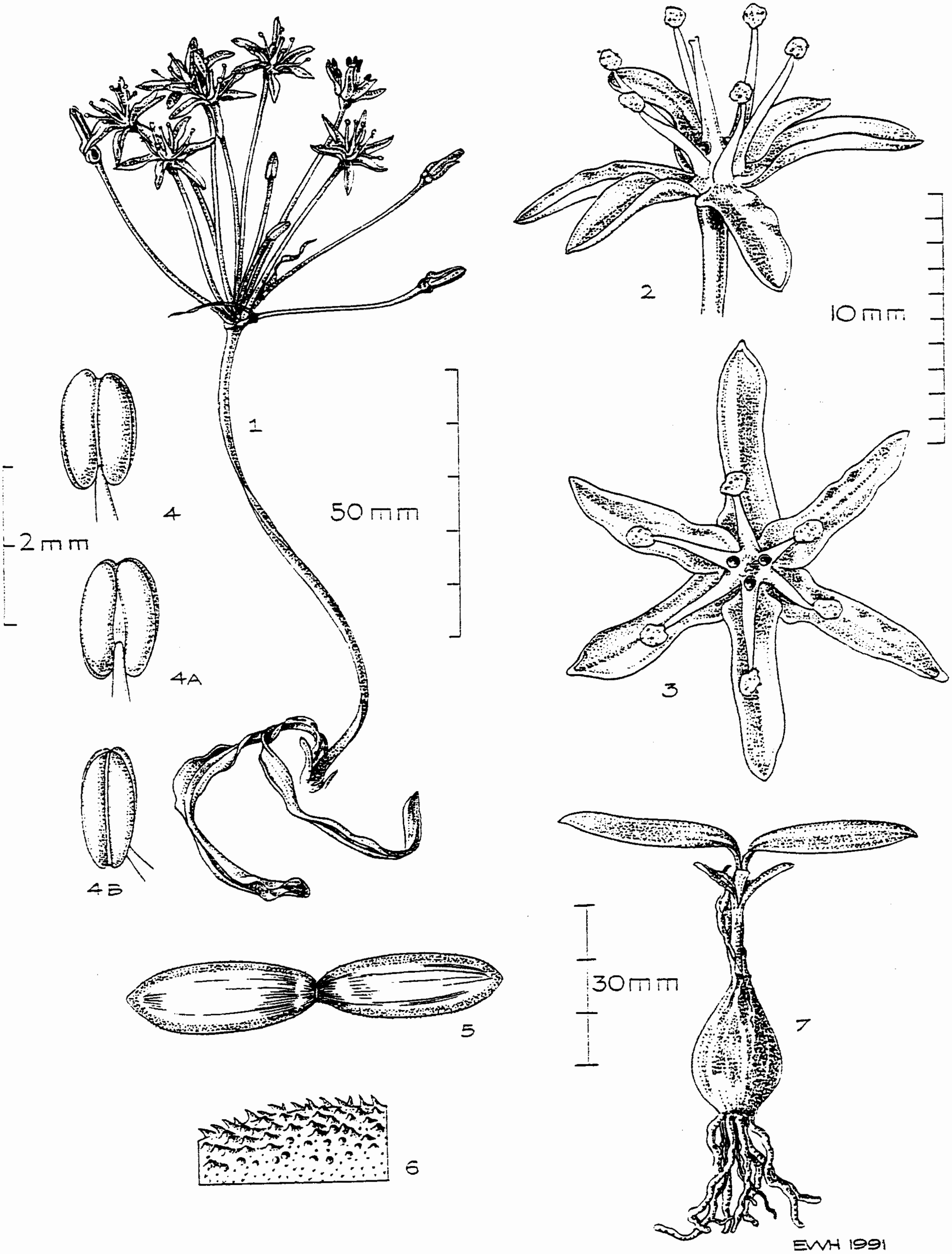


FIGURE 9.29-- *Strumaria merxmuelleriana* 1, inflorescence; 2-3, flowers showing small nectar droplets as base of narrow inner filaments; 4, anther attachment, dorsal view, 4A, ventral view; 4B, lateral view; 5, upper leaf surfaces showing rough edges; 6, close up of scabrid edge of adaxial leaf surface; 7, vegetative habit. Drawn from *Williamson 3669*.

recently discovered specimens (*Williamson 3669, Williamson 3676* and *Snijman 306*).

Distribution and habitat: Known only from the elevated area of the Springbok district where the bulbs grow in sandy soils, along seasonal watercourses, under bushes or in the open (Figure 9.48).

Specimens examined

--2917 (Springbok): approximately 2 km S of Kosies (-BA), fl 1 Apr 1987, *Williamson 3669* (NBG); fl 26 Apr 1987, *Williamson 3676* (NBG); Klipdam golf course, 3,5 km W of Okiep (-DB), *Müller-Doblies 79113c* (K, PRE); near turnoff to farm Nooitgedacht, 23 km from Springbok to Wildepaardehoek Pass (-DD), *Snijman 306* (NBG, PRE).

14. **Strumaria massoniella** (D.& U. Müller-Doblies) Snijman, comb. nov. Type: Cape, E of Gifkop, 5 km E of Kromrivier on Loeriesfontein/Kliprand road, 10 Aug 1980, *Müller-Doblies 80077c* (PRE, holo.!; B, GRA, GZU, K!, M, MO, NBG, S, STE, Z, Herb. M-D.).

Gemmaria massoniella D. & U. Müller-Doblies: 33 (1985).

Bulb solitary, ovoid, 15--19 mm diam., with a fine felt-like covering, pale yellow within; neck 50--80 mm long. *Leaves* absent at anthesis, 2, appressed to the ground, ovate to suborbicular, 23--30 (-50) x 18--23 mm, convex on the adaxial surface, concave on the other; adaxial surface with dense marginal hairs 0,5--1,0 (-1,3) mm long, otherwise glabrous. *Inflorescence* slightly to widely spreading, 60--70 mm across; scape flexuose, 80--120 mm long, 2--5 mm diam., dark wine-red proximally, leaden-grey above; spathe valves lanceolate, 13--25 x 2--5 mm; bracteoles up to 3,5 mm long. *Flowers* 9--14, initially somewhat clustered, spreading later, stellate, pale pink, with an olive green dorsal median stripe on each tepal, ageing to deeper pink, scented; pedicels straight, 25--43 mm long, leaden-grey flushed with pink. *Tepals* free to the base, outspread or occasionally slightly deflexed, oblong-lanceolate 3,5--8,5 x 1,2--2,0 mm, channelled. *Stamens* equalling or slightly shorter than the tepals, widely spreading; filaments separate, up to 5 mm long, adnate to the broadened style base, somewhat bulbous proximally subulate distally; anthers subcentrifixed, 1,8 mm long and wine-red before opening; pollen cream-coloured. *Ovary* with an unknown number of ovules. *Style* slightly exceeding the stamens, up to 9 mm long, depressed-conoidal basally, extending into narrowly tapering terete column distally, with nectar collecting in 3 droplets between the base and inner filaments. *Chromosome number* unknown. Figure 9.30.

Flowering time: Only known in cultivation. April to May, at Kirstenbosch Botanic Garden.

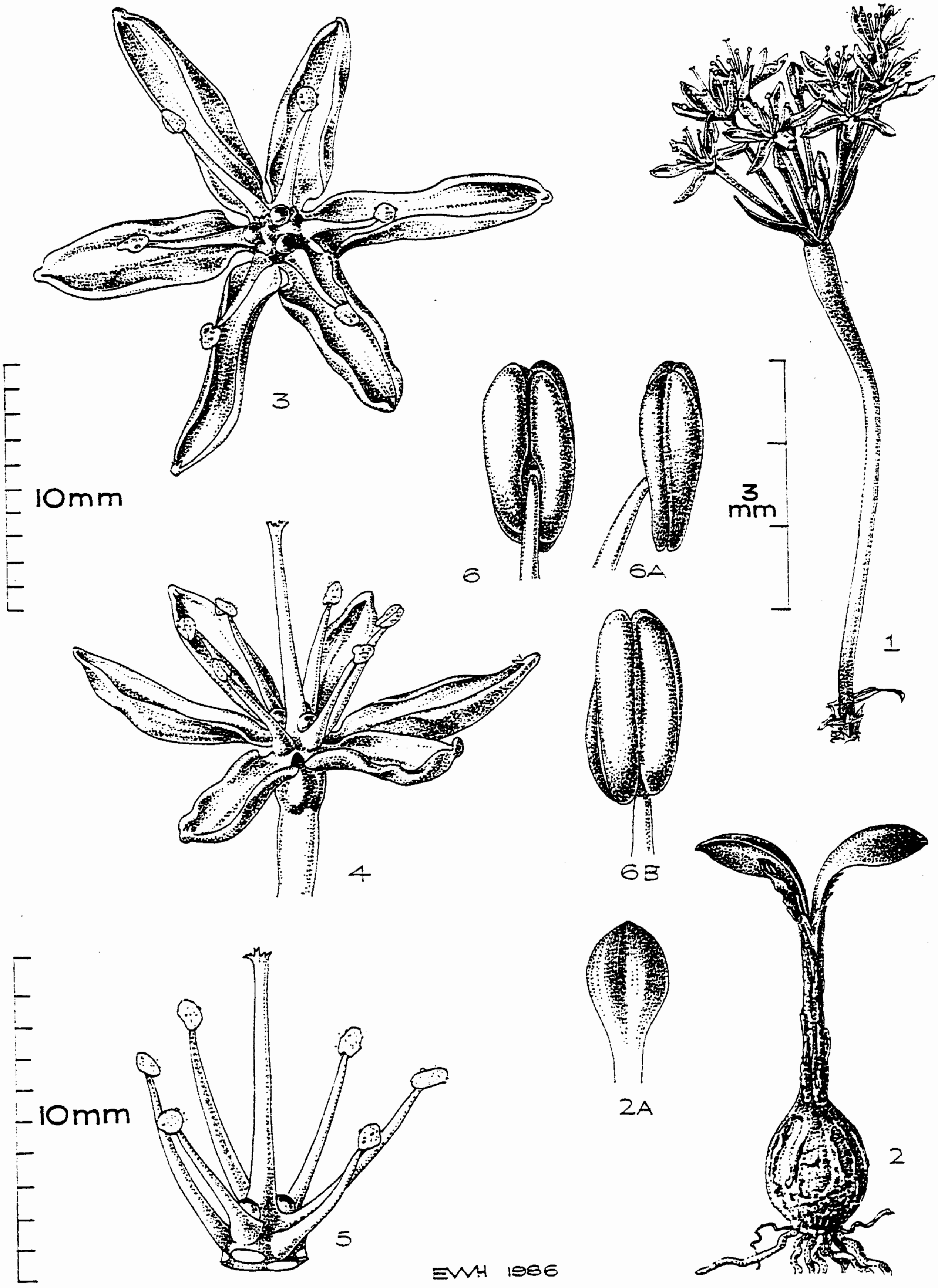


FIGURE 9.30-- *Strumaria massoniella*: **1**, inflorescence, life size; **2**, vegetative habit, life size, **2A**, adaxial leaf surface; **3-4**, whole flowers; **5**, androecium and style; **6**, anther attachment, dorsal view, **6A**, lateral view, **6B**, ventral view. Drawn from *Schelpe 8218*.

Diagnostic features: This poorly known species is closely related to *S. merxmuelleriana* and *S. karooica*. The original diagnosis of *S. massoniella* stresses that leaf position and leaf covering distinguish it from its allies. The appressed leaves are stated to distinguish it from *S. karooica* and the ciliate leaves to separate it from *S. merxmuelleriana* (Müller-Doblies 1985). Field studies have since shown that appressed leaves are characteristic of *S. karooica* in nature, unlike the erect leaves shown in Barker's illustration (Barker 1935), probably drawn from a bulb in cultivation. Furthermore, leaf pubescence in *S. karooica* has been observed to be somewhat variable. The leaves are usually glabrous with minutely scabrous margins, but occasionally the adaxial surface may be softly and sparsely pubescent, with hairs up to 3 mm long. These characters therefore do not reliably retain their diagnostic value. Thus, from current data, the only characters which remain to distinguish *S. massoniella* are the typically "hump-backed" appearance of the leaves. The flowers, which have channelled tepals, are very similar to those of *S. merxmuelleriana* but unlike those of *S. karooica* with plane tepals. *Strumaria massoniella* inhabits a region of extremely unreliable rainfall, a factor which appears to limit flowering. The discovery of further plants during a favourable season may resolve the uncertain status of this taxon, but until such material becomes available, *S. massoniella* is maintained as a separate species on the basis of its uniquely shaped leaves.

Distribution and habitat: Strumaria massoniella is sparsely scattered on sandy plains west of Loeriesfontein towards Vaalputs in western Bushmanland, a flat semi-arid region with an elevation of 1000 m and a sparse covering of low succulent shrubs (Figure 9.48).

Specimens examined

--3018 (Kamiesberg): Vaalputs (-BA), *Schelpe 8218* (NBG).

--3019 (Loeriesfontein): E of Gifkop, 5 km E of Kromrivier on Kliprand road (-CC), *Müller-Doblies 80077c* (K, PRE).

15. **Strumaria karooica** (W.F. Barker) Snijman, comb. nov. Syntypes: Cape, Laingsburg division, Matjiesfontein, *J.D. Logan & J. Archer* 1933, April 1915, *Pearson* sub *NBG 2499/14* (BOL), lecto.!, here designated.

Hessea karooica W.F. Barker: 32 (1935). *Periphanes karooica* (W.F. Barker) Leighton: 82 (1948). *Gemmaria karooica* (W.F. Barker) D. & U. Müller-Doblies: 33 (1985).

Bulb ovoid, 15--25 mm diam.; outer covering fibrous, cream to brown; inner tunics yellowish; neck absent or reaching up to 40 mm long. *Leaves* absent at anthesis, 2, usually appressed to the ground, occasionally suberect, varying from obovate to ovate, elliptical or elliptical-lanceolate, 18--60 x 15--20 mm, narrowed to 2--4 mm at the base,

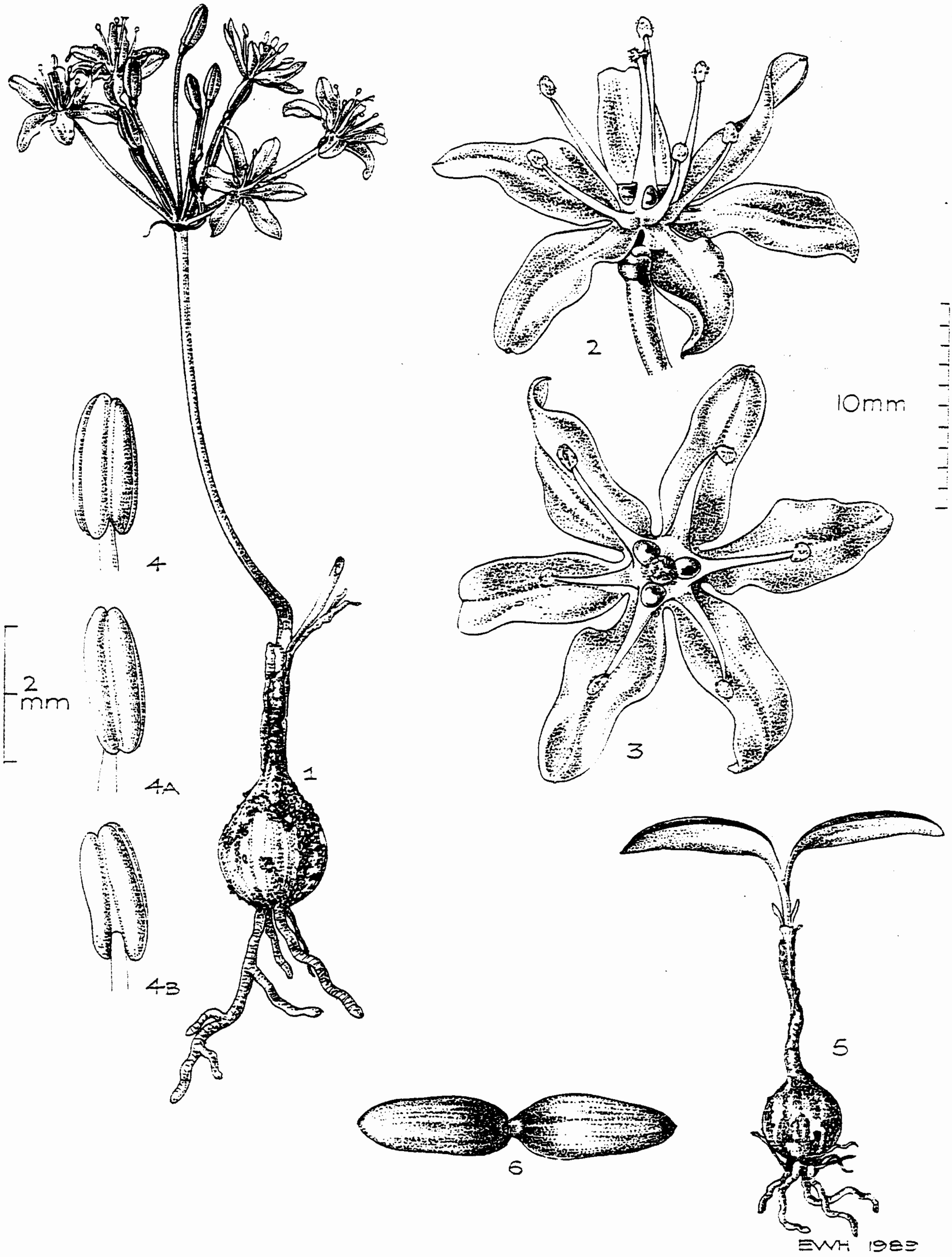


FIGURE 9.31-- *Strumaria karooica*: **1**, flowering habit, life size; **2-3**, whole flowers; **4**, anther attachment, ventral view, **4A**, lateral view, **4B**, dorsal view; **5**, vegetative habit, life size; **6**, adaxial surface of leaves. Drawn from *Snijman 1165.*

with both surfaces glabrous, rarely the adaxial surface sparsely covered with long, white patent hairs (up to 3 mm long); margin minutely ciliate, sometimes reddened; subtended by a subterranean amplexicaul cataphyll and non-amplexicaul prophyll. *Inflorescence* widely spreading, (30-) 40--80 mm across; scape erect to flexuose, 50--80 mm long, 1,5--3,0 mm diam., reddish towards the base, breaking off at the base in fruit; spathe valves narrowly lanceolate, up to 25 x 2--5 mm; bracteoles up to 10 mm long. *Flowers* (4-) 6--14, spreading, stellate, pale pink with a deeper pink median dorsal stripe on each tepal, ageing to deep pink, scentless; pedicels straight to upwardly curved, 20--40 mm long. *Tepals* free to the base, outspread, oblong-lanceolate, 6--8 mm x 1,5--3,0 mm, plane-surfaced with somewhat undulate edges. *Stamens* equalling or somewhat shorter than the tepals, somewhat spreading; filaments separate, adnate to the swollen style base, somewhat bulbous proximally, anthers subcentrifixed, ± 2 mm long and pink to wine-red before opening; pollen cream-coloured. *Ovary* with up to 2--3 ovules per locule. *Style* up to 6 mm long, more or less equalling the stamens, with a broad somewhat conoidal base, tapering and slender distally, with nectar collecting in 3 droplets between the base and inner filaments. *Seeds* ± 2 mm diam. *Chromosome number* $2n = 20$. Figure 9.31.

Flowering time: March to April.

Diagnostic features: Of all the species of subsection Gemmaria, *S. karooica* has the most attractive flowers, due to the plane-surfaced, pink, widely-spreading tepals. The ovate to elliptical leaves arise from a yellow-fleshed bulb and are usually glabrous with minutely ciliate margins. Only rarely are the leaves softly pubescent adaxially. Previously the species was thought to have upright leaves, as shown in the illustration accompanying the original description (Barker 1935). Plants in the field however have leaves appressed to the ground. Closest allies are *S. massoniella* and *S. merxmuelleriana*.

Distribution and habitat: Records indicate that the species is confined to the southern Roggeveld escarpment, extending southwards to Matjiesfontein near Laingsburg in the Little Karoo, at elevations of 900--1200 m (Figure 9.48). The species inhabits open, flat clayey sites, usually amongst doleritic or shaley rocks. Populations comprise small, fairly dense aggregations of a few hundred bulbs, in association with sparse renosterveld.

Specimens examined

--3120 (Williston): 16 km from Middelpos towards Sutherland (-CD), fl 25 Mar 1988, *Snijman 1165* (K, MO, NBG, PRE).

--3220 (Sutherland): farm Wolvedans between Middelpos and Sutherland (-AB), fl 25 Mar 1988, *Snijman 1167* (K, NBG, PRE); Sutherland commonage (-BC), fl 10 Mar 1988, *Forrester & Leitch s.n.* (NBG); fl 25 Mar 1988, *Snijman 1168* (MO, NBG, PRE).

--3320 (Montagu): Laingsburg division, Matjiesfontein (-BA), fl Apr 1915, *Pearson* sub *NBG 2499/14* (BOL); fl 13 Apr 1933, *Logan & Archer* in Herb. Bol. *A600* (BOL); fl Apr 1923, *Frith* sub *Marloth 1161* (PRE).

16. Strumaria gemmata Ker-Gawl.in The botanical magazine 39: t. 1620 (1814); Schultes & Schultes: 792 (1830). Type: figure in The botanical magazine 39: t. 1620 (1814), lecto.!, designated by Müller-Doblies (1985).

Imhofia gemmata (Ker-Gawl.) Herbert: 291 (1837); Kunth: 628 (1850). *Hessea gemmata* (Ker-Gawl.) Benth. & Hook.: 721 (1883); Baker: 23 (1888), 192 (1896). *Periphanes gemmata* (Ker-Gawl.) Leighton: 82 (1948). *Gemmaria gemmata* (Ker-Gawl.) Salisb. ex D. & U. Müller-Doblies: 29 (1985).

Imhofia burchelliana Herbert: 290 (1837); Kunth: 627 (1850). Syntypes: Cape, Uniondale division, between Krakeel River and Roode Krans River in Lange Kloof, 13 March 1814, *Burchell 4954* (K!); Uniondale division, between Roode Krans River and Groot River in Langekloof, 14 March 1814, *Burchell 4967* (K, lecto.!), here designated. *Imhofia burchelliana* Herbert var. *virescens* Herbert: 291 (1837); Kunth: 627 (1850). Type: Cape, Hopetown division, *Burchell 2683* (K, holo.!). *Hessea burchelliana* (Herbert) Benth. & Hook.: 721 (1883).

Imhofia bergiana Kunth: 627 (1850). Type: Cape of Good Hope, *Bergius* (B, holo.)

Strumaria undulata Berg. ex Kunth: 627 (1850) nom. illeg., non *S. undulata* Jacq.:50 (1797). 360 (1795). Type: As for *Imhofia bergiana* Kunth.

Bulb solitary or sometimes forming bulblets, ovoid to globose, 10--35 mm diam., with lightly fibrous brownish outer tunics, yellowish within; neck up to 45 mm long, occasionally lacking. *Leaves* absent or incipient at anthesis, 2, recurved to prostrate, varying from broadly to narrowly elliptical to lorate, 40--90 (-200) x 5--25 mm, with long, soft hairs covering the adaxial surface or occasionally the margins only, rarely entirely glabrous, with minutely ciliate margins, subtended by a subterranean amplexicaul cataphyll and non-amplexicaul prophyll. *Inflorescence* widely spreading, 50--220 mm across; scape straight to somewhat flexuose, 50--400 mm long, 1--3 mm diam., pale green to wine-red with a grey bloom, breaking off at the base in fruit; spathe valves lanceolate, 10--25 x 2--3 mm; bracteoles up to 7 mm long. *Flowers* (2-) 6--14, spreading, stellate, pale lemon or occasionally cream-coloured, with a thickened green midrib, flushed with wine-red dorsally, becoming reddish with age, scentless; pedicels inwardly curved to straight, 40--85 mm long, leaden-grey to wine-red. *Tepals* free to the base, outspread, oblanceolate, 4--8 x 2,5--3,5 mm, shortly clawed, bearing a solid shiny translucent gibbosity at the base of the ventral surface, more or less crisped and involute on the edges. *Stamens* equalling the tepals, spreading; filaments separate, adnate to the broadened style base, somewhat

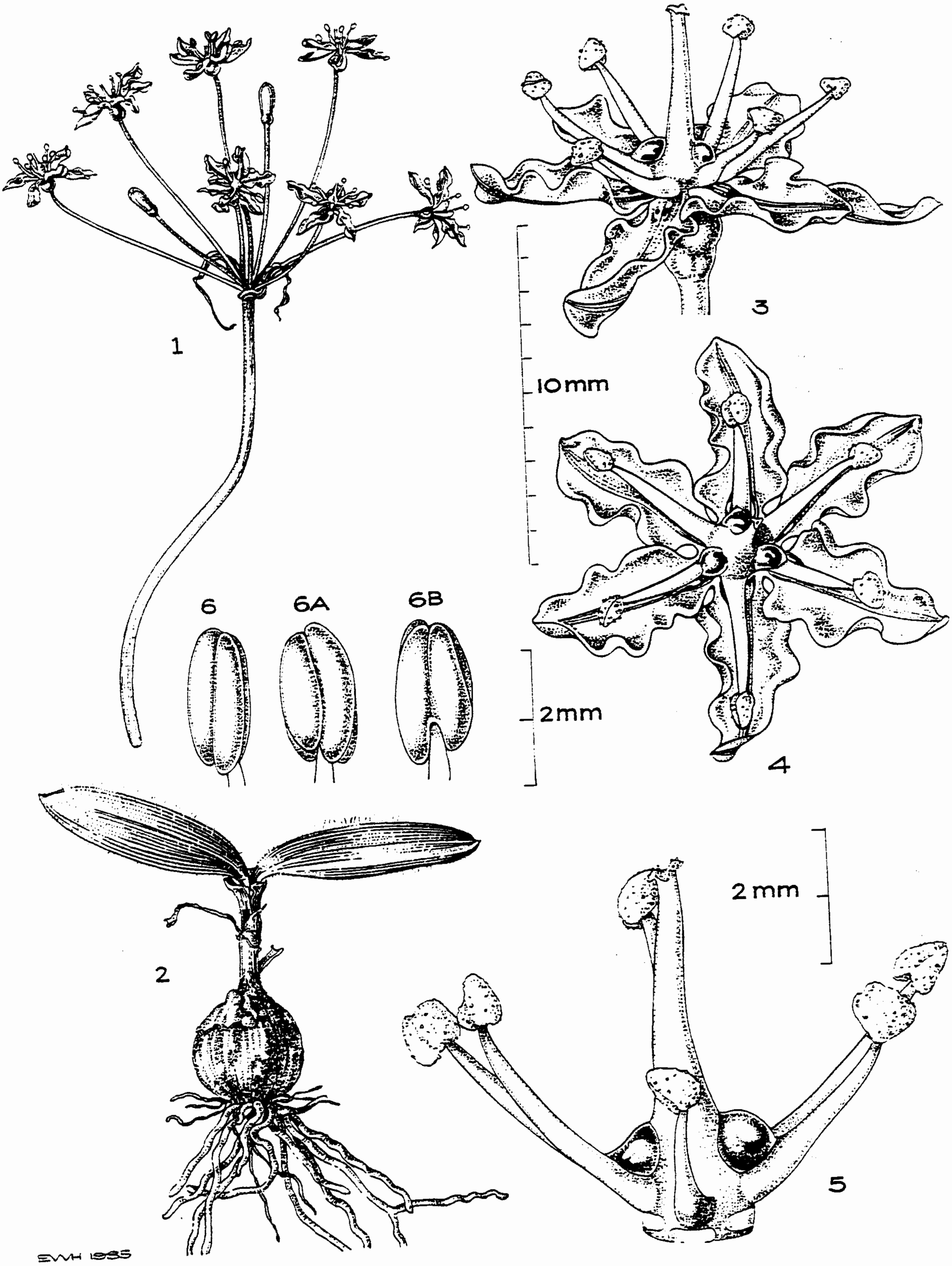


FIGURE 9.32-- *Strumaria gemmata*: 1, inflorescence, life size; 2, vegetative habit, life size; 3-4, whole flowers; 5, androecium and style; 6, anther attachment, lateral view, 6A, ventral view, 6B, dorsal view. Drawn from *Mathews 1226*.

bulbous proximally, subulate above, up to 5 mm long; anthers subcentrifixed, 2--3 mm long before opening, lemon to reddish pink; pollen pale lemon. *Ovary* with up to 3--5 ovules per locule. *Style* up to 6 mm long, equalling the stamens,tapering smoothly upwards from a broad obscurely conoidal base. *Seeds* $\pm$ 2 mm diam. *Chromosome number* $2n = 20$. Figure 9.32.

Flowering time: Usually between February and April, occasionally extending to May in the southern areas.

Diagnostic features: Strumaria gemmata is the only species in the genus with pale lemon flowers. Furthermore, it is the only species with distinctly crisped tepals. A feature not found elsewhere in the subtribe is the development of a solid shining translucent gibbosity on each tepal, which appears to mimic nectar beneath the filament attachment. The leaves are indistinguishable from those of other pubescent-leaved species of subsection Gemmaria but show greater variation in the extent of the covering. Collections from the extreme west show the greatest reduction in pubescence and often the leaf margins are only scabrid. Elsewhere in its distribution range the species usually has some pubescence.

Distribution and habitat: The distribution of *S. gemmata* is confined to semi-arid areas in the south-eastern and eastern regions of the Cape Province. Scattered records have been made throughout the Great Karoo and Little Karoo where the species occupies a range of habitats, in soils varying from clayey to loamy sand, either on stony slopes, flats or occasionally near marshes. In the southern Cape, populations are confined to limestone flats, between Bredasdorp and Riversdale (Figure 9.50). Throughout the distribution range the associated vegetation differs widely. Populatons have been recorded in renosterveld, Valley Bushveld and grassland. Within populations the bulbs may either be abundant or occasional.

Specimens examined

--3025 (Colesberg): near Plewman Siding (-CC), fl 26 Feb 1952, *Acocks 16307* (K, PRE).

--3123 (Victoria West): Victoria West division, Hutchinson (-CA), fl 13 Mar 1918, *Burtt-Davy 17593* (BOL).

--3124 (Hanover): N slopes of Sneeuwberg, between Hanover and Graaff-Reinet (-CB), fl Feb, *Bolus 1817* (BOL, K, SAM).

--3125 (Steynsberg): Middelberg division, Bangor farm (-AC), fl Mar 1918, *Bolus 14132* (BOL).

--3126 (Queenstown): Summit of Andriesberg, near Bailey (-DB), fl Jan 1897, *Galpin 2271* (BOL, K, PRE).

--3224 (Graaff Reinet): Kendrew (-DA), fl 15 Mar 1930, *Galpin 10057* (PRE).

--3321 (Ladismith): Phesantefontein (-CC), *Bayer 494* (NBG); Huis River Pass (-DA), fl 24 Mar 1940, *Lewis 717* (SAM); fl 3 Mar 1973, *Bayliss BS5636* (K); Huis River Mountains (-BC), *Compton 8674* (NBG).

--3322 (Oudtshoorn): Oudtshoorn (-CA), fl 8 Apr 1906, *A. Taylor s.n.* (PRE); *Lavranos & Pehlemann 20613* (NBG, PRE); Witberg, E of Robinsons Pass (-CC), *Mathews 1226* (NBG, PRE).

--3323 (Willowmore): Uniondale division, hills near Avontuur (-CA), fl Mar 1922, *Fourcade 2088* (BOL); *Bayer 521* (NBG); Uniondale, near De Hoop farm (-CB), *Snijman 374* (NBG).

--3324 (Steytlerville): Baviaanskloof, near Smitskraal (-CB), fl 10 Mar 1985, *Vlok 956* (K, MO, NBG, PRE).

--3325 (Port Elizabeth): Uitenhage, Koega River (-CB), *Zeyher s.n.* (K); fl Mar, *Zeyher 4107* (BOL, K); Uitenhage (-CD), *Zeyher s.n.* (K, SAM); near Uitenhage (-CD), fl 21 Apr 1893, *Schlechter 2571* (BOL, PRE, SAM); Redhouse, near Port Elizabeth (-DC), fl May 1915, *Paterson 1010* (BOL); New Brighton, Port Elizabeth district (-DC), *West s.n.* (BOL).

--3326 (Grahamstown): Alicedale (-AC), fl Apr 1924, *Rogers 27771* (BOL, K).

--3420 (Bredasdorp): De Hoop Nature Reserve, Melkkamer (-AB), *Van Wijk & Fellingham 2261* (NBG); between De Hoop and Bredasdorp (-AC), *Thomas s.n.* (NBG); near De Hoop homestead (-AD), fl 10 Apr 1957, *Levyns 10685* (BOL); De Hoop (-AD), fl 8 Apr 1957, *Barker 8708* (NBG); Potberg, Swellendam (-BC), fl Apr 1947, *Levyns 8170* (BOL); Cape Infanta (-BD), *Goldblatt 5629* (NBG).

--3421 (Riversdale): Soetmelksrivier, 17 miles W of Albertinia (-AB), fl 11 Apr 1962, *Lewis 5915* (NBG, PRE).

--*Imprecise localities:* farm Roturua, Fauresmith district, fl 16 Mar 1939, *Liebenberg 3637* (PRE); Hopetown division, *Burchell 2683* (K); Colesberg division, near Hondeblafs River, fl 6 Mar 1813, *Burchell 2702* (K); between Rietfontein and Plettenbergs Beacon, Colesberg, fl 7 Mar 1813, *Burchell 2727* (K); Albert division, fl Feb 1840, *Drege 3517a* (E, K); district of Albert, *Cooper 575* (K); near Biesjesfontein, Somerset East, *Bolus s.n.* (SAM); near Naauwpoort, *Bolus s.n.* (BOL); Zwartkops, Koega and Zondags Riviere, fl Feb-Mar, *Ecklon & Zeyher 103* (SAM); Uniondale division, between Krakeel River and Roode Krans River, Langekloof, fl 13 Mar 1814, *Burchell 4954* (K); Uniondale division, between Roode Krans River and Groot River, Langekloof, fl 14 Mar 1814, *Burchell 4967* (K); near Groot River, Langekloof, *Burchell 4978* (K); hills N of Ganzkraal, Long Kloof, fl Mar 1922, *Fourcade 2088* (BOL); Korenplaats, Riversdale district, fl Mar 1909, *Muir* ex *Herb. Galpin 5374* (BOL, PRE); Riversdale division, fl Apr 1914, *Muir s.n.* (BOL).

17. **Strumaria leipoldtii** (L. Bolus) Snijman, comb. nov. Type: Cape, Clanwilliam division, Olifants River Dam, April 1929, *Leipoldt* in *Herb. Afr. Bol. 19140* (BOL, holo.!; K!).

Hessea leipoldtii L. Bolus: 147 (1930). *Periphanes leipoldtii* (L. Bolus) Leighton: 82 (1948). *Gemmaria leipoldtii* (L. Bolus) D. & U. Müller-Doblies: 30 (1985).

Bulb ovoid, 15--30 mm diam., with light brown fibrous outer tunics; inner scales whitish; neck up to 25 mm long or absent. *Leaves* absent at anthesis, 2(-3), oblong-oval to broadly lorate, 40--140 x 17--35 mm, glabrous on both surfaces; adaxial surface dark green; margin densely fringed with 1--3 mm long soft, white hairs; subtended by a non-amplexicaul prophyll and an amplexicaul cataphyll which may protrude slightly above ground and turn green or reddish brown. *Inflorescence* widely spreading, 50--140 mm across; scape flexuose, 40--150 mm long, ± 3 mm diam., breaking off at the base in fruit; spathe-valves linear-lanceolate, 15--25 x 2--3 mm; bracteoles up to 6 mm long. *Flowers* 8--15, ascending to spreading, stellate, white with a pale green or darker pink dorsal median stripe on each tepal; pedicels straight to upwardly curved, 40--60 mm long. *Tepals* free to the base, outspread, ovate-lanceolate, 5--10 x 2--3 mm, slightly channelled. *Stamens* slightly shorter than the tepals, spreading; filaments separate, adnate to the broadened style base, with the inner filaments broader basally than the outer, both whorls distinctly bulbous proximally, tapering upwards; anthers subcentrifixed, 2 mm long and cream to wine-red before opening; pollen cream-coloured. *Ovary* with 2--3 ovules per locule. *Style* lengthening to ± 5 mm, with the proximal third somewhat bulbiform, tapering into a slender column distally. *Seeds* ± 3 mm diam. *Chromosome number* unknown. Figure 9.33.

Flowering time: From the end of March to early April.

Diagnostic features are the leaves, which are typically broad (15--35 mm across) and densely fringed with long soft hairs, while both adaxial and abaxial surfaces are glabrous. Florally *S. leipoldtii* cannot be separated easily from other small, white-flowered species of subsection Gemmaria. It appears to be most closely related to *S. discifera* and *S. chaplinii*.

Distribution and habitat: Considerable confusion surrounds the whereabouts of the type locality of *S. leipoldtii.* L. Bolus (1930) described the species as having been found "on the hills near the weir in the Olifant's River Dam, about 32 miles from Clanwilliam". The Bulshoek Dam is located 16 miles north of Clanwilliam, thus the distance given by L. Bolus is possibly the total distance travelled to and from the collection site (Figure 9.49). The species is also known from near Lamberts Bay, where it grows on sandstone rock ledges with a southern aspect, along the seasonal Jachalsrivier. Associated plants are succulent shrubs, particularly the narrowly distributed *Pteronia onobromoides* DC. and

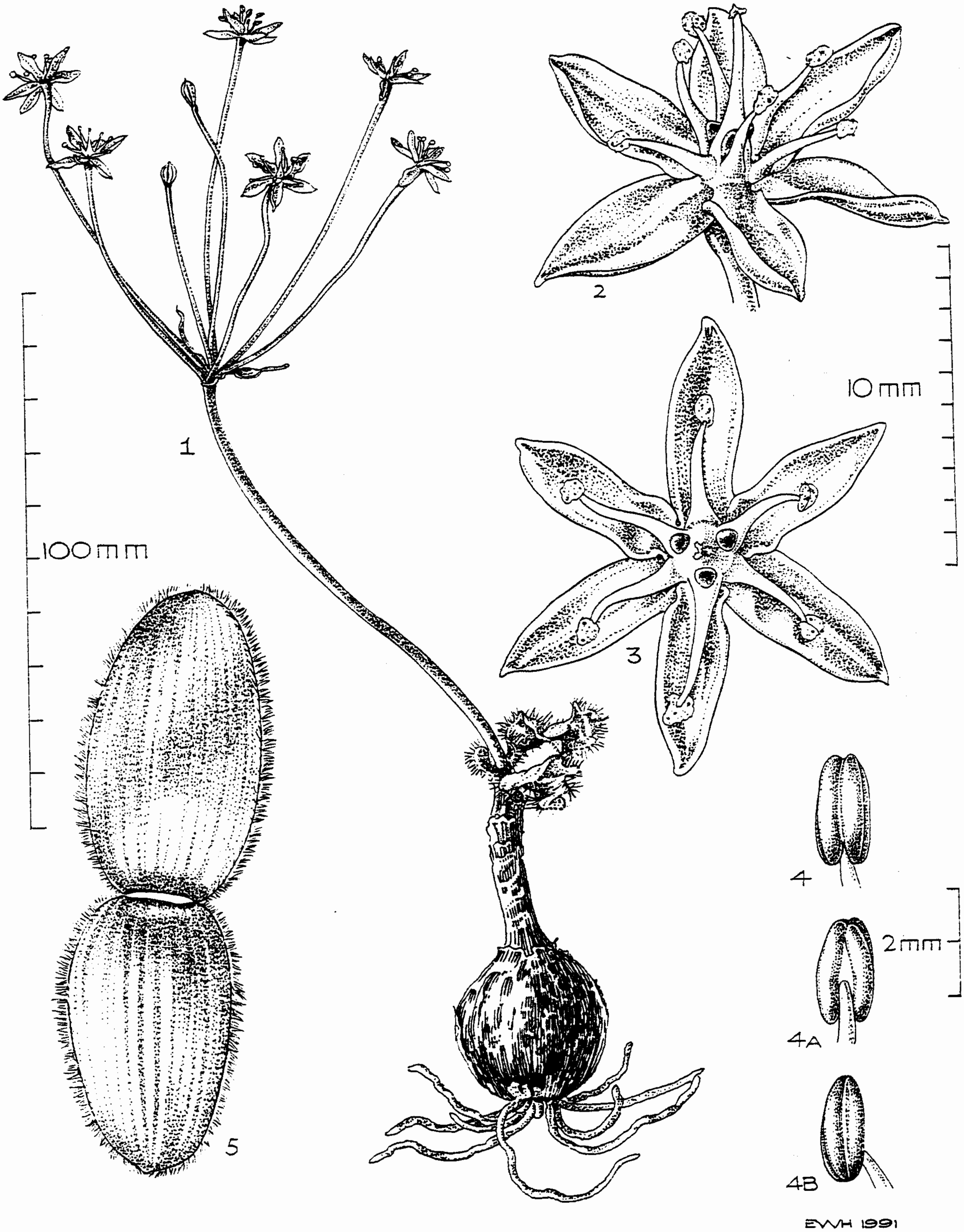


FIGURE 9.33-- *Strumaria leipoldtii*: 1, inflorescence, life size; 2-3, whole flowers showing nectar droplets between inner filaments and style; 4, anther attachment, dorsal view, 4A, ventral view; 4B, lateral view; 5, vegetative habit, life size. Drawn from *Snijman 1244*.

Senecio tortuosa DC. Despite recent attempts to map the species' distribution, the population from the type locality has not been re-located and only one small population on the outskirts of Lamberts Bay has been found. This locality, situated close to a quarry, renders *S. leipoldtii* the most threatened of the *Strumaria* species.

Specimens examined

--3218 (Clanwilliam): Lamberts Bay, N of Jachalsrivier (-AB), fl Apr 1927, *Pole Evans* sub *V. Nouhuys 18* (PRE); *Snijman 1244* (NBG); Lamberts Bay (-AB), *Wagener s.n.* (NBG 95031, NBG 84203).

--Imprecise locailities: Clanwilliam, *Leipoldt 4225* (BOL); possibly Nieuwoudtville, *Leipoldt* sub *NBG 188/46* (NBG); Olifants River Dam, fl Apr 1929, *Leipoldt* in *Herb. Afr. Bol. 19140* (BOL, K).

18. **Strumaria chaplinii** (W.F.Barker) Snijman, comb. nov. Type: Cape, Malmesbury division, Langebaan, 15 Mar 1944, *Chaplin 9* sub *NBG 154/44* (NBG, holo.!; PRE!).

Hessea chaplinii W.F. Barker: 130 (1944). *Gemmaria chaplinii* (W.F. Barker) D. & U. Müller-Doblies: 29 (1985).

Bulb solitary, subglobose, 15--20 mm across, with brown fibrous outer tunics, whitish within; neck extending up to 30 mm. *Leaves* absent at anthesis, 2, prostrate, narrowly obovate-oblong to lorate, 15--65 x 5--10 mm; adaxial surface green, covered with 0,2--6,0 mm long, white, patent hairs; abaxial surface glabrous, green or flushed with red proximally; subtended by a subterranean amplexicaul cataphyll and non-amplexicaul prophyll. *Inflorescence* widely spreading, 40--150 mm across; scape somewhat flexuose, 35--10 mm long, 2--3 mm diam., green to pinkish with a grey bloom, abscising at the base in fruit; spathe valves linear-lanceolate, 10--30 x 3--7 mm; bracteoles up to 20 mm long. *Flowers* 4--14, spreading, stellate, white with a reddish or greenish-brown dorsal median stripe on each tepal, ageing to darker shades of pink, scentless; pedicels straight to upwardly curved, 20--80 mm long, concolorous with the scape. *Tepals* free to base, outspread, ovate-lanceolate, 5--6 x 1,5--2,75 mm, plane-surfaced. *Stamens* slightly shorter than the tepals, spreading; filaments separate, adnate to the broadened style base with the inner whorl attached higher up than the outer, both whorls somewhat bulbous-based, tapering distally; anthers subcentrifixed, 2 mm long and wine-red before opening; pollen whitish. *Ovary* with 1--4 ovules per locule. *Style* up to 5 mm long, equalling the stamens, tapering smoothly upwards from a broad depressed-conoidal base, with nectar collecting in 3 droplets between the base and inner filaments. *Seeds* 3,0--3,5 mm diam. *Chromosome number* $2n = 20$. Figure 9.34.

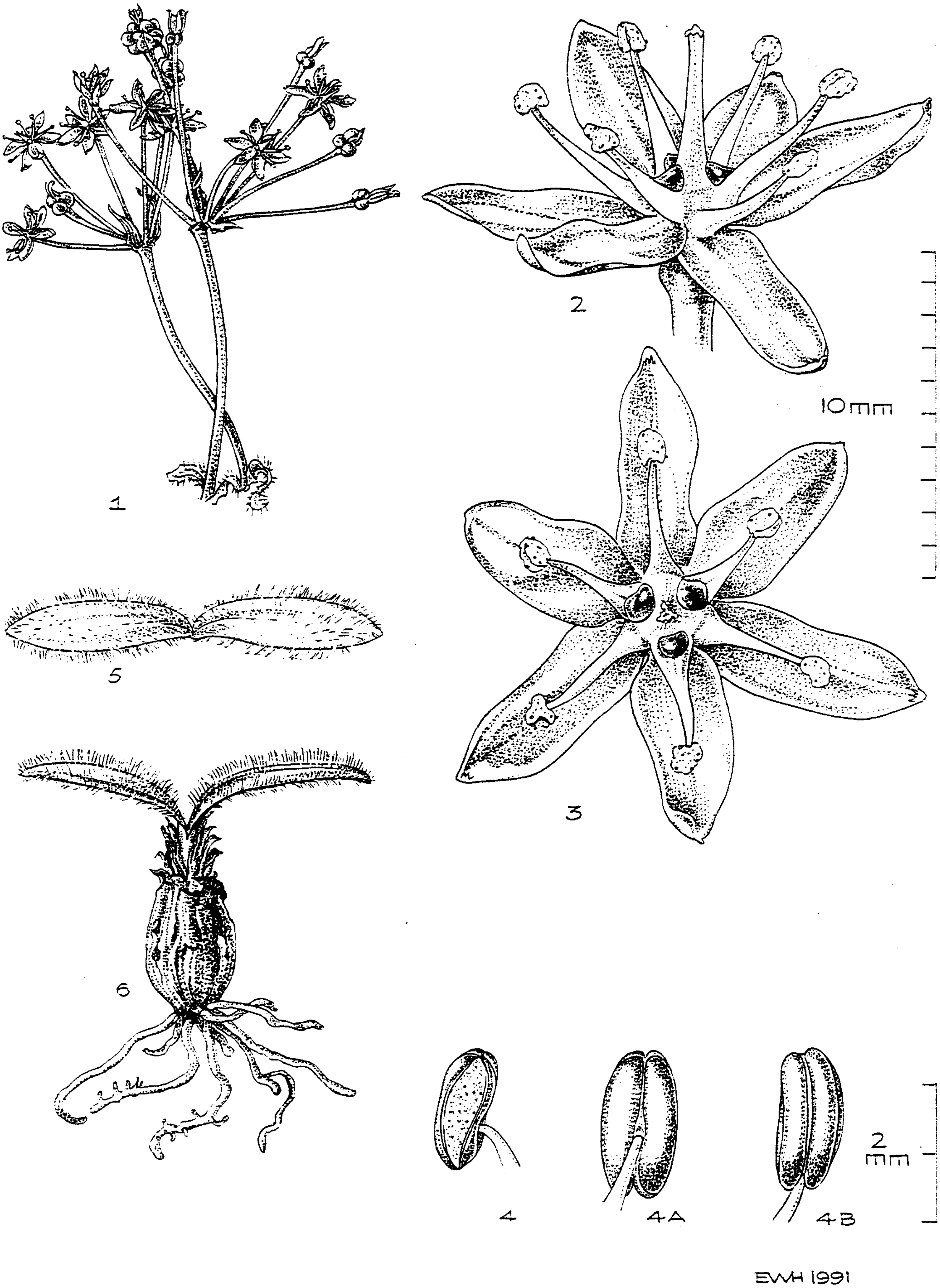


FIGURE 9.34-- *Strumaria chaplinii* 1, inflorescences, life size; 2-3, whole flowers showing nectar droplets in axils of inner filaments; 4, anther attachment, lateral view, 4A, ventral view; 4B, dorsal view; 5-6, vegetative habit, life size. Drawn from *Duncan 28*.

Flowering time: From the middle of March to April.

Diagnostic features: Strumaria chaplinii forms a close alliance with *S. discifera* and *S. leipoldtii* and more remotely so with *S. villosa*, all of which occur further north in the western Cape Province. Each of these species has densely pubescent leaves and similarly-sized, predominantly white, stellate flowers. The flowers of *S. chaplinii* are characteristically flat and open, with plane-surfaced tepals. The style is broadest at the extreme base and extends smoothly upwards without the sculpturing found at the base of the style in *S. discifera*. The fleshy inner scales of its bulb are white, easily distinguishing it from *S. villosa*, which has yellow-fleshed bulbs. The pubescent adaxial leaf surface distinguishes it from the smooth-surfaced, densely fringed leaves of *S. leipoldtii*.

Distribution and habitat: Confined to granite outcrops along the coast between St. Helena Bay and Saldanha Bay in the south-western Cape (Figure 9.49), where the bulbs are densely aggregated in shallow humus-rich soil, around the margins or in fissures of large boulders. *Strumaria chaplinii* grows sympatrically with *S. tenella* subsp. *tenella* in Langebaan but is usually in fruit when *S. tenella* begins to flower in May. Apart from a rich bulbous flora, the granite rocks also support a dwarf succulent community. The species is currently under threat from coastal development in the Langebaan area.

Specimens examined

--3217 (Vredenburg): Paternoster (-DD), *Barker 10239* (NBG).

--3318 (Cape Town): Langebaan (-AA), 15 Mar 1944, *Chaplin 9* sub *NBG 154/44* (NBG, PRE); *Barker 10431* (NBG); *Duncan 28* (K, NBG, PRE).

5.3.3 Section Bokkeveldia

Section **Bokkeveldia** (D. & U. Müller-Doblies) Snijman, stat. nov. Type: *Strumaria watermeyeri* L. Bolus.

*Bokkeve*ldia D. & U. Müller-Doblies: 27 (1985).

Bulbs with whitish inner tunics, rarely yellowish. foliage leaves 2 or rarely 3, exserted simultaneously above ground, sheathed basally by a cataphyll. Flowers funnel-shaped; pedicels as long or slightly longer than the perigone.

Species 5.

19. Strumaria perryae Snijman in Bothalia 22 (in press). Type: Cape, between Grasberg and Theunisdrift, NW of Nieuwoudtville, 15 May 1980, *Perry 997* (NBG, holo. K, PRE, MO).

Bulb solitary, globose, 10--15 mm diam, with lightly fibrous light brown outer tunics, whitish within; neck up to 45 mm long. *Leaves* absent at anthesis, 2, suberect to recurved, narrowly lorate to lanceolate, 50--150 (-250) x 2,5--5,0 mm, softly pubescent with hairs up to 2 mm long on both surfaces, flushed with red towards the base of the abaxial surface, subtended by a subterranean amplexicaul cataphyll and non-amplexicaul prophyll. *Inflorescence* somewhat clustered, 25--30 mm across; scape erect to flexuose, 50--165 (-240) mm long, ± 1 mm diam., reddish pink with a grey bloom, rarely pubescent, breaking off at the base in fruit; spathe valves linear-lanceolate, 15--20 x 1--2 mm; bracteoles up to 6 mm long. *Flowers* 3--11, more or less ascending, widely funnel-shaped, scentless; pale pink with a deeper pink median dorsal band on each tepal, turning deep pink with age; pedicels straight to upwardly curved, 20--30 (-60) mm long, pale green to reddish pink. *Tepals* shortly adnate to the filaments for up to 1 mm, otherwise free, the outer spreading more widely than the inner, oblong-lanceolate, 10--17 x 2,5--4,0 mm. *Stamens* suberect to slightly spreading, exserted beyond the tepals; filaments separate, up to 17 mm long, with the outer and inner whorls adnate to the style base for up to 2,5 mm and 3,5 mm respectively; anthers subcentrifixed, ± 3 mm long before opening, dark maroon; pollen cream-coloured. *Style* up to 19 mm long, equalling or slightly exceeding the stamens, slightly thickened and trigonous proximally, tapering gradually upwards; with nectar collecting in 3 droplets between the style and inner filaments. *Seeds* 2,0--2,5 mm diam. *Chromosome number* $2n = 20$. Figure 9.35.

Flowering time: May, but commencing in April when cultivated.

Diagnostic features: The long, lorate, pubescent leaves and somewhat funnel-shaped flowers of *S. perryae* are characteristics also found in *S. pubescens* and *S. aestivalis*, and indicate a close affinity amongst these species. The narrow leaves of *S. perryae* are diagnostic, being at most 5 mm across. In contrast, *S. pubescens* and *S. aestivalis* have leaves more than 10 mm wide and have the derived character state of yellow inner bulb tunics. The adnation of all the filaments to the style is well developed, reaching a length of 3,5 mm. This feature is paralleled in specimens of *S. salteri* and *S. watermeyeri* which occur further south on the escarpment towards Clanwilliam; and in *S. aestivalis* from near Loeriesfontein in the north. In *S. perryae*, *S. salteri*, and *S. watermeyeri* the inner filaments are closely adnate to the style and the efferent canal, which conducts nectar from the septal nectaries to the sinus between the inner filaments and style is only microscopically visible. *Strumaria aestivalis* shows greater specialisation of this character, in that the nectar well between the inner filament and style is clearly visible.

Distribution and habitat: *Strumaria perryae*, a rare species, is known from a single small population on the northern Bokkeveld escarpment between Grasberg and Theunisdrift north west of Nieuwoudtville. The population inhabits clayey soil in association with low karroid shrubs (Figure 9.51).

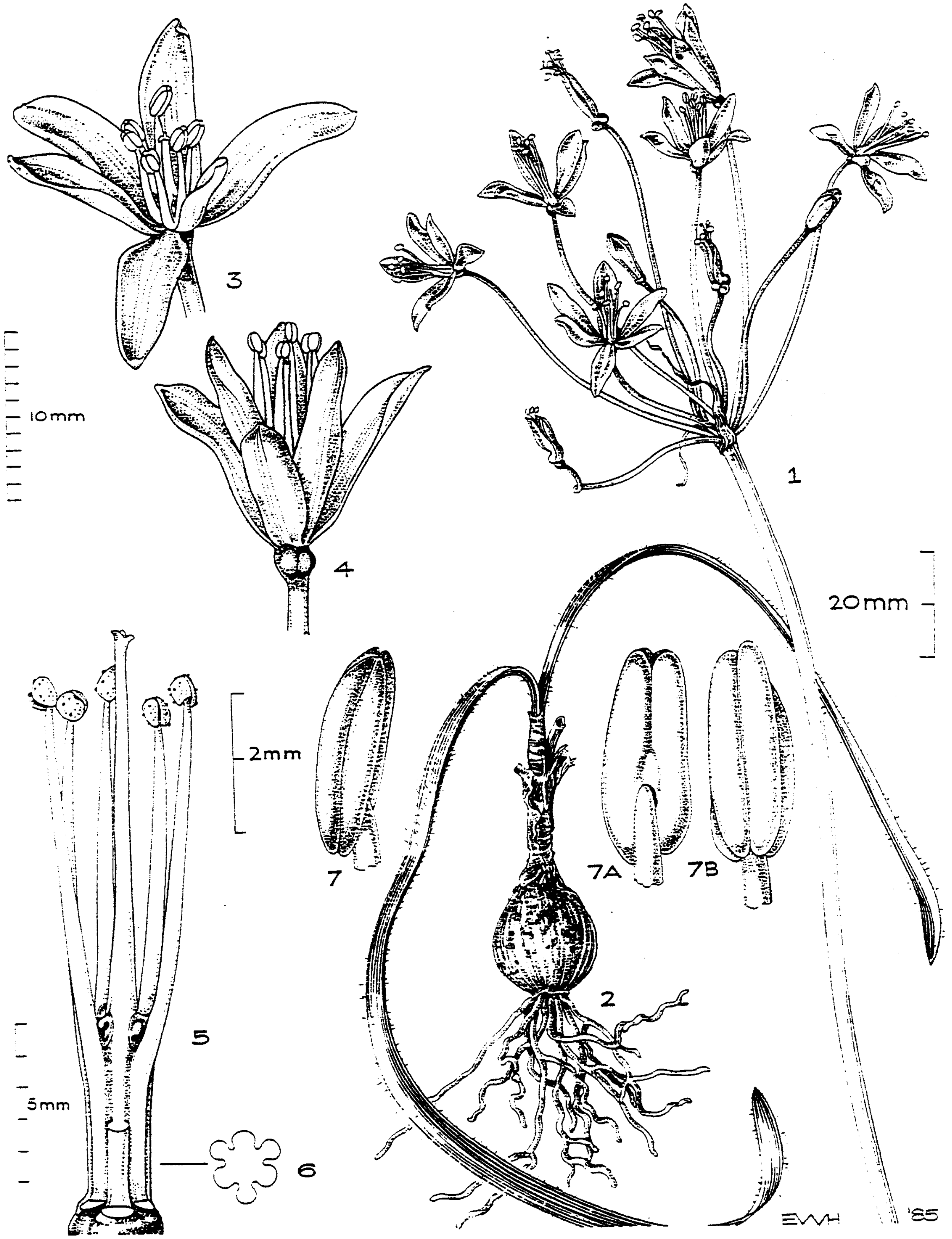


FIGURE 9.35-- *Strumaria perryae*: 1, inflorescence, life size; 2, vegetative habit, life size; 3-4, whole flowers; 5, flower with tepal and one stamen removed to show adnation of filaments to style; 6, transverse section through androecium and style; 7, anther attachment, lateral view, 7A, dorsal view; 7B, ventral view. Drawn from *Perry 997*.

Etymology: The species honours Miss Pauline Perry, who assisted me on many expeditions to Namaqualand and the Roggeveld and who first discovered this recently described species. She also nurtured the living collections of the Amaryllideae at the Karoo National Botanic Garden in Worcester, thus facilitating my studies in the family.

Specimens examined

--3119 (Calvinia): between Grasberg and Theunisdrift, NW of Nieuwoudtville (-AA), *Perry 997* (K, MO, NBG, PRE); approximately 7 km from Grasberg homestead towards Theunisdrift (-AA), fl 8 May 1985, *Snijman 867* (NBG).

20. Strumaria pubescens W. F. Barker in Journal of South African Botany 9: 147 (1943). Type: Cape, Laingsburg division, Ngaapkop, 25 February 1943, *Compton 14417* sub *NBG 151/43* (NBG, holo.!; BOL!).

Bokkeveldia pubescens (W. F. Barker) D. & U. Müller-Doblies: 28 (1985).

Bulbs subglobose to ovoid, 15--35 mm diam., often clumped; outer covering softly fibrous, light brown; inner tunics yellowish; neck up to 100 mm long. *Leaves* absent at anthesis, 2 (-3), spreading, lorate, 45--230 x 10--27 mm, light green; adaxial surface usually covered with 2--4 mm long, soft, white hairs, occasionally glabrous, somewhat canaliculate towards the base; abaxial surface flushed with red basally, glabrous; margin softly hairy; subtended by a subterranean amplexicaul cataphyll and a non-amplexicaul prophyll. *Inflorescence* a lax to fairly dense umbel, 20--80 mm across; scape straight, up to 170 mm long, 1,5--3,0 mm diam., light green to reddish brown breaking off at the base in fruit; spathe valves lanceolate, 13--30 x 1--4 mm; bracteoles up to 3 mm long. *Flowers* 4--30, more or less ascending, funnel-shaped, delicate pink with a darker pink median dorsal band, becoming tinged with mauve with age, scented; pedicels straight to upwardly curved, 18--40 mm long, light green to reddish brown. *Tepals* shortly adnate to the filaments for 0,5--2,5 mm, otherwise free, narrowly oblanceolate, 10--20 x 2,5--4,0 mm broad. *Stamens* more or less half as long as the tepals, suberect,; filaments separate, up to 10 mm long, with the outer slightly shorter than the inner, both whorls shortly adnate to the style base for up to 2,5mm; anthers subcentrifixed, dark maroon to cream-coloured; pollen cream-coloured. *Style* up to 7,5 mm long, equalling the stamens, thickened and trigonous proximally, narrowing smoothly upwards. *Seeds* ± 3 mm diam. *Chromosome number* $2n = 20$. Figure 9.36.

Flowering time: February to March, occasionally extending into April.

Diagnostic features: Strumaria pubescens is readily distinguished by its funnel-shaped flowers in which the tepals remain imbricate, until they spread outward in the distal third. The stamens are conspicuously shorter than the tepals, reaching little more than half

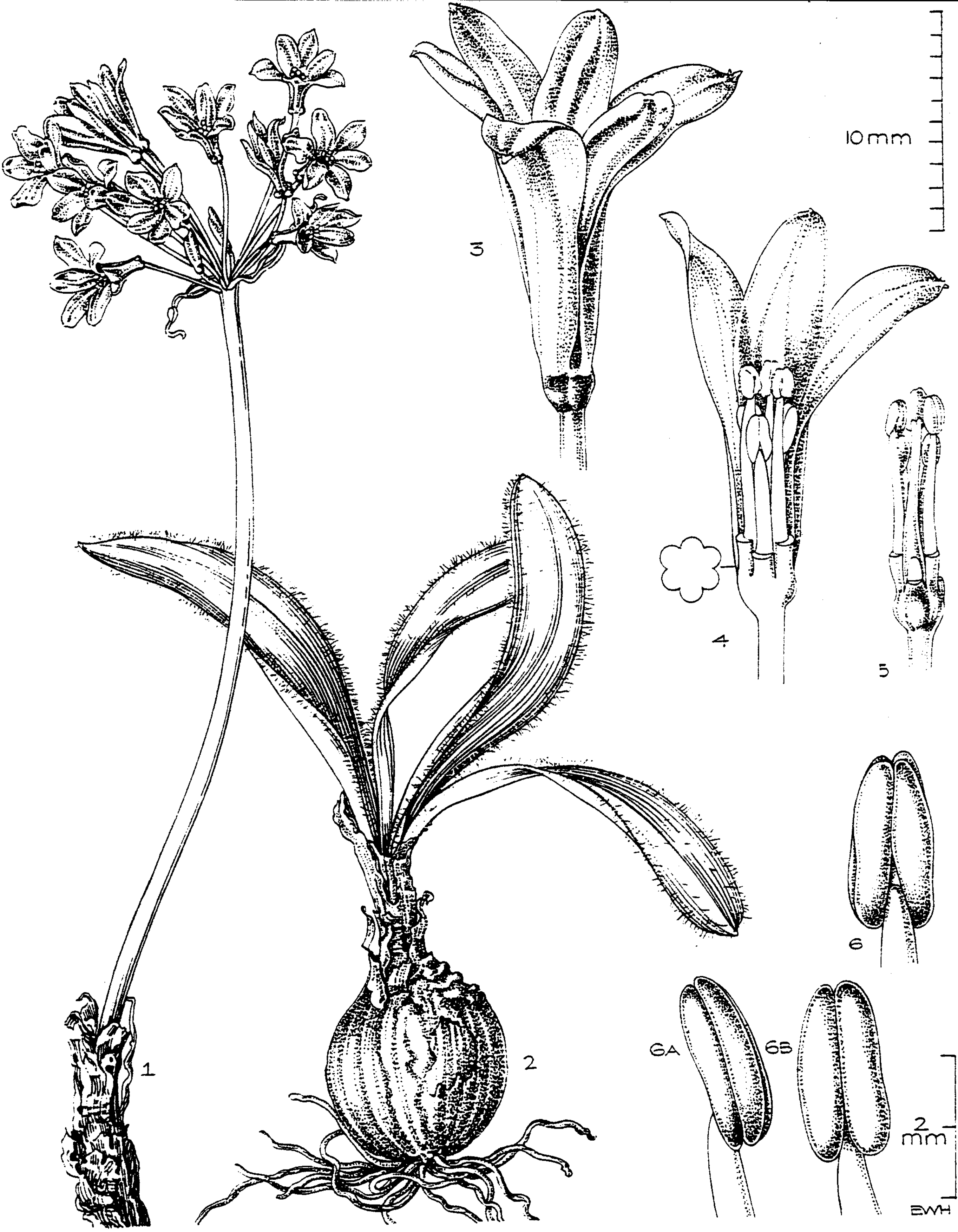


FIGURE 9.36-- *Strumaria pubescens*: 1, inflorescence, life size; 2, vegetative habit, life size; 3, whole flower; 4, flower with three tepals removed and transverse section showing adnation of tepals to filaments and style; 5, flower with tepals and one stamen removed; 6, anther attachment, dorsal view; 6A, lateral view, 6B, ventral view. Drawn from *Snijman 1164.*

the length of the tepals and are thus almost hidden in the lower tubular half of the flower. The broad, long, pubescent, strap-shaped leaves are most easily confused with those of its close ally *S. aestivalis*. In *S. pubescens*, however, only the adaxial surface is hairy, in contrast to both surfaces in *S. aestivalis*.

Distribution and habitat: Originally *S. pubescens* was known only from the karroid hills near Matjiesfontein in the Laingsburg district. A second population has since been discovered on the Gannaga Pass, ascending the Roggeveld escarpment towards Middelpos, approximately 150 km to the north west (Figure 9.51). The species grows on fairly steep, south-facing slopes in clayey soil, in the overhang of shaley rock ledges, at elevations of approximately 1000 m. The populations are extremely localised and small, with the bulbs densely aggregated together.

Variation: The species shows considerable variation in size between populations. Specimens from the type locality are depauperate in comparison to the northern collections, and attain only half the size of these specimens, both florally and vegetatively. The luxuriance of the growth of the bulbs from the Gannaga Pass is thought to be due to favourable local conditions of the humus-rich soil and deep shade in which they were found. Thus the original description has been amplified to include this variation in size.

Specimens examined

--3220 (Sutherland): Gannaga Pass, SW of Middelpos (-AA), fl 25 Mar 1988, *Snijman 1164* (K, MO, NBG, PRE, S).

--3320 (Montagu): Laingsburg division, Ngaapkop (-BA), fl 25 Feb 1943, *Compton 14417* sub *NBG 151/43* (NBG, BOL); fl 20 Mar 1944, *Compton 15603* (NBG).

21. **Strumaria aestivalis** Snijman in Bothalia 22 (in press). Type: Cape, farm Langberg, NW of Loeriesfontein, fl ex NBG 31 January 1984, *Perry 1991* (NBG, holo,; PRE, K, MO).

Bulb solitary or occasionally forming bulblets, ovoid, 20--40 mm diam, with the outer covering fibrous, ranging from brown to cream-coloured, yellowish within; neck up to 70 mm long, rarely absent. *Leaves* absent at anthesis, 2 (-3), recurved, lorate, 80--280 x 15--26 mm, canaliculate, both surfaces densely pubescent with long, patent, silky white hairs; amplexicaul cataphyll shortly exserted, tipped with red, soon withering down; non-amplexicaul prophyll hidden in the bulb. *Inflorescence* widely spreading, 60--100 mm across; scape 60--100 mm long, 2,5--4,0 mm diam., pale green to glaucous, sometimes flushed with pink, pubescent or glabrous, breaking off at the base in fruit; spathe valves lanceolate, 30--50 x 5--7 mm; bracteoles up to 20 mm long. *Flowers* 10--20, spreading,

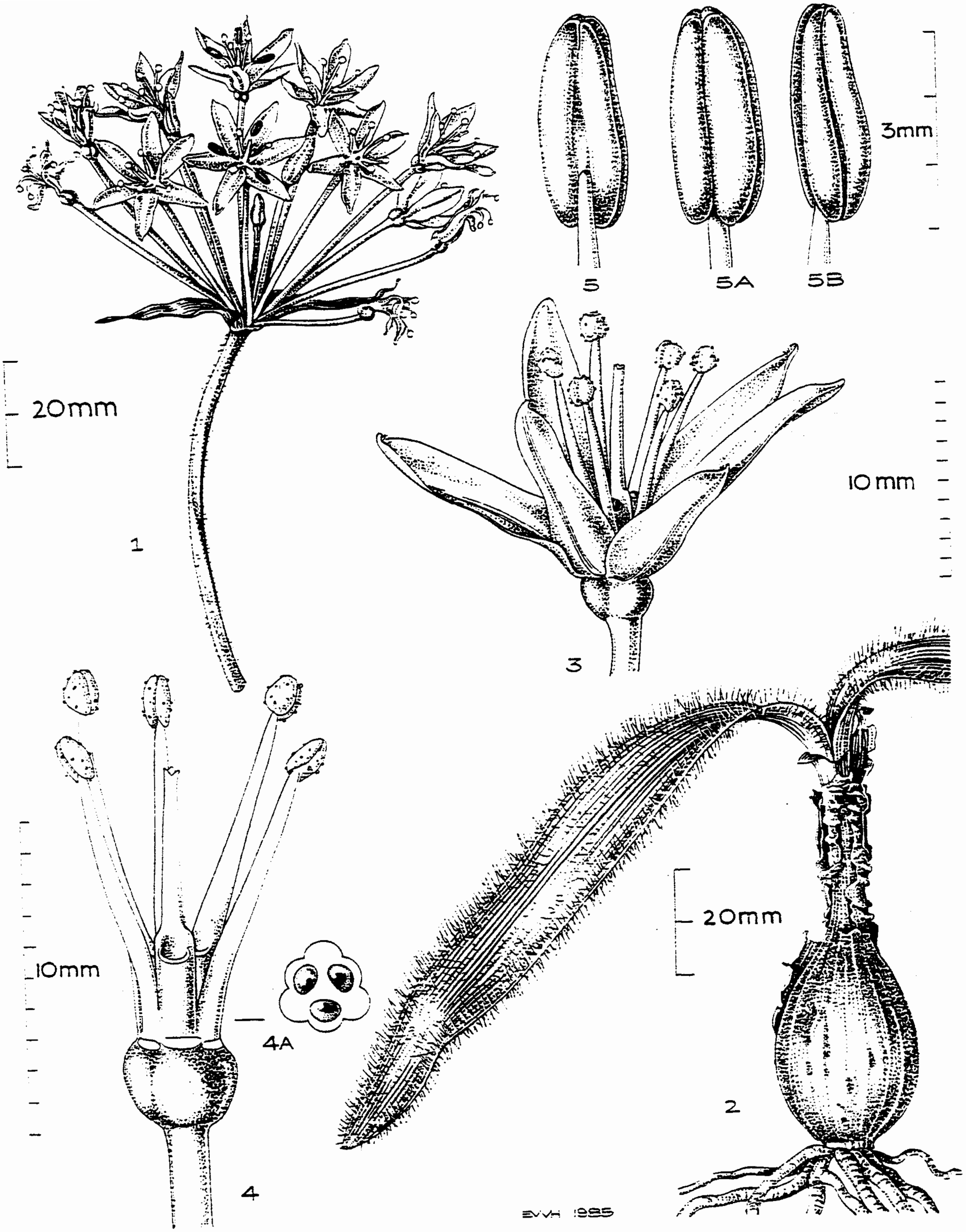


FIGURE 9.37-- *Strumaria aestivalis*: 1, inflorescence, life size; 2, vegetative habit, life size; 3, whole flower; 4, flower with tepals and one stamen cut away one third along its length, 4A, transverse section through androecium and style to show three nectar wells; 5, anther attachment, dorsal view, 5A, ventral view, 5B, lateral view. Drawn from *Perry 1991.*

widely funnel-shaped, white, with a pale pink median dorsal band on each tepal, turning deeper pink with age, heavily scented; pedicels straight to upwardly curved, 40--55 mm long, pale greenish pink. *Tepals* free to the base, spreading, oblong-lanceolate, 12--14 x 3--5 mm. *Stamens* equalling the tepals, spreading slightly from near the base; filaments separate, 7--10 mm long, adnate to the broadened style base for up to 4 mm; the inner face of the inner whorl free with only the lateral margins adnate to the broadly triquetrous style, thus forming 3 tubular nectar wells; anthers subcentrifixed, ± 3 mm long before opening, wine-red; pollen cream-coloured. *Ovary* with 1--2 ovules per locule. *Style* up to 17 mm long, broadly triquetrous in the proximal third, tapering and slender distally. *Seeds* 4--6 mm diam. *Chromosome number* $2n = 20$. Figure 9.37.

Flowering time: January.

Diagnostic features: Of all the species of subgenus Gemmaria, *S. aestivalis* is remarkable in having wide nectar wells formed by the fusion of the lateral margins of the inner filaments to the sharp edges of the triquetrous style: a specialised character state also well developed in subgenus Strumaria; and which indicates parallel development in the two groups. Vegetatively *S. aestivalis* most closely resembles *S. pubescens,* in having yellow-fleshed bulbs and broadly lorate pubescent leaves.

Distribution and habitat: Strumaria aestivalis has been recorded from only one locality in the north western foothills of the Langberg, north west of Loeriesfontein (Figure 9.51), where the population is confined to the south east facing banks of a seasonal stream. Bulbs are aggregated in the shade of rocks or low shrubs, amongst shale chips overlying clayey soil, at elevations of 950 m. This site falls within a zone in which the probability of rain is greatest in March (Zucchini & Adamson 1984), east of the predominantly winter rainfall area where *Strumaria* is centered. The species is typically summer-flowering and responds rapidly to scattered thunder-showers which fall during the summer months.

Specimens examined

--3018 (Kamiesberg): Farm Langberg, NW of Loeriesfontein (-DB), *Perry 1991* (K, MO, NBG, PRE); fl 20 Jan 1986, *Snijman 1006* (MO, NBG).

22. **Strumaria watermeyeri** L. Bolus in Annals of the Bolus Herbarium 3:78 (1923); Barker: t. 398 (1930). Type: Cape, Nieuwoudt. [Nieuwoudtville], Apr 1918, *E.B. Watermeyer* sub *NBG 745/15* (Bol, neo.!, K!), here designated.

Bokkeveldia watermeyeri (L. Bolus) D. & U. Müller-Doblies: 27 (1985).

Bulb solitary, ovoid, 11--20 mm diam., with outer tunics lightly fibrous and light greyish-brown, whitish within; neck up to 50 mm long. *Leaves* absent at anthesis, 2 (-3), usually appressed to the ground, rarely suberect, varying from elliptical to ovate to ovate-lanceolate, 13--45 x 8--17 mm, leathery; adaxial surface dark green, pustulate and glutinous towards the margin; abaxial surface light green, sometimes flushed with red basally, smooth, subtended by a subterranean amplexicaul cataphyll and non-amplexicaul prophyll; seedling glabrous or more or less pubescent. *Inflorescence* unilaterally or equally spreading 15--50 mm across; scape straight to somewhat flexuose, 20--110 mm long, 1--2 mm diam., green to reddish pink, breaking off at the base in fruit; spathe valves lanceolate, 10--25 x 2--5 mm; bracteoles up to 10 mm long. *Flowers* 4--11, either somewhat secund or erecto-patent,varying from funnel-shaped to broadly funnel-shaped, delicate pink or occasionally white, usually banded with darker pink dorsally, ageing to deep pink, without a scent; pedicels straight, 12--30 mm long, green to reddish pink. *Tepals* cut to the base, adnate to the base of the filaments for up to 8 mm, spreading slightly in the proximal two-thirds, becoming outspread distally, oblanceolate, 7--23 x 2--3 mm, with the proximal half either much attenuated or without a narrow proximal claw. *Stamens* equalling or longer than the tepals, suberect to slightly spreading; filaments separate, 8--26 mm long, adnate to the style base for 0,5--4,0 mm, subulate; anthers subcentrifixed, 2,5--3,0 mm long before opening, dark maroon; pollen cream-coloured. *Ovary* with up to 3--6 (-8) ovules per locule. *Style* 11--21 mm long, equalling or slightly longer than the stamens, slightly thickened and trigonous proximally, tapering smoothly upwards, with nectar collecting in 3 sinuses formed by the attachment with the inner filaments. *Seeds* ± 2 mm diam. *Chromosome number* $2n = 20$. Figure 9.38.

Flowering time: From April until the first half of May.

Diagnostic features: The dark green leaves, appressed to the ground, with the pustulate glutinous edge, make *S. watermeyeri* quite distinct. The close contact with the substrate often results in sand grains adhering to the edge of the upper surface of the leaves. The flowers are variable, enabling two subspecies to be recognised. Those of *S. watermeyeri* subsp. *watermeyeri* are long and funnel-shaped with the proximal two-thirds of the tepals extended into a narrow claw which is adnate to the filaments for up to 8 mm. The smaller more widely funnel-shaped flowers of *S. watermeyeri* subsp. *botterkloofensis* have the tepal/filament adnation reduced to 0,5 mm. *Strumaria watermeyeri* is most closely related to *S. salteri*.

Typification: The holotype cited in the original description (*E. watermeyer sub NBG 997/16*) was originally grown at the National Botanic Garden, Kirstenbosch, where it flowered two or three times (L. Bolus 1923). However, no specimen has been preserved at BOL and no isotype has been located at K. Moreover no other material was cited in the protologue, thus according to Article 7.4 of the International Code of Botanical Nomenclature (Greuter *et al.* 1988) selection of a neotype is necessary. The neotype designated here flowered five years prior to the first publication of the species and the herbarium sheet was annotated by L. Bolus as *Strumaria watermeyeri*.

22a. **Strumaria watermeyeri** subsp. **watermeyeri.**

Inflorescence unilaterally spreading, 20--80 mm across; scape 35--110 mm long. *Flowers* somewhat secund and horizontally spreading, funnel-shaped. *Tepals* adnate to filaments for 2,5--8,0 mm, slightly spreading in the proximal two-thirds, otherwise outspread, 14--23 x 2--3 mm, with the proximal half much attenuated into a narrow claw. *Stamens* longer than the tepals, slightly spreading; filaments separate, 15--24 mm long, adnate to the style base for 2--4 mm.

Distribution and habitat: Confined to the Bokkeveld and Koebee Mountains of the north-western Cape, at an altitude of approximately 700--800 m (Figure 9.51). Populations inhabit open sites, in shallow sand overlying exposed sandstone sheets, amongst arid fynbos.

Specimens examined

--3119 (Calvinia): Nieuwoudtville (-AC), *Middlemost* sub *NBG 528/37* (NBG); fl 17 Apr 1937, *Compton 6586* (NBG); *Watermeyer* sub *NBG 745/15* (BOL, K); *Smith s.n.* (SAM); Vanrhyns Pass (-AC), *Hutchinson 792A* (K); top of Vanrhyns Pass (-AC), fl 24 Apr 1971, *Tölken 4003* (BOL); *Perry 1008* (NBG); fl 5 May 1932, *Salter 2143* (BOL); fl 30 Apr 1946, *Smith 6482* (NBG); *Smith 6483* (NBG); fl 15 Apr 1971, *Thomas s.n.* (NBG); farm Arendskraal, SW of Nieuwoudtville (-AC), *Perry 1815* (NBG, PRE); fl 22 Apr 1982, *Snijman 598* (MO, NBG); Grasberg, Calvinia division (-AC), fl Apr 1932, *Ryder & son* sub *NBG 2276/30* (BOL); *Lavranos & Bleck 20849* (NBG); Glen Lyon farm, near Nieuwoudtville (-AC), fl 10 Apr 1961, *Barker 9668* (NBG); Bokkeveldberge, between Nieuwoudtville and Vanrhynsdorp (-AC), fl 9 Apr 1978, *Norris s.n.* (NBG); 1 km NW of Oorlogskloof homestead (-AC), *Snijman 1075* (NBG); farm Lokenberg, S of Nieuwoudtville (-CA), fl 8 May 1971, *Hall 3969* (NBG); farm Papkuilsfontein, SE of Nieuwoudtville (-CA), *Snijman 899* (NBG, PRE); summit of Tierberg, above Koebee Pass (-CA), *Snijman 1173* (NBG, PRE).

--Imprecise locality: Namaqualand, *Caporn* sub *NBG 747/15* (BOL).

22b. **Strumaria watermeyeri** subsp. **botterkloofensis** (D. & U. Müller-Doblies) Snijman, comb. nov. Type: Cape, Calvinia district, Botterkloof, top of pass, 1 September 1980, ca. 700 m, *U. & D. Müller-Doblies 80127z* (PRE, holo.!; B, K!, Herb. M-D.).

Bokkeveldia watermeyeri subsp. *botterkloofensis* D. & U. Müller-Doblies: 27 (1985).

Inflorescence equally spreading, 20--50 mm across; scape straight to somewhat flexuose, 20--65 mm long. *Flowers* erecto-patent, broadly funnel-shaped. *Tepals* adnate to the filaments for 1 mm, slightly spreading in the proximal half, otherwise outspread,

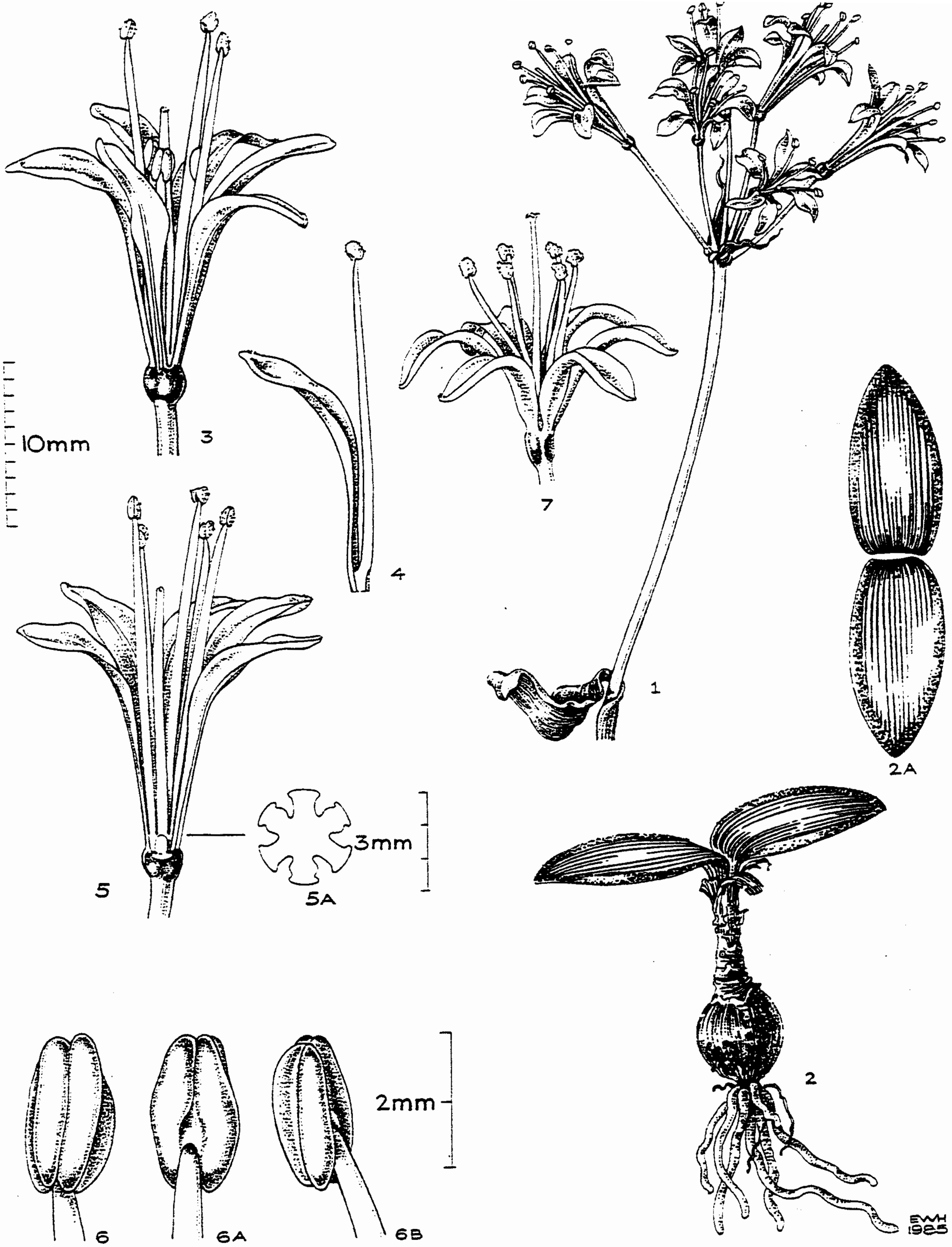


FIGURE 9.38-- *Strumaria watermeyeri*, 1 & 3-6, subsp. *watermeyeri*, 7, subsp. *botterkloofensis*: 1, inflorescence, life size; 2, vegetative habit, life size, 2A, adaxial surface of leaves; 3, whole flower; 4, tepal adnate to filament; 5, flower with one tepal and stamen removed, 5A, transverse section through base of flower; 6, anther attachment, ventral view, 6A, dorsal view, 6B, lateral view. Drawn from *Lavranos 20849* 1-6, and *Snijman 1079* 7.

oblanceolate, without a narrow proximal claw, 7--11 x 2--3 mm. *Stamens* more or less equalling the tepals, slightly spreading; filaments separate, 8--10 mm long, adnate to the style base for 0,5 mm.

Distribution and habitat: Known populations of *S. watermeyeri* subsp. *botterkloofensis* occur on the summit of the Botterkloof Pass, on a mountain range south east and somewhat isolated from the most southerly known populations of *S. watermeyeri* subsp. *watermeyeri* (Figure 9.51). This subspecies is also restricted to shallow sandy pans on exposed sandstone sheets in association with arid fynbos elements.

Specimens examined

--3119 (Calvinia): Botterkloof (-CD), fl Apr--May 1947, *Lewis 2376* (SAM); fl 29 Apr 1947, *Barker 4514* (NBG); fl 15 Apr 1958, *Martin 1152* (NBG); *Müller-Doblies 80127z* (PRE); *Snijman 1079* (NBG).

23. **Strumaria salteri** W.F. Barker in Journal of South African Botany 10: 131 (1944). Type: Cape, Clanwilliam division, Pakhuis, 16 April 1940, *Salter 7508* sub *NBG 986/38* (NBG, holo.!).

Bokkeveldia salteri (W. F. Barker) D. & U. Müller-Doblies: 28 (1985).

Bulb solitary, ovoid, 13--30 mm diam., with lightly fibrous greyish brown outer tunics, whitish within; neck up to 70 mm long or lacking. *Leaves* absent or incipient at anthesis, 2 (-3), usually appressed to the ground, lorate to narrowly elliptical or ovate, 25--100 x 13--28 mm; adaxial surface dark green, glabrous; abaxial surface light green, sometimes flushed with red basally; margin minutely ciliate; subtended by a subterranean amplexicaul cataphyll and non-amplexicaul prophyll. *Inflorescence* a lax umbel, 35--100 mm across; scape flexuose, 60--210 mm long, 1,5--3,0 mm diam., wine-red, sometimes tinged with green, breaking off at the base in fruit; spathe valves broadly lanceolate, 15--30 x 3,0--4,5 mm; bracteoles up to 10 mm long. *Flowers* 5--14, spreading, widely funnelform, glistening pink with a contrasting reddish pink median band on both surfaces of each tepal, ageing to darker pink, scentless; pedicels straight to upwardly curved, 25--55 mm long, wine-red, occasionally green. *Tepals* free to the base, spreading, often recurved above, oblanceolate, 15--29 x 4,0--5,5 mm. *Stamens* longer or equalling the tepals, suberect to slightly spreading; filaments separate, up to 22 mm long, adnate to the style base for 2,0--3,5 mm, with the inner whorl attached slightly higher than the outer; anthers subcentrifixed, 2--3 mm long before opening, deep maroon; pollen cream-coloured. *Ovary* with (2-) 4--7 (-9) ovules per locule. *Style* up to 20 mm long, equalling the stamens, somewhat thickened and trigonous proximally, tapering smoothly upwards, with nectar collecting in 3 sinuses formed by the attachment with the inner filaments. *Seeds*

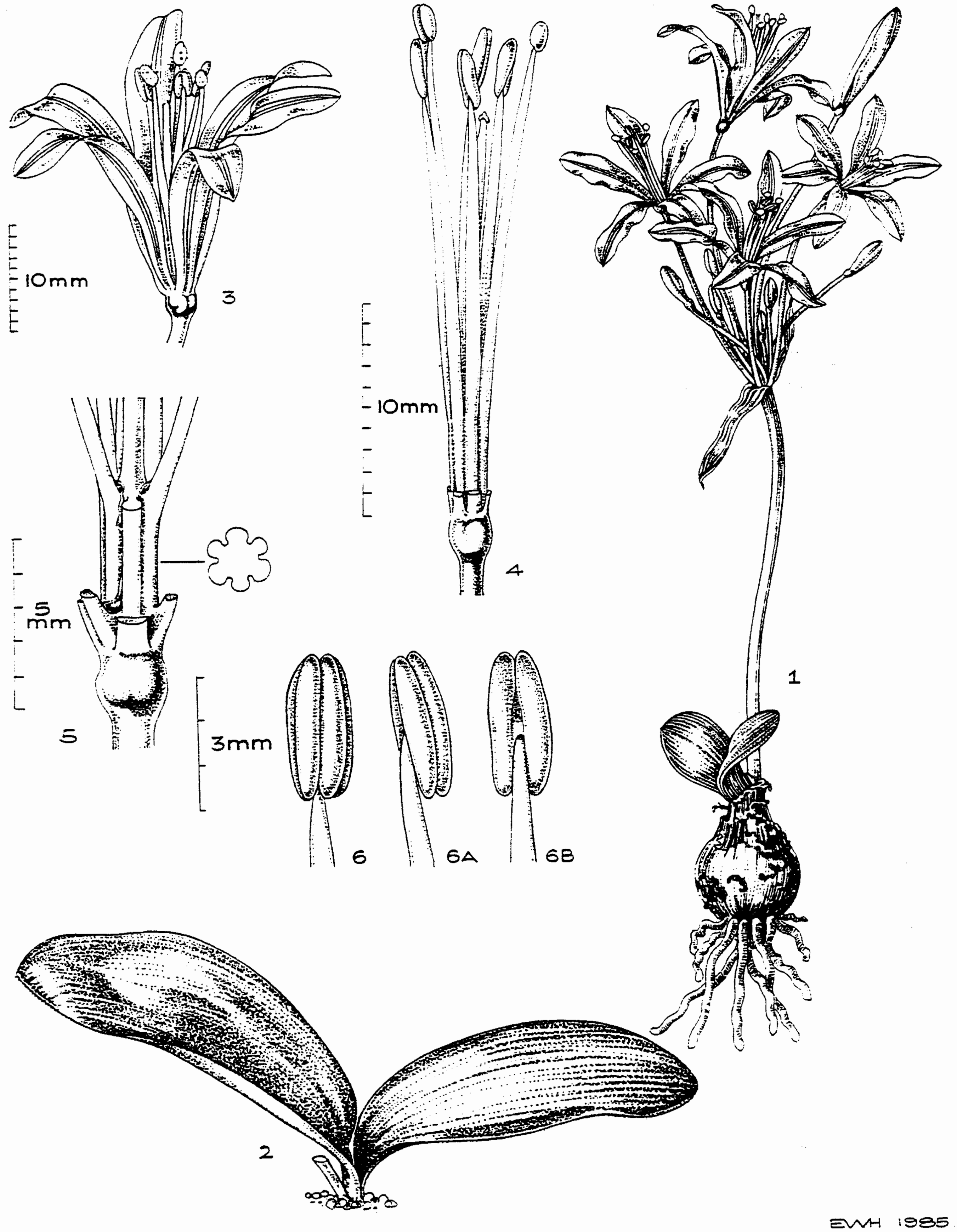


FIGURE 9.39-- *Strumaria salteri*: **1**, habit, life size; **2**, mature leaves, life size; **3**, whole flower; **4**, flower with tepals removed; **5**, portion of flower with tepals and one stamen removed to show adnation of filaments to style; **6**, anther attachment, ventral view, **6A**, lateral view, **6B**, dorsal view. Drawn from *Snijman 254*.

2,0--2,5 mm diam. *Chromosome number* $2n = 20$. Figure 9.39.

Flowering time: May. Cultivated bulbs flower from April.

Diagnostic features: Strumaria salteri is undoubtedly the most showy species in the genus. The widely funnel-shaped flowers and bifoliate leaves, appressed to the ground, place it close to *S. watermeyeri*, from which it is easily distinguished by its minutely ciliate leaves and tepals which are free from the stamens and somewhat broader than those of *S. watermeyeri* (4--5 mm as apposed to 2,5--3,5 mm wide).

Distribution and habitat: Previously known with certainty only from the Pakhuisberge, east of Clanwilliam in the western Cape, *S. salteri* is now also recorded northwards along the adjacent Nardouw mountains and Olifants River Valley (Figure 9.51). Populations are confined to seasonally moist sandstone outcrops, in humus-rich sandy pockets, at elevations between 300 and 900 m. The vegetation bordering these open sites is arid fynbos or marginal succulent Karoo.

Variation: Known populations at the northern and southern limits of the narrow distribution belt show a trend towards floral dimorphism. Specimens from the Pakhuis Pass have stamens which more or less equal the length of the tepals, whereas in the north the stamens exceed the tepals by up to 4 mm. If further data corroborate these initial observations, the formal recognition of subspecies may become justifiable.

Specimens examined

--3118 (Vanrhynsdorp): Nardouwsberg, N end of the plateau (-DC), *Lavranos & Bleck 22989* (NBG); Nardouwsberg plateau, near farm Grootfontein (-DD), *Duncan 286* (NBG); farm Krommevallei on W bank of Olifantsrivier, N of Clanwilliam (-DD), fl 10 May 1990, *Paterson-Jones 63* (NBG).

--3219 (Wuppertal): 25,8 Km from Clanwilliam along Pakhuis road (-AA), fl 21 May 1980, *Snijman 254* (NBG, PRE); *Perry 1321* (NBG).

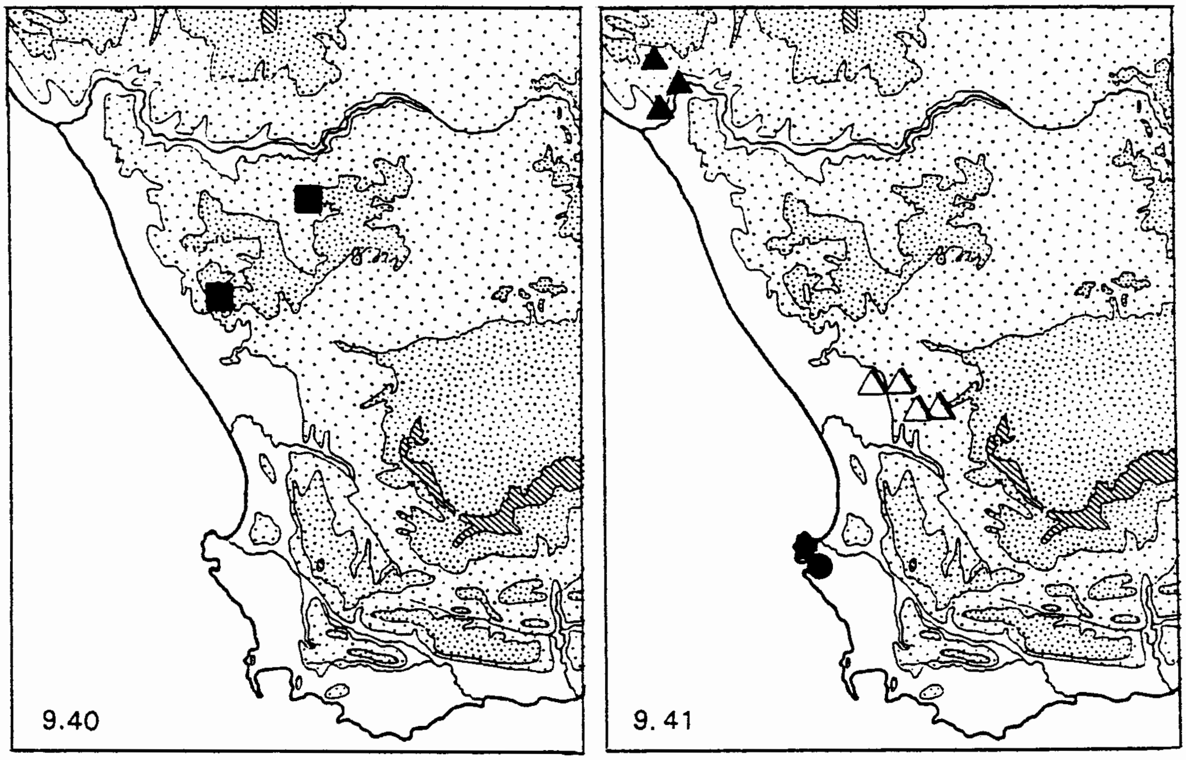
--Imprecise localities: Clanwilliam division, Pakhuis, *Salter 7508* sub *NBG 986/38* (NBG); Vanrhynsdorp-Nieuwoudtville, *Leipoldt* sub *NBG 32/40* (BOL, NBG, PRE).

6. Doubtful species

Strumaria undulata Jacq., Collectanea 5: 50 (1797); Willd.: 32 (1799); Schultes & Schultes: 791 (1830); Herbert: 288 t. 29,13 (1837); D. Dietr.: 1187 (1840); Kunth: 624 (1850); Baker: 104 (1888), 217 (1896), non Berg. ex Kunth: 627 (1850) (= *S. gemmata* Ker-Gawl.). Type: figure in Jacq., Icones plantarum rariorum 2: t. 360 (1795), lecto.!, designated by Müller-Doblies (1985).

Nesynstylis undulata (Jacq.) Raf.: 123 (1838). *Eudolon undulata* (Jacq.) Salisb. ex Baker: 217 (1896).

All currently known species of *Strumaria* share the character state of stamens adnate to the style. *Strumaria undulata* is exceptional in that it is described by Jacquin (1797) as having filaments clearly not connate with the style. To date no material collected in southern Africa matches the type of the species, (Müller-Doblies 1985, pers. obs.), namely the illustration of a plant originally cultivated in Austria. *Strumaria undulata* is regarded as an uncertain species and the interpretation of the floral morphology is treated as doubtful.



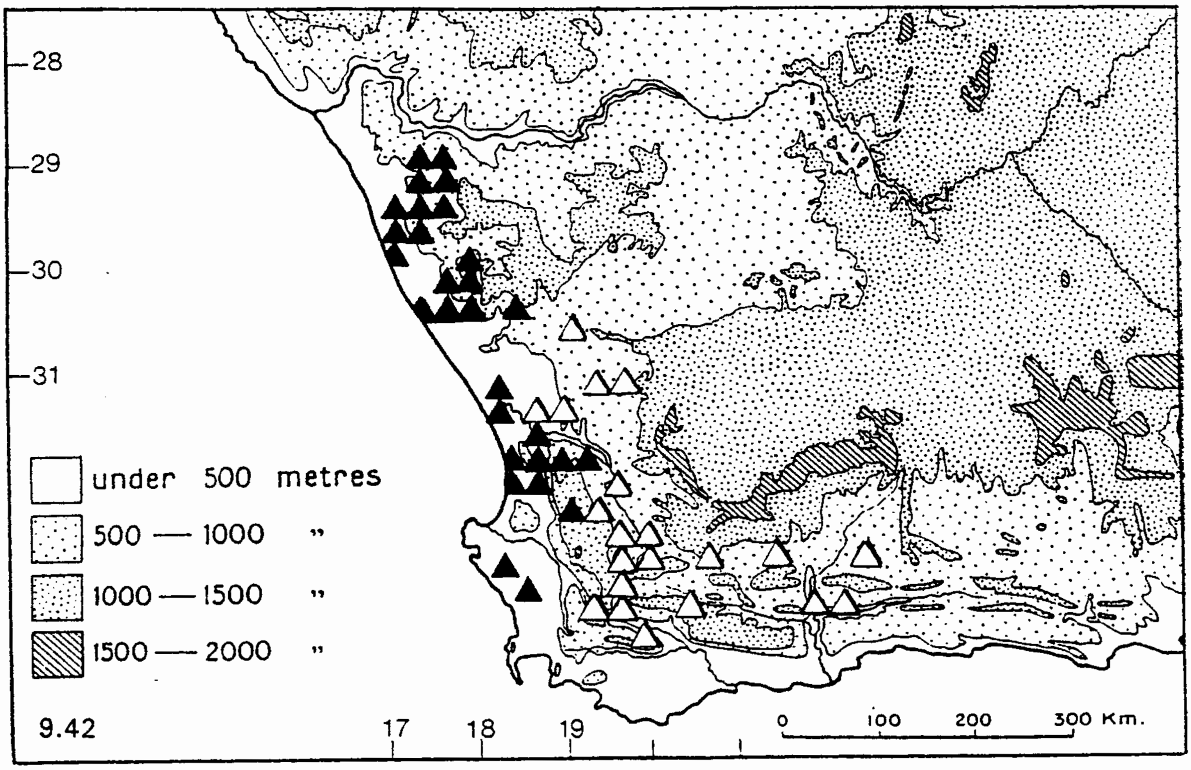


FIGURE 9.40 & 41-- Distribution of: 40, *Kamiesbergia stenosiphon;* 41, (▲) *Namaquanula bruce-bayeri*, (△) *N. pulcherrima*, (●) *N. mathewsii.*

FIGURE 9.42-- Distribution of (▲) *Hessea breviflora*, (△), *H. stellaris.*

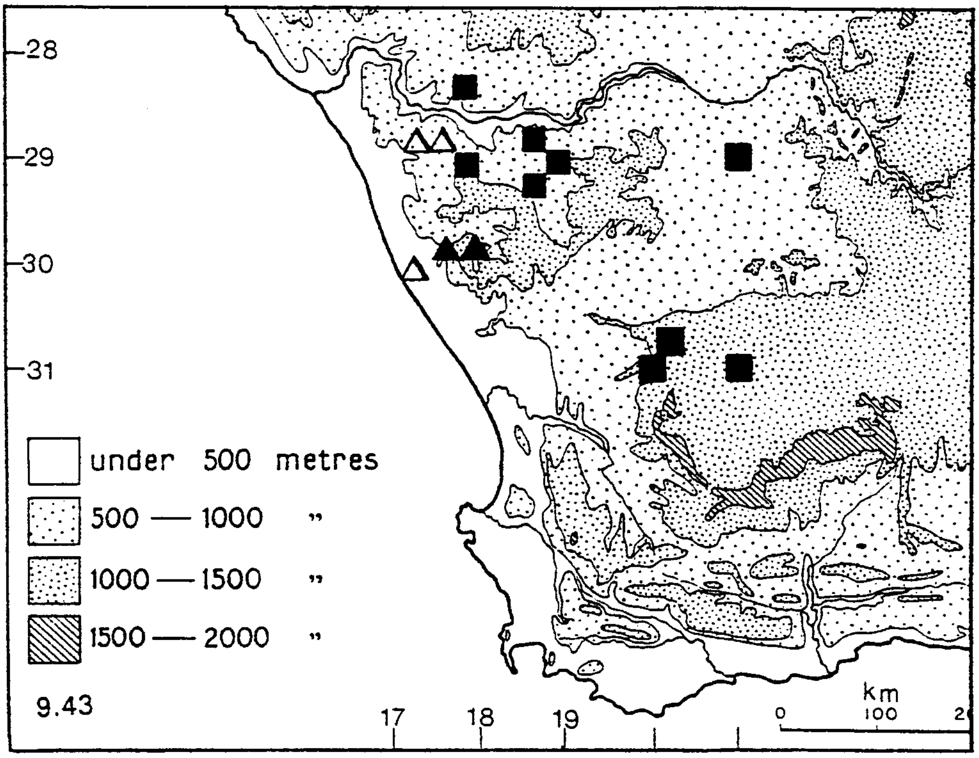


FIGURE 9.43-- Distribution of

(■) *Hessea speciosa,*

(△) *H. pilosula,*

(▲) *H. incana.*

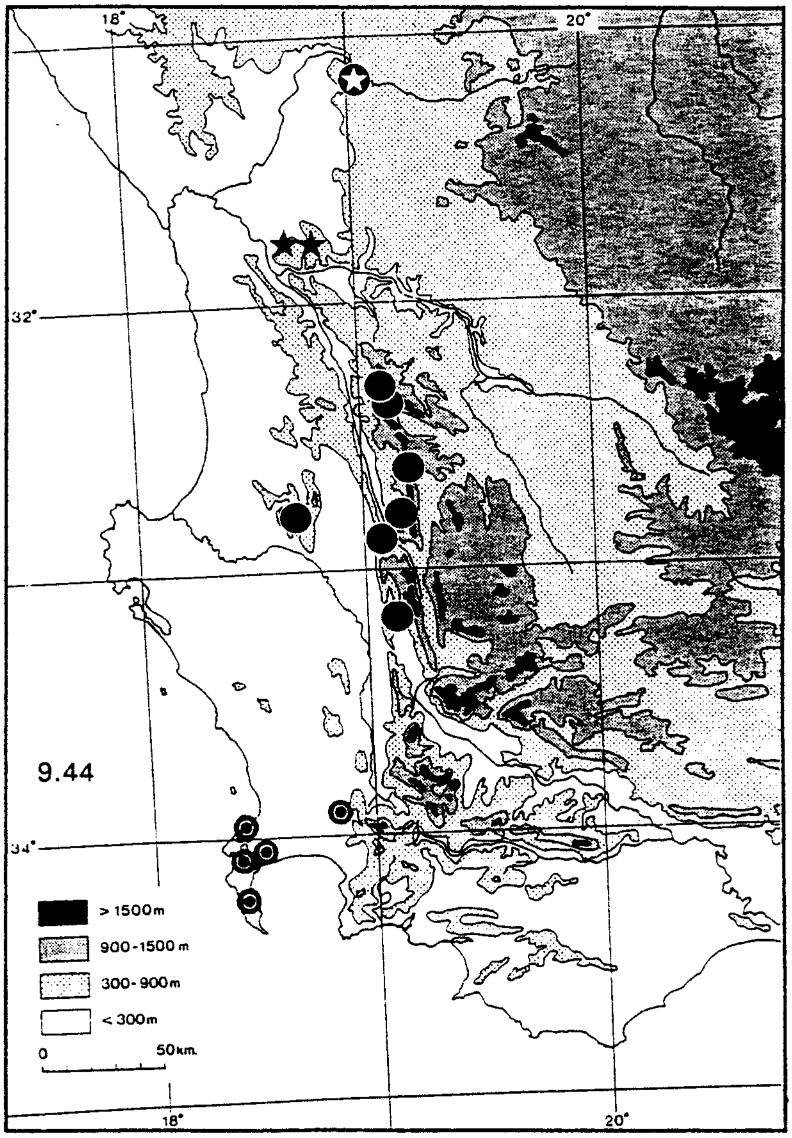


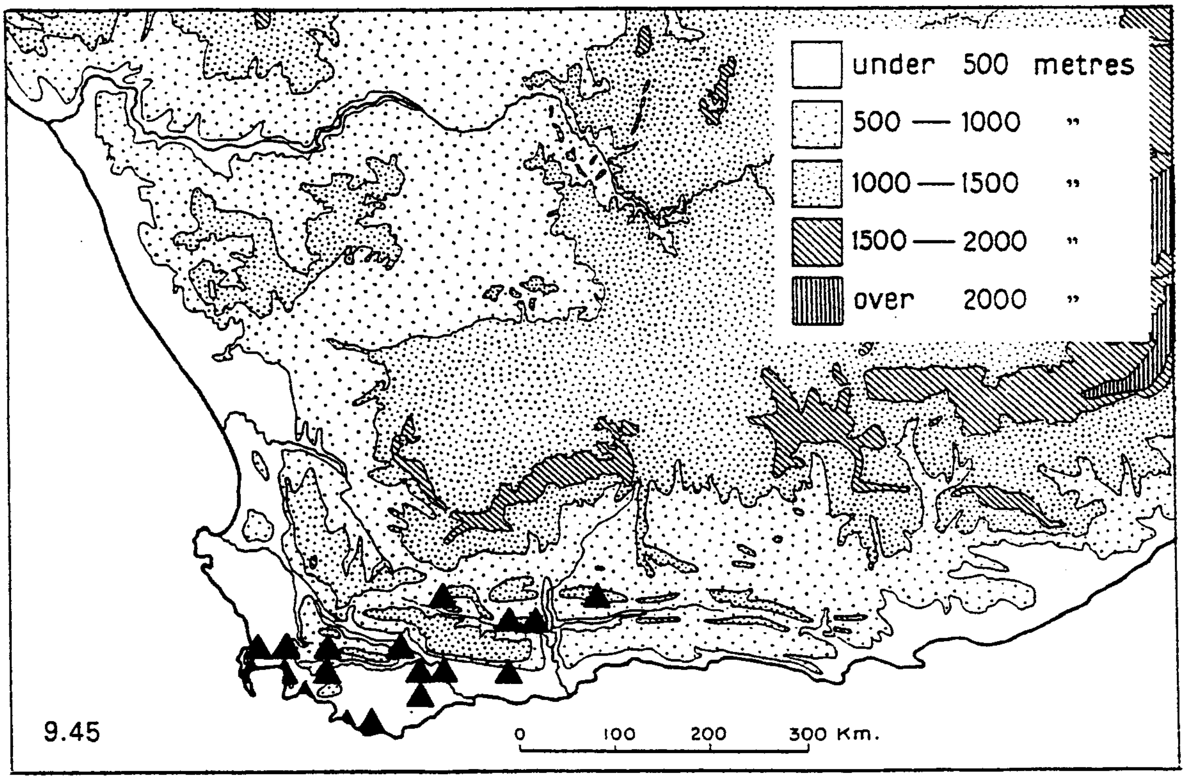
FIGURE 9.44-- Distribution of

☆ *Hessea pusilla,*

★ *H. undosa,*

(●) *H. monticola,*

(⊙) *H. cinnamomea.*



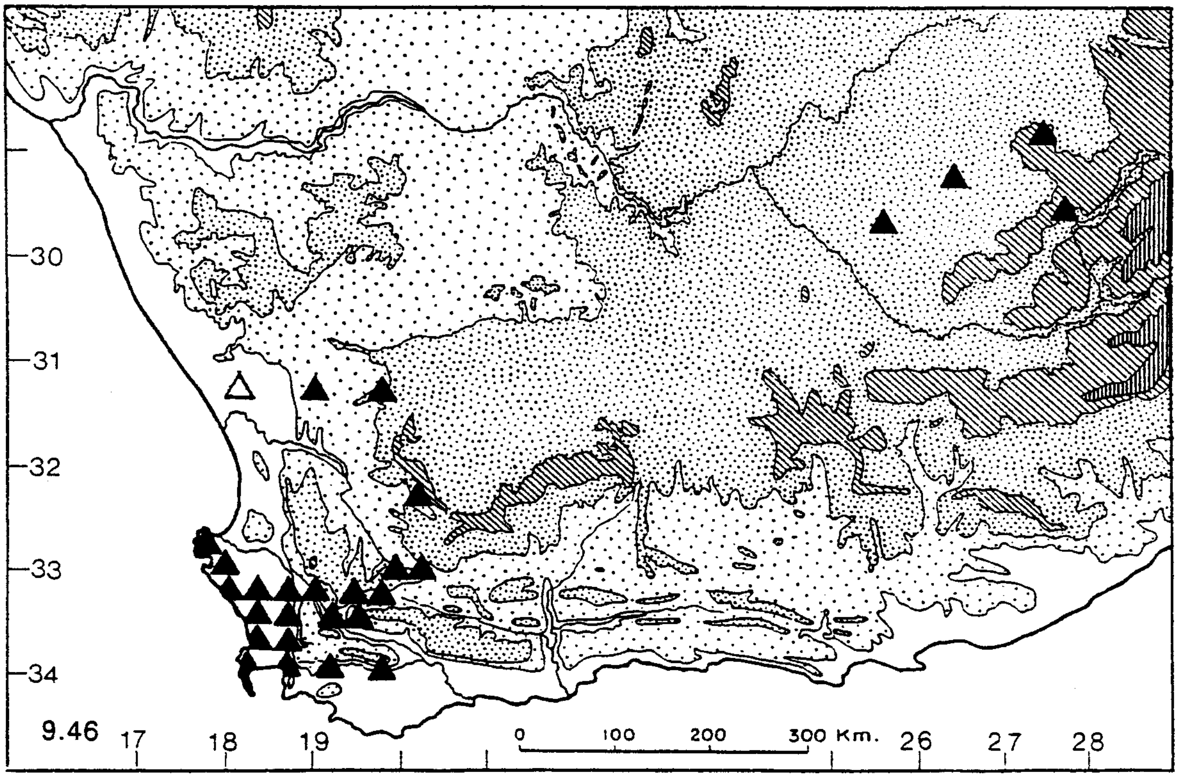
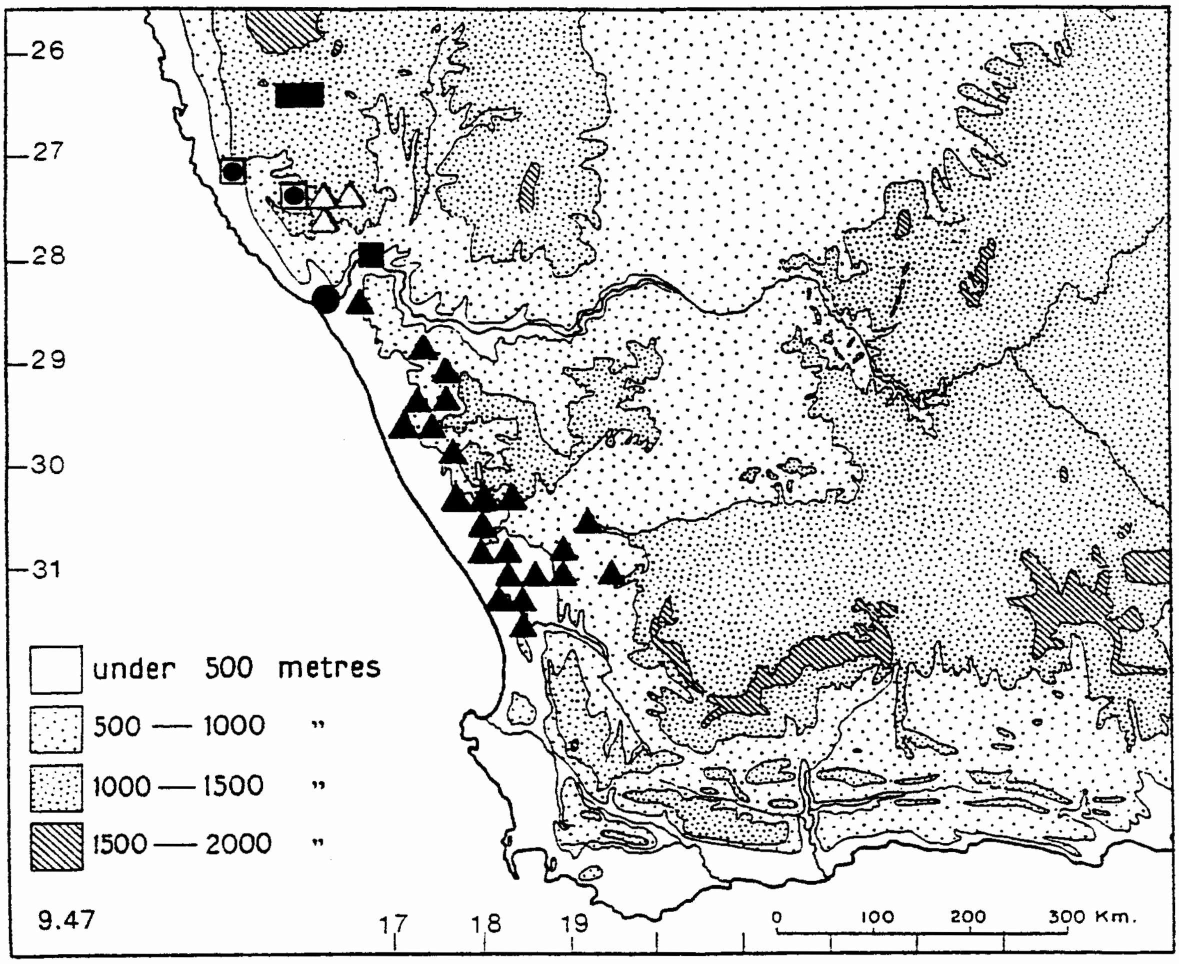
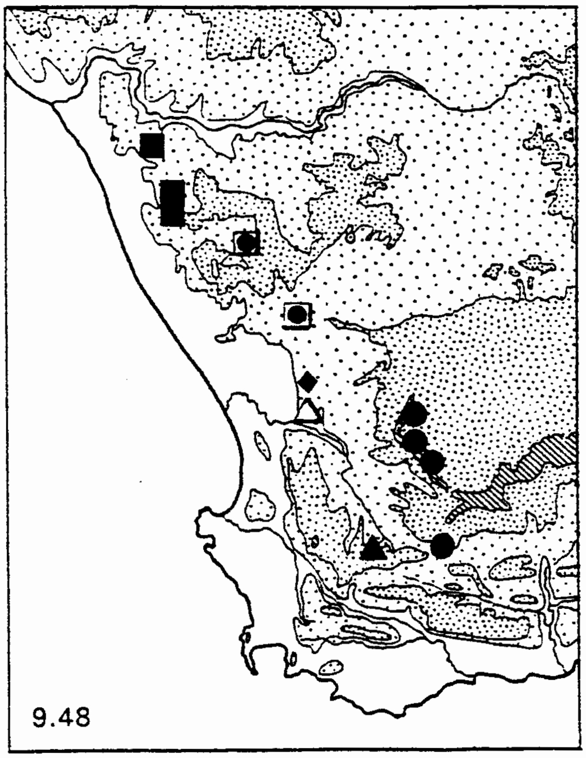


FIGURE 9.45-- Distribution of *Carpolyza spiralis*.

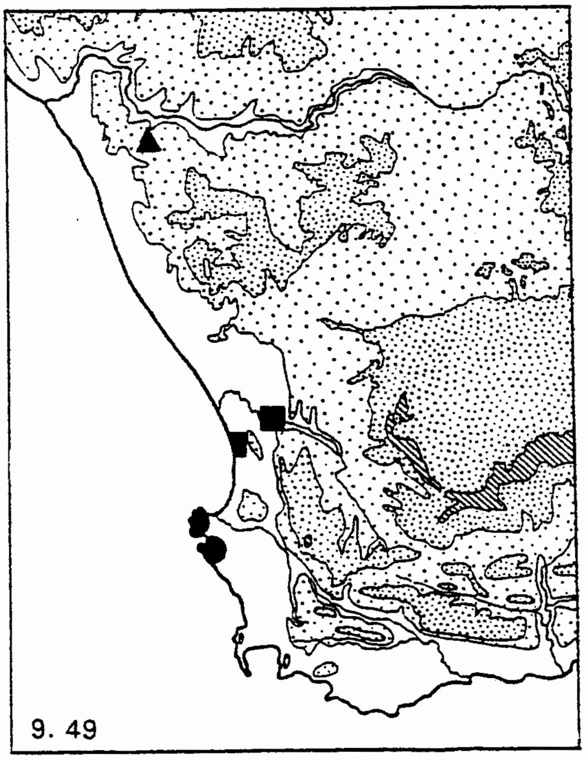
FIGURE 9.46-- Distribution of *Strumaria* subgenus Tedingea (▲) *S. tenella,* (△) *S. pygmaea*.



9.47



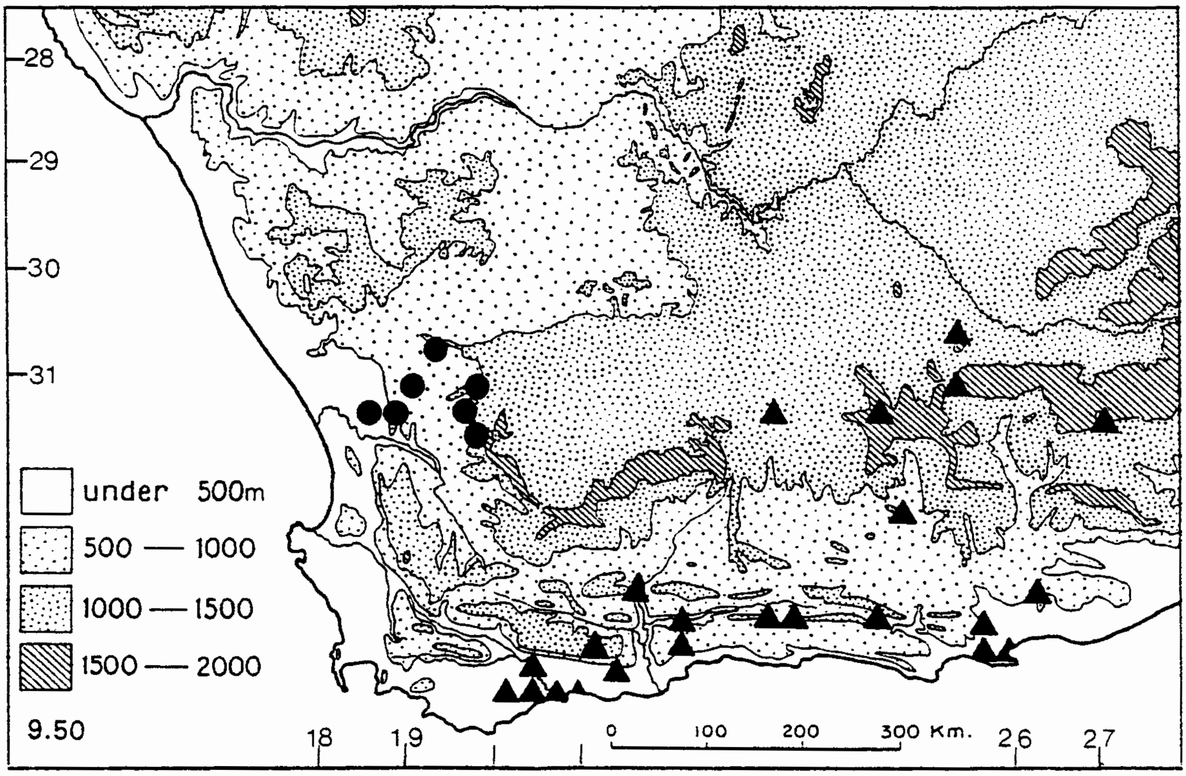
9.48



9. 49

FIGURE 9.47-- Distribution of *Strumaria* subgenus Strumaria (●) *S. bidentata,* (▣) *S. phonolithica,* (■) *S. barbarae,* (△) *S. hardyana,* (▲) *S. truncata.*

FIGURE 9.48 & 49-- Distribution of *Strumaria* subgenus Gemmaria: 48, (◆) *S. picta,* (△) *S. unguiculata,* (▲) *S. karoopoortensis,* (■) *S. merxmuelleriana,* (▣) *S. massoniella,* (●) *S. karooica*; 49, (▲) *S. villosa,* (■), *S. leipoldtii,* (●) *S. chaplinii.*



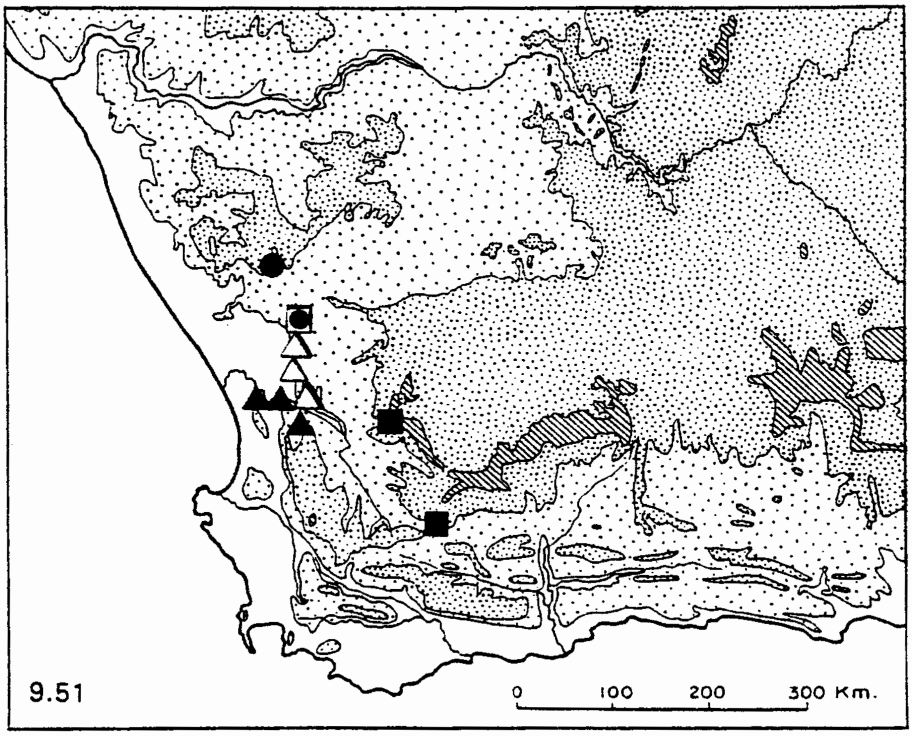


FIGURE 9.50-- Distribution of *Strumaria* subgenus Gemmaria (▲) *S. gemmata,* (●) *S. discifera.*

FIGURE 9.51-- Distribution of *Strumaria* section Bokkeveldia (△) *S. watermeyeri,* (▲) *S. salteri,* (■) *S. pubescens,* (▣) *S. perryae,* (●) *S. aestivalis.*

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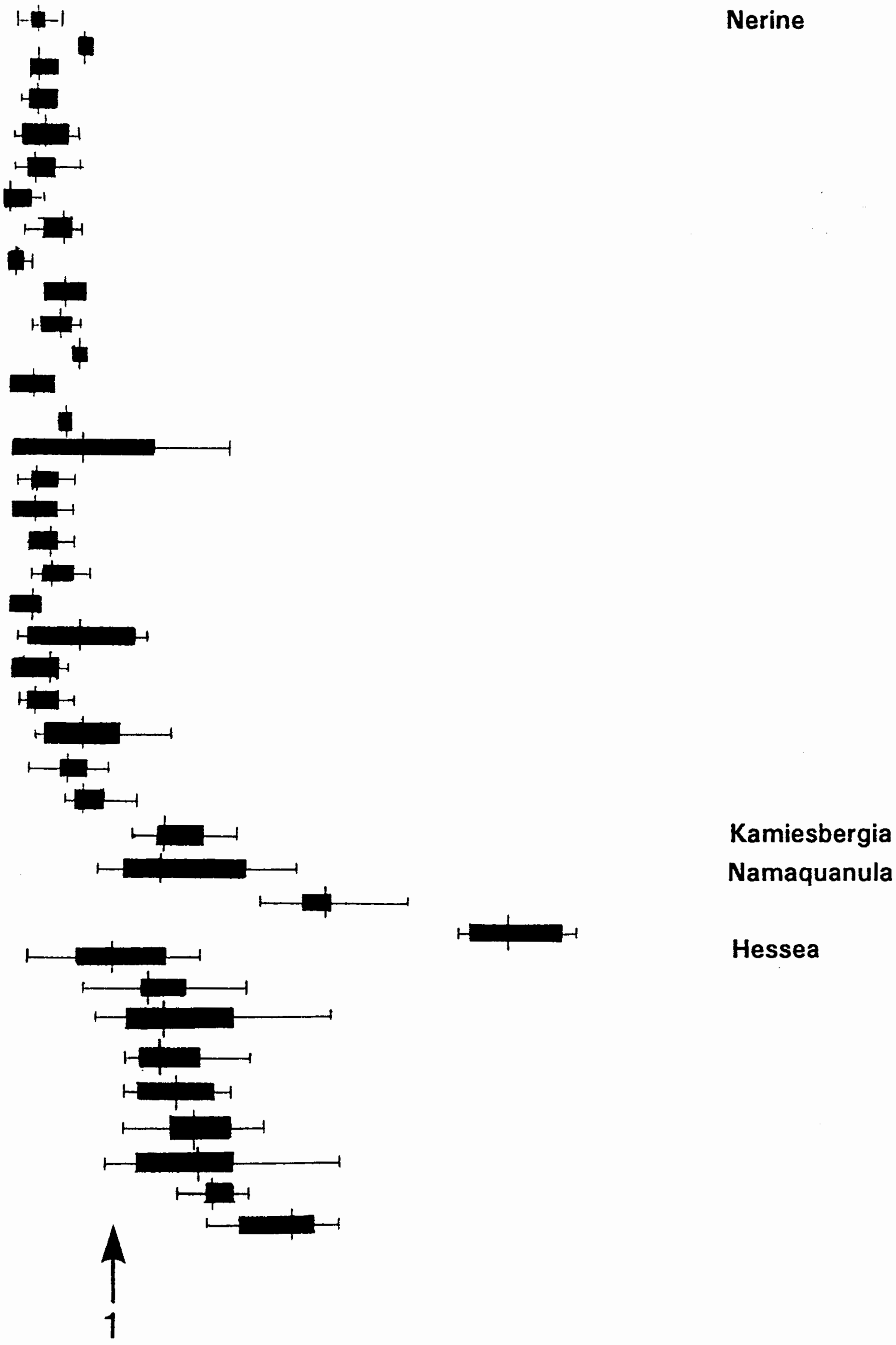
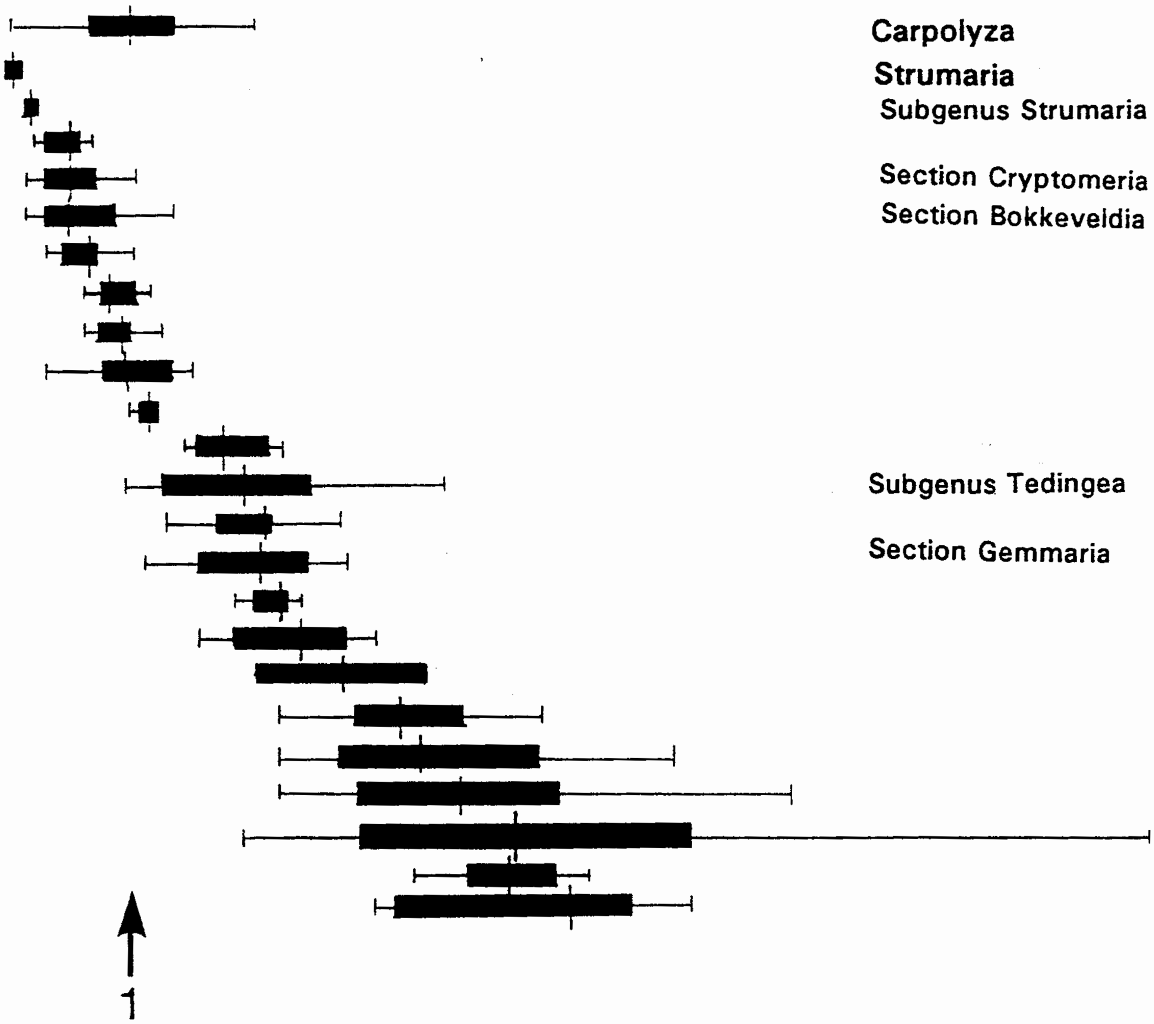
APPENDIX 1-- Specimens dissected for bulb morphology. Voucher specimens are retained at NBG. The *Nerine* specimens are from living material at the Kirstenbosch National Botanic Garden.

Species	Collector or Source	Locality
Carpolyza spiralis (L'Herit.) Salisb.	Müller-Doblies 8258	Cape: ex Karoo Botanic Garden, Worcester
" " "	Rourke 1831	Cape: Soetanysberg, 3419 DD
" " "	E.G. Oliver s.n.	Cape: Kuilsrivier, 3318 DC
Hessea breviflora Herbert	Snijman 853	Cape: Boontjieskloof, 3219 AA
H. cinnamomea (L'Herit.) Durand & Schinz	Snijman 1136	Cape: Cape of Good Hope Nature Reserve,3418 AD
H. incana Snijman	Snijman 1180	Cape: farm de Kuilen, 3018 AA
H. monticola Snijman	Snijman 976	Cape: Elandskloof, 3219 CA
H. pilosula D. & U. Müller-Doblies	Snijman 1134	Cape: near Steinkopf, 2917 BA
H. pusilla Snijman	Snijman 1072	Cape: Perdekraal, 3119 AA
H. speciosa Snijman	Snijman 1210	Cape: 36km NE of Downes, 3120 AC
H. stellaris (Jacq.) Herbert	Snijman 1202	Cape: Varkkloof, 3219 CB
" " " "	Walters s.n.	Cape: Sandhills, 3319 DA
H. undosa Snijman	Snijman 1178	Cape: Gifberg, 3118 DD
Kamiesbergia stenosiphon Snijman	Snijman 1175	Cape: Kamiesberg, 3018 AC
" " "	Snijman 1179	" " "
" " "	Snijman 1192	" " "
Namaquanula bruce-bayeri D. & U. Müller-Doblies	Van Berkel 549	Namibia: Witputz, 2716 DC
N. mathewsii (W.F. Barker) Snijman	Snijman 840	Cape: farm Soutkuil, 3318 AA
(= *Gemmaria mathewsii*)	Snijman 842	Cape: farm Skaapplaas, 3119 CB
N. pulcherrima (D. & U. Müller-Doblies)	Snijman 855	Cape: farm Soetwater, 3119 CB
Snijman (= *Gemmaria pulcherrima*)	Snijman 871	Cape: Nieuwoudtville, 3119 CB)
Nerine appendiculata Baker	NBG 44/79	Natal: Van Reenen, 2829 AD
N. alta W.F. Barker	NBG 78/80	Cape: Blackwoods, 3227 CB
N. angulata L. Bolus	NBG 38/80	Cape: Glengotha, 3227 AC
N. bowdenii Watson	NBG 73/80	Natal: Weza Forest, 3029 DA
N. duparaquetiana Baker	NBG 748/84	Cape: ex hort Kirstenbosch
N. filamentosa W.F. Barker	NBG 50/80	Cape: Aardoffplaas, 3227 AC
N. filifolia Baker	NBG 47/80	Cape: NW of Gasea siding, 3227 CB
N. flexuosa Herbert	NBG 39/80	Cape: near Bedford, 3226 CA
N. gaberonensis Brem. & Oberm.	Duncan 249	Cape: near Kakamas, 2820 DC
N. gibsonii Douglas	NBG 290/76	Cape: near Cala, 3127 DA
N. humilis (Jacq.) Herbert	NBG 461/59	Cape: Montagu, 3320 CC
N. krigei W.F. Barker	NBG 567/65	Cape: Kaffir Drift, 3327 AC
N. masonorum L. Bolus	NBG 828/20	Transkei: Mqanduli, 3128 DD
N. pancratioides Baker	NBG 139/82	Natal: Hebron, 3029 CB
N. pudica Hooker f.	J.C. Paterson-Jones 40	Cape: Greyton, 3419 BA
N. sarniensis (L.) Herbert	NBG 105/44	Cape: Genadendal, 3419 BA
N. undulata (L.) Herbert	Bruyns 3664	Cape: Badspoort, 3321 DB
Strumaria aestivalis Snijman	Snijman 1006	Cape: farm Langberg, 3018 DB
S. bidentata Schinz	Bayer 1027	Cape: Beauvallon, 2816 DA
"	Van Jaarsveld & Kuhn 8221	Cape: Alexander Bay, 2816 DA
S. chaplinii (W.F. Barker) Snijman (= *Gemmaria chaplinii*)	Duncan 28	Cape: Langebaan, 3318 AA

Species	Collector or Source	Locality
S. discifera Marloth ex Snijman subsp. *bulbifera* Snijman	Perry & Snijman 2042	Cape: Nieuwoudtville, 3119 AC
S. discifera subsp. *discifera*	Snijman 443	Cape: Koebee Pass, 3118 DB
" " "	Snijman 261	Cape: near Klawer, 3118 DA
S. gemmata Ker-Gawl. (= *Gemmaria gemmata*)	Mathews 1226	Cape: Witberg, 3322 CC
S. hardyana D. & U. Müller-Doblies	Lavranos & Pehlemann 21197	Namibia: farm Aub, 2716 DB
" "	Lavranos & Pehlemann 21246	Namibia: near Rosh Pinah, 2716 DC
S. karooica (W.F. Barker) Snijman (= *Gemmaria karooica*)	Snijman 1168	Cape: Sutherland, 3220 BC
S. karoopoortensis (D. & U. Müller-Doblies) Snijman (= *Gemmaria karoopoortensis*)	Perry 1278	Cape: Fonteinskop, 3319 BB
S. leipoldtii (L. Bolus) Snijman (= *Gemmaria leipoldtii*)	Snijman 1244	Cape: Lamberts Bay, 3218 AB
S. perryae Snijman	Perry 997	Cape: near Grasberg, 3119 AA
S. picta W.F. Barker (= *Bokkeveldia picta*)	Perry 1337	Cape: Mensieskraal, 3119 CA
	Snijman 1227	Cape: Papkuilsfontein, 3119 CA
S. pubescens W.F. Barker (= *Bokkeveldia pubescens*)	Snijman 1164	Cape: Gannaga Pass, 3220 AA
S. salteri W.F. Barker (= *Bokkeveldia salteri*)	Lavranos & Bleck 22989	Cape: Nardouwsberg, 3118 DD
S. pygmaea Snijman (= *Hessea spiralis* Baker)	Snijman 862	Cape: Kersbosvlei II, 3118 AD
S. truncata Jacq.	Hiemstra 493	Cape: Wildepaardehoek Pass, 2917 DC
" "	Snijman 282	Cape: near Garies, 3018 CB
S. tenella (L.f.) Snijman subsp. *tenella* (= *Tedingea tenella*)	Snijman 517	Cape: Voelfontein, 3220 AD
	Snijman 856	Cape: Nieuwoudtville, 3119 AC
" "	Snijman 1207	Cape: Botterkloof, 3119 CD
S. tenella subsp. *orientalis* Snijman	I.B. Oliver 313	O.F.S.: Bloemfontein, 2926 AA
S. unguiculata (W.F. Barker) Snijman (= *Gemmaria unguiculata*)	Snijman 854	Cape: Doring River bridge, 3119 CC
S. villosa Snijman	Perry 1544	Cape: E of Kosies, 2917 BA
S. watermeyeri L. Bolus subsp. *watermeyeri* (= *Bokkeveldia watermeyeri* subsp. *watermeyeri*	Snijman 899	Cape: Papkuilsfontein, 3119 CA

APPENDIX 2-- Bar diagram for ratio of pedicel length to perigone length in species of *Nerine, Kamiesbergia, Namaquanula, Hessea, Carpolyza* and *Strumaria*. Each bar represents the range with the median marked and the 1st and 3rd quartiles shown by the heavy bar.




Carpolyza
Strumaria
Subgenus Strumaria
Section Cryptomeria
Section Bokkeveldia
Subgenus Tedingea
Section Gemmaria
1

APPENDIX 3-- Specimens examined anatomically for floral morphology. Voucher specimens are retained at NBG.

Species	Collector or Source	Locality
Carpolyza spiralis (L'Herit.) Salisb.	Van Zijl s.n.	Ex hort, Constantia.
Hessea breviflora Herbert	Van Jaarsveld 5371	Cape: Sannagas, 2917 DC
H. cinnamomea (L'Hérit.) Durand & Schinz	Snijman 1038	Cape: Good Hope Nature Reserve, 3418 AD
H. incana Snijman	Snijman 1180	Cape, De Kuilen, 3018
H. monticola Snijman	Hugo s.n.	Cape: Dasklip Pass, 3219 CC
Kamiesbergia stenosiphon Snijman	Snijman 1175	Cape: Kamiesberg, 3018 AC
Namaquanula mathewsii (W.F. Barker) Snijman (= *Gemmaria mathewsii*)	Snijman 840	Cape: Soutkuil, 3318 AA
N. pulcherrima (D.& U. Müller-Doblies) Snijman (= *Gemmaria pulcherrima*)	Snijman 1022	Cape: SW of Grootdrif, 3118 BD
Nerine filamentosa W.F. Barker	NBG 50/80	Cape: Aardoffplaas, 3227 AC
N. masonorum L. Bolus	NBG 828/20	Transkei: Mganduli, 3128 DD
Strumaria aestivalis Snijman	Perry 1991	Cape: farm Langberg, 3018 DB
S. bidentata Schinz	Van Jaarsveld & Kuhn 3221	Cape: Alexander Bay, 2816 DA
S. gemmata Ker-Gawl. (= *Gemmaria gemmata*)	Vlok 956	Cape: Baviaanskloof, 3324 CB
S. picta W.F. Barker (= *Bokkeveldia picta*)	Perry 1337	Cape: Mensieskraal, 3119 CA
S. pubescens W.F. Barker (= *Bokkeveldia pubescens*)	Snijman 1164	Cape: Gannaga Pass, 3220 AA
S. salteri W.F. Barker (= *Bokkeveldia salteri*)	Lavranos & Bleck 22989	Cape: Nardouwsberg, 3118 DD
" "	Perry 1321	Cape: Pakhuis, 3219 AA
" "	Snijman 251	Cape: Pakhuis, 3219 AA
S. tenella (L.f.) Snijman subsp. *tenella* (= *Tedingea tenella*)	Snijman 856	Cape: Gien Lyon, 3119 AC
S. tenella subsp. *orientalis* Snijman	I.B. Oliver 313	O.F.S.: Bloemfontein, 2926 AA
S. truncata Jacq.	Barker 10192	Cape: N of Vanrhynsdorp, 3118 DA
"	Bayer 2759	Cape: SW of Loeriesfontein, 3019 CD
"	Duncan 257	Cape: Bulletrap, 2917 DA

APPENDIX 4-- Specimens examined by SEM for pollen morphology. Voucher specimens of *Hessea*, *Kamiesbergia* and *Strumaria* are retained at NBG. The remaining specimens are from living material at the Kirstenbosch National Botanic Garden.

Species	Collector or Source	Locality
Amaryllis belladonna L.	Manning s.n.	Cape: Kirstenbosch Botanic Garden, 3318 CD
Boophane disticha (L.f.) Herbert	Van Jaarsveld 5794	Cape: Langberg, 3319 DC
Brunsvigia marginata (Jacq.) Aiton	J.C. Paterson-Jones s.n.	Cape: Franschhoek, 3319 CC
Crinum moorei Hook.f.	NBG 569/70	Natal: Ngome Forest, 2731 DC
Hessea breviflora Herbert	Snijman 255	Cape: Pakhuis, 3219 AA
H. cinnamomea (L'Hérit.) Durand & Schinz	Snijman 1038	Cape: Good Hope Nature Reserve, 3418 AD
H. monticola Snijman	Abrahams 294	Cape: Kleinjongenskraal, 3219 AC
H. stellaris (Jacq.) Herbert	Goldblatt 6089	Cape: Matjiesfontein, 3320 BA
Kamiesbergia stenosiphon Snijman	Snijman 1175	Cape: Kamiesberg, 3018 AC
Nerine appendiculata Baker	NBG 135/86	Natal: Van Reenen, 2829 AD
N. filamentosa W.F. Barker	NBG 148/85	Cape: farm Glenhum, 3227 AC
N. gaberonensis Brem. & Oberm.	NBG 407/87	Cape: Augrabies National Park, 2828 CB
N. huttoniae Schonl.	NBG 114/86	Cape: Cango Caves, 3322 AC
N. masonorum L. Bolus	NBG 828/20	Transkei: Manduli, 3128 DD
Strumaria aestivalis Snijman	Perry 1991	Cape: Langberg, 3018 DB
" "	Snijman 1006	Cape: Langberg, 3018 DB
S. karooica (W.F. Barker) Snijman (= *Gemmaria karooica*)	Perry 3644	Cape: Fransplaas, 3220 AB
S. picta W.F. Barker (= *Bokkeveldia picta*)	Snijman 1227	Cape: Papkuilsfontein, 3119 CA
S. salteri W.F. Barker (= *Bokkeveldia salteri*)	Perry 1321	Cape: Pakhuis, 3219 AA
S. truncata Jacq.	Duncan 245	Cape: near Soebatsfontein, 2917 DC
"	Perry 1057	Cape: W of Steinkopf, 2917 BA

APPENDIX 5-- Specimens examined microscopically for seed testa morphology. Voucher specimens of *Hessea, Kamiesbergia, Namaquanula* and *Strumaria* are retained at NBG. The remaining specimens are from living material.

Species	Collector or Source	Locality
Amaryllis belladonna L.	Snijman s.n.	Cape: Uitkyk Pass, 3219 AC
Ammocharis coranica (Ker-Gawler)	KG 268/89	Cape: ex Karoo Botanic Garden, Worcester
Boophane disticha (L.f.) Herbert	NBG 909/82	Cape: Hamburg, 3327 AD
B. flava W.F. Barker ex Snijman	Snijman 602	Cape: Glen Lyon, 3119 AC
B. pulchra W.F. Barker	Perry 1046	Cape: W of Steinkopf, 2917 BA
Brunsvigia bosmaniae Leighton	Snijman 275	Cape: Karkams, 3017 BD
B. litoralis R.A. Dyer	NBG 884/82	Cape: Humewood, 3325 DC
B. minor Lindl.	NBG 1196/82	Cape: Arendskraal, 3119 AC
B. orientalis (L.) Aiton ex Ecklon	Snijman s.n.	Cape: Milnerton, 3318 CD
B. radula (Jacq.) Aiton	NBG 886/82	Cape: Kamiesberg, 3018 AC
Crinum variabile (Jacq.) Herbert	NBG 892/82	Cape: Bowesdorp, 3017 BB
Carpolyza spiralis (L'Hérit.) Salisb.	Müller-Doblies 8258	Cape: ex Karoo Botanic Garden, Worcester
Cybistetes longifolia (L.) Milne-Redh. & Schweick.	Van Zijl s.n.	Cape: ex hort, Constantia
Hessea breviflora Herbert	Van Jaarsveld & Drijfhout 5305	Cape: Wildepaardehoek Pass, 2917 DC
" "	Williamson 3431	Cape: near Arabies, 2917 BB
H. pusilla Snijman	Snijman 1072	Cape: Perdekraal, 3119 AA
Kamiesbergia stenosiphon Snijman	Snijman 1175	Cape: Kamiesberg, 3018 AC
Namaquanula mathewsii (W.F. Barker) Snijman (= *Gemmaria mathewsii*)	Snijman 842	Cape: Skaapplaas, 3318 AA
Nerine appendiculata Baker	NBG 44/79	Natal: Van Reenen, 2829 AD
N. duparquetiana Baker	NBG 748/84	Cape: ex hort, Kirstenbosch
N. filamentosa W.F. Barker	NBG 148/85	Cape: Cathcart, 3227 AC
N. filifolia Baker	NBG 877/75	O.F.S.: Harrismith district
N. krigei W.F. Barker	NBG 878/75	O.F.S.: Harrismith district
Strumaria aestivalis Snijman	Perry 1991	Cape: Langberg, 3018 DB
S. chaplinii (W.F. Barker) Snijman (= *Gemmaria chaplinii*)	NBG 220/73	Cape: Paternoster, 3217 DD
S. gemmata Ker-Gawl. (= *Gemmaria gemmata*)	Vlok 956	Cape: Baviaanskloof, 3324 CB
S. karooica (W.F. Barker) Snijman (= *Gemmaria karooica*)	Forrester & Leitch s.n.	Cape: Sutherland, 3220 BC
S. karoopoortensis (D. & U. Müller-Doblies) Snijman (= *Gemmaria karoopoortensis*)	Perry 1278	Cape: Fonteinskop, 3319 BB
S. pygmaea Snijman (= *Hessea spiralis*)	Snijman 862	Cape: Kersbosvlei II, 3118 AD
S. truncata Jacq.	Duncan 257	Cape: Bulletrap, 2917 DA
"	Perry 1057	Cape: W of Steinkopf, 2917 BA

APPENDIX 6-- Specimens examined for chromosome cytology. Voucher specimens are retained at NBG.

Species	Collector or Source	Locality
Hessea breviflora Herbert	Barker 9868	Cape: Darters Grave, 3017 BD
"	Perry 690	Cape: N of Clanwilliam, 3118 DD
"	Pretorius 11	Cape: N of Citrusdal, 3218 BD
"	Snijman 853	Cape: Boontjieskloof, 3219 AA
"	Van Jaarsveld & Drijfhout 5305	Cape: Wildepaardehoek Pass, 2917 DC
H. cinnamomea (L'Hérit.) Durand & Schinz	Snijman 1038	Cape: Good Hope Nature Reserve, 3418 AD
H. incana Snijman	Snijman 1180	Cape: De Kuilen, 3018 AA
H. pilosula D. & U. Müller-Doblies	Snijman 1131	Cape: Near Koufontein, 2917 BC
H. pusilla Snijman	Snijman 1072	Cape: Perdekraal, 3119 AA
H. speciosa Snijman	Snijman 1163	Cape: N of Downes, 3120 AC
H. stellaris (Jacq.) Herbert	Goldblatt 6089	Cape: Matjiesfontein, 3320 BA
"	Perry 990	Cape: Rietfontein, 3119 BC
H. undosa Snijman	Snijman 1178	Cape: Matsikammaberg, 3118 DD
Kamiesbergia stenosiphon Snijman	Snijman 1175	Cape: Kamiesberg, 3018 AC
Namaquanula bruce-bayeri D. & U. Müller-Doblies	Williamson 3405	Cape: Beesbank, 2816 BC
Strumaria chaplinii (W.F. Barker) Snijman (= *Gemmaria chaplinii*)	Duncan 28	Cape: Langebaan, 3318 AA
S. discifera Marloth ex Snijman subsp. *bulbifera* Snijman	Perry & Snijman 204	Cape: Nieuwoudtville, 3119 AC
S. discifera subsp. *discifera*	Bayer 1853	Cape: Bloukranz Pass, 3119 DA/DB
" "	Perry 1014	Cape: E of Nieuwoudtville, 3119 AC
" "	Snijman 261	Cape: near Klawer, 3118 DA
S. karooica (W.F. Barker) Snijman (= *Gemmaria karooica*)	Snijman 1168	Cape: Sutherland, 3220 BC
S. karoopoortensis (D. & U. Müller-Doblies) Snijman (= *Gemmaria karoopoortensis*)	Perry 1278	Cape: Fonteinskop, 3319 BB
S. merxmuelleriana (D. & U. Müller-Doblies) Snijman (= *Gemmaria merxmuelleriana*)	Snijman 306	Cape: Nooitgedacht, 2917 DD
S. pubescens W.F. Barker (= *Bokkeveldia pubescens*)	Snijman 1164	Cape: Gannaga Pass, 3220 AA
S. pygmaea Snijman (= *Hessea spiralis*)	Snijman 862	Cape: Kersbosvlei II, 3118 AD
S. watermeyeri L. Bolus subsp. *botterkloofensis* (D. & U. Müller-Doblies) Snijman (= *Bokkeveldia watermeyeri* subsp. *botterkloofensis*)	Snijman 1079	Cape: Botterkloof, 3119 CD

Index with Taxon Numbers

Taxa upheld in this work are indicated in bold.