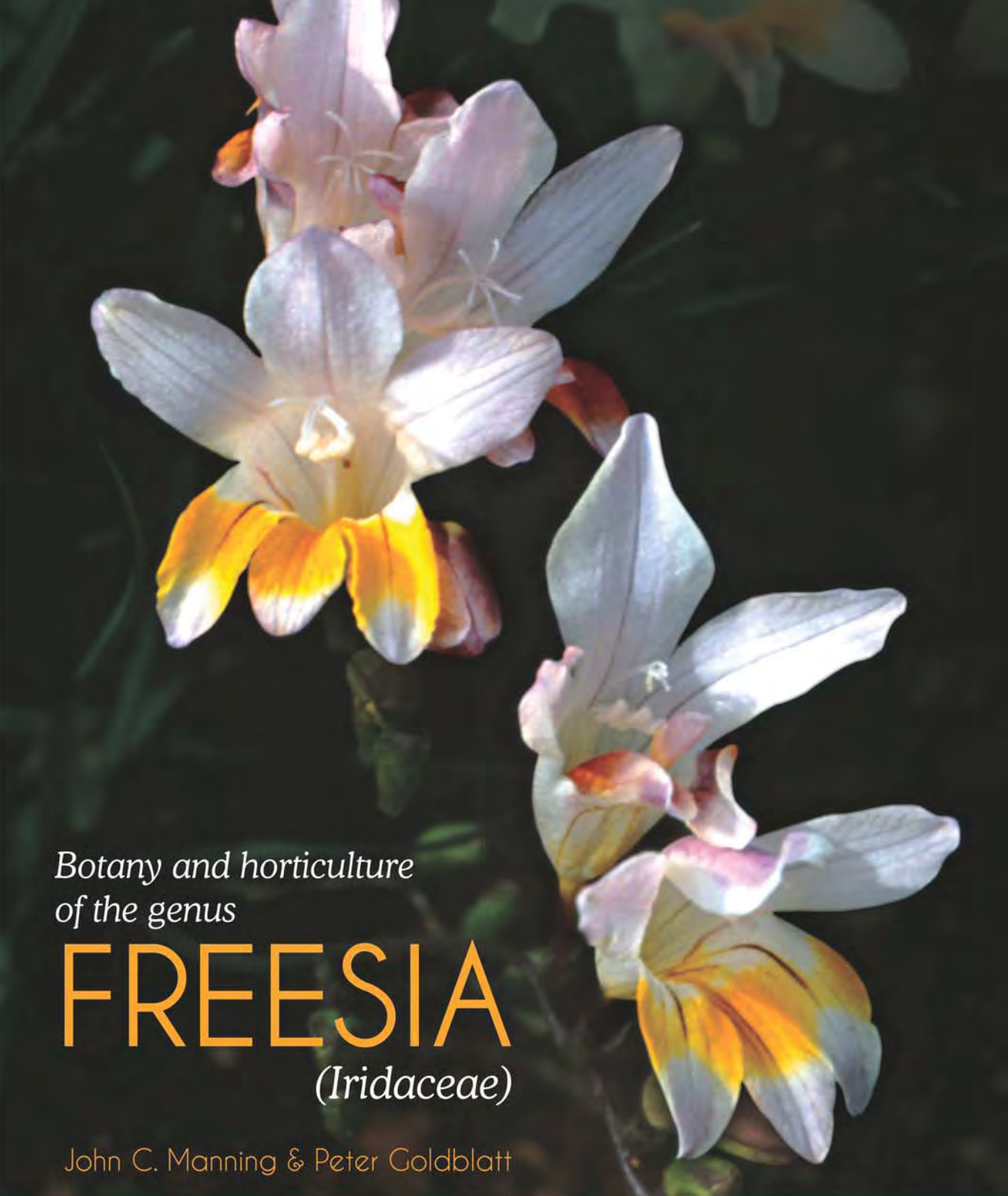




*Botany and horticulture
of the genus*

FREESIA

(Iridaceae)

John C. Manning & Peter Goldblatt

STRELITZIA

This series has replaced *Memoirs of the Botanical Survey of South Africa* and *Annals of the Kirstenbosch Botanic Gardens* which SANBI inherited from its predecessor organisations.

The plant genus *Strelitzia* occurs naturally in the eastern parts of southern Africa. It comprises three arborescent species, known as wild bananas, and two acaulescent species, known as crane flowers or bird-of-paradise flowers. The logo of the South African National Biodiversity Institute is based on the striking inflorescence of *Strelitzia reginae*, a native of the Eastern Cape and KwaZulu-Natal that has become a garden favourite worldwide. It symbolises the commitment of the Institute to champion the exploration, conservation, sustainable use, appreciation and enjoyment of South Africa's exceptionally rich biodiversity for all people.

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FRONT COVER: *Freesia fucata*
BACK COVER: top: *Freesia grandiflora* subsp. *grandiflora*
middle: *F. corymbosa*
bottom: *F. verrucosa*

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*S*TRELITZIA 27

Botany and horticulture of the genus



by

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2010



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New combination, species and statuses in *Strelitzia* 27 (2010)

Freesia grandiflora (Baker) Klatt subsp. ***occulta*** J.C.Manning & Goldblatt, subsp. nov., 111

Freesia leichtlinii Klatt subsp. ***alba*** (G.L.Mey.) J.C.Manning & Goldblatt, stat. et comb. nov., 70

Freesia praecox J.C.Manning & Goldblatt, sp. nov., 65

Freesia subgen. ***Viridibractea*** (Goldblatt) J.C.Manning & Goldblatt, stat. nov., 50

Freesia viridis (Aiton) Goldblatt & J.C.Manning subsp. ***crispifolia*** (Goldblatt) J.C.Manning & Goldblatt, comb. nov., 55



Auriol Batten

We have great pleasure in dedicating this volume to Auriol Batten in recognition of her unfailing talent and enthusiasm in this and other projects that we have shared with her, notably the revisions of '*Gladiolus* in southern Africa' and of '*Crocasmia* and *Chasmanthe*'. It has always been a great pleasure to work with Auriol, and her clear vision and incisive mind have been an inspiration. She started work on this project a year before her ninetieth birthday and completed the paintings the year after—a remarkable achievement by a remarkable artist.

The photograph depicts Auriol holding the Lifetime Achievement Award for Botanical Art, which she received at the Kirstenbosch Biennale in September 2008.

A decorative illustration in the top left corner featuring stylized orange flowers and thin, curving stems that branch out across the top of the page.

Auriol Batten

Auriol Ursula Batten is South Africa's finest living botanical artist. Born in Pietermaritzburg, KwaZulu-Natal Province, South Africa in 1918, she graduated with a B.Sc degree from the local university in 1937, majoring in Botany and Geography, and went on to pursue a career teaching at various schools in the Natal midlands. Her interest in flower painting stems from her school years, where she received instruction from two dedicated mistresses in botany and art, later studying art at the nearby Durban Technical College. She remained in the province until 1945 when she moved to East London, where she lives today.

After settling down in East London she devoted her spare time to painting and the result was the publication in 1966 of *Wild flowers of the Eastern Cape Province*, a collaborative venture between herself and another local artist, Hertha Bokelmann. This was the first wild flower guide to the region and its genesis and production were due entirely to her creative and scientific efforts. The sumptuous *Flowers of southern Africa* followed in 1986, in which she illustrated 100 species, again accompanied by text written and compiled entirely by herself. She was awarded a Gold Medal by the RHS that year and her international reputation as a botanical artist was cemented. In 2000 she was awarded a Gold Medal

at the Inaugural Exhibition of Botanical Art, Kirstenbosch Biennale, followed in 2008 by the Lifetime Achievement Award at the Kirstenbosch Biennale in recognition of her contribution to botanical art in South Africa.

Auriol has illustrated several botanical monographs, including works on *Dierama*, *Gladiolus* and most recently *Crocasmia*, and individual paintings have appeared in *Curtis's Botanical Magazine* and *Flowering Plants of Africa*. Her talents as an artist are matched by her scientific insight and many of the plates in these works owe their completeness to her persistence in acquiring fruiting stages long after the initial work was done. Her work was chosen for the exhibition Art in Science at the International Botanical Congress, Missouri in 1999 and is in the collections of the South African National Biodiversity Institute and of the Royal Botanical Garden, Edinburgh.

Her interest in wild flowers extends far beyond their illustration. She is a founder member of the Border Wildflower Society and still serves on the board of various conservation bodies. For these and her continued dedication to botanical matters in general she has received various civic decorations and in 1994 was awarded an honorary doctorate by Rhodes University.

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Abstract

Freesia Klatt (Iridaceae: Crocoideae) is characterized by its regularly netted corm tunics, sharply deflexed or horizontal flower spike, deeply divided style branches, verrucose or papillate capsules, and subglobose seeds with a glossy, smooth or lightly wrinkled testa lacking secondary ornamentation. The genus comprises 16 species distributed through sub-Saharan Africa, with a marked centre of diversity in the winter rainfall region of the southwestern Cape. Molecular and morphological evidence suggest a new classification in which the tubular-flowered species previously segregated as subgen. *Anomatheca* (Ker Gawl.) J.C.Manning & Goldblatt do not comprise a monophyletic lineage but represent three independent origins for the gullet-flowered species. These data support the recognition of two subgenera, based on the texture of the floral bracts: subgen. *Freesia* (8 spp.) is defined by its soft-textured, green or translucent floral bracts, often with dark brown tips; and subgen. **Viridibractea** (Goldblatt) J.C.Manning & Goldblatt (8 spp.) is recognized by firm-textured, green bracts with narrow translucent margins. Floral chemistry provides additional novel data supporting this topology: β -ionone and dihydro- β -ionone are characteristic of all fragrant species in subgen. *Viridibractea* but are absent from subgen. *Freesia*.

In subgen. *Freesia*, plants of *F. grandiflora* from Macuba, in north-central Mozambique, with unusually short filaments and a consistently pink perianth are recognised as subsp. **oc-culta** J.C.Manning & Goldblatt. Within subgen. *Viridibractea*, *Freesia viridis* (Aiton) Goldblatt & J.C.Manning is segregated as the monotypic sect. *Alatae*, defined by several autapomorphies, notably a winged stem, greenish or brown flowers, and a 1-banded pollen operculum. The remaining

species in the subgenus comprise sect. *Viridibractea*, defined by two derived characters: a papillate stem and oblique seeds with swollen raphe. Species boundaries in sect. *Viridibractea* are particularly problematic, and the recent discovery of several new, locally endemic species has necessitated a re-examination of the taxonomy of the group. The development of axillary cormels in *F. alba* and *F. leichtlinii* is a previously overlooked feature that is diagnostic for the two species, and populations until now recognized at species level as *F. alba*, are distinguishable from *F. leichtlinii* only on the basis of their white rather than pale yellow or cream-coloured flowers. They are accordingly reduced to subspecific rank as subsp. **alba** (G.L.Mey.) J.C.Manning & Goldblatt. Subspecific rank is also re-introduced in *F. viridis* for inland populations with falcate, mostly crispulate leaves and shortly lanceolate tepals, which are distinguished as subsp. **crispifolia** (Goldblatt) J.C.Manning & Goldblatt from coastal populations with narrowly lanceolate leaves and attenuate tepals. The new species *F. praecox* J.C.Manning & Goldblatt is recognized for early-flowering populations with narrow leaves from the southern Riviersonderend Mountains that were previously included in *F. alba* but which differ from it in ecology and in lacking axillary cormels. This revision covers morphology, anatomy, molecular relationships, floral biology, taxonomy, horticultural history and cultivation. Each species is described and fully illustrated in colour and black-and-white, with complete synonymy, notes on ecology, and distribution maps. A complete analysis of the floral scent chemistry of 13 taxa is presented.

Keywords: floral chemistry, *Freesia* Klatt, horticulture, Iridaceae, new species, southern Africa, taxonomy



Introduction

Freesia Klatt is one of the smaller of the African genera of Iridaceae, a large family of almost 2 000 species in $\pm$ 65 genera (Goldblatt & Manning 2008) and which includes popular garden ornamentals such as *Iris* L., *Crocus* L., *Gladiolus* L., *Sparaxis* Ker Gawl., *Watsonia* Mill. and, of course, *Freesia*. The genus has a long history of cultivation in Europe, dating back to the late eighteenth century, and together with *Gladiolus* and *Iris* ranks as one of the horticulturally most important genera in the family. Its colourful, highly fragrant flowers have made it especially popular as a cut flower (Bryan 1995) and in recent years, annual sales in the United Kingdom have reached over 110 million stems (Fu *et al.* 2007). Astonishingly, the numerous cultivars have been derived from repeated crosses between just two species and their offspring. Wild species are almost unknown in cultivation and certainly not in commercial numbers.

Freesia, a member of the largely African subfamily Crocoideae, is recognized primarily by its sharply inclined to horizontal spike, deeply divided style branches, and verrucose capsules (Goldblatt & Manning 1995). Other features that characterize the genus are its mostly conical (rather than subglobose) corms with regularly netted corm tunics, often composed of fine, pale fibres. The leaves are anatomically unusual in Crocoideae in lacking a submarginal vein or sclerenchyma trace, with support provided instead by columnar, thick-walled epidermal cells at the leaf margin (Rudall 1995). Other features of the genus that are derived in the subfamily are the subglobose seeds with smooth or slightly wrinkled testa without visible cell outlines, and the basic chromosome number $x = 11$. The pollen of *Freesia* is typical of subfamily Crocoideae, with the striking exception of *F. viridis* (Aiton) Goldblatt & J.C.Manning, which has a 1-banded operculum rather than the usual 2-banded one.

The position of *Freesia* within the subfamily Crocoideae has only recently become clear. The divided style branches initially suggested a relationship with the widespread African genus *Lapeirousia* Pourret, now placed in the subtribe Watsonieae, and several of the narrow-tubed species were accordingly included by Baker (1896) in *Lapeirousia* subgen. *Anomatheca*. A close relationship between these two genera has now been discounted: the axial corm development and smooth seeds of *Freesia* are fundamentally different from *Lapeirousia*, which has axillary corm development, colliculate seeds, and unspecialized leaf margin anatomy. These anatomical differences led Goldblatt & Manning (1995) to suggest that *Freesia* might instead be allied to *Tritonia* Ker Gawl. and *Crocasmia* Planch., with which the pattern of corm development, seed structure and leaf anatomy are consistent. Subsequent analysis of DNA sequences of several plastid regions (Goldblatt *et al.* 2005) showed that *Freesia* is in fact immediately related to *Crocasmia* and *Devia* Goldblatt & J.C.Manning, which have similar smooth seeds but notched, not deeply divided style branches, and that these three genera are together allied to *Xenoscapa* (Goldblatt) Goldblatt & J.C.Manning, which also shows the unusual divided style branches but has unspecialized, angular seeds with a sculpted, areolate or foveate testa. Some species of *Crocasmia*, as well as *Devia*, have finely wrinkled and warty capsules like those of *Freesia*, providing independent evidence for a close relationship between the three genera. The four genera *Freesia*, *Crocasmia*, *Devia* and *Xenoscapa* all share a similar, derived leaf marginal anatomy and the derived basic chromosome number $x = 11$, and are now regarded as comprising tribe Freesieae within subfamily Crocoideae (Goldblatt *et al.* 2006).

Freesia is centred in the southwestern and southern Cape in the southern African winter rainfall region, with two species extending northwards along the eastern seaboard through tropi-

cal East Africa, one reaching as far north as the Imatong Mountains in southern Sudan. The genus contains 16 species, one of which is newly described here.

As currently circumscribed, *Freesia* comprises the two subgenera *Anomatheca* and *Freesia* (Manning & Goldblatt 2005), usually treated until recently as independent genera (Goldblatt & Manning 1995). This classification is essentially a legacy of the historical significance that was accorded to flower shape in the family but recent studies have repeatedly concluded that flower shape is extremely labile, even among closely allied species, and in itself is not necessarily a good indicator of relationships. The results of a molecular analysis presented here suggest that the relationships among the species need to be radically re-assessed. Preliminary indications of the need for this were already present in an earlier morphological cladistic study (Goldblatt & Manning 1995), and a new classification is presented here.

The last taxonomic revision of *Freesia* was carried out when the species were still segregated

between *Anomatheca* and *Freesia* s. str. (Goldblatt 1972, 1982). Several improvements in our understanding of the taxonomy of the species have been introduced since then, including not only the incorporation of the two genera within an expanded *Freesia* but also the description of two new species (Manning & Goldblatt 2001, 2005) and the reduction of another to synonymy (Goldblatt & Manning 2000). Furthermore, recent field work has made it necessary to re-evaluate the circumscription of *F. alba* (G.L.Mey.) Gumbel., resulting in the conclusion that the species differs from *F. leichtlinii* Klatt only in flower colour and is thus more appropriately reduced to a subspecies within it. Finally, narrow-leaved, early-flowering populations from the southern foothills of the Riviersonderend Mountains that were previously included in *F. alba* lack the axillary cormels that are now understood to characterize the species, and they are accordingly recognized as a distinct taxon, *F. praecox*. These advances in our understanding of *Freesia* have rendered the current treatments of the genus out of date and necessitate a new, comprehensive treatment of this important and charismatic genus.



Materials and methods

Morphology and palynology: this study is based on an examination of living plants in the field and of specimens in the following herbaria: BOL, K, MO, NBG, NH, NU, PRE and SAM (acronyms as in Holmgren *et al.* 1990). The abbreviation of authors' names follows Brummitt & Powell (1992). Pollen was collected from herbarium specimens and visualized in Fuchsin jelly (Beattie 1971; Kearns & Inouye 1993).

Floral chemistry: the floral chemistry of 11 species and two subspecies of *Freesia* from across the genus was investigated by headspace analysis and a combination of capillary gas chromatography and mass spectrometry, following the methodology established by Kaiser (1995, 1997, 2000, 2006). Plants were either sampled directly from natural populations or from cultivated specimens originally collected in the wild (Tables 4–6, Appendix). Two or more flowering stems were sampled at a time, providing an approximation of the scent spectrum for each population investigated.

Molecular phylogeny: all infrageneric taxa (species and varieties) in *Freesia* were sampled with the exception of *F. leichtlinii* subsp. *leichtlinii* and *F. laxa* subsp. *azurea*. The three genera *Devia*, *Crocasmia* and *Xenoscapa*, previously found to be closely related to *Freesia* (Reeves *et al.* 2001; Goldblatt *et al.* 2006) were included as outgroup taxa (Table 3). One individual of *Lapeirousia* was also included and used as an external outgroup taxon.

DNA extraction and amplification: total genomic DNA was isolated from fresh or silica-gel-dried leaves using the 2× CTAB method of Doyle & Doyle (1987) with minor modifications. All taxa are stored in the DNA bank at Kirstenbosch (www.nbi.ac.za/frames/researchfram.htm; not *Crocasmia mathewsiana*) and at the Royal Botanic Gardens, Kew (www.rbgekew.org.uk/data/dnaBank/homepage.html).

Five DNA regions from the plastid genome were sequenced: a portion of the coding region *matK* ($\pm$ 850 BP—bootstrap percentage), the *trnL* intron and associated *trnL*-F spacer, and the *rpl32-trnL* and *trnQ-5' rps16* spacers. Primers XF and 5R (see www.kew.org/barcoding) were used to amplify the selected portion of the *matK* gene. Primer pairs c-d and e-f were used to amplify the *trnL* intron and *trnL*-F spacer, respectively (hereafter the *trnL*-F region) (Taberlet *et al.* 1991). The *trnL*-F region was generally amplified in one reaction using primers c and f, although in some cases the intron and spacer were amplified separately. The *rpl32-trnL* and *trnQ-5' rps16* spacers were amplified using primers designed by Shaw *et al.* (2007). Polymerase Chain Reactions (PCR) for *matK*, *rpl32-trnL* and *trnQ-5' rps16* were performed in 40 μ l reactions containing 4 units of Taq polymerase (Promega Corporation, Madison, USA), 8 μ l of 5X Gotaq Flexi buffer (supplied by the manufacturer), 2.4 μ l of 25 mM MgCl₂, 4 μ l of bovine serum albumine (BSA; 0.4 %), 0.8 μ l of dNTPs (10mM), and 2 μ l of each primers (10 mM). For the *trnL*-F region, PCRs were performed using 25 μ l reactions prepared using the ReddyMix PCR Master mix (Thermo Scientific, Fife, UK) with 0.5 μ l of 0.4 % BSA and 0.5 μ l of each primers. All amplifications were performed on a 9700 GeneAmp thermocycler from ABI (Applied Biosystems, Warrington, Cheshire, UK). The following program was used for *matK* and *trnL*-F: 1–2 min. at 94°C, 30–33 cycles of 1 min. at 94°C, annealing at 50°C (*trnL*-F) or 53°C (*matK*) for 1 min., 1.5 min. at 72°C, and a final extension of 4 min. at 72°C. The following parameters were used for the amplification of the *rpl32-trnL* and *trnQ-5' rps16* spacers: 5 min. at 80°C, 30 cycles of 1 min. at 95°C, annealing at 50°C for 1 min., 4 min. at 65°C, and a final extension of 5 min. at 65°C. All PCR products were purified using the Nucleospin® Extract II minicolumn kit from Macherey-Nagel (Düren, Germany) and eluted in the buffer provided by the manufacturer. Cy-

cle sequencing reactions were performed in 10 μ l volumes using 0.5 μ l of BigDye® Terminator cycle sequencing chemistry (v3.1; ABI) and the same primers as for PCR. Cycle sequencing products were purified using a Biomek NX S8 automated station (Beckman Coulter, Fullerton, CA, USA) and complementary strands were sequenced on a ABI 3730 automated sequencer (Applied Biosystems).

Phylogenetic analyses: the program SEQUENCHER 4.1 (Gene Codes Corp., Ann Arbor, Michigan, USA) was used to assemble complementary strands and verify base-calling. All DNA regions were easily aligned by eye in Phylogenetic Analysis Using Parsimony (PAUP version 4.0b10) (Swofford 2002). We used the maximum

parsimony criterion as implemented in PAUP (Swofford 2002) and a heuristic search approach to reconstruct phylogenetic relationships in *Freesia*. Combined analyses were performed using 1 000 random addition replicates and tree bisection and reconnection (TBR) branch swapping, saving 10 trees per replicate. Support for each clade was assessed using the bootstrap method (Felsenstein 1985) as implemented in PAUP with 1 000 bootstrap replicates, TBR branch swapping, simple addition sequence with MulTrees option in effect (keeping only 10 trees per replicate). We used the following categorization to describe bootstrap percentages (BP): 50–74 %, weak; 75–89 %, moderate; 90–100 %, strong. *La-peirousia pyramidalis* was defined as outgroup in all analyses.





Taxonomic history

Species of *Freesia* first found their way to Europe in the mid-seventeenth century at a time of rising interest in Cape plants. The Dutch botanist, Nicolaas Burman, described both *F. caryophyllacea* and *F. corymbosa* (Burm.f.) N.E.Br. in 1768 from living plants in cultivation in The Netherlands, following the taxonomic convention of the day in naming them in the genus *Gladiolus* on account of their markedly zygomorphic flowers. *Freesia* as a genus was only established a century later (Klatt 1866), and although accepted henceforth as correct, the name was in fact nomenclaturally superfluous and only recently conserved against the earlier *Lomenia* Pourret (Goldblatt 1980). The name finds its origin in *Freesea* Eckl. (1827), published without a description and thus illegitimate. Ecklon's (1827) intention was to segregate various species of *Tritonia* with zygomorphic flowers from their actinomorphic allies, and his concept of the genus thus differs greatly from Klatt (1866). Kuntze (1891) attempted to rectify this by substituting the name *Nymanina* for Klatt's usage but succeeded only in rendering *Nymanina* nomenclaturally illegitimate and superfluous by citing *Freesia* Klatt in synonymy (McNeil *et al.* 2006: Art. 52.1). Reichenbach (1828) had earlier proposed the name *Waitzia* for *Tritonia*, which at the time included some species of *Freesia*, and combinations in that genus are listed below in the synonymy of individual species. *Waitzia* is a later synonym of *Tritonia* and is, in addition, illegitimate, being a homonym of *Waitzia* J.C.Wendl. (Wendland 1808), a genus of Asteraceae. The confusion was extended in 1846 by Heynhold who, realizing that *Waitzia* Rchb. was a homonym, transferred the species in Reichenbach's genus to *Montbretia* DC., among them several we now know as *Freesia*.

Charming, though diminutive, *Freesia verrucosa* is easily grown away from its native habitat, and was widely cultivated in Europe in the late 18th century. It, too, was referred to the genus

Gladiolus when described in 1782 by Linnaeus fil. under the name *G. junceus* (itself an illegitimate homonym), based on specimens collected by C.P. Thunberg in 1772–1774. The species was the subject of much confusion, perhaps in part because the name was so inappropriate (*junceus* means rush-like), and was later named independently as *Ixia verrucosa* by Benedict Vogel in 1784 and as *Ixia emarginata* by the French scientist Jean Lamarck in 1789, given two different names by the English botanist R.A. Salisbury in 1796, *Gladiolus amabilis* and *G. pulchellus*, and named *G. polystachyus* by Henry Andrews in 1799.

A further five species of *Freesia* were named in quick succession during the last decades of the eighteenth century, followed by another two in the nineteenth century. The establishment of the South African College (later the University of Cape Town) and Kirstenbosch Gardens (now Kirstenbosch National Botanical Garden) in Cape Town led directly to the discovery and description of four additional species in the first decades of the twentieth century. A further two species were recognized in the opening years of the twenty-first century, and we describe the latest addition to the genus here (Table 1). These names were not, however, the only ones to appear over this period, and most species of *Freesia* suffered having more than one name applied to them by different botanists. In many instances the species were also described in various genera, depending on the shape of their flowers.

The first attempt at a comprehensive treatment of *Freesia* in its classic sense was that of the British botanist, J.G. Baker (1892, 1896), who recognized just the single species *Freesia refracta*, which he divided into three varieties corresponding to *F. refracta*, *F. corymbosa* and *F. leichtlinii* subsp. *alba* as treated here. Baker's understanding of the genus was derived primarily

from information supplied to him by the amateur horticulturist, M. Foster, Professor of Physiology at Cambridge, and he remained uncertain of the exact application of some of the other names current at the time, mentioning two additional species in a footnote: *F. xanthospila* (now a synonym of *F. caryophyllacea*) and *F. leichtlinii*, which he knew only from illustrations. Like most botanists at the time, Baker restricted the genus *Freesia* to the species with large, funnel-shaped flowers. The slender-tubed species were treated as the distinct genus *Anomatheca* or were referred either to *Lapeirousia* or to *Watsonia*.

Baker's treatment of *Freesia* differed greatly from a contemporary revision of the genus by Klatt (1895), who presciently united the genera *Freesia* and *Anomatheca* under the latter, older name. Klatt's treatment was, however, ignored by subsequent botanists in favour of the retention of the two as distinct genera. The description of several new species of *Freesia* in the early decades of the twentieth century by the South African botanist H.M.L. (Louisa) Bolus, stimulated the first modern treatment of *Freesia* s. str. by the English botanist N.E. Brown (1935). Although many of Brown's nineteen species are nothing more than minor colour and leaf variants, he was the first to recognize the important

difference in bract texture that characterizes the two subgenera recognized here. Fifty years later, Brown's plethora of poorly defined species was reduced to eleven and the correct application of the early superfluous names was finally resolved by Goldblatt in his revisions of *Anomatheca* (1972) and *Freesia* (1982).

The history of *Anomatheca* predates that of *Freesia* by some sixty years. *Anomatheca verrucosa*, the first species to be described, was originally placed in the genus *Gladiolus* by Linnaeus fil. (1782), following the rather broad definition of the genus at the time, but was independently described in the genus *Ixia* by Vogel (1784) on account of its apparently $\pm$ symmetrical flowers, despite the evidence of the fine painting drawn from living plants, which clearly shows the flowers to be slightly zygomorphic. *Anomatheca* as a genus was established for the species by the British botanist, John Bellenden Ker Gawler (1804) and was recognized until Baker (1892) reduced it to a subgenus of *Lapeirousia*. Subsequently reinstated by Goldblatt (1971), the genus was finally united with *Freesia* following a morphological cladistic analysis (Goldblatt & Manning 1995). *Freesia*, although the later name, was conserved over *Anomatheca* in the interest of promoting nomenclatural stability (Goldblatt &

TABLE 1.—Chronology of *Freesia* species. Approximate dates of discovery are given plus the first publication of each species

Species	Discovery	Description
<i>F. caryophyllacea</i>	< 1768	Burman f. (1768)
<i>F. corymbosa</i>	< 1768 (?1752)	Burman f. (1768)
<i>F. verrucosa</i>	< 1769 (?1752)	Linnaeus f. (1782) [as <i>Gladiolus junceus</i>]
<i>F. laxa</i>	1773	Thunberg (1823)
<i>F. viridis</i>	?1774	Aiton (1789)
<i>F. sparrmanii</i>	1775	Thunberg (1814)
<i>F. refracta</i>	1786–1795	Jacquin (1795)
<i>F. grandiflora</i>	1858	Baker (1876)
<i>F. leichtlinii</i>	< 1872	Klatt (1874)
<i>F. andersoniae</i>	1889	Bolus (1927)
<i>F. speciosa</i>	1918	Phillips & Brown (1921)
<i>F. fergusoniae</i>	1926	Bolus (1927)
<i>F. praecox</i>	1931	This work
<i>F. occidentalis</i>	1932	Bolus (1933c)
<i>F. fucata</i>	1975	Manning & Goldblatt (2001)
<i>F. marginata</i>	2000	Manning & Goldblatt (2005)

Manning 1993). *Anomatheca* was later formally recognized at subgeneric level as *Freesia* subgen. *Anomatheca* (Manning & Goldblatt 2005) but in this study we no longer recognize it at any level.

The generic name *Anomaza* Lawson ex Salisb. has often been regarded as a synonym of *Anomatheca* (Goldblatt 1972) and consequently would now be treated as a synonym of *Freesia*. *Anomaza* appeared in the literature in a long article by the British botanist R.A. Salisbury (1812) dealing with the cultivation and nomenclature of bulbous plants, simply as '*Anomaza excisa* Laws., Cat. 2' (this unpublished document is probably no longer extant). The genus *Anomaza* was not formally described by Salisbury, even lacking a diagnosis, and is thus not validly published, and nor is the species *A. excisa*. The name was only associated with *Anomatheca* because Salisbury

included as synonyms of *A. excisa* a number of names that represent *Anomatheca verrucosa*. Also cited under *Anomaza excisa*, however, was *Ixia excisa* L.f., which is evidently the basionym for *A. excisa*. *Ixia excisa* is a later synonym of *Geissorhiza ovata* (Burm.f.) Aschers. & Graebn. and *Anomaza* is therefore synonymous with *Geissorhiza*. Both Lawson and Salisbury evidently considered *Ixia excisa* to be the earliest name for *Anomatheca verrucosa*, an error explained by the similarity of the flowers and leaves of the two species. As an illegitimate name, the identity of *Anomaza* has no nomenclatural significance. More intriguing is the possibility that *Anomaza* is merely an orthographic or typographic error for *Anomatheca*. Whatever its origin, *Anomaza* cannot be regarded as a generic synonym of *Anomatheca* or *Freesia* and it has no place in the nomenclature of either genus.





Morphological characters of taxonomic significance

Corms: species of *Freesia* are small to moderate-sized, deciduous geophytes, producing an underground corm that is replaced annually. The corm is more or less globose-conical in *F. grandiflora* and *F. laxa* (Figure 1) but is conical or narrowly conical in all other species (Figures 2–4). The outer tunics are characteristically pale in colour, and finely to somewhat coarsely fibrous, forming a regularly netted lattice as they decay. Corm formation is through enlargement of the basal internodes of the flowering stem and is thus axial. Vegetative reproduction is typically through the production of cormels from the base of the current season's corm. In *F. leichtlinii*, in which the corm is deeply buried, cormels are produced firstly in the axils of the lower leaves along the subterranean portion of the stem, followed by the development of additional cormels at the base of the parent corm late in the season as the plants enter dormancy. In other species the basal cormels are mostly significantly smaller than the main replacement corm but in *F. leichtlinii* the difference in size between them is much less, resulting in the production of what appears to be a cluster of similar-sized corms rather than a definite 'parent' corm with associated cormels. Axillary cormels are also developed occasionally in the leaf axils in *F. grandiflora* (Baker) Klatt. This species is unique in the genus in developing scaly rhizomes from the base of the corm (Figure 1A). These resume growth at the beginning of the next growth cycle and develop a cormel at the apex which subsequently becomes independent of the parent corm as the rhizome shrivels.

Stem, leaves and floral bracts: stems of most species are slender and cylindrical in cross-section (Figures 1; 2; 4) but *Freesia viridis* has a flattened, strongly angled or winged stem (Figure 3). Species in sect. *Viridibractea* have stems that are either densely and minutely puberulous throughout their length or at least sparsely puberulous toward the base (Figure 4). This is most

evident in young plants and often becomes less clear with age. The inflorescence axis is typically sharply deflexed and $\pm$ horizontal or inclined in both flower and in fruit (Figures 2–4) but is only weakly inclined or even suberect in *F. grandiflora* and sometimes *F. laxa* (Thunb.) Goldblatt & J.C.Manning (Figure 1).

Isobilateral leaves, typical of most Iridaceae, are produced in a two-ranked fan. Leaf number ranges among species from 4–14, varying somewhat within species. The lower leaves are basal and the uppermost leaf, which is usually inserted on the stem some distance above the others, is typically bladeless or may have a short blade. The leaf blades are narrowly lanceolate to oblong-lanceolate, or falcate, and usually plane but the edges are weakly to strongly undulate or crisped in *Freesia laxa* subsp. *crispifolia* and sometimes slightly so in *F. verrucosa* (B.Vogel) Goldblatt & J.C.Manning. The midrib is usually slightly raised or thickened but the margins are unthickened (Figures 5; 6A). *Freesia marginata* is unusual in the genus in developing a prominent, thickened submarginal vein (Figure 6B), a characteristic that is found elsewhere in the genus, only occasionally in *F. refracta* (Jacq.) Klatt. Leaves in *Freesia* species are typically thin-textured and bright green but *F. marginata* has moderately thick, leathery leaves and the leaves of *F. fucata* J.C.Manning & Goldblatt and some populations of *F. refracta* are decidedly glaucous. The leaf apex in most species is acute but in some, especially *F. caryophyllacea* (Burm.f.) N.E.Br., *F. fergusoniae* L.Bolus and *F. occidentalis* L.Bolus, it is typically obtuse.

The leaf fan in *Freesia grandiflora* and *F. laxa* (Figure 1) is invariably erect but in most other species can be more or less sharply inclined so that the leaves are held at an angle to the ground (Figure 2) or even pressed closely to it, a characteristic that is best expressed in young plants in



FIGURE 1.—Morphology of *Freesia* subgen. *Freesia*. A–D, *Freesia grandiflora* subsp. *grandiflora*: A, corm; B, foliage; C, inflorescence; D, half flower and front view. E, *F. grandiflora* subsp. *occulta*: half flower and flower. F, G, *F. laxa* subsp. *laxa*: F, inflorescence; G, flower, front view. H, *F. verrucosa*, flower, side view, three-quarter view and half flower. Scale bar: 10 mm. Artist: John Manning.



FIGURE 2.—Morphology of *Freesia* subgen. *Freesia*. A–D, *Freesia occidentalis*: A, corm; B, inflorescence and foliage; C, half flower, side view and front view; D, bracts, outer (left), inner (right). E, F, *F. refracta*: E, half flower, whole flower and front view; F, bracts, outer (left), inner (right). G, H, *F. corymbosa*: G, whole flower and front view; H, bracts, outer (left), inner (right). I, *F. speciosa*, half flower, whole flower and front view. Scale bar: 10 mm. Artist: John Manning.



FIGURE 3.—Morphology of *Freesia* subgen. *Viridibractea* sect. *Alatae*. *Freesia viridis* subsp. *viridis*: A, corm; B, foliage and inflorescence; C, flower, front view, whole flower and half flower; D, capsule; E, seed. Scale bar: A–D, 10 mm; E, 2 mm. Artist: John Manning.



FIGURE 4.—Morphology of *Freesia* subgen. *Viridibractea* sect. *Viridibractea*. A–F, *Freesia fucata*: A, whole plant; B, half flower; C, flower, front view; D, bracts, outer (left), inner (right); E, capsules; F, seed. G, *F. fergusoniae*, half flower and flower, front view. H, I, *F. leichtlinii* subsp. *alba*: H, flower, front view and half flower; I, bracts, outer (left), inner (right). J, *F. sparrmanii*, whole flower, side view, front view and half flower. Scale bar: 10 mm. Artist: John Manning.

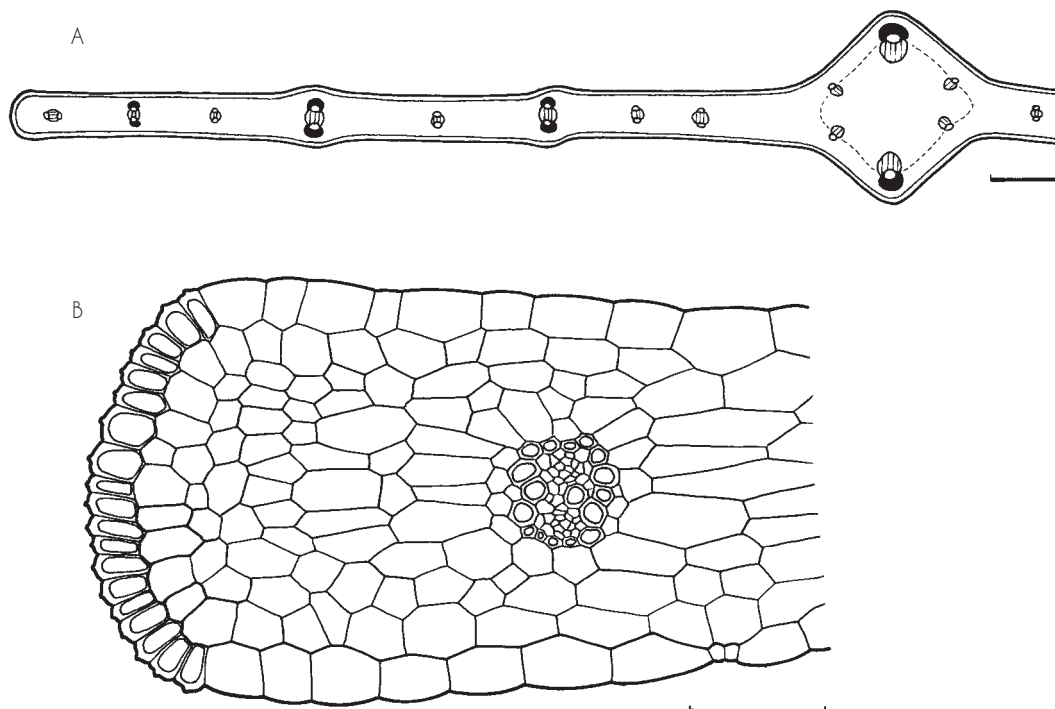


FIGURE 5.—Leaf anatomy of *Freesia caryophyllacea*. A, t/s of half leaf, sclerenchyma shaded and xylem hatched; B, detail of leaf margin showing thickened, columnar marginal epidermal cells and submarginal vascular bundle. Scale bar: A, 250 μm ; B, 50 μm . Artist: John Manning.

sunny sites. This feature is most strongly developed in species of sect. *Viridibractea*, particularly *F. caryophyllacea*, *F. fergusoniae* and *F. marginata*. The degree of flexing appears to depend strongly on the ambient light level, both in the wild and in cultivation, and flexure of the leaf fan is also strongly associated with the production of shorter leaves with blunt or rounded tips. Although initially thought to be a species-specific characteristic, the orientation and shape of the leaves are influenced by environmental factors to the extent that the utility of the character for species identification is limited.

Anatomically, the leaves are characterized by lacking a submarginal vein or sclerenchyma strand, with mechanical strengthening provided instead by radially elongated and thickened marginal epidermal cells (Figures 5; 6).

Floral bracts in *Freesia* are unusually variable in texture compared to other genera of Crocoideae, and textural differences form the morphological basis of the new subgeneric classification that is proposed here. Half of the genus, treated here as subgen. *Freesia*, has relatively thin-textured bracts. In *F. grandiflora* and *F. laxa*, the bracts are green throughout, or paler and submembranous in the upper half, which is probably the ancestral state for the genus, matched in allied genera of Freesieae. Other species in the subgenus have semi-transparent, membranous bracts that become dry and papery from the tips as the flowers open. The bracts and bracteoles across this group are $\pm$ brown-tipped, most conspicuously in the species with dry bracts, with the exception of *F. refracta* and *F. verrucosa*, in which the bracts are uniformly pale. Brown-tipped bracts were treated as derived in the group by Goldblatt & Manning (1995) and would thus rep-

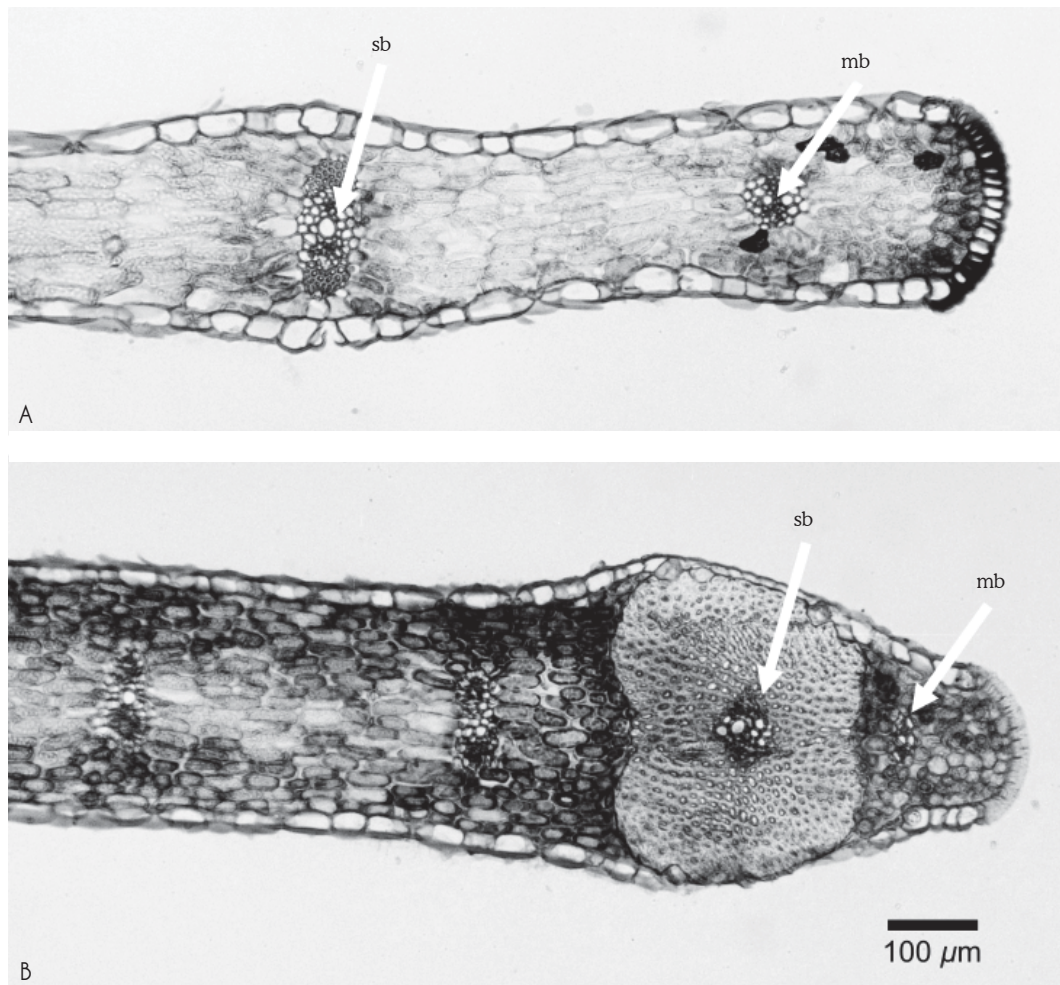


FIGURE 6.—Leaf margin anatomy in *Freesia* (from Manning & Goldblatt 2005). A, *F. caryophyllacea*; B, *F. marginata*. sb, submarginal vascular bundle; mb, marginal vascular bundle.

represent a synapomorphy for subgen. *Freesia*. The outer bracts are moderately long, mostly 7–20 mm long, in *F. andersoniae* L.Bolus, *F. grandiflora*, *F. laxa* and *F. speciosa* L.Bolus but shorter, 4–8 mm long, in the remaining species.

In the other half of the genus, treated here as subgen. *Viridibractea*, the bracts are thick-textured or foliar, and green with narrow, transparent margins. These firm-textured bracts are evidently derived in the genus (Goldblatt & Man-

ning 1995) and thus represent a synapomorphy for subgen. *Viridibractea*. The outer bracts are usually acute or apiculate but in *Freesia fucata* and sometimes in *F. praecox* (Figure 7E) they are $\pm$ tricuspidate. The inner bracts are apically forked and usually slightly shorter than the outer.

Flowers: the flowers in *Freesia* are of two main morphological types that until now formed the basis for the generic or infrageneric classification of the group. Phylogenetic analysis suggests that



FIGURE 7.—Morphology of *Freesia praecox*. A, whole plant; B, foliage and inflorescence; C, front view of two flowers; D, half flower; E, bracts, outer (left and top), inner (right); F, capsules; G, seed. Scale bar: A–F, 10 mm; G, 2 mm. Artist: John Manning.

these two floral types should be interpreted as floral syndromes and thus a reflection of adaptations to different groups of pollinating insects, rather than as signals of phylogenetic affinities.

The four species *Freesia grandiflora*, *F. laxa*, *F. verrucosa* and *F. viridis* have tubular or salver-shaped flowers with a slender perianth tube, either cylindric throughout or expanding slightly and evenly from the base, and tepals that are similar in size and equally spreading or recurved (Figures 1; 3). This floral type defined the genus *Anomatheca*. The stamens are inserted near the mouth of the tube and are included, shortly exerted, or conspicuously exerted. Flowers of *F. grandiflora*, *F. laxa* and *F. verrucosa* are pink or pink to red (rarely white or lilac), and either unscented or weakly scented during the day, whereas *F. viridis* has greenish flowers, often flushed maroon, that are either unscented or sweetly scented only at night.

The remaining twelve species share the classic, deeply gullet-shaped, freesia-type flower that traditionally defined the genus (Figures 2; 4). The funnel-shaped floral tube is divided into a narrowly tubular lower portion that expands $\pm$ abruptly at the level of the filament insertion into a broadly cylindrical upper portion as long as or more usually longer than the lower portion. The stamens are almost always included, rarely shortly exerted. The lower, tubular portion of the tube is typically $\pm$ half as long as the upper cylindrical part but there is some variation within species in the relative length of the two parts of the floral tube, especially in *Freesia leichtlinii* subsp. *alba* and *F. corymbosa*. *Freesia sparrmanii* (Thunb.) N.E.Br. is unusual in having the lower portion of the perianth tube invariably as long as or longer than the upper portion.

Perianth colour varies among the gullet-flowered species from white to pale yellow, rarely pale to deep pink or deep yellow, but always with dark yellow or orange markings on all or some of the lower tepals. The outer surface of the tepals is often flushed with dull purple. The flowers are typically more or less two-lipped with the dorsal tepal largest and suberect, and the lower tepals recurved. Eastern populations of *Freesia leichtlinii* subsp. *alba* are exceptional in having $\pm$ equal tepals. Within this group, *F. corymbosa*, *F. occidentalis*, *F. refracta* and *F. speciosa* have dis-

tinctive, ovate-cordate inner tepals, sometimes with the inner margins of the lower lateral tepals sharply upcurved (Figure 2). Flower size ranges from $\pm$ 30 mm long up to 60 or 70 mm in the large-flowered species, *F. andersoniae* and *F. speciosa*. The flowers are always fragrant, with the striking exception of *F. sparrmanii*, which always has unscented flowers. Floral scent is typically strong and dominated by the scent of violets or a combination of violets and roses in subgen. *Viridibractea* but it often has a slightly sour or bitter aspect in subgen. *Freesia*.

Corolla form and coloration, highly variable within many genera of Crocoideae, is often a notoriously unreliable indicator of relationships within the subfamily (Goldblatt & Manning 2006) as it is liable to significant variation through selection for different pollination systems. Although superficially similar in general form to certain species of *Gladiolus*, *Sparaxis* and *Tritonia*, morphological evidence suggests that the gullet-shaped flowers found in *Freesia* represent a unique floral type. Other gullet-flowers in the family typically have the upper portion of the floral tube flared and much shorter than the lower portion, with the stamens thus partially exerted, and the lower three tepals joined basally beyond the level at which the upper tepals separate from the tube so that the flowers are distinctly bilabiate. In *Freesia*, those species with gullet flowers have a broadly cylindrical upper portion that is mostly $\pm$ as long as the lower part of the tube and completely includes the filaments, and all six tepals separate from the tube at the same level. This unusual flower form thus appears to represent a synapomorphy for the genus. The extensive orange or deep yellow marking on the margins of the lower tepals in the gullet-flowered species of *Freesia* is another unique feature and thus constitutes a second possible synapomorphy for the genus. The phylogenetic origin of this flower type is not clear but it may have developed through enlargement of the upper portion (distal to the filament insertion) of an ancestral tubular flower as found in *Xenoscapa*, *Devia* and some species of *Crocasmia*.

Phylogenetic analysis of the species (see Phylogenetic relationships, p. 22) suggests that the *Freesia*-type gullet flower is most parsimoniously interpreted as basic in the genus, with salverform

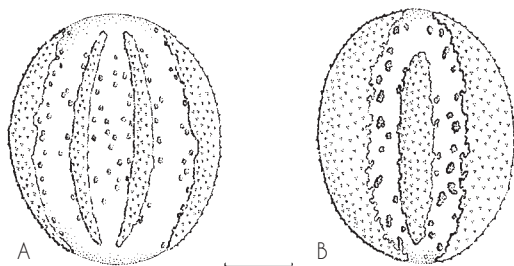


FIGURE 8.—Pollen morphology in *Freesia* illustrating operculum banding patterns. A, *F. grandiflora*; B, *F. viridis*. Scale bar: 20 μ m. Artist: John Manning.

or tubular flowers having arisen independently twice or three times.

Pollen: the monosulcate, operculate pollen with microporate, spinulate exine of *Freesia* (Figure 8) is ancestral in subfamily Crocoideae. All *Freesia* species examined have a 2-banded operculum, with the notable exception of *F. viridis*, which has a 1-banded operculum (Table 2). A 2-banded operculum is basic in subfamily Crocoideae and is found in the related genera *Crocasmia* and *Devia* (Goldblatt *et al.* 1991) but not *Xenoscapa*, which has pollen with a 1-banded operculum (Goldblatt & Manning 1995). It is

most parsimonious to treat the 1-banded condition as derived from the 2-banded, in which case the 1-banded operculum of *F. viridis* constitutes a further autapomorphy for this unusual species.

Fruit and seeds: all species produce broadly ovoid, 3-lobed capsules that are finely verrucose in the upper portion, at least when fresh. Mature capsules are leathery in texture and dehisce in the upper half to expose the seeds. The seeds are $\pm$ globose, with a glossy testa lacking visible cellular outlines (secondary sculpturing) (Figure 9). The testa is reddish brown or brown in most species but is bright reddish or orange in fresh seeds of *Freesia grandiflora* and *F. laxa*, although darkening within a day or two. Smooth when fresh, the seeds develop slight wrinkles as they dry. Apart from *F. viridis* (Figure 9H, I), all members of subgen. *Viridibractea* are readily distinguished by their oblique seeds in which the raphe side is $\pm$ swollen (Figure 9J–O). A conspicuous swelling of the seed coat at the raphe is also characteristic of *F. laxa* (Figure 9A) and sometimes *F. grandiflora* (Figure 9B). The latter is unique in its campylotropous seeds, as all other species have anatropous seeds.

Development of the seed coat follows the usual pattern in Crocoideae (Figure 10). Ovules

TABLE 2.—Pollen grain operculum banding pattern in *Freesia*

Taxon	Operculum	Voucher data
Subgen. <i>Freesia</i>		
<i>F. andersoniae</i>	2-banded	Manning 2934 (NBG)
<i>F. corymbosa</i>	2-banded	Manning 2885 (NBG)
<i>F. grandiflora</i>	2-banded	Jansen 7879 (MO) (Goldblatt <i>et al.</i> 1991); Kurzweil 1677 (NBG) (Goldblatt & Manning 1995)
<i>F. laxa</i>	2-banded	<i>ex hort</i> (Goldblatt <i>et al.</i> 1991); Karsten s.n. (NBG)
<i>F. occidentalis</i>	2-banded	Goldblatt 4069 (MO) (Goldblatt <i>et al.</i> 1991)
<i>F. refracta</i>	2-banded	Goldblatt 2841 (MO) (Goldblatt <i>et al.</i> 1991)
<i>F. speciosa</i>	2-banded	Goldblatt, Porter & Manning 12177 (NBG)
<i>F. verrucosa</i>	2-banded	Goldblatt 2933 (MO) (Goldblatt <i>et al.</i> 1991); Vlok 329 (NBG)
Subgen. <i>Viridibractea</i>		
<i>F. fergusoniae</i>	2-banded	Schutte-Vlok 858 (NBG)
<i>F. leichtlinii</i> subsp. <i>alba</i>	2-banded	Goldblatt & Manning 12257 (NBG)
<i>F. praecox</i>	2-banded	Manning 2921 (NBG)
<i>F. sparrmanii</i>	2-banded	McDonald 1192 (NBG)
<i>F. viridis</i>	1-banded	Goldblatt 3640, 7190 (MO) (Goldblatt <i>et al.</i> 1991); Hall 4212, Williamson 3526 (NBG) (Goldblatt & Manning 1995); Hall 2414 (NBG)

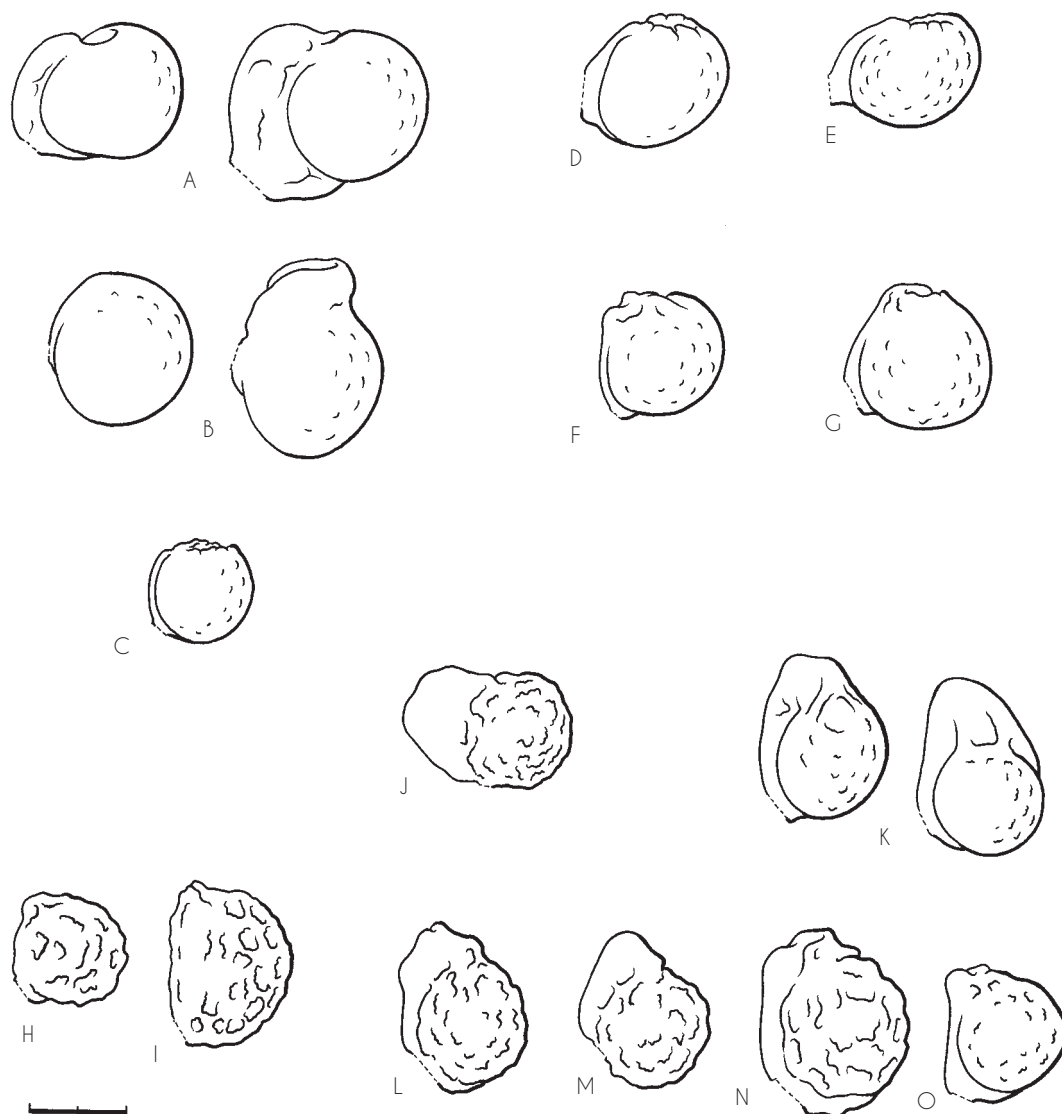


FIGURE 9.—Seed morphology in *Freesia*. A, *F. laxa*; B, *F. grandiflora*; C, *F. verrucosa*; D, *F. viridis* subsp. *viridis*; E, *F. viridis* subsp. *crispifolia*; F, *F. speciosa*; G, *F. occidentalis*; H, *F. refracta*; I, *F. corymbosa*; J, *F. sparrmanii*; K, *F. leichtlinii* subsp. *alba*, Riversdale (left), Plettenberg Bay (right); L, *F. fergusoniae*; M, *F. caryophyllacea*; N, *F. fucata*; O, *F. marginata*. Scale bar: 2 mm. Artist: John Manning.

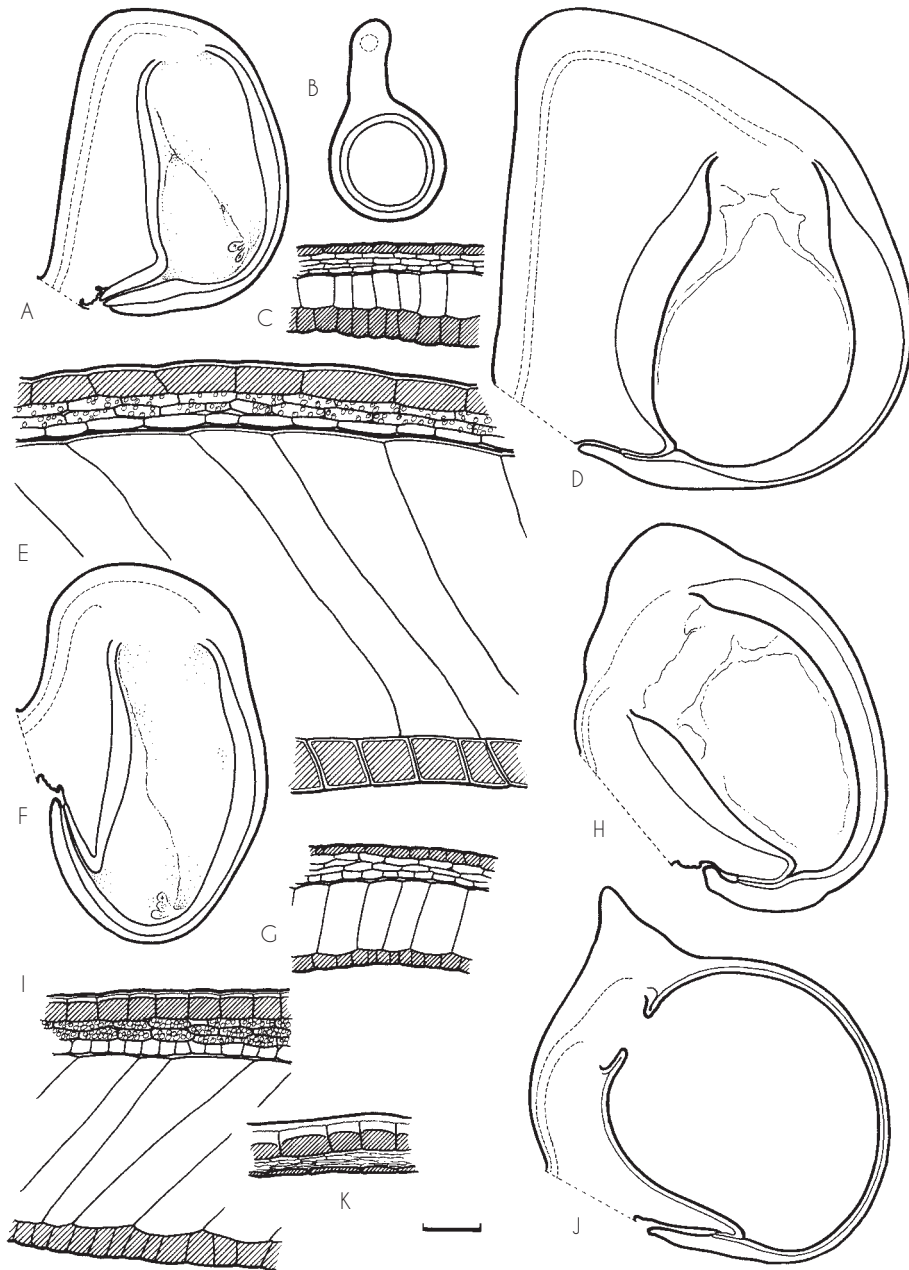


FIGURE 10.—Seed development in *Freesia*. A–E, *Freesia caryophyllacea*: A, l/s ovule; B, t/s ovule; C, detail of integuments; D, fully formed seed; E, detail of coat of fully formed seed. F–K, *F. grandiflora*: F, l/s ovule; G, detail of integuments; H, developing seed; I, detail of coat of developing seed; J, ripe seed; K, detail of coat of ripe seed. Various enlarged. Artist: John Manning.

are bitegmic with a 2-layered tegmen (inner integument) and 3- or 4-layered testa (outer integument). No additional cell layers are formed during seed development. The tegmen is crushed during ripening and only the testa contributes significantly to the mature seed coat. The swollen or inflated raphe that is characteristic of subgen. *Viridibractea* and also *Freesia grandiflora* and *F. laxa* in subgen. *Freesia* is evident in the ovule, which is remarkably similar to that in the related genus *Crocasmia* (Goldblatt *et al.* 2004). Unlike *Crocasmia*, however, the raphe enlarges considerably in these species during seed development. The reddish or orange pigmentation of the mature seeds of *F. grandiflora* appears to be localized in the thickened outer wall of the epidermis.

Seed dispersal mechanisms have not been studied in the genus but most species lack any obvious adaptations for dispersal and we assume

that they rely on passive, mainly short-distance dispersal of the seeds. The swollen raphe in subgen. *Viridibractea* possibly assists in myrmecochory but dispersal of seeds by ants has not been seen. *Freesia laxa* and *F. grandiflora* are apparently exceptional in the genus in relying on birds for seed dispersal. The fresh seeds in these two species are bright red or orange (darkening within a day or so) and may appear to frugivorous birds as small berries, which are eaten and thus dispersed, although only anecdotal observations exist for this (Mauve s.n. PRE). Dispersal in *F. laxa* is almost certainly deceptive as the seeds lack evident rewards but possibly not in *F. grandiflora*. Although the seed coat in this species is not fleshy, the raphe in fresh seed is highly hydrated, and the testal layers are significantly richer in starch grains than the seeds of other species such as *F. caryophyllacea* and may thus have some nutritional value.





PHYLOGENETIC RELATIONSHIPS

by Félix Forest, Irina Tatarenko, John Manning & Peter Goldblatt

Phylogenetic analysis of DNA sequences of several plastid regions places *Freesia* as sister to the genera *Crocasmia* and *Devia*, with these three genera in turn sister to *Xenoscapa*. These four genera are now regarded as comprising tribe Freesieae within subfamily Crocoideae (Goldblatt *et al.* 2006).

Crocasmia is a small genus of eight species of relatively robust, orange- to scarlet-flowered plants primarily of temperate grasslands and forested habitats along the eastern seaboard of southern and tropical East Africa; one species is endemic to Madagascar and another is restricted to high elevations in Namaqualand in western South Africa. Floral form within the genus is variable, reflecting adaptation to pollination by birds, bees, and butterflies but most species have gullet- or trumpet-shaped flowers. *Devia* is a monotypic, strongly xeromorphic genus from the higher parts of the western escarpment on the edge of the southern African winter rainfall region. It is unusual in its evergreen habit and small, pale pink, tubular flowers. *Xenoscapa* comprises two species from winter rainfall South Africa and southern Namibia, and is characterized by its obtuse, prostrate leaves and single-flowered spikes of salver-shaped, whitish or pink flowers. These patterns suggest that *Freesia* originated in southwestern Africa, with indirect dating of the molecular tree placing the divergence of the genus in the mid-Miocene (12–15 million years ago) (Goldblatt *et al.* 2005).

Within *Freesia* the relationships among the species remain incompletely resolved although the introduction of molecular techniques has provided new insights. The genus was historically divided into two groups (treated as genera or subgenera) on the basis of flower morphology

(Manning & Goldblatt 2005). Subgen. *Anomatheca* was characterized by tubular or salver-shaped flowers with the filaments inserted in the upper part of the tube near the mouth, and subgen. *Freesia* by deeply gullet-shaped flowers with the filaments inserted near the middle of the tube at the junction between the narrowly tubular lower portion and the broadly cylindrical upper part.

A preliminary morphological cladistic analysis of the genus (Goldblatt & Manning 1995) retrieved *Freesia* in the classical sense as monophyletic, based on a combination of gullet-shaped flowers, included stamens, strong floral scent, and a whitish to yellow perianth. Although this combination of characters appears at first glance to be a compelling collection, it is highly likely that several, at least, are not independent states, thus significantly reducing the morphological evidence for the monophyly of the group. In the same analysis, the four species of *Anomatheca* were retrieved as a grade comprising three distinct lineages, one of them including the two red-flowered taxa *F. grandiflora* and *F. laxa*, linked on the basis of their brown-tipped floral bracts, which were treated as apomorphic but homoplasious as they occurred elsewhere in the genus.

The clear implication from this morphological cladistic analysis, that the tubular-flowered species did not comprise a monophyletic lineage, was not implemented in the infrageneric classification presented by Manning & Goldblatt (2005), who followed tradition in treating them as a single lineage (as subgen. *Anomatheca*). The phylogenetic analysis of plastid DNA sequence data presented here (Figure 11, Table 3) provides additional and independent evidence for a

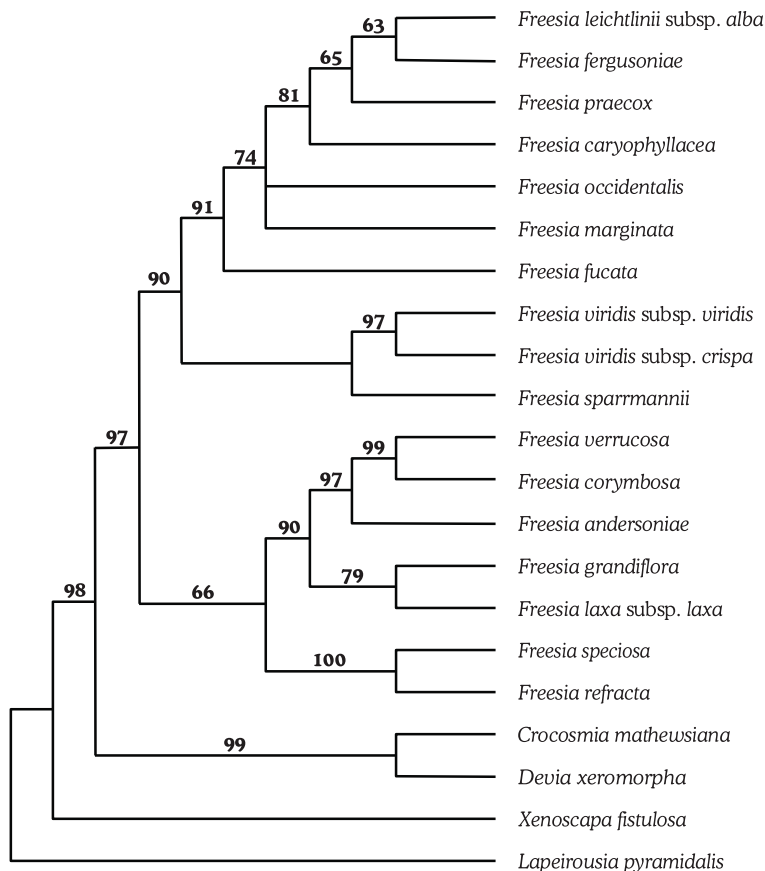


FIGURE 11.—Strict consensus tree of *Freesia* based on analysis of five plastid regions. Bootstrap percentages over 50 % are shown above the branches.

more complex relationship between the tubular- and gullet-flowered species.

Results: the combined matrix includes 3 798 characters of which 3 211 are constants, 587 are variable and 142 (3.7 %) are potentially parsimony informative. The combined analysis resulted in only three most parsimonious trees (of 708 steps), with a consistency index of 0.68 (calculated excluding uninformative sites) and a retention index of 0.74.

Freesia is strongly supported as monophyletic (97 BP), with a dichotomy at the crown node of the genus in the strict consensus tree (Figure 11).

The first clade of this dichotomy is only weakly supported (66 BP) but comprises two strongly supported groups, one consisting of *F. speciosa* and *F. refracta* (100 BP), together sister to a group (90 BP) in which the pair *F. grandiflora*–*F. laxa* subsp. *laxa* (79 BP) is sister to three other species (*F. andersoniae*, *F. corymbosa*, *F. verrucosa* (97 BP). The second clade comprises two groups, the first comprising an unsupported sister relationship between *F. sparrmannii* and the two subspecies of *F. viridis*, and the second well supported (91 BP) and encompassing the remainder of the genus as a grade of seven species. *F. fucata* is the first diverging lineage in this grade, followed by *F. occidentalis* and *F. margi-*

nata. The only topological discrepancy among the three most parsimonious trees resulting from the combined analysis lies in the position of *F. occidentalis* and *F. marginata*, which are interchangeably second and third in this grade or are sisters. The last four species form a moderately supported clade (81 BP), in which *F. caryophyllacea* is sister to *F. praecox* and the pair *F. leichtlinii* subsp. *alba*–*F. fergusoniae* (Figure 11); none of these relationships are well supported.

A phylogenetic analysis (not shown) based on the low-copy nuclear gene coding for xanthine deshydrogenase (Xdh) is generally concordant with the plastic combined analysis presented here but with much less resolution and support. One exception is the placement of *Freesia sparrmanii* within the clade comprising (among others) *F. refracta* and *F. grandiflora*, rather than sister to the *F. viridis* subspecies.

Discussion: the most significant implication of the molecular phylogeny is that the tubular-flowered species represent two or three independent origins from among the gullet-flowered species. Evidence from morphology (notably the red flowers and the orange or red seeds with inflated raphe), and from ecology and biogeography (the largely subtropical and tropical distribution), reinforces the molecular evidence that the summer rainfall species *Freesia grandiflora* and *F. laxa* are sister taxa, evidently derived from an ancestor with gullet-shaped flowers and soft-textured, brown-tipped bracts. The third tubular-flowered species, *F. verrucosa*, appears to be independently derived from within the same group but its precise relationships are unclear. The affinities of the fourth tubular-flowered species, *F. viridis*, in contrast, lie with the second group of gullet-flowered species, those with firm-textured, green bracts. In the light of this it is significant that *F. viridis*,

TABLE 3.—Voucher data for molecular analysis

Species	Voucher	LHMS/Kew bank
<i>Freesia andersoniae</i>	Free State, Fauresmith, <i>ex hort.</i> NBG467/93	584/28380
<i>F. caryophyllacea</i>	Western Cape, Onrus, <i>ex hort.</i> NBG317/87	581/28377
	Eastern Cape, Joubertina, Goldblatt & Porter 12506 (NBG), <i>ex cult.</i>	
<i>F. corymbosa</i>	NBG141/85	585/28381
<i>F. fergusoniae</i>	Western Cape, Riversdale, Goldblatt & Manning 12252 (NBG)	–/31346
<i>F. fucata</i>	Western Cape, Villiersdorp, Manning 2271 (NBG)	
<i>F. grandiflora</i>	KwaZulu-Natal, without precise locality, <i>ex cult.</i> NBG2/89	587/28383
<i>F. laxa</i> subsp. <i>laxa</i>	KwaZulu-Natal, Annerley, <i>ex hort.</i> NBG131/82	–/35187
<i>F. leichtlinii</i> subsp. <i>alba</i>	Western Cape, Plettenberg Bay, <i>ex hort.</i> NBG796/71	586/28382
<i>F. marginata</i>	Western Cape, Worcester, Manning 2734 (NBG)	–/31347
<i>F. occidentalis</i>	Western Cape, Karooport, Manning 2769 (NBG)	579/28375
<i>F. praecox</i>	Western Cape, Riviersonderend, Manning 2921 (NBG)	–/31348
<i>F. refracta</i>	Western Cape, De Doorns, Walters 505 (NBG)	
<i>F. sparrmanii</i>	Western Cape, Swellendam, <i>ex hort.</i> NBG144/85	583/28379
<i>F. speciosa</i>	Western Cape, Ladismith, Goldblatt, Porter & Manning 12177 (NBG)	628/28433
<i>F. verrucosa</i>	Western Cape, Oudtshoorn, Goldblatt & Porter 11840 (NBG)	686/28461
<i>F. viridis</i> subsp. <i>viridis</i>	Western Cape, Saldanha, Goldblatt & Porter 12899 (NBG)	588/28384
<i>F. viridis</i> subsp. <i>crispifolia</i>	Western Cape, Clanwilliam, Hall 904 (NBG)	–/35186
<i>Crocsmia mathewsiana</i>	Mpumalanga, Graskop, Goldblatt & Manning 9830 (NBG)	–/1175
<i>Devia xeromorpha</i>	Northern Cape, Sneeukskrans, Snijman & Manning 1194 (NBG)	–/11506
<i>Lapeirousia pyramidalis</i>	Western Cape, Vanrhynsdorp, Barker 6439 (NBG)	
<i>Xenoscapa fistulosa</i>	Western Cape, without precise locality, Chase 11508 (K)	–/11508

alone among the tubular-flowered species, has bracts of this type and texture. This alliance may receive additional support from the presence of ionones in the floral scent, diagnostic of subgen. *Viridibractea*. Although *F. viridis* is weakly associated with *F. sparrmanii* in the molecular analysis, morphological evidence, notably the puberulous stem and inflated seed raphe, favours a closer association between *F. sparrmanii* and the other gullet-flowered species in the clade. Whatever its precise relationships, *F. viridis* is a highly distinctive species with several autapomorphies, namely the winged stem, green to almost brown flowers with strongly curved floral tube, and a 1-banded pollen operculum.

The scattered placement of the three species *Freesia corymbosa*, *F. occidentalis* and *F. refracta* in the analysis is unexpected and without any morphological support. These species are very similar in appearance and are considered to be closely allied (Goldblatt 1982). Differences between them lie primarily in the degree of pigmentation of the bract tips, the shape of the leaf apices, and subtle differences in flower colour. In the face of their overwhelming morphological similarity it is more likely that some form of horizontal gene transfer stemming from past

hybridization events is the explanation for their dispersed positions in the molecular analysis. The inclusion of nuclear gene sequences in the analysis may resolve this issue.

The plastid molecular analysis thus supports the separation of the genus into two main groups, treated here as subgenera and morphologically characterized by different, apparently derived bract types. Within subgen. *Freesia* it is evident that *F. grandiflora* and *F. laxa* represent sister taxa but relationships among the remaining species are unclear. There is no support for a particularly close relationship between *F. andersoniae* and *F. speciosa* as was suggested by Goldblatt (1982), primarily on the basis of their unusually large flowers. Within subgen. *Viridibractea* it is most likely that *F. viridis* is sister to the remaining species, which form a close-knit assemblage defined morphologically by their puberulous stems and oblique seeds with conspicuously swollen raphe. Relationships within the latter group are incompletely resolved but unscented, small-flowered *F. sparrmanii* appears to be sister to the remaining species, all of which are highly fragrant. Among the latter, the yellow-flowered *F. leichtlinii* and *F. fergusoniae* may be closely allied.





SYSTEMATICS

Freesia Eckl. ex Klatt in Linnaea 34: 672 (1866), name conserved against *Lomenia* Pourr. [= *Watsonia*] (Goldblatt 1980) and against *Anomatheca* Ker Gawl. (Goldblatt & Manning 1993). Type species: *Freesia refracta* (Jacq.) Klatt [lecto., designated by Goldblatt 1982: 56].

Anomatheca Ker Gawl.: 227 (1804). Type species: *Anomatheca juncea* Ker Gawl. = *Freesia verrucosa* (B. Vogel) Goldblatt.

Nymanina Kuntze: 701 (1891), illegit. superfl. name for *Freesia* Klatt. Type species: as for *Freesia*.

Small to medium-sized deciduous geophytes; corm subglobose to narrowly conical, rounded at base; outer tunics of pale, fine- to coarse-textured, netted fibres; cataphylls up to 3, soft-textured, pale, green or flushed purple. Stem erect or sometimes shortly decumbent, usually terete but flattened and winged in *F. viridis*, often branched, smooth or sparsely to densely papillate. Leaves 4–13, lower 3–11 ± basal and suberect to prostrate, linear-lanceolate to lanceolate, falcate or oblong, acute to obtuse, midrib lightly to moderately thickened, margins unthickened, usually plane, rarely undulate or crispulate (*F. viridis* subsp. *crispifolia*), uppermost 1 or 2 leaves cauline, usually without blade. Inflorescence a spike, lightly to sharply deflexed and horizontal, secund and ± scalloped, up to 14-flowered. Bracts either firm-textured and green with narrow, hyaline margin, or pale and papery or membranous and then usually tipped dark brown; outer bracts acute, apiculate or tricuspidate, inner smaller and forked apically. Flowers weakly to strongly zygomorphic, either ± salver-shaped with subequal tepals ± evenly spreading, or funnel-shaped and bilabiate with upper tepals larger and suberect and lower recurved, mostly white or cream-coloured to pale yellow, often flushed purple on reverse, but also pink, red or green to brown, lower tepals often with yellow to orange nectar guides,

often fragrant; perianth tube either subcylindrical and expanding slightly and evenly from base or near apex, or funnel-shaped and narrowly tubular below but ± abruptly expanded near middle into broadly cylindrical or flared distal part; tepals subequal or upper larger and sometimes hooded, oblong to lanceolate, inner tepals oblong or ovate-cordate. Stamens unilateral, arched or ± straight, inserted either near mouth or near middle of tube at base of broader distal portion, usually included but sometimes exerted; anthers oblong-linear, held opposite upper tepal. Style filiform, curving behind or over anthers, dividing into 3 slender branches, each branch divided into 2 recurving arms. Capsules subglobose to oblong, 3-lobed, rough and papillate to verrucose throughout or in upper half. Seeds several per locule, subglobose, sometimes with raphe and chalaza inflated or swollen, smooth or wrinkled, testa dry and glossy reddish brown, rarely bright orange to red when fresh. Basic chromosome number: $x = 11$ (Goldblatt 1982).

16 spp., mainly winter rainfall South Africa but extending into southern Namibia and eastern subtropical and tropical Africa.

Named after Dr Friedrich Heinrich Theodor Freese, a physician at Kiel, Germany, and friend of C.F. Ecklon, nineteenth century plant collector. Ecklon (1827) had originally intended to honour Freese in the genus *Freesea* [sic], based on long-tubed species of *Tritonia* and *Ixia* but Ecklon's name lacks a formal description and is thus illegitimate. *Freesia* was formally described by the German botanist, F.W. Klatt (1866), who applied the name in a different sense to that originally intended by Ecklon, as well as changing Ecklon's spelling. Klatt's reinterpretation of the genus has its roots in specimens distributed by Ecklon with the manuscript name *Freesea odorata* (now *Freesia corymbosa*), one of the three species included in the genus by Klatt.

Key to species

- 1a Flowers $\pm$ salver- or trumpet-shaped with floral tube slender and cylindrical throughout or widening gradually from base and inflated only in upper 5 mm (Figures 1G; 3C), 1–3 mm diam. at mouth; tepals subequal and $\pm$ spreading or recurved; stamens inserted in upper 5 mm of floral tube; lower tepals without extensive yellow markings, often with small median mark at base of lower tepals:
 - 2a Stems 2-angled or -winged; floral tube sharply bent in upper part and mouth facing down; flowers green or brownish; anthers included 9. *F. viridis*
 - 2b Stems round in section; floral tube straight or slightly curved, mouth facing sideways or upwards; flowers white, mauve, pink or red; anthers exerted:
 - 3a Leaves < 100 mm long, much shorter than inflorescence, oblong, obtuse-apiculate; bracts 4.0–5.5 mm long; perianth tube 15–20 mm long; flowers pink 5. *F. verrucosa*
 - 3b Leaves usually > 100 mm long, often as long as or longer than inflorescence, linear-lanceolate to lanceolate, acute-apiculate; bracts (4–)5–20 mm long; perianth tube 20–40 mm long; flowers red, pink, pale blue or white:
 - 4a Perianth tube > twice as long as tepals; upper tepal 9–15 mm long; filaments 3–4 mm long, scarcely exerted; anthers 4 mm long 1. *F. laxa*
 - 4b Perianth tube $\pm$ as long as tepals or slightly longer; upper tepal 22–32 mm long; filaments (6–)15–25 mm long, exerted (2–)10–20 mm; anthers 5.5–8.0 mm long 2. *F. grandiflora*
- 1b Flowers funnel-shaped, floral tube with narrowly tubular lower portion $\pm$ abruptly expanded into broadly cylindrical distal portion (Figures 2I; 4H, J), 5–15 mm diam. at mouth; stamens inserted near middle or in lower half of tube, at junction between lower and upper portions; lower tepals usually with extensive yellow markings:
 - 5a Floral bracts thin-textured, membranous or papery, pale green or translucent and dry, usually with dark tips; stems smooth; seeds subglobose, without inflated raphe:
 - 6a Bracts 7–13 mm long; flowers normally 50–65 mm long; filaments 18–32 mm long:
 - 7a Leaves 100–200 mm long, acute; flowers white to cream-coloured, boldly marked with purple lines in throat; tepals ovate to elliptic; filaments 18–25 mm long 3. *F. andersoniae*
 - 7b Leaves 25–100 mm long, obtuse or subacute; flowers pale yellow, at most with pale purple lines in throat; tepals suborbicular; filaments 27–33 mm long 4. *F. speciosa*
 - 6b Bracts 4–8 mm long; flowers normally 25–40 mm long; filaments 10–14 mm long:
 - 8a Bracts uniformly pale-coloured; leaves usually $\pm$ as long as stem 7. *F. refracta*
 - 8b Bracts brown-tipped; leaves usually $\pm$ half as long as stem:
 - 9a Leaves obtuse or subacute, (5–)7–18(–25) mm wide; bracts lightly tipped with dark brown; flowers white or cream-coloured, sometimes flushed pale lilac or mauve . . . 8. *F. occidentalis*
 - 9b Leaves acute to acuminate, 2–7(–10) mm wide; bracts with pronounced dark brown tips; flowers usually pale yellow sometimes flushed dull purple, or pale to deep pink 6. *F. corymbosa*
 - 5b Floral bracts firm-textured, green with narrow membranous margins; stems puberulous or papillate, at least towards base; seeds obliquely globose, with inflated raphe:
 - 10a Floral tube narrowly funnel-shaped, lower portion 12–15 mm long and $\pm$ as long as or slightly longer than upper portion (Figure 4J); lower tepals 4–5 mm wide; flowers unscented 10. *F. sparrmanii*
 - 10b Floral tube funnel-shaped, lower portion $\pm$ half as long as upper portion (Figure 4H); lower tepals 5–12 mm wide; flowers always fragrant:
 - 11a Plants usually with deeply buried corms, bearing cormels in one or more lower leaf axil; coastal in sandy soils 15. *F. leichtlinii*
 - 11b Plants with shallow corms, bearing cormels at base of parent corm, never in leaf axils; inland in loamy or clay soils:
 - 12a Corm tunics of soft, thin-textured fibres (< 0.1 mm diam.); flowers mostly with yellow or orange markings on lower median tepal only; flowering June–July 14. *F. praecox*

- 12b Corm tunics of wiry, coarse-textured fibres (at least some > 0.2 mm diam.); flowers mostly with yellow or orange markings on all three lower tepals:
 13a Flowers creamy yellow or bright yellow; number of leaves (5–)7–13; flowering (June) July to August 16. *F. fergusoniae*
 13b Flowers white; number of leaves 4–7(–9); flowering April to July:
 14a Leaves erect, glaucous, acuminate, 4–5 mm wide 11. *F. fucata*
 14b Leaves erect or prostrate, green or glaucous, subacute to acute, 6–15(–20) mm wide:
 15a Leaves medium-textured, with prominent midrib but no evident submarginal vein 13. *F. caryophyllacea*
 15b Leaves firm-textured and leathery, with inconspicuous midrib and prominent submarginal vein 12. *F. marginata*

Freesia subgen. Freesia

Anomatheca Ker Gawl. in König & Sims, *Annals of Botany* 1: 227 (1804). *Lapeirousia* subgen. *Anomatheca* (Ker Gawl.) Baker: 173 (1892). *Freesia* subgen. *Anomatheca* (Ker Gawl.) J.C.Manning & Goldblatt: 172 (2005). Type species: *Anomatheca verrucosa* (B.Vogel) Goldblatt = *Freesia verrucosa* (B.Vogel) Goldblatt & J.C.Manning.

Plants small to medium-sized. Stem rounded in section, smooth. Leaves erect to prostrate, blades lanceolate to oblong, plane, acute or obtuse. Spike suberect or inclined. Bracts soft-textured, either soft-herbaceous and green throughout or drying from apex, or entirely membranous and translucent, often brown-tipped. Flowers either funnel-shaped with slender proximal portion of tube widening ± abruptly into cylindrical distal portion and tepals unequal, upper largest and erect, lower spreading, or ± salver-shaped with straight tube narrowly cylindrical throughout or widening gradually from base and tepals ± equal and spreading or recurved, blue or pink to red with red markings on lower tepals, or white or pale to deep pink or yellow with dark yellow or orange markings on lower tepals, unscented or scented. Stamens shortly to well exerted, or included. Seeds subglobose or with inflated raphe, smooth or rugulose, reddish brown but sometimes orange to red when fresh.

1. ***Freesia laxa*** (Thunb.) Goldblatt & J.C. Manning in *Systematic Botany* 20: 171 (1995). *Gladiolus laxus* Thunb.: 50 (1823). *Lapeirousia laxa* (Thunb.) N.E.Br.: 24 (1928). *Meristostigma laxum* (Thunb.) A.Dietr.: 597 (1832). *Anomatheca laxa* (Thunb.) Goldblatt: 442 (1971). Type: South Africa, [Eastern Cape], without precise locality but probably Uitenhage District in De-

cember 1773, Thunberg UPS-THUNB1039 (UPS-THUNB, holo.–microfiche!).

Anomatheca cruenta Lindl.: t. 1369 (1830). *Lapeirousia cruenta* (Lindl.) Baker: 173 (1892). *Freesia cruenta* (Lindl.) Klatt: 187 (1894). Type: South Africa, [Eastern Cape], without precise locality, Lindley s.n. (GCE, holo.!).

Lapeirousia grandiflora Jacq.: 120 (1836), illegit. superfl. name for *Anomatheca cruenta* Lindl. Type: Illustration in *Annales de flora et de Pomone* 4: 122 (1836).

Lapeirousia graebneriana Harms: 366 (1901). Type: Tanzania, Iringa District, Uhehe, Ufuagi, 14 March 1899, Goetze 748 (B, holo.!, BR, iso.!).

Plants (150–)200–500 mm high; corm globose-conical, 10–15 mm diam., developing cormels at base; tunics of fine-textured fibres; stem erect, sometimes with 1(2) branches. Leaves 6–9, suberect, usually shortly overtopping spike, narrowly lanceolate, (40–)100–400 × 4–10(–15) mm, acute to acuminate, soft-textured with midrib moderately thickened. Spike slightly or moderately deflexed, (1)2–6(–14)-flowered. Bracts ovate, (4–)5–8(–14) mm long, acute, soft and herbaceous, green with reddish brown tips, inner bracts slightly shorter. Flowers 25–40 mm long, red to pink, lilac or pale blue, rarely white, base of lower three tepals each with dark red, purple or violet blotch, unscented; perianth tube cylindrical but slightly expanded near apex, (20–)25–35(–40) mm long, slightly or more strongly curved in upper 4 mm; tepals subequal but inner 3 broader, uppermost somewhat reflexed, others spreading, elliptic to obovate, 9–15 × 4–8 mm. Filaments erect, mostly 3–5 mm long, inserted 2 mm below mouth of tube and exerted 1–3 mm; anthers ± 4 mm long. Style dividing between base of anthers and tips. Capsules oblong-ovoid, three-lobed, 10–12(–15) × 8–10 mm, papillate (sometimes obscurely). Seeds subglobose with

highly inflated raphe, 2.5–3.0 mm diam., smooth and glossy, bright red when fresh but soon darkening to reddish brown. *Flowering time*: variable in any locality, from June to April, most often from October to December. Plate 1; Figure 1F, G.

Etymology: Latin *laxus*, flaccid, loose, alluding to the appearance of the plant.

Distribution and ecology: widely distributed along the eastern seaboard of southern Africa from east of Port Elizabeth (with a single, early, unlocalized record from 'Uitenhage') along the coast and through the Eastern Cape and Kwa-Zulu-Natal Midlands to southern Mozambique, inland to Mpumalanga in South Africa and Swaziland (Figure 12). Further north the species has been recorded from Zambia, eastern Zaïre, Tanzania, western Kenya, eastern Uganda and in the Imatong Mountains of southern Sudan.

Plants favour friable soils, growing in small colonies in coarse sandy soil in coastal scrub and inland on the edges of bush and forest, often in rocky situations. Flowering time varies greatly, often in a single locality, but is usually from early to late summer. *Freesia laxa* has been in cultivation in Europe since 1830 and is still grown today. It is now naturalized locally on waste ground in Australia around Sydney and along the northern coast of New South Wales (Cooke 1986), and in southern China, Mauritius, Réunion, Madeira, and in the United States of America in Florida and most likely other southern states, doubtless through escapes from cultivation.

Freesia laxa is self-fertile, a condition favoured by the branching of the style opposite the anthers at a level where the stigmas are sure to contact the pollen. The species, unlike others in the genus, appears to hybridize relatively freely in cultivation, and viable crosses have been produced with *F. sparrmanii* and *F. viridis*. The *F. viridis* × *laxa* hybrid is an attractive deep maroon-red but the flowers are small, as might be expected from the parentage, and although vigorous, the cross has no horticultural merit beyond its curiosity.

The tubular, red flowers of subsp. *laxa* display the features associated with pollination by butterflies but the shift in colour to lilac or blue in subsp. *azurea* suggests the intriguing possibility that this subspecies is entering a guild of plants

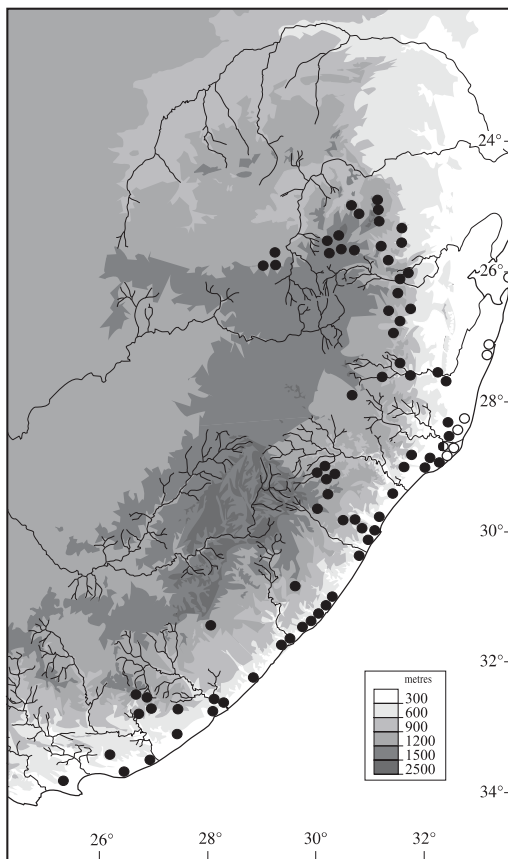


FIGURE 12.—Known distribution of *Freesia laxa* in southern Africa: subsp. *laxa*, ●; subsp. *azurea*, ○.

pollinated by long-proboscid, tangle-veined flies of the genus *Stenobasipteron* (Nemestrinidae), which are known to visit several plants with similar flowers along the eastern seaboard of southern Africa (Potgieter & Edwards 2005).

Diagnosis and relationships: *Freesia laxa* is evidently closely allied to *F. grandiflora*, with which it shares subglobose-conical rather than narrowly conical corms, suberect spikes of brilliant scarlet flowers (pale lilac in subsp. *azurea*), and seeds that are bright orange or red when fresh. Both species are restricted to forest or savanna in regions of summer rainfall. Although treated as varieties by some authors in the past, the two taxa are quite distinct in floral and vegetative features.

Freesia laxa is generally smaller-flowered, and although the two species overlap in the absolute length of the perianth tube, the relative length of the tube compared to the tepals is distinctly different. The tube in *F. laxa* is relatively longer, more than twice as long as the tepals, which spread horizontally from the base and measure 9–15 mm long, and the filaments are very short, 3–4 mm long, and scarcely exerted from the tube. *Freesia grandiflora*, by comparison, has a tube $\pm$ as long as the tepals or only slightly longer, larger and somewhat cupped tepals $\pm$ 20–30 mm long, and filaments 15–25 mm long exerted 10–20 mm beyond the tube, rarely (subsp. *occulta*) only $\pm$ 6 mm long and exerted $\pm$ 2 mm.

The seeds of *Freesia laxa* are also often slightly larger and have a swollen raphe forming a semicircular rim around one half of the seed, whereas seeds of *F. grandiflora* are either globose with the raphe not swollen or if it is swollen then it is very short, with the swelling forming a knob on one end of the seed rather than a semicircular rim. The two species have very different modes of vegetative multiplication. Plants of *F. laxa* invariably produce several sessile cormels around the base of the mother corm but these are rarely found in *F. grandiflora*. Instead, plants develop thick, creeping rhizomes, covered with papery bracts, or very occasionally sessile cormels may be produced in the axils of the lower leaves. Ecologically the two species are largely complementary, with *F. laxa* typically found in more temperate montane or maritime environments, whereas *F. grandiflora* occupies drier and hotter habitats. Unusually, both species have been recorded naturally around Pretoria, notably in the Fountains Valley and at Irene. Although *F. laxa* typically flowers earlier than *F. grandiflora*, as at Fountains, where it was collected by local botanist Inez Verdoorn on 28 December 1928 (Verdoorn 628) compared with a collection of *F. grandiflora* on 25 March 1929 (Verdoorn 781); at Irene both species were collected in flower on 10 January 1906 by R. Leendertz (Leendertz 698, 4061). No natural hybrids have, however, been recorded.

History: *Freesia laxa* was most likely first collected in the Eastern Cape in 1773 by Swedish botanist Carl Peter Thunberg. Despite being one of the earliest species of *Freesia* to be discovered, it was only named fifty years later, as *Gladiolus laxus* Thunb. The identity of *G. laxus* remained un-

certain for over 100 years, during which time the species was independently described under the name *Anomatheca cruenta* by the English botanist, John Lindley in 1830 from plants of South African origin that were flowered in Britain. It became widely known in horticulture under this name, or the later combination *Lapeirousia cruenta*, and is still offered as such today in trade catalogues.

Thunberg's name was revived when N.E. Brown (1928) made the combination *Lapeirousia laxa* after examining the type material of *Gladiolus laxus*. The posthumously published name *L. grandiflora* Jacq. (1836), based on an illustration of a cultivated specimen, is rendered nomenclaturally superfluous by the citation of the earlier name *L. cruenta* in synonymy (McNeil *et al.* 2006: Art. 52.1).

Key to subspecies

- 1a Flowers pink to red (rarely white) with dark red markings on lower tepals; upper tepal 10–15 $\times$ (4)–5–8 mm; style dividing at or above middle of anthers 1a. subsp. *laxa*
- 1b Flowers lilac, pale bluish or white with violet or indigo markings on lower tepals; upper tepal 9–11(–12) $\times$ 4(–5) mm; style dividing below middle of anthers 1b. subsp. *azurea*

1a. subsp. *laxa*

Flowers pink to red (rarely white), usually paler on reverse, lower three tepals each with dark red blotch at base; perianth tube 20–35(–40) mm long; tepals 10–12(–15) $\times$ 4–8 mm. **Filaments** exerted 1.5–2.0 mm. **Style** dividing between middle and apex of anthers. Plate 17; Figure 1F, G.

Distribution and ecology: the typical subspecies is widely distributed along the eastern coast and near interior of South Africa, from near Port Elizabeth eastward through the Eastern Cape and KwaZulu-Natal and inland through Swaziland to Ohrigstad in Mpumalanga and Pretoria in Gauteng, and thence discontinuously through eastern tropical Africa to western Kenya, eastern Uganda and southern Sudan. It does not appear to occur in Zimbabwe, northern Mozambique or southern Malawi but is recorded from Zambia and southern Tanzania.

Although favouring rocky habitats on the edge of bush clumps and afrotemperate forest,



PLATE 2.—*Freesia grandiflora*

subsp. *laxa* is also found in coastal forest and bush near sea level in northern KwaZulu-Natal. Plants have been recorded in flower from August to January but peak flowering south of the equator is between November and January, and May to July north of the equator.

The flowers, although usually bright red, vary considerably in the exact shade, ranging from pink through crimson to orange-red, with occasional white mutants also recorded. Early collections made by the South African botanists, John Medley Wood and Rudolf Marloth in the late nineteenth century around Durban, notably on the Berea, are especially large-flowered, with a perianth tube 35–40 mm long and tepals up to 15 × 8 mm. Unfortunately this fine form of the species is now almost certainly extinct due to urbanization.

1b. **subsp. *azurea*** Goldblatt & Hutchings in Novon 3: 146 (1993). Type: Mozambique, Inhaca Island, 20 July 1980, *De Koning & Navunga 8312* (LMU, holo.!; BR!, K!, MO!, SRGH!, iso.).

Flowers lilac, pale bluish or white, lower three tepals each with dark blue to violet blotch at base; perianth tube 25–35 mm long; tepals 9–11(–13) × 4(–5) mm. *Filaments* exerted 1–3 mm. *Style* dividing between base and middle of anthers.

Etymology: Latin *azureus*, pure deep blue, referring to the flower colour and markings.

Distribution and ecology: subsp. *azurea* is restricted to coastal habitats between Richards Bay in northern KwaZulu-Natal and Massinga in central Mozambique. Plants grow in coarse, sandy soils, either in exposed sites such as grassy dunes or in light shade. Flowering is in winter and early spring, between June and September, unlike the typical subspecies, which flowers mainly in late spring and summer, between November and January.

2. ***Freesia grandiflora*** (Baker) Klatt in Dur. & Schinz, *Conspectus florae africanae* 5: 187 (1894). *Anomatheca grandiflora* Baker: 337 (1876). *Lapeirousia grandiflora* (Baker) Baker: t. 6924 (1887), illegit. homonym, not *L. grandiflora* Jacq. (1836) (= *F. laxa* (Thunb.) Goldblatt & J.C.Manning). Type: Mozambique, mouth of Luabo [Luaua] River, 30 May 1858, *Kirk s.n.* (K, lecto., designated by Goldblatt 1993: 53).

Tritonia graminifolia Baker: 195 (1892). *Lapeirousia graminifolia* (Baker) L.Bolus: 135 (1929b). Type: South Africa, [Mpumalanga], near Lydenburg, November 1874, *Bolus 2651* (K, holo.).

Freesia rubella Baker: 868 (1901). Type: Mozambique, Delagoa Bay [Maputo], 1890, *Junod 166* (Z, holo.).

Plants (120–)200–600 mm high; corm globose-conical, 10–15 mm diam., producing thick, scaly rhizomes 20–40 mm long, tunics of fine fibres or almost papery; stem erect, usually unbranched but sometimes with 1(–4) branches, rarely developing cormels in axils of lower leaves. *Leaves* 6–9, suberect, usually reaching to base of spike or shortly above, lanceolate, (40–)100–300 × (6–)8–20 mm, acute, soft-textured with moderately thickened midrib. *Spike* suberect or weakly deflexed, becoming erect or suberect in fruit, 2–6-flowered. *Bracts* soft and herbaceous, green with dark reddish brown tips, ovate, 10–20 mm long, acute, inner bracts two thirds as long. *Flowers* 30–50 mm long, usually red, more rarely pinkish red or pink, base of lower three tepals with darker red blotch, unscented; perianth tube cylindrical below, expanded and funnel-shaped in upper 3 mm, 20–30 mm long, straight or slightly curved above; tepals subequal with inner three slightly larger and uppermost largest, suberect below and spreading above, oblanceolate, upper tepals 22–32 × 7–10 mm, lower 21–26 mm long. *Filaments* erect and unilateral, (6–)15–25 mm long, inserted (2–)3–4 mm below mouth of tube and exerted 12–20 mm; anthers 5.5–8.0 mm long. *Style* usually dividing between middle and apex of anthers, rarely below anthers. *Capsules* oblong, 3-lobed, 8–10 × 7–8 mm, papillate, sometimes weakly. *Seeds* subglobose, 2.0–3.5 mm diam., with or without inflated chalaza and raphe, campylotropous with very short raphe, smooth or lightly wrinkled, deep orange or red when fresh but soon darkening. *Flowering time*: mainly January to April. Plates 2; 17B; Figure 1A–E.

Etymology: Latin *grandiflorus*, large-flowered.

Distribution and biology: *Freesia grandiflora* has a scattered distribution through the eastern parts of southern and tropical Africa, from KwaZulu-Natal in the south, where it is recorded from the coast north of Durban and the Ingwavuma District, through the northern provinces of South Africa as far west as Rustenburg and Zeerust (Figure 13), and through Swaziland and Mozambique to

Zambia and southern Tanzania. It typically grows in humus-rich soils in scrub, deciduous woodland or more rarely forest, sometimes along streams. Plants have also been recorded occasionally on termite mounds. Although the species prefers subtropical climates, it has also been collected in temperate forests in the Soutpansberg, Steelpoortberg and Wolkberg, where it may occur in deep shade in dense populations.

The tubular, scarlet (rarely pink) flowers with well-exserted stamens appear to be adapted for butterfly pollination but, as with most species in the genus, no observations are available. The glossy orange or reddish brown seeds, which

are conspicuously displayed on the plant by the widely spreading fruit walls, are evidently adapted for dispersal by fruit-eating birds, as they resemble small berries. Although no published observations on this are known, the Pretoria botanist, Amelia Mauve (née Obermeyer) noted on one of her collections (*Mauve s.n.* PRE) that plants which appeared in her garden had probably been introduced by birds. The species is evidently palatable and not only has the foliage been recorded as being grazed by eland (*Hofmeyr 186* PRE) but the corms have been recorded as having been uprooted by animals as well (*Reid 1101* PRE).

The production of rhizomes in this species is an unusual feature that is not common in South African Iridaceae. The thick rhizomes, covered with overlapping scales, appear to be produced late in the growing season and are thus rarely evident on herbarium specimens, which are anyway often cut above the corm. Even those with attached corms from the current season have evidently been pulled from the ground, leaving the previous season's corm and its rhizome/s behind. The rhizomes spread from the base of the parent corm, giving rise to a terminal cormel only at the end of the second season, after which they wither and sever the connection between the daughter corm and the parent plant. Similar rhizomes are produced by *Crocasmia aurea* (Goldblatt *et al.* 2004), another member of the tribe Freesieae with a very similar ecology. Both species are woodland or forest plants from southern and tropical Africa, both produce flowers that are evidently adapted for butterfly pollination, and both produce seeds adapted for bird dispersal. The rhizomatous habit in the two species accounts for their frequent occurrence in dense populations in suitable habitats, and bird dispersal is almost certainly responsible for their widespread distribution.

Plants from near Mocuba in central Mozambique with pink flowers and unusually short filaments (Figure 1E), represent a distinct local variant that we recognize as subsp. *occulta*. Pink-flowered plants with filaments of normal length have been recorded from near Numbi in the Kruger National Park in South Africa, although other collections from the Park have the usual red flowers. The are included in subsp. *grandiflora*. A key to the subspecies and the description of subsp. *occulta* appear in the addendum, p. 111.

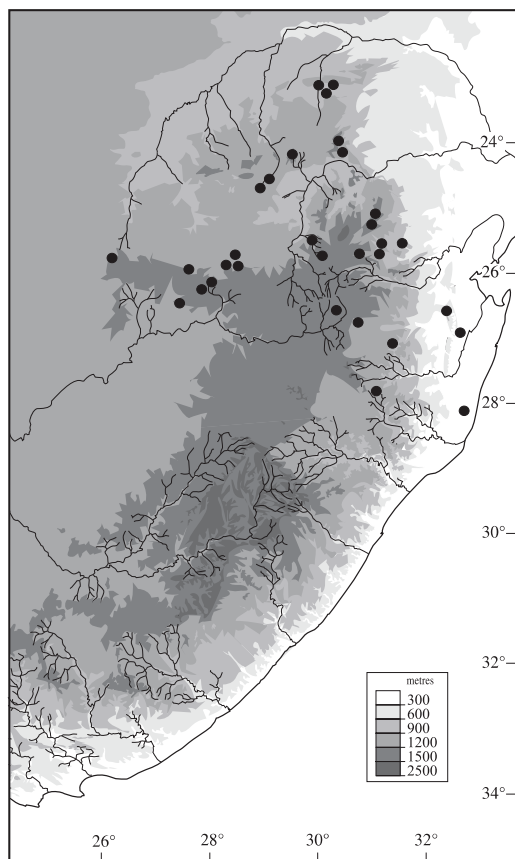


FIGURE 13.—Known distribution of *Freesia grandiflora* in southern Africa.

Diagnosis and relationships: *Freesia grandiflora* is undoubtedly closely allied to *F. laxa*, the only other species that favours woodland or savanna in the summer rainfall region, and both share unusual, scarlet flowers, subglobose-conical corms, and seeds that are brightly coloured when fresh. *Freesia grandiflora* is distinguished by its larger flowers with the dorsal tepal 22–32 mm long, a relatively shorter tube at most only slightly longer than the dorsal tepal, and long filaments, 15–20 mm long, and well exerted from the tube. *Freesia laxa* has smaller tepals, 9–15 mm long, a relatively longer tube more than twice as long as the tepals, and very short filaments, 3–4 mm long, only very shortly exerted. The characteristic rhizomes are not developed in *F. laxa*, which relies for vegetative reproduction on sessile cormels that develop around the base of the parent corm.

History: the species was first collected in Mozambique in 1858 by Sir John Kirk, who accompanied David Livingstone's Zambezi expedition. First described by Baker (1876) as *Anomatheca grandiflora*, the species was later transferred to the genus *Lapeirousia* (Baker 1887) under the illegitimate combination, *L. grandiflora* Baker (preoccupied by the name *L. grandiflora* Jacq.), where it was treated by most botanists despite the decision by Klatt (1895) to include the species of *Anomatheca* in *Freesia*. Baker (1892, 1901) subsequently redescribed the species twice for specimens that differed in no significant way from his *Anomatheca grandiflora*, first as *Tritonia graminifolia* for plants collected near Lydenburg and later as *Freesia rubella* for specimens from Delagoa Bay in southern Mozambique. The species was also sometimes treated as a form of *F. laxa* but its status as a distinct species is quite clear.

3. ***Freesia andersoniae*** *L. Bolus* in South African Gardening and Country Life 17: 337 (1927). Type: South Africa, [Northern Cape], Herbert District, September 1925, *Anderson* 760 (BOL, lecto!., designated by Goldblatt 1982: 86).

Plants 100–250(–300) mm high; corm conical, 15–25 mm diam., tunics light brown, of medium- to coarse-textured fibres; stem smooth but minutely verrucose on angles below each flower, erect, usually simple but with one or two branches in well-grown specimens. *Leaves* 10–14, in-

clined to suberect, $\pm$ as long as stem, narrowly lanceolate, 100–200 $\times$ 4–10 mm, acute to sub-attenuate. *Spike* deflexed, 2–5-flowered. *Bracts* dry and membranous or papery, translucent with brown veins and rust-coloured speckling on apices, ovate, 7–10(–13) mm long, acute, inner bracts up to 2 mm longer. *Flowers* 50–60 mm long, white to cream-coloured, base of lowermost tepal and inner edges of lower lateral tepals flushed orange, all three lower tepals with dark brownish midline and with dark chevrons in sinuses, strongly lily-scented; perianth tube funnel-shaped, 35–45 mm long with basal tubular portion 15–20 mm long, widening rather abruptly into cylindrical-flared upper portion; tepals unequal, dorsal largest, suberect, obovate, 12–16 $\times$ 10–12 mm, upper laterals narrower, broadly elliptical, lower tepals recurved, elliptical, 10–15 $\times$ 17–19 mm. *Filaments* arcuate, 18–25 mm long, inserted at base of widened upper portion, included; anthers 7–9 mm long. *Style* dividing between base and middle of anthers. *Capsules* short-oblong or oblong-ovoid, 3-lobed, (7–)10–12 $\times$ 8–10 mm, warty or papillate. *Seeds* subglobose or with chalaza slightly swollen, 2.5–3.0 mm diam., smooth, glossy dark or reddish brown. *Flowering time:* August to early October, rarely as early as late May. Plates 3; 17C.

Etymology: named for Mrs Ethel Anderson who collected the type and sent it to botanist Louisa Bolus in Cape Town.

Distribution and ecology: *Freesia andersoniae* is the only member of the genus with gullet-shaped flowers to occur entirely outside the southern African winter rainfall region. It is scattered across the central plateau of South Africa in the drainage basins of the Orange and Vaal Rivers, from the Kuruman Hills on the southern fringes of the Kalahari in the north southwards to near Carnarvon in the west and to Aliwal North and the Sneeu Berg near Middelburg in the east (Figure 14). The species is typically restricted to the lower, southern slopes of the dolerite and dolomite outcrops that are scattered across the calcareous plains of the Orange–Vaal basin, and is relatively common on the koppies around Kimberley. Plants are locally abundant, often growing wedged among the rocks in the thick red clays derived from the igneous rock. Here they are protected from predation by baboons, porcupines, and other herbivores and also benefit from



PLATE 3.—*Freesia andersoniae*

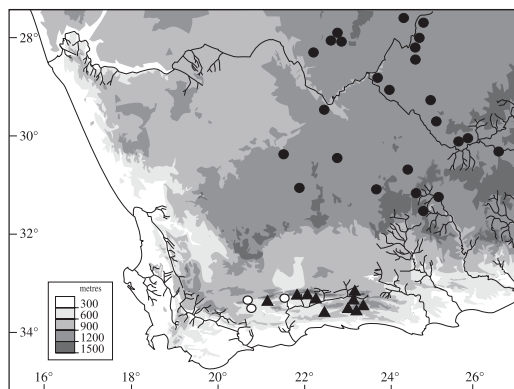


FIGURE 14.—Known distribution of *Freesia andersoniae*, ●; *F. speciosa*, ○; *F. verrucosa*, ▲.

cooler root temperatures and extra moisture. The corms sprout in response to the late summer or autumn showers that characterize the climate of the region, and plants are well grown by early winter although flowering is delayed until spring, by which time the leaves are already drying off. The species is evidently frost-hardy, and the plants with their firm-textured, almost waxy flowers are remarkably drought-tolerant.

Freesia andersoniae is patently palatable as it is heavily grazed, especially in drier years when other herbage is scarce. Even in less heavily stocked areas, however, the species is shy to flower in years with poor autumn rains.

The species is unusual among the gullet-flowered members of the genus in remaining fragrant throughout the night. This, coupled with the dominance of the chemical linalool (common in moth-pollinated flowers) suggests that the flowers may be at least partially moth-pollinated.

Diagnosis and relationships: *Freesia andersoniae* has an erect, almost smooth stem and thin-textured, membranous or papery bracts with large, white flowers, 50–60 mm long, that are marked with characteristic purple chevrons in the tepal sinuses. Although florally very different, preliminary DNA sequence data suggest a relationship with *F. laxa* and *F. grandiflora*, the only other species in the genus restricted to the summer rainfall region. Morphologically, however, *F. andersoniae*

is more likely to be confused with the large-flowered *F. speciosa*, from which it is distinguished by its relatively longer and narrower, acute leaves, white to cream-coloured flowers marked internally with purple lines down the sinuses in the gullet, ovate to elliptical inner tepals less than 10 mm wide, and filaments 18–25 mm long. *Freesia speciosa* typically has blunt, rather broad leaves and pale yellow flowers with distinctive, almost suborbicular inner tepals, and longer filaments, 27–33 mm long.

History: the species was described in 1929 by Cape Town botanist Louisa Bolus from plants collected in the Herbert District south of Kimberley in September 1925 by local resident, Mrs Ethel Anderson, for whom it was named. This was not the earliest record of the species, however, and it appears to have been first collected in 1889 near Douglas by F. Orpen, and later in August 1899 from near Middelburg by D.F. Gilfillan. At the time, the plants were included in a very broadly defined *Freesia refracta*, as were several collections from the early years of the 20th century, including one from Warrenton made by Miss Adams in 1903 and another from Hopetown made by the botanist Rudolph Marloth in 1916. The initial misidentification of the species stems from the inclusion at this time, under the name *F. refracta*, of *F. leichtlinii* subsp. *alba*, the eastern forms of which have flowers that are superficially similar to those of *F. andersoniae* in their size and proportions.

4. ***Freesia speciosa*** L.Bolus in South African Gardening and Country Life 19: 385 (1929a). Type: South Africa, [Western Cape], between Bonnievale and Barrydale (cultivated at the Karoo Garden, Whitehill), 22 August 1929, Archer s.n. BOL19027 (BOL, holo.!).

Freesia sparrmannii [as 'sparrmannii'] var. *flava* N.E.Br.: t. 11 (1921). *Freesia flava* (N.E.Br.) N.E.Br.: 27 (1935). Type: South Africa, [Western Cape], Ladismith District, 30 October 1918 (fl. in cult. Pretoria 19 September 1919), Shand s.n. PRE15786 (PRE, holo.!).

Plants (80–)120–200(–300) mm high; corm conical, 15–30 mm diam., tunics light brown, of medium- to coarse-textured fibres; stem smooth but minutely verrucose on angles below each flower, erect, usually simple but with up to four branches in well-grown specimens. *Leaves* 5 or



PLATE 4.—*Freesia speciosa*

6, inclined to suberect, usually $\pm$ half as long as stem, oblong, 25–100 $\times$ 14–20 mm, obtuse to subobtusely apiculate, firm-textured or softer. *Spike* deflexed, 3–6-flowered. *Bracts* membranous, green below when young but dry in upper two thirds, later translucent with brown veins and rust-coloured speckling on apices, ovate, 8–10 mm long, acute but lower bracts tricuspidate, inner bracts up to 1 mm longer. *Flowers* 50–70 mm long, pale creamy yellow, base of lowermost tepal and inner edges of lower lateral tepals flushed orange, all three lower tepals with brown midline, strongly lily-scented, with sour or bitter aspect during day; perianth tube funnel-shaped, 35–50 mm long with basal tubular portion 15–20 mm long, widening $\pm$ abruptly into cylindrical-flared upper portion; tepals unequal, dorsal largest, suberect, broadly ovate to suborbicular, 15–18 $\times$ 14–15 mm, upper laterals narrower, elliptical, lower tepals recurved, lower laterals broadly elliptical to suborbicular, 14–15 $\times$ 11–12 mm, lower median oblong, 14–15 $\times$ 7–8 mm. *Filaments* arcuate, 27–33 mm long, inserted at base of widened upper portion, included; anthers 6–7 mm long. *Style* dividing at or slightly beyond anther apices. *Capsules* short-oblong or oblong-ovoid, 3-lobed, 9–13 $\times$ 8–10 mm, warty or papillate. *Seeds* globose, 2.5–3.0 mm diam., smooth or finely wrinkled, glossy dark or reddish brown. *Flowering time*: mid-August to September. Plates 4; 17D; Figure 2I.

Etymology: Latin *speciosus*, showy, splendid.

Distribution and biology: this showy but rarely collected species is endemic to the western Little Karoo, where it has been collected from the Anysberg eastwards to Calitzdorp (Figure 14). *Freesia speciosa* occurs in small, localized populations on cooler, south-trending stony slopes in open Succulent Karoo shrubland, typically in rather loamy soil formed from decaying sandstone, in sandstone alluvium, or with the corms wedged in cracks on south-facing sandstone cliffs in humus, but not in the sandier soils derived from local quartzite formations.

The species is unusual among the gullet-flowered members of the genus in remaining fragrant throughout the night. This, coupled with the dominance of linalool in the scent profile (common in moth-pollinated flowers) suggests that the flowers may be at least partially moth-

pollinated. The floral scent chemistry changes during the night, when the distinct sour or bitter aspect that is present during the day disappears to leave a clean, lily-like scent.

Diagnosis and relationships: *Freesia speciosa* is a distinctive species with rather broad, blunt, often somewhat succulent leaves and large, pale creamy yellow flowers, 50–70 mm long, with broadly elliptical or suborbicular lower lateral tepals, 11–12 mm wide. It has the largest flowers in the genus, and is most likely to be confused with *F. andersoniae* from the interior Upper Karoo, which has similar bracts and large flowers. The leaves of *F. andersoniae* are narrow, pointed and firm-textured, and the white or cream-coloured flowers are boldly marked with purple streaks along the sinuses in the gullet, with narrower lower lateral tepals up to 9 mm wide, and shorter filaments, 18–25 mm long.

History: *Freesia speciosa* was described in 1921 by N.E. Brown, who treated it as a variety of *F. sparrmanii*, based on plants collected a few years earlier by a Mr J. Shand of Ladismith and cultivated at the then Botanical Research Institute in Pretoria. Although attributed to both E.P. Phillips and N.E. Brown (Goldblatt 1982), the name *F. speciosa* var. *lutea* is explicitly attributed to Brown alone in the publication (Brown 1921). This association between what are, in effect, the largest and the smallest-flowered species in the genus, is incomprehensible to modern botanists but at that time, Brown was applying the name *F. sparrmanii* var. *alba* to the large-flowered plants here treated as *F. leichtlinii* subsp. *alba*. Following his partial untangling of the names, N.E. Brown (1935) subsequently raised the taxon to species status, as *F. flava*. In the interim, however, the species had been independently described under the name *F. speciosa* by the Cape Town botanist, Louisa Bolus, from a cultivated plant grown at the Karoo Botanical Garden at Whitehill, which flowered in August 1929. It had originally been collected in the wild in the Barrydale District some time previously by Joseph Archer, the first curator of the Karoo Garden. This name therefore has priority at species level. Curiously, Brown (1935) failed to associate Bolus's species with his *F. flava*, which he distinguished from *F. speciosa* by its acute, rather than obtuse, leaves.



PLATE 5.—*Freesia verrucosa*

5. ***Freesia verrucosa*** (B.Vogel) Goldblatt & J.C.Manning in *Systematic Botany* 20: 171 (1995). *Ixia verrucosa* B.Vogel in Trew: t. 24, f. 2 (1784). *Anomatheca verrucosa* (B.Vogel) Goldblatt: 442 (1971). Type: without precise locality, figure in Trew, *Plantae rariora* 3: 8, t. 24, f. 2 (1784).

Gladiolus junceus L.f.: 94 (1782), illegit. homonym, not *G. junceus* Burm.f. (1768) (= *Geissorhiza aspera* Goldblatt). *Lapeirousia juncea* Ker Gawl.: t. 606 (1802), now regarded as a new name from this date. *Anomatheca juncea* (Ker Gawl.) Ker Gawl.: 227 (1804). *Peyrousia juncea* (Ker Gawl.) Poir.: 364 (1826). *Meristostigma junceum* (Ker Gawl.) Steud.: 130 (1841). *Freesia juncea* (Ker Gawl.) Klatt: 187 (1894). Type: South Africa, without precise locality, Thunberg s.n. LINN59.25 [as '*Gladiolus falcatus*'] (LINN, holo.-microfiche!).

Ixia emarginata Lam.: 342 (1789). Type: South Africa, without precise locality, Herb. Lamarck (P. holo.!).

Gladiolus amabilis Salisb.: 41 (1796). Type: unknown.

Gladiolus pulchellus Salisb.: 39 (1796). Type: unknown.

Gladiolus polystachyus Andr.: t. 66 (1799). *Gladiolus paniculatus* Pers.: 45 (1805), illegit. superfl. name for *G. polystachyus* Andr. Type: illustration in Andr., *The botanist's repository*: t. 66 (1799).

Ixia elliptica Thunb.: 4 (1803). Type: [South Africa], without precise locality, Thunberg UPS-THUNB897 (UPS-THUNB, holo.!).

Gladiolus excisus Jacq.: 46 (1804). Type: illustration in Jacq., *Plantarum rariorum horti caesarei schoenbrunnensis* 4: t. 491 (1804).

Ixia gawleri Schrad.: 67 (1810), illegit. superfl. name for *Gladiolus amabilis* Salisb. Type: illustration in Curtis's *Botanical Magazine* 17: t. 606 (Ker Gawl. 1802).

Plants 80–200 mm high; corm conical, 10–15 mm diam., tunics of fine- to medium-textured fibres; stem erect, usually 1–5-branched. *Leaves* 7–10, suberect, usually $\pm$ one third as long as stem, oblong, (15–)20–80 $\times$ 3–9 mm, obtuse-apiculate, margins sometimes slightly undulate, soft-textured with moderately thickened midrib. *Spike* slightly deflexed to horizontal, (4–)8–10(–15)-flowered. *Bracts* soft-textured, herbaceous, obovate, 4.0–5.5 mm long, green below but soon becoming pale, flushed pinkish distally with reddish veins, inner bracts slightly shorter. *Flowers* 20–30 mm long, bright pink (rarely mauve), base of lower three tepals or only median tepal with whitish or pale yellowish blotch outlined with dark pink, unscented or lightly scented; perianth tube subcylindrical and

expanding slightly from base to apex, 15–20 mm long, straight or slightly curved in upper 5 mm; tepals subequal or upper three slightly larger, spreading, elliptic to oblanceolate, 8–11 $\times$ 3–4 mm. *Filaments* arcuate, 6–7 mm long, inserted 4–5 mm within tube and shortly exerted; anthers $\pm$ 3 mm long. *Style* dividing opposite middle of anthers. *Capsules* short-oblong to subglobose, 3-lobed, 6–7 $\times$ 6 mm, papillate. *Seeds* subglobose, 1.5–2.0 mm diam., smooth, glossy reddish brown. *Flowering time*: late August to October. Plates 5; 17E; Figure 1H.

Etymology: Latin *verrucosus*, warty, for the rough surface of the capsules.

Distribution and ecology: *Freesia verrucosa* is recorded from the Little Karoo between Ladismith and Willowmore, extending eastwards into the intermontane valleys of the Langkloof from Avontuur to Kareedouw (Figure 14). The species grows in stony clay soils derived from shales of the Bokkeveld Series, in open renosterveld shrubland. Plants occur scattered in small colonies along roadsides or in stony washes, rarely in any numbers but occasionally in more dense concentrations.

The narrowly funnel-shaped, pink flowers, which appear in late spring, seem to be adapted for pollination by nectar-feeding bees and we have observed visits by *Anthophora* species (Apidae: Anthophorinae). The species is unique in the genus in having flowers that close up completely at night.

Diagnosis and relationships: *Freesia verrucosa* is recognized by its spreading fan of short, blunt leaves, short bracts 4.0–5.5 mm long, and declinate or horizontal spikes of narrowly funnel-shaped pink flowers with a slender tube 15–20 mm long. The seeds, 1.5–2.0 mm in diameter, are the smallest in the genus. The relationships of the species have generally been accepted to lie among the tubular-flowered species previously treated as the genus *Anomatheca*, particularly *F. laxa*, which has similar-shaped flowers. There are, however, no other significant similarities between these two taxa and preliminary DNA sequence data suggest instead a relationship with *F. corymbosa*. This alliance may be supported by the very short bracts, 4.0–5.5 mm long, but the hypothesis requires further testing.



PLATE 6.—*Freesia corymbosa*

The species may be confused with *Tritonia tugwelliae* from the southwestern Great Karoo by the superficial similarity in inflorescence and flowers but the latter has falcate, attenuate leaves with undulate or crisped margins, a slightly longer tube, reflexed lower tepals, and undivided style branches.

History: the first documented wild collections of both *Freesia verrucosa* and *F. laxa* are those of Swedish botanist C.P. Thunberg in the Eastern Cape, who gathered the material during one of his extended collecting trips from Cape Town to Humansdorp and Port Elizabeth, either in 1772 or in 1773. Thunberg was accompanied on these trips by the gardener Francis Masson, despatched by Sir Joseph Banks to collect plants for the Royal Botanic Gardens, Kew and responsible for the introduction of numerous South African plants to England. Thunberg was not, however, the first to collect the species, which was first described by B.C. Vogel from plants cultivated in Germany some years before this. Vogel's description accompanied a watercolour painting of a plant in flower that was published in C.J. Trew's *Plantae rariores* (1784) but the original painting was completed before Trew's death in 1769, meaning that the species must have been collected in South Africa before the Thunberg-Masson expedition. It is likely that Trew's plants were collected on the exploratory expedition mounted by the Governor of the Cape Colony, Ryk Tulbagh, under the command of Ensign August Frederik Beutler and accompanied by the plant collector, Hendrik Beenke. The expedition left Cape Town in 1752 for the eastern part of the Colony, travelling along the southern Cape coast and then cutting inland to Oudtshoorn and through the Langkloof, where Beenke could easily have encountered *F. verrucosa*.

Thunberg's own collection was the basis for *Gladiolus junceus*, described in 1782 by the younger Linnaeus. Although the specimen in Thunberg's herbarium is correctly named, Linnaeus f. misidentified the duplicate specimen lodged in the Linnaean herbarium as *Gladiolus falcatus* (now *Lapeirousia falcata*) but it is clear that the description of *G. junceus* is based on this specimen, which thus constitutes the type despite being incorrectly inscribed (Goldblatt 1972). The species was subsequently given no less than eight different specific epithets in the course of 30 years, which is not to say

that it was re-collected during this time. Two of these names are illegitimate replacements of existing names while others are based on illustrations, some quite probably drawn from cultivated specimens ultimately derived from plants introduced to Europe by Masson. The species is still relatively poorly collected today despite being quite common in the wild.

Although the earliest name for the species, *Gladiolus junceus* L.f., is an illegitimate later homonym for *G. junceus* Burm.f. (now *Geissorhiza aspera* Goldblatt), the species continued to be known under the epithet *juncea* when Ker Gawler placed it in his new genus *Anomatheca* (Ker Gawler 1804) and later when F.W. Klatt transferred the species of *Anomatheca* to *Freesia*. The nomenclatural issue was partly resolved by Goldblatt (1972) but the epithet '*juncea*' is to be treated as a new name from 1802 when Ker Gawler first used it in *Lapeirousia*.

The plant named *Anomaza excisa*, published by R.A. Salisbury in 1812 but based on a manuscript of W. Lawson, has often been associated with what is now *Freesia verrucosa*. *Anomaza excisa* is actually a combination based on *Ixia excisa* L.f., which is itself a later synonym of what is currently *Geissorhiza ovata* (Goldblatt 1982). *Ixia excisa* was associated with *F. verrucosa* largely because it has similar pink flowers with a narrow perianth tube and fairly broad, obtuse leaves. Floral details such as the style branches, as well as the corms are quite different. The combination in the genus *Anomaza* may simply be a typographic or orthographic error for *Anomatheca* but the name is in any case illegitimate.

6. ***Freesia corymbosa*** (Burm.f.) N.E.Br. in Kew Bulletin 1929: 132 (1929). *Gladiolus corymbosus* Burm.f.: 2 (1768). Type: South Africa, without precise locality (cultivated in Europe), *Burman s.n.* (G-Herb. Burman, holo.!).

Tritonia odorata Lodd., The botanical cabinet 19: t. 1820 (1832), nom. nud., without description. *Waitzia odorata* (Lodd.) Heynh.: 854 (1841).

Freesia odorata Eckl. ex Klatt: 672 (1866), illegit. superfl. name for *F. sparrmanii*. *F. refracta* var. *odorata* (Eckl. ex Klatt) Baker: 167 (1892). Type: South Africa, [Eastern Cape], heights between the Bushmans and Kariaga Rivers, *Ecklon & Zeyher Irid 108* (GH, holo.; K!, LD!, MO!, P!, PRE!, iso.).

Freesia aurea E.G.Hend. ex Gumb.: 392 (1896). *F. corymbosa* var. *aurea* (E.G.Hend. ex Gumb.) N.E.Br.: 16 (1935). Type: [South Africa], without locality or date, Gumbleton s.n. (K, holo!).

Freesia armstrongii W.Watson: 195 (1898). Type: South Africa, [Eastern Cape], Humansdorp Dist. (cultivated at Royal Botanic Gardens, Kew), *Armstrong s.n.* (K, holo!).

Freesia metelerkampiae L.Bolus: 337 (1927). Type: South Africa, without precise locality (cultivated in Cape Town), July–August 1927, *Metelerkamp s.n.* (BOL, holo!).

Freesia brevis N.E.Br.: 263 (1933), illegit. superfl. name for *F. metelerkampiae* L.Bolus. Type: illustration in South African Gardening and Country Life 17: 336 (Bolus 1927) (a figure of the type of *F. metelerkampiae* when alive).

Plants (120–)150–400(–600) mm high; corm conical or globose, 12–30 mm diam., tunics light brown, of medium- to coarse-textured fibres, sometimes forming neck; stem smooth, erect, usually branched, with up to four branches in well-grown specimens. *Leaves* 7–10, erect, usually $\pm$ half as long as stem, narrowly lanceolate, (40–)60–200 $\times$ 2–7(–10) mm, acute, rarely oblong-lanceolate and obtuse. *Spike* horizontal or deflexed, (3–)6–10-flowered. *Bracts* membranous becoming dry, oblong to oblanceolate, 4–8 mm long, translucent or flushed pale pinkish, with brown veins and dark brown tips, obtuse or rarely apiculate, inner bracts slightly shorter to slightly longer, with dark brown tips. *Flowers* 25–35(–40) mm long, usually pale to deep yellow, pale to deep pink, or rarely white, with base of tube, lowermost tepal and inner margins of lower lateral tepals bright yellow to orange, lower tepals with brownish midline running into tube, unscented or weakly scented; perianth tube funnel-shaped, 20–25(–35) mm long with basal tubular portion 5–10(–20) mm long and strongly curved at tip, widening abruptly into flared upper portion; tepals unequal, dorsal largest, suberect, broadly ovate-cordate, 8–12 $\times$ 7–10 mm, upper laterals narrower, ovate, lower tepals recurved, lower laterals broadly ovate-cordate with margins strongly upcurved, 7–11 $\times$ 8–10 mm, lower median ovate, 7–10 $\times$ 4–8 mm. *Filaments* arcuate, 13–15 mm long, inserted at base of widened upper portion, included; anthers 5–6 mm long. *Style* dividing at or slightly beyond anther apices. *Capsules* subglobose or oblong, 3-lobed, 6–8 $\times$ 6–8 mm, papillate. *Seeds* globose with flattened chalaza, 2.0–3.5 mm diam., slightly wrinkled, glossy reddish brown. *Flowering time*: usually late

August to October, rarely as early as May. Plates 6; 17F, G; Figure 2G,H.

Distribution and ecology: *Freesia corymbosa* is fairly widespread in the southern Cape, where it has been recorded from the foothills of the Swartberg at Toorwater in the west through the Langkloof and adjacent valleys to Grahamstown and King William's Town, and even as far east as Butterworth (Figure 15). Plants grow in loamy or sandy soils in rocky conglomerate, sandstone or shale, in open renosterveld and Succulent Karoo scrub or grassy fynbos.

The species is very variable in flower colour. The flowers are typically pale yellow with a darker throat and lower tepals but are deep yellow around Port Elizabeth. This form, named *Freesia aurea*, was used extensively in early *Freesia* breeding. Rose- or deep pink-flowered populations are not uncommon in the Langkloof, near Haarlem, Joubertina and Zuurbron, and near Hankey, and were also originally described as a separate species, *F. armstrongii* in 1898. This pink-flowered variant was important in introducing a range of new colours into the hybrids being raised in Europe and North America at the turn of the nineteenth and early twentieth centuries.

The length of the lower part of the perianth tube in *Freesia corymbosa* is variable. Mostly 5–8 mm across the range of the species, it is often longer, up to 10 mm long, in populations around Port Elizabeth, and is exceptionally long, 15–20 mm, in a collection from the southern foothills of the Zuurberg, near Enon. Flowers of *F. corymbosa* are not particularly fragrant, and those of many populations are scentless. The scent is variously described by collectors as faint and sweet or unpleasantly peppery.

Diagnosis and relationships: *Freesia corymbosa* is distinguished from the similar *F. refracta* and *F. occidentalis* by its usually obtuse bracts, which are prominently tipped with dark brown for up to 0.5 mm, the dark staining typically extending onto the body of the bract (Figure 2H), and often by its more brightly coloured flowers, mostly pale to deep yellow but also pink, or rarely white. *F. refracta*, which mostly has dull yellowish or greenish flowers, has bracts that are uniformly pale without brown tips (Figure 2F) and leaves that are mostly as long as the stem rather than half as

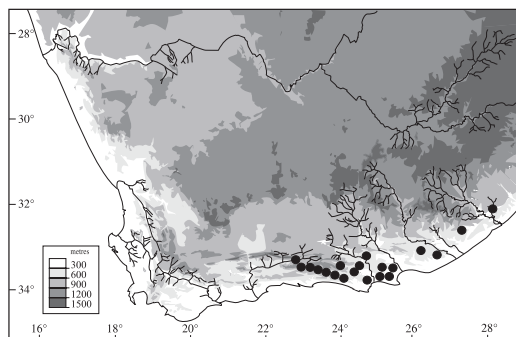


FIGURE 15.—Known distribution of *Freesia corymbosa*.

long or less. The flowers of *F. occidentalis* have the upper tepals uniformly creamy yellow or flushed with pale lilac, and rather rounded lower tepals, and although this species from the Ceres Karoo and adjacent highlands shares brown-tipped bracts with *F. corymbosa*, the bracts in *F. occidentalis* are invariably acute and only lightly tipped with brown on the apiculus itself and not on the body of the bract (Figure 2D). The leaves in *F. occidentalis* are typically oblong and obtuse, whereas they are mostly narrowly lanceolate and acute in *F. corymbosa*.

History: *Freesia corymbosa* and *F. caryophyllacea* appear to be the first species in the genus known in Europe. Both were described in 1768 by N.L. Burman from plants cultivated in the Netherlands but the original collector(s) and dates of collection are unfortunately not recorded. One possibility, which we have likewise suggested for *F. verrucosa*, is that *F. corymbosa* was collected on the exploratory expedition that left Cape Town in 1752 for the eastern parts of the Cape Colony under the command of Ensign August Frederik Beutler, accompanied by the plant collector Hendrik Beenke. The expedition would have cut inland to Oudtshoorn and thence through the Langkloof, where *F. corymbosa* is common.

The name *Freesia corymbosa*, like many others of Burman's, was overlooked by later botanists with the result that Klatt (1866) independently described the species as *F. odorata* from specimens that had been distributed under that name by C.F. Ecklon. Unfortunately, Klatt included the earlier name *F. sparrmanii* Thunb. in his description, thereby unwittingly rendering

the name *F. odorata* an illegitimate superfluous name (McNeil et al. 2006: Art. 52.1). Klatt further confused the identity of the species by also including under *F. odorata* specimens of *F. refracta* and even *F. leichtlinii*, as well as the illegitimate *Tritonia odorata* Lodd. (1832), thereby causing considerable difficulty in the correct application of the name (Brown 1935). The species was known under the names *F. odorata* Eckl. ex Klatt or *F. refracta* var. *odorata* (Eckl. ex Klatt) Baker until well into the twentieth century and it was only in 1935 that N.E. Brown established the correct application of these names. As a result of the general confusion that existed between *F. corymbosa* and *F. refracta* at the time, the typical form of *F. corymbosa* was redescribed in 1929 under the name *F. metelerkampiae* by Louisa Bolus, and Brown (1933) himself published the superfluous name *F. brevis* based on an illustration of the type of *F. metelerkampiae*.

The more striking and attractive colour variants of the species were initially treated as distinct species. The pink-flowered form was described in 1898 as *Freesia armstrongii* for collections made by William Armstrong, although James Bowie, a collector for the Royal Botanic Gardens, had originally recorded it much earlier, in 1820 or 1821. Bowie sent corms of this variant back to the Royal Botanic Gardens at Kew, where they were successfully grown and flowered. Plants with more intensely yellow flowers were recognized as *F. aurea*, a name later reduced to varietal status as *F. corymbosa* var. *aurea* by N.E. Brown (1935). Both of these colour forms were subsequently included in *F. corymbosa* without any rank by Goldblatt (1982).

7. *Freesia refracta* (Jacq.) Klatt in *Linnaea* 34: 673 (1866). *Gladiolus refractus* Jacq.: t. 241 (1795). *Gladiolus resupinatus* Pers.: 45 (1805), illegit. superfl. name for *G. refractus* Jacq. *Tritonia refracta* (Jacq.) Ker Gawl.: 228 (1804). *Waitzia refracta* (Jacq.) Heynh.: 855 (1841). *Montbretia refracta* (Jacq.) Endl. ex Heynh.: 418 (1847). *Nymanina refracta* (Jacq.) Kuntze: 701 (1891). Type: illustration in Jacq., *Icones plantarum rariorum* 2: t. 241 (1795).

Freesia hurlingii L.Bolus: 112 (1933a). Type: South Africa, [Western Cape], Bonnievale, 23 August 1931, *Hurling* & Neil s.n. (BOL, lecto!), designated by Goldblatt 1982: 74; BOL, isolecto!).



PLATE 7.—*Freesia refracta*

Plants (80–)150–400(–600) mm high; corm conical or $\pm$ globose, 12–30 mm diam., tunics light brown, of fine- to medium-textured fibres, forming short neck; stem smooth, suberect, usually branched, with up to four branches in well-grown plants. *Leaves* 7–10, erect, half as long to $\pm$ as long as stem, narrowly lanceolate-attenuate, (60–)100–300 $\times$ 2–7(–10) mm, acute, sometimes glaucous, rarely with prominent marginal vein. *Spike* horizontal or deflexed, (4)5–10(–12)-flowered. *Bracts* membranous becoming dry, translucent or flushed pale pinkish with brown veins, oblong to oblanceolate, 4–8 mm long, obtuse to apiculate, inner bracts slightly shorter to slightly longer. *Flowers* 25–35 mm long, pale greenish yellow or dull white, more or less strongly flushed purplish on reverse and at base of tube, lowermost tepal and inner margins of the lower lateral tepals bright orange, all three lower tepals with dark brownish midline, either unscented or strongly scented of rose and violet with spicy undertones; perianth tube funnel-shaped, 16–25 mm long with basal tubular portion 5–8(–9) mm long, widening abruptly into flared upper portion; tepals unequal, dorsal largest, suberect, broadly ovate-cordate, 8–12 $\times$ 7–10 mm, upper laterals narrower, ovate, lower tepals recurved, lower laterals broadly ovate-cordate with margins strongly upcurved, 7–11 $\times$ 8–10 mm, lower median ovate, 7–10 $\times$ 4–8 mm. *Filaments* arcuate, 10–14 mm long, inserted at base of widened upper portion of tube, included; anthers 5–6 mm long. *Style* dividing at or slightly beyond anther apices. *Capsules* subglobose or oblong, 3-lobed, 6–10 $\times$ 6–8 mm, papillate. *Seeds* globose with flattened chalaza, 2.0–2.5 mm diam., lightly wrinkled, glossy reddish brown. *Flowering time*: mid-July to early September. Plates 7; 17H; Figure 2E, F.

Distribution and ecology: *Freesia refracta* is relatively common in the drier interior valleys of the southwestern Cape, where it has been recorded from the Hex River Valley near De Doorns, along the length of the Breede River Valley from Rawsonville and Worcester in the west to the mouth of the river at Port Beaufort, and along the southern Cape coast to Gouritz River Mouth in the east, with a westward extension along the southern foothills of the Langeberg and Riviersonderend Mountains (Figure 16). It is also common through the Little Karoo, from the Anysberg in the west to De Rust in the east. The species grows in drier, stony soils on a variety of

substrates, typically shales of the Bokkeveld series but also sandstone alluvium overlying shales, and on limestone outcrops. The associated vegetation varies from Succulent Karoo shrubland on shale through transitional fynbos on alluvium to coastal thicket on limestone.

Populations from the Breede River Valley and its tributaries are relatively uniform, with narrow, attenuate leaves as long as the stem and 3–7(–10) mm wide but plants from the Little Karoo are more variable, with broader, acute leaves. A collection from the Warmwaterberg near Barrydale has exceptionally short and broad leaves, less than half the length of the stem and 12–16 mm wide. Another variant from dry sites along the Anysberg and near Kammanassie Dam, its easternmost limit, has short, stiff, slightly glaucous leaves with the marginal vein and midrib more strongly thickened than usual.

Diagnosis and relationships: *Freesia refracta* is one of a group of three similar vicariant species that also includes *F. occidentalis* from the interior Swartruggens and Cedarberg, the Tanqua River Basin and extreme western Great Karoo, and *F. corymbosa* from the eastern Little Karoo and Langkloof eastwards to the Transkei. These three species share small flowers with prominent lower tepals, the two laterals distinctly ovate-cordate with the inner margins sharply upcurved, and small, membranous bracts. *F. refracta* is distinguished in this alliance by its uniformly pale bracts. Plants typically have rather long, narrow leaves $\pm$ as long as the stem and 3–8 mm wide. Flower colour varies from dull white to pale yellowish but the perianth is usually tinged greenish, with deep yellow to orange markings on the lower tepals. The species is most likely to be confused with *F. corymbosa*, especially around Oudtshoorn, where the ranges of the two species approach one another, but the bracts in *F. corymbosa* have characteristic dark brown tips. *Freesia occidentalis* from the Ceres Karoo to the west has mostly shorter, blunter leaves, white to pale creamy yellow flowers with obtuse tepals, and bracts that are lightly but quite evidently tipped with brown.

History: *Freesia refracta* was described and illustrated in 1795 by Nicolaus von Jacquin, Director of the Imperial Gardens at Schönbrunn, Vienna during the latter half of the eighteenth



PLATE 8.—*Freesia occidentalis*

century. Although the collector and date are not recorded, the plants are very likely to have been gathered by one of the two gardeners, Franz Boos or Georg Scholl, who had been despatched to the Cape in 1786 to collect for the Imperial Gardens. In keeping with the generic concepts of the time, the species was originally described in the genus *Gladiolus*.

A great deal of confusion surrounded the application of the names of the various species of *Freesia* that had been described by the end of the nineteenth century. This confusion led Louisa Bolus to redescribe the species in 1933 as *F. hurlingii*, under the misapprehension that the name *F. refracta* applied to what we now know as *F. leichtlinii* subsp. *alba*. For many years all of the gullet-flowered species of *Freesia* were called *F. refracta*, especially in horticultural circles, and even today in the horticultural trade and in some local floras, species such as *F. leichtlinii* subsp. *alba* can be found under that name.

8. ***Freesia occidentalis*** L.Bolus in South African Gardening 23: 266 (1933c). Type: South Africa, [Western Cape], Nieuwefontein, precise locality not given, September 1932, Compton 4723 (BOL, lecto.!, designated by Goldblatt 1982: 77; K, isolecto.!).

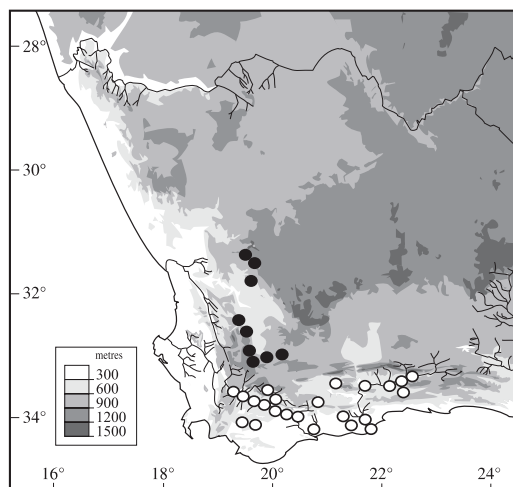


FIGURE 16.—Known distribution of *Freesia refracta*, ○; *F. occidentalis*, ●.

Freesia framesii L.Bolus: 245 (1934). Type: South Africa, [Northern Cape], Calvinia District (cultivated in Cape Town), September 1934, Ross *Frames ex E. Skatfe* BOL21366 (BOL, holo.!).

Plants 80–300(–600) mm high; corm conical, 15–20 mm diam., tunics light brown, of medium- to coarse-textured fibres, forming neck; stem smooth, erect, usually branched, with up to four branches in well-grown specimens. *Leaves* 7–10, erect or inclined, $\pm$ half as long to as long as stem, oblong to lanceolate, 40–120(–300) $\times$ (5–) 7–18(–25) mm, obtuse to subacute, apiculate. *Spike* horizontal or deflexed, (3–)6–9-flowered. *Bracts* membranous becoming dry, translucent or flushed pale pink with brown veins and tips, oblanceolate to oblong, 5–8 mm long, apiculate, inner slightly shorter to slightly longer, with brown tips. *Flowers* 30–35 mm long, white to pale creamy yellow, sometimes flushed mauve or pink, base of tube sometimes bright orange, lowermost tepal and inner margins of lower lateral tepals bright yellow, all three lower tepals with dark brownish midline, strongly rosy violet-scented with peppery overtones; perianth tube funnel-shaped, 20–25 mm long with basal tubular portion 6–11 mm long and strongly curved at tip, widening abruptly into flared upper portion; tepals unequal, dorsal largest, suberect, broadly ovate-cordate, 8–12 $\times$ 7–10 mm, upper laterals narrower, ovate, lower tepals recurved, lower laterals broadly ovate-cordate with margins strongly upcurved, 7–11 $\times$ 8–10 mm, lower median ovate, 7–10 $\times$ 4–8 mm. *Filaments* arcuate, 13–15 mm long, inserted at base of widened upper portion, included; anthers 5–6 mm long. *Style* dividing at or slightly beyond anther apices. *Capsules* subglobose or oblong, 3-lobed, 6–10 $\times$ 6–8 mm, papillate. *Seeds* globose with flattened chalaza, 2.0–2.5 mm diam., lightly wrinkled, glossy reddish or purplish brown. *Flowering time*: mainly mid-August to late September, rarely early August. Plates 8; 17I; Figure 2A–D.

Etymology: Latin *occidentalis*, from the west, alluding to the westerly distribution of the species, mistakenly assumed to be more extreme than it actually is.

Distribution and ecology: rarely seen and even less often collected, *Freesia occidentalis* is restricted to the fringes of the arid basin of the Ceres or Tanqua Karoo, from just southwest of Calvinia in the north, along the eastern ridges and foothills

of the Cedarberg and Swartuggens Mountain ranges that flank its western edge, to Karooport in the south, and thence eastward along the foot of the Bonteberg to Pieter Meintjies siding at the western edge of the Great Karoo (Figure 16). Occupying the drainage basin of the upper Doring River in the rain shadow of the Cold Bokkeveld Mountains and higher peaks of the Cedarberg, the Ceres Karoo is a semi-desert depression of gravelly flats occasionally punctuated by outcrops of tillite and dolerite. *Freesia occidentalis* grows either in arid fynbos on rocky slopes in Table Mountain and Witteberg sandstone, or in low shrubland at the transition between renosterveld and Succulent Karoo, where plants grow in loamy soils along the foothills of the mountains where the sandstone grades into the fine-grained Karoo shales of the valley bottom, in rocky alluvium, or less commonly in shale outcrops. The species favours south-trending slopes or drainage lines where it benefits from extra moisture in this arid area.

Plants from north of the Doring River Valley, on the edge of the Bokkeveld Escarpment just south of Calvinia, are relatively robust, typically more than 150 mm tall with leaves up to 20 mm wide, bearing white or cream-coloured flowers with the lower tepals and lower part of the tube bright orange. Populations south of the Doring River Valley are seldom more than 200 mm tall with leaves mostly less than 10 mm wide, and flowers that are conspicuously and attractively flushed with mauve or lilac.

Diagnosis and relationships: *Freesia occidentalis* is distinguished from the similar *F. refracta* and *F. corymbosa* by its obtuse or subacute leaves, typically shorter than the flowering spike, its white or creamy yellow flowers, sometimes flushed pale pink or mauve, with rather blunt tepals, and its brown-tipped bracts (Figure 2D). The flowers of *F. refracta* and *F. corymbosa* are usually yellowish or greenish, sometimes flushed dull purple, or pink or white (*F. corymbosa*), typically with rather acute tepals. *F. refracta*, which occurs between Worcester and Oudtshoorn, is distinguished by its generally longer, narrow, acute leaves and its uniformly pale bracts; and *F. corymbosa*, which ranges from the eastern Little Karoo through the Langkloof and into the Eastern Cape, by its more obtuse bracts that are very prominently tipped with dark brown (Figure 2H).

History: this species is one of several described by Cape Town botanist H.M.L. (Louisa) Bolus in the early decades of the twentieth century. The description and illustration of *Freesia occidentalis*, which appeared in November 1933, were based on plants that flowered at the Karoo Garden at Whitehill in August of that year, and which were originally collected by R.H. Compton, long-time Director of the National Botanic Gardens at Kirstenbosch, in September 1932 on the Farm Nieuwefontein. Although the precise locality is not given in Compton's collecting register, it is almost certainly the farm of that name in the central Tanqua River Basin. Louisa Bolus, however, identified the locality with a location north of Vanrhynsdorp in southern Namaqualand, an error which placed the species far west of its relatives and prompted her choice of epithet. It may also have encouraged her to describe *F. framesii* the following year for plants that had been collected near Calvinia by the Cape Town succulent enthusiast, Percy Ross Frames, and which had flowered in the garden of Mrs E. Skaife in Cape Town.

***Freesia* subgen. *Viridibractea* (Goldblatt)**

J.C. Manning & Goldblatt, stat. nov., *Freesia* sect. *Viridibractea* Goldblatt in *Journal of South African Botany* 48: 56 (1982). Type species: *Freesia alba* (G.L.Mey.) Gumbel. = *Freesia leichtlinii* subsp. *alba* (G.L.Mey.) J.C. Manning & Goldblatt.

Plants small to medium-sized; stem either winged in section and smooth, or rounded in section and puberulous, at least below. *Leaves* erect to prostrate, blades lanceolate to oblong, plane or undulate-crispulate, acute or obtuse. *Spike* inclined or horizontal. *Bracts* firm-textured, herbaceous and green with narrow, translucent margin. *Flowers* either funnel-shaped with slender proximal portion of tube widening $\pm$ abruptly into cylindrical distal portion and tepals unequal, upper largest and erect, lower spreading, white or pale to deep yellow with dark yellow or orange markings on lower tepals, or $\pm$ tubular with tube widening gradually from base and sharply curved distally, tepals $\pm$ equal and recurved, yellowish green or brownish, unscented or scented. *Stamens* included or shortly exserted. *Seeds* subglobose or with inflated raphe, smooth or rugulose, reddish brown.

Freesia sect. **Alatae** J.C.Manning & Goldblatt in Novon 15: 172 (2005). Type species: *Freesia viridis* (Aiton) Goldblatt & J.C.Manning.

Stem compressed and laterally winged. *Leaves* erect or suberect, falcate, acute to attenuate, plane or undulate-crispulate. *Flowers* green to brownish or maroon, scented or evidently unscented at night, tubular, tube sharply curved apically, tepals $\pm$ equally recurved, lanceolate. *Filaments* included. *Seeds* subglobose, without inflated raphe.

9. ***Freesia viridis*** (Aiton) Goldblatt & J.C. Manning in Systematic Botany 20: 172 (1995). *Gladiolus viridis* Aiton: 481 (1789). *Tritonia viridis* (Aiton) Ker Gawl.: 231 (1804). *Waitzia viridis* (Aiton) Kreysig: 52 (1829). *Montbretia viridis* (Aiton) Voigt: 610 (1845). *Lapeirousia viridis* (Aiton) L.Bolus: 276 (1932). *Anomatheca viridis* (Aiton) Goldblatt: 37 (1971). Type: South Africa, [Western Cape], Swartland, without exact locality or date, Masson s.n. (BM, holo.).

Plants 100–300(–500) mm high; corm conical, 10–30(–40) mm diam., tunics of fine- to coarse-textured fibres, sometimes extending upwards as neck; stem erect, flattened and 2-winged, usually simple but with up to five branches. *Leaves* 4–8, suberect or more rarely prostrate, half as long to slightly longer than stem, narrowly lanceolate to oblong, or falcate, (30–)50–150(–200) $\times$ 4–15(–25) mm, acute to attenuate, rarely obtuse-acuminate, margins plane to strongly crispulate or undulate, soft-textured or leathery with moderately thickened midrib. *Spike* deflexed, (3)4–10-flowered. *Bracts* herbaceous and firm-textured, green, often flushed pinkish at tips, ovate, 5–10(–25) mm long, obtuse, inner slightly shorter. *Flowers* 20–40 mm long, yellowish green to olive green or $\pm$ strongly flushed with brown or maroon, unscented or rose-scented at night; perianth tube subcylindrical, expanding gradually from base to apex, 15–25 mm long, curved sharply downward in upper 5–7 mm with oblique mouth; tepals subequal with upper three slightly larger, recurved from base, lanceolate and obtuse to linear-lanceolate and attenuate, 6–15 $\times$ 1–2 mm. *Filaments* arcuate, 5–7 mm long, inserted 4–6 mm below mouth at bend in tube, included or very shortly exserted; anthers shortly protruding from tube, $\pm$ 3 mm long. *Style* dividing at base of anthers. *Capsules* oblong or subglo-

bose, 3-lobed, 10–15 $\times$ 8–10 mm, rough or papillate when fresh. *Seeds* globose, 2.0–3.0 mm diam., wrinkled, glossy reddish brown. *Flowering time*: mid-May to mid-August, rarely to October. Plate 9; Figure 3.

Etymology: Latin *viridis*, green, referring to the flower colour.

Distribution and biology: *Freesia viridis* is widely scattered through the western coastal parts of the winter rainfall region, from southern Namibia through Namaqualand and the Olifants River Valley to Yzerfontein and Mamre north of Cape Town (Figure 17). The species occurs on a wide variety of substrates, mostly in coastal thicket and Succulent Karoo shrubland, rarely in arid fynbos. The slender form and dull colouring of the flowers render the plants very difficult to locate and they are more conspicuous when in fruit. The flowers, which are invariably unscented during the day, may become pleasantly fragrant at night, releasing a rose-like scent. Some plants or populations do not produce floral scent at all, and in those that do, the timing of scent release is somewhat variable, sometimes early in the evening but in other instances commencing as late as 22:00.

Freesia viridis, unlike most other species in the genus (with the notable exception of *F. laxa*), is self-fertile and the flowers set seed without cross-pollination. The nocturnal fragrance, dull colour, and slender perianth tube with included anthers are strong evidence that the species is adapted for pollination by moths. The lack of floral scent in some plants, however, suggests that the species may rely more heavily on self-pollination. Viable hybrids have been produced in cultivation with *F. laxa* but not with any of the gullet-flowered species, but this may be more a reflection of the relative promiscuity of *F. laxa* than anything else (see that species for additional discussion).

The leaves of *Freesia viridis* are extremely bitter, in contrast to the bland and inoffensive foliage of the other species that we have tasted. Self-fertility and unpalatable foliage may explain the success of this species, which persists even in heavily overgrazed veld, and its relatively wide range, which contrasts sharply with the narrow distributions of other *Freesia* species of the southern African winter rainfall zone.

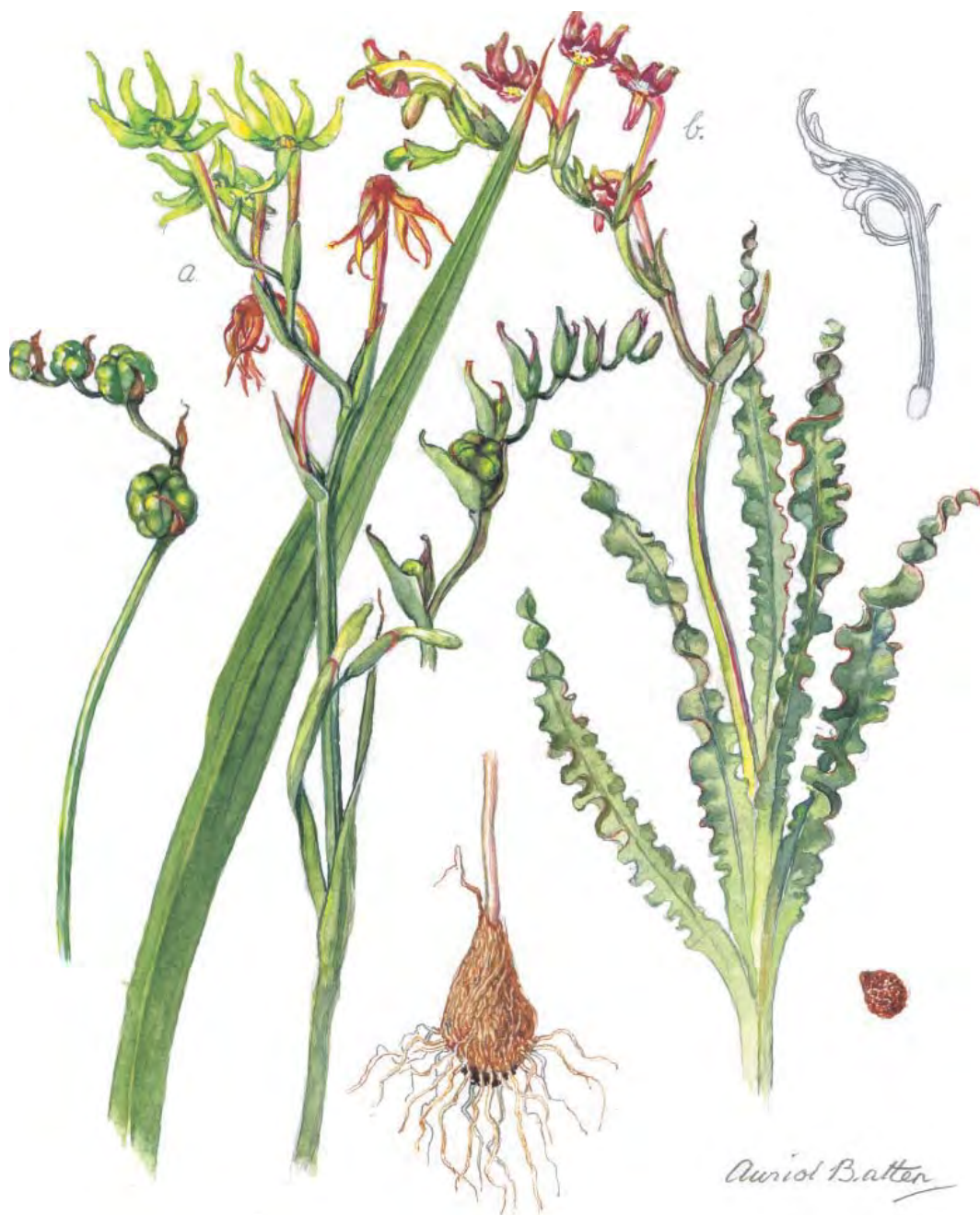


PLATE 9.—*Freesia viridis*: a, subsp. *viridis*; b, subsp. *crispifolia*.

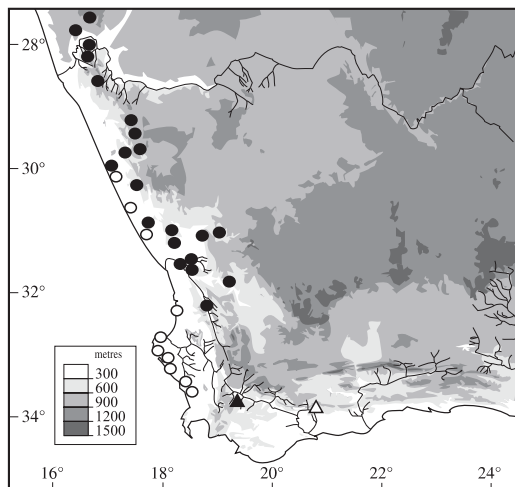


FIGURE 17.—Known distribution of *Freesia viridis* subsp. *crispifolia*, ●; subsp. *viridis*, ○; *F. sparrmanii*, △; *F. fucata*, ▲.

Diagnosis and relationships: *Freesia viridis* is a highly unusual species that was until now regarded as isolated within the genus, the numerous autapomorphies and lack of evident synapomorphies making its relationships difficult to assess. Its unusual flowers, which are probably adapted to pollination by moths, are unmatched in the genus. Other derived features not related to pollination biology are the flattened and winged stems, which contrast with the smoothly cylindrical stems of the other species, and the one-banded pollen operculum.

The lack of any evident close relatives among the other tubular-flowered species prompted our placement of the species in a separate section of subgen. *Anomatheca* (Manning & Goldblatt 2005). DNA sequence data, however, support an alliance with the gullet-flowered species of sect. *Viridibractea*, and the marked similarity in bract morphology and texture between *Freesia viridis* and these species, ignored until now, provides strong morphological support for this association. Possible additional, weak support may come from floral scent chemistry, which shows the production of small quantities of ionone in *F. viridis* subsp. *crispifolia*, a carotenoid-derived chemical that has been otherwise recorded in

Freesia only among members of subgen. *Viridibractea*.

History: this curious-looking plant was first collected along the Cape west coast, probably near Langebaan, in the late eighteenth century by the Scottish plant collector Francis Masson, sent out to the Cape of Good Hope to collect plants for the Royal Botanic Gardens, Kew. Masson arrived in Cape Town on 30 October 1772 on board Capt. Cook's ship *Resolution* and his first two collecting trips were both towards the east of Cape Town (Gunn & Codd 1981). It was only in the spring of 1774 that he travelled up the west coast, in the company of Swedish botanist Carl Thunberg, and it is here that they could have encountered *Freesia viridis* for the first time. Material introduced by Masson and cultivated at Kew formed the basis of W.T. Aiton's description of the species. Its cultivation in the Calcutta gardens of the British East India Company (Voigt 1845) is curious as it is neither useful nor especially attractive. Like many other zygomorphic Iridaceae at the time, *F. viridis* was first placed in the genus *Gladiolus*, subsequently passing in turn through several different genera, including *Tritonia*, *Lapeirousia* and *Anomatheca*, before being transferred to *Freesia* (Goldblatt & Manning 1995).

The marked difference between the flat-leaved southern coastal populations and those with crispulate leaves from inland to the north, led to the recognition of two subspecies in *Anomatheca viridis* (Goldblatt 1972). This distinction was later abandoned (Goldblatt 1983) and thus not maintained when the species was transferred to *Freesia* (Goldblatt & Manning 1995). On further consideration, however, the relatively consistent morphological difference in the leaf margins and to some extent in flower shape and colour, combined with a difference in geography and habitat, appear to us to warrant subspecific status.

Key to subspecies

- 1a Leaves narrowly lanceolate to lanceolate, mostly 4–10 mm wide, margins plane; tepals (6–)10–18 mm long 9a. subsp. *viridis*
- 1b Leaves lanceolate to falcate, up to 25 mm wide, margins ± crispulate or undulate; tepals 6–10 mm long 9b. subsp. *crispifolia*



PLATE 10.—*Freesia sparrmanii*

9a. subsp. **viridis**

Leaves narrowly lanceolate to lanceolate, plane, acuminate, (2–)4–10(–15) mm wide. *Flowers* yellowish green, or green flushed with dark purple; tepals oblong-lanceolate to narrowly lanceolate and attenuate, (6–)10–18 mm long. Plate 18a; Figure 3.

Distribution and ecology: subsp. *viridis* is strictly a coastal taxon, most commonly encountered between Yzerfontein and Stompneus Bay south of the Berg River Mouth but occurring in isolated populations further north along the Namaqualand coast, at Brand-se-Baai, Groen River Mouth, and near Hondeklip Bay. Plants occur on granite, shale or limestone outcrops in coastal thicket within sight of the sea, and grow in pockets of loamy soil or in rock crevices. The narrowly lanceolate leaves are typically soft-textured with plane margins and the flowers are usually uniformly yellowish green or sometimes flushed with dark maroon, mostly with rather slender and tapering tepals. At least some plants from Langebaan and those from Groen River Mouth produce a pronounced fragrance at night but others are apparently unscented.

9b. subsp. **crispifolia** (Goldblatt) J.C. Manning & Goldblatt, comb. nov. *Anomatheca viridis* subsp. *crispifolia* Goldblatt in Contributions from the Bolus Herbarium 4: 87 (1972). Type: South Africa, [Western Cape], Clanwilliam, July 1894, Leiboldt 161 (BOL, holo.!, NBG!, PRE!, iso.).

Leaves oblong-lanceolate to falcate, margins slightly undulate to tightly crispulate, 5–10(–25) mm wide. *Flowers* dull green or brownish to maroon; tepals oblong-lanceolate to lanceolate, 6–10 mm long. Plate 18b.

Etymology: Latin *crispifolius*, with crisped leaves.

Distribution and ecology: subsp. *crispifolia* is distributed along the near interior of the West Coast from Clanwilliam in Western Cape, through the Knersvlakte and central Namaqualand in Northern Cape as far north as the Aurore Mountains in southern Namibia. Plants are not edaphically specific, and have been collected on stony shale, clay, cyanite, granite or sandstone, and even in loamy clay covered with quartzite pebbles, from near the coast to just over 100 km

inland. The corms are often wedged in crevices in rock outcrops.

The subspecies is characterized by leaves with $\pm$ strongly crisped margins, and brownish green to maroon flowers with somewhat shorter and blunter tepals than subsp. *viridis*. Flowers are occasionally scented at night but more often appear to be unscented. Populations from the Richtersveld and southern Namibia in the extreme north of its range are characterized by short, often rather prostrate leaves with very weakly crisped margins.

Freesia sect. **Viridibractea** Goldblatt in Journal of South African Botany 48: 56 (1982). Type species: *Freesia alba* (G.L.Mey.) Gumb. = *Freesia leichtlinii* subsp. *alba* (G.L.Mey.) J.C. Manning & Goldblatt.

Stem rounded in section, sparsely to densely papillate-puberulous. *Leaves* erect, inclined or prostrate, acute or obtuse. *Flowers* funnel-shaped with slender proximal portion of tube widening $\pm$ abruptly into cylindrical distal portion, tepals unequal, upper largest and erect, lower spreading, white or pale to deep yellow with dark yellow or orange markings on lower tepals. *Filaments* inserted at base of widened upper portion, included. *Seeds* obliquely subglobose, with inflated raphe.

10. **Freesia sparrmanii** (Thunb.) N.E.Br. in The Flowering Plants of South Africa 1: t. 11 (1921). *Gladiolus sparrmanii* [as '*sparrmannii*'] Thunb.: 191 (1814). *Ixia sparrmanii* (Thunb.) Roem. & Schult.: 285 (1822). *Meristostigma sparrmanii* (Thunb.) Steud.: 130 (1841). Type: South Africa, [Western Cape], exact locality unknown but probably at or near Grootvadersbos, September–October 1775, Sparrman s.n. (S, lecto.!, designated by Goldblatt 1982: 63; S, isolecto.!).

Plants (100–)150–250 mm high; corm conical, 10–25 mm diam., tunics pale, of fine-textured fibres; stem erect or flexed outward above uppermost sheath and then suberect, minutely papillate in lower half, usually with two to five branches. *Leaves* 5–9, erect, $\pm$ as long as the stem, linear to narrowly lanceolate, tapering above, 70–200 $\times$ (2–)3–8(–9) mm, acute. *Spikes* deflexed, (3–)5–8(–11)-flowered. *Bracts* herbaceous and firm-textured, green with hyaline



PLATE 11.—*Freesia fucata*

margins, flushed purple apically, obovate, (3–) 4–6(–7) mm long; inner bracts slightly shorter. *Flowers* (30–)35–40 mm long, white, flushed dull purple on reverse of tepals, base of lower median tepal with oblong yellow-orange mark in midline, unscented; perianth tube narrowly funnel-shaped, 20–27 mm long with basal narrow part 12–15 mm long, widening into wider, flared upper portion; tepals unequal, dorsal largest and suberect, ovate, 10–11 × ± 7 mm, upper laterals slightly narrower, lower tepals recurved, narrowly ovate, 7–8(–10) × 4–5 mm. *Filaments* arcuate, 10–14 mm long, inserted at base of widened upper portion, included; anthers 4.0–4.5 mm long. *Style* dividing ± 2 mm beyond anther apices. *Capsules* oblong or subglobose, 3-lobed, 10–12 × 8–10 mm, papillate. *Seeds* obliquely subglobose with inflated chalaza and raphe, 2.0–2.5 mm diam., smooth, glossy reddish brown. *Flowering time*: late September to late October. Plates 10; 18C; Figure 4J.

Etymology: named after the Swedish naturalist, Anders Sparrman, who first collected the species in 1775.

Distribution and ecology: this attractive species, with branched spikes of dainty white flowers flushed with purple on the outside, has a very local distribution on forest margins and in clearings on the forest floor along the southern foothills of the Langeberg between Suurbraak and Heidelberg, a distance of little more than 25 km (Figure 17). Although an early collection (Ecklon & Zeyher 4027) was reportedly made along the Buffeljags River just east of Swellendam, modern collections of the species are all from rather further east, on the Grootvadersbos Forest Reserve and adjacent farms north of Heidelberg. Plants occur in localized populations in light shade in moist, loamy clay and often thrive on roadside banks. They flower in late spring, from early September to October, rarely to early November, and are quite lacking in fragrance.

Although successful crosses between gullet- and tubular-flowered species of *Freesia* usually fail, *Freesia sparrmanii* has been successfully crossed with *F. laxa* subsp. *laxa* (information until now unpublished). The resulting hybrid, perfectly intermediate between the two species, is of no horticultural interest.

Diagnosis and relationships: *Freesia sparrmanii* is somewhat isolated from the other species in sect. *Viridibractea* by its unscented, small flowers with a relatively longer lower portion of the tube. It is distinguished from other gullet-flowered species by its slender flowers with narrow tepals no more than 5 mm wide and a narrowly funnel-shaped tube with the slender, lower portion 12–15 mm long and ± as long as or slightly longer than the upper part. In other gullet-flowered species the lower portion of the tube is almost invariably shorter than the upper. The distinction between the two parts of the perianth tube is also less marked in *F. sparrmanii* than in the other gullet-flowered species.

History: this rare species was first collected in 1775 by the Swedish physician and naturalist, Anders Sparrman, probably from near Grootvadersbosch, where he stayed briefly during his travels in the erstwhile Dutch colony, although the exact locality is not recorded. It was described by C.P. Thunberg in 1814 as a species of *Gladiolus*, in keeping with the broad and rather vague concept of that genus that prevailed in the 18th and early 19th centuries but was subsequently included in *Freesia refracta* until 1935, when N.E. Brown recognized that it represented a distinct species.

The spelling of the species epithet is a matter of some confusion. Thunberg used the form '*sparrmannii*', whereas some authors omitted the second 'r', thus *sparrmannii*. This is the conserved spelling of the genus name *Sparrmannia*. We follow the recommendation in the Code of Botanical Nomenclature (McNeil *et al.* 2006: Art. 60C.4), which suggests that for epithets based on personal names the customary spelling of the personal name should not be modified, and thus adopt the spelling used by Sparrman himself, with a single 'n'.

11. ***Freesia fucata*** J.C.Manning & Goldblatt in *Bothalia* 31: 189 (2001). Type: South Africa, Western Cape, Villiersdorp District, 5.5 km along Doornrivier Road, Farm Die Hoek, 10 July 2000, Manning 2271 (NBG, holo.!).

Plants 150–300 mm high; corm conical, 15–20 mm diam., tunics pale, of medium-textured fibres, accumulating with age and forming neck around



PLATE 12.—*Freesia marginata*

base of stem; stem flexed outward above uppermost sheath and then suberect, minutely papillate, usually with one or two branches. *Leaves* 5 or 6, inclined to suberect, usually $\pm$ as long as stem, linear-lanceolate, 80–250 $\times$ 4–5 mm, tapering above, acute. *Spike* lightly deflexed, 4–9-flowered. *Bracts* herbaceous and firm-textured, green with hyaline margins, obovate, 6–10(–13) mm long, tricuspidate, inner slightly shorter. *Flowers* (30–)35–47 mm long, white flushed dull purple on reverse of tepals, base of lower tepals marked yellow-orange with dark midline, strongly violet-scented; perianth tube funnel-shaped, 20–30 mm long with tubular lower portion 6–7 mm long, widening $\pm$ abruptly into flared upper portion; tepals unequal, dorsal largest, suberect, ovate, 11–18 $\times$ 8–11 mm, upper laterals slightly narrower, oblong, lower tepals recurved, lower laterals narrowly ovate, 10–14 $\times$ 6–8 mm, lower median oblong, 10–16 $\times$ 5–6 mm. *Filaments* arcuate, 13–15 mm long, inserted at base of widened upper portion, included; anthers 7–8 mm long. *Style* dividing at or slightly beyond anther apices. *Capsules* oblong, 3-lobed, (6–)9–12 $\times$ (6–)7–10 mm, papillate. *Seeds* obliquely subglobose with inflated chalaza and raphe, 2.5–3.0 mm diam., wrinkled, glossy reddish brown. *Flowering time*: July. Plates 11; 18D; Figure 4A–F.

Etymology: Latin *fucatus*, painted or stained, alluding to the boldly marked flowers.

Distribution and biology: *Freesia fucata*, a local endemic of the Hoeks River Valley south of Villiersdorp in the southwestern Cape, is known from just two or three populations (Figure 17). Plants grow in clay soils derived from shales of the Bokkeveld Series in open renosterbos shrubland, occurring in small colonies along roadsides or in stony washes, sometimes in quite dense concentrations but always rather localized. They flower during the winter, in July.

Diagnosis and relationships: *Freesia fucata* is distinguished from other early-flowering species of sect. *Viridibractea* by its narrow, glaucous, almost grass-like leaves, 4–5 mm wide, and three-toothed bracts. The rather variable *F. caryophyllacea*, which also extends into the Worcester Valley, typically has more or less prostrate, rather broader leaves, 10–16 mm wide, and although western populations of *F. caryophyllacea*, centred around Bredasdorp, have subacute and of-

ten quite long leaves, 5–9 mm wide, these are never as narrow nor as long as in *F. fucata*.

History: the species was first collected at the type locality in 1975 by the Worcester dentist, I.B. Walters, who had a keen interest in the local flora and collected extensively in the Worcester Valley. His collections were misidentified as *Freesia refracta* on account of their narrow leaves until we encountered living plants in the winter of 1999, when it became obvious that they represented an undescribed member of sect. *Viridibractea*.

12. ***Freesia marginata*** J.C.Manning & Goldblatt in Novon 15: 168 (2005). Type: South Africa, Western Cape, between Worcester and Roberston, 25 May 2002, Manning 2734 (NBG, holo.!).

Plants 40–100 mm high, usually $\pm$ prostrate; corm conical, 15–20 mm diam., tunics of pale, medium-textured fibres, accumulating with age and forming long neck around base of stem; stem flexed outward above uppermost leaf sheath and then prostrate or horizontal, densely puberulous, simple or rarely with one branch. *Leaves* (4)5 or 6(7), prostrate or rarely erect, slightly shorter than to half as long as stem, oblong to lanceolate, 20–50(60) $\times$ 6–15 mm, acute, leathery and $\pm$ glaucous, with prominent submarginal vein. *Spike* declinate, 4–10-flowered. *Bracts* herbaceous and firm-textured, green with hyaline margins, obovate, 5–7 mm long, tricuspidate or upper bracts obtuse with prominent central cusp tipped rust-brown, inner bracts slightly longer, 7–8 mm long. *Flowers* (30–)33–37 mm long, white usually lightly flushed purple on reverse of tepals, base of lower tepals marked yellow-orange and usually with dark midline, strongly violet-scented; perianth tube funnel-shaped, 18–25 mm long, with tubular basal portion 6–10 mm long, widening $\pm$ abruptly into flared upper portion; tepals unequal, dorsal largest, erect, obovate, 12–15 $\times$ 7–8 mm, upper laterals slightly narrower, oblong-lanceolate, lower tepals recurved, oblong-lanceolate, 11–13 $\times$ 4.0–5.5 mm. *Filaments* arcuate, 15–17 mm long, inserted at base of widened upper portion of perianth tube, included; anthers 5.0–5.5 mm long. *Ovary* ovoid, 3 mm long; style dividing below or opposite anther apices. *Capsules* oblong or subglobose, 3-lobed, (5–)6–10 $\times$ 5–10 mm, minutely papillate when fresh. *Seeds* obliquely subglobose

with slightly to moderately inflated chalaza and raphe, 2.0–3.0 mm diam, slightly wrinkled, glossy reddish or purplish brown. *Flowering time*: late May to early June. Plates 12; 18E.

Etymology: Latin *marginatus*, margined, referring to the prominent submarginal vein on the leaves.

Distribution and ecology: this highly localized species is known from just two small populations in the Breede River Valley between Worcester and Roberston in the southwestern Cape (Figure 18). Plants are more or less restricted to gravelly or stony washes, where they grow in decaying sandstone with the corms deeply buried in sandy loam in rock crevices among open Succulent Karoo shrubland. Plants are typically low-growing with prostrate leaves and $\pm$ prostrate inflorescences, although individuals growing in the shade of small bushes develop suberect leaves. The stem usually remains prostrate in fruit and the capsules lie on the ground, often becoming lightly covered by soil. Plants may occur in quite dense concentrations, and the species is one of the earliest to come into bloom, flowering in early winter.

Diagnosis and relationships: *Freesia marginata* closely resembles *F. caryophyllacea* in its flowers, prostrate and $\pm$ obtuse leaves, and early flowering but is quite distinct from that species in the leathery texture of the leaves, their more or less glaucous colouring, inconspicuous pseudomidrib, and most especially in the prominent submarginal vein. This is clearly visible in both fresh and dried leaves as a translucent strand $\pm$ 0.5 mm in from the leaf margin (Figure 6B). The leaves of *F. caryophyllacea* are mostly softer and bright green with a prominent midrib and invisible submarginal vascular bundle (Figure 6A). *Freesia caryophyllacea* is mostly restricted to renosterbos shrubland on stony clay soils and is relatively widespread in the Western Cape, occurring throughout the Breede River Valley and Overberg, from Bot River and Caledon to Bredasdorp. The species flowers across its range anywhere between April and June but populations in the Breede River appear to flower in mid- or late June. *Freesia marginata*, in contrast, occurs on decaying sandstone in Succulent Karoo shrubland and flowers some weeks earlier than this, in late May or early June. The curious tricuspidate bracts of *F. marginata* are also found

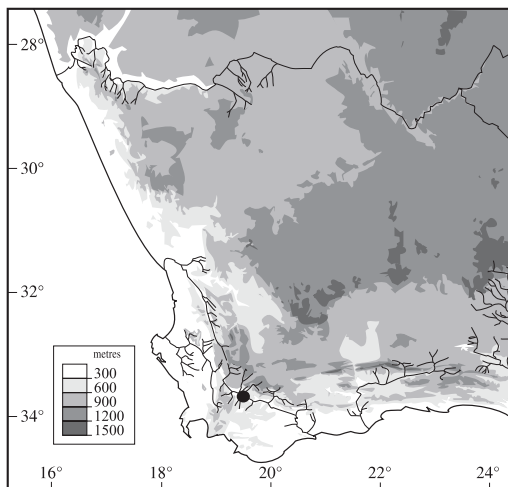


FIGURE 18.—Known distribution of *Freesia marginata*.

in *F. fucata*, another local endemic in the same valley system.

History: described in 2005, *Freesia marginata* was first collected in 2000 by Deon Kotze, horticulturist at the Karoo Botanic Garden, who showed us living plants in the collection in June 2001. Although past flowering, the distinctive leaves were a clear indication that the plants represented an undescribed species, and we collected type material the following year.

13. ***Freesia caryophyllacea*** (Burm.f.) N.E.Br. in Kew Bulletin 1929: 134 (1929). *Ixia caryophyllacea* Burm.f.: 1 (1768). *Antholyza caryophyllacea* (Burm.f.) Roem. & Schult.: 448 (1817). *Anisanthes caryophyllaceus* (Burm.f.) Klatt: 344 (1882). Type: South Africa, without locality (cult.), Burman s.n. (G, holo.).

Gladiolus xanthospilus DC. in Redouté 3: t. 124 (1805), syn. nov. *Freesia xanthospila* (DC.) Klatt: 673 (1866). *Tritonia xanthospila* (DC.) Ker Gawl. ex Spreng: 154 (1824). *Waitzia xanthospila* (DC.) Heynh.: 855 (1841). *Montbretia xanthospila* (DC.) Heynh.: 418 (1846). Type: South Africa, without precise locality, cultivated in France, illustration in Redouté, Les Liliacées 3: t. 124 (1805).

Freesia herbertii Klatt ex N.E.Br. (See Addendum on p. 111)

Freesia parva N.E.Br.: 9 (1935). Type: South Africa, [Western Cape], near Elim, 24 April 1896, R. Schlechter 7727 (K, lecto.), designated by Goldblatt: 65 (1982); BOL, isolecto.).

Freesia elimensis L.Bolus: 168 (1933b). Type: South Africa, [Western Cape], 8 miles [13 km] from Bredasdorp on Elim road, 22 April 1933, W.F. Barker & L. Bolus NBG697/33 (BOL, holo.!; BOL, iso.!).

Plants 30–100 mm high, usually $\pm$ prostrate; corm conical, 10–15 mm diam., tunics of pale, medium-textured fibres, sometimes accumulating with age and forming long neck around base of stem; stem flexed outward above uppermost leaf sheath and then prostrate or horizontal, rarely suberect, densely puberulous, simple or rarely with one branch. *Leaves* 5–7(–9), prostrate or rarely erect, usually slightly shorter than stem, rarely as long, oblong to lanceolate, (20–)30–100(–120) $\times$ 6–15(–20) mm, subacute or obtuse, thin-textured or leathery. *Spike* declinate, 3–10-flowered. *Bracts* herbaceous and firm-textured, green with hyaline margins, obovate, 5–8 mm long, inner slightly shorter. *Flowers* 30–40 (–60) mm long, white flushed purple on reverse of tepals, base of lower tepals marked yellow-orange and usually with dark midline, unscented or violet-scented; perianth tube funnel-shaped, 20–30 mm long with basal tubular portion 5–8 (–12) mm long, widening $\pm$ abruptly into flared upper portion; tepals unequal, dorsal largest, erect, elliptical to obovate, 17–25(–30) $\times$ 8–12 mm, upper laterals slightly narrower, oblong-lanceolate, lower tepals recurved, oblong-lanceolate, 14–20 $\times$ 6–8 mm. *Filaments* arcuate, 13–20 mm long, inserted at base of widened upper portion of perianth tube, included or slightly exerted; anthers 4–6 mm long. *Ovary* ovoid, 3 mm long; style dividing at or just beyond anther apices. *Capsules* oblong or subglobose, 3-lobed, 8–10 $\times$ $\pm$ 10 mm, papillate. *Seeds* obliquely globose with inflated chalaza and raphe, 2.0–3.0 mm diam., wrinkled, glossy reddish brown. *Flowering time*: mid-April to early June. Plates 13; 18F.

Etymology: Latin *caryophyllaceus*, of the scent of cultivated pinks and carnations in the family Caryophyllaceae but quite inappropriate to the actual scent of the species.

Distribution and ecology: this low-growing species is common in the southwestern Cape lowlands, in the region known locally as the Overberg, but it occurs along the length of the Breede River Valley, from Romans River just south of Tulbagh in the west to Heidelberg in the east, and southwards from the foothills of the Rivierson-

derend Mountains near Greyton, through Caledon and Napier to Bredasdorp, with a westerly extension along the coast to Hermanus and with outlying populations near Grabouw (Figure 19). *Freesia caryophyllacea* is typically found on gravelly clay soils in renosterveld shrubland although it also occurs near the coast in sandy loam in fynbos or thicket. South of Bredasdorp the species is found along the foothills of limestone ridges, where it thrives in loamy pockets along the edge of scrub. Flowering is in late autumn or winter, from April to June, with the plants generally coming into flower about a month or so after the first rains of the season. Plants flower especially well in veld that has been burned the preceding summer.

The leaves of *Freesia caryophyllacea* range from short and blunt, and disposed in a prostrate fan along the ground in exposed situations, to narrower and more acute, and held suberect or upright in shaded situations under shrubs. The leaves are usually shorter than the spike, rarely as long. The inflorescence is also typically sharply inclined and held almost horizontally along the ground but it too may become suberect in suitable situations. Although typically 30–40 mm long, the flowers on some plants along the foot of the Riviersonderend Mountains may be much larger, 50–60 mm long. All three lower tepals are usually marked with deep golden yellow or orange, which turns a chestnut-brown with age but some plants have just the lower median or lower laterals marked. The species is usually pleasantly scented, sometimes only lightly so, but some plants appear to lack fragrance entirely.

A peculiarity of the plants from Heuningrug south of Bredasdorp is their propensity to form short, thread-like stolons, at the end of which a new corm develops. This feature was seen in several plants from Die Poort but has not been observed in more typical populations of the species.

Diagnosis and relationships: *Freesia caryophyllacea* is generally easily recognized by its relatively short, blunt or subacute leaves, often borne in a prostrate fan, and by its $\pm$ horizontal inflorescence, typically with rather large bracts. The white flowers are flushed with purple and marked on some or all of the lower tepals with golden yellow blotches that turn brown as the



PLATE 13.—*Freesia caryophyllacea*

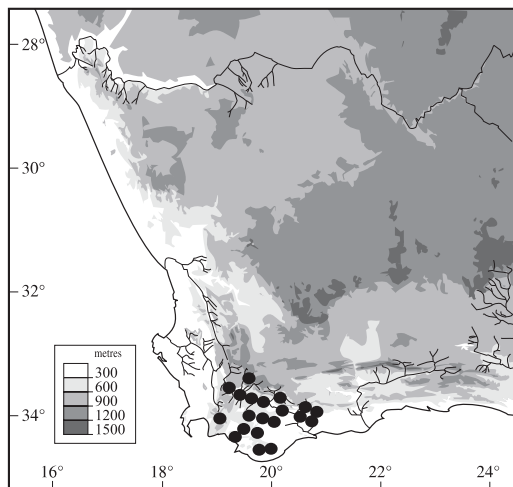


FIGURE 19.—Known distribution of *Freesia caryophyllacea*.

flowers age. The species flowers in late autumn or winter, from April to June, rarely into July.

The forms with narrower, suberect leaves and flowers with just the median lower tepals marked with yellow that occur on coastal limestones around Bredasdorp, particularly the ridge known as the Heuningrug, are somewhat anomalous in the species. Originally described as a separate species, *Freesia elimensis*, in 1933 by H.M.L. Bolus, this treatment was followed by Goldblatt (1982), who suggested that the species might be of hybrid origin between *F. caryophyllacea* and *F. alba* (now *F. leichtlinii* subsp. *alba*). These populations were subsequently treated as a form of *F. caryophyllacea* (Goldblatt & Manning 2000) but it may not be without significance that they grow together with *F. leichtlinii* subsp. *leichtlinii*, and some introgression is therefore theoretically possible. Plants from coastal rock outcrops at Hermanus and Onrus, often with suberect leaves and just the lower median tepal marked, are also somewhat deviant from typical *F. caryophyllacea* and pose some problems in identification. Previously treated in *F. alba* (Goldblatt 1982; Goldblatt & Manning 2000), they lack the characteristic axillary cormels of that taxon and flower much earlier, in June and July.

The relatively broad leaves of *Freesia caryophyllacea* serve to distinguish it from *F. fucata*, which has very narrow, acute leaves and unusual, tricuspidate bracts. Another white-flowered species from near Roberston, *F. marginata*, has leathery leaves with a distinct submarginal vein, quite visible in both fresh and dry material, but otherwise resembles *F. caryophyllacea* in its short, prostrate leaves and early flowering.

Plants with narrower, suberect leaves may be confused with western forms of white-flowered *Freesia leichtlinii* subsp. *alba* but are readily distinguished from this species of the sandy coastal forelands by their earlier flowering and complete lack of cormels in the lower axils of the leaves. A much more difficult distinction is that between narrow-leaved forms of *F. caryophyllacea* and *F. praecox*. The latter, which is known so far only from the lower slopes of the Riviersonderend Mountains, has soft, fine-textured corm tunics, suberect leaves that taper evenly and gradually to attenuate-acute apices, and flowers that typically have only the lower median tepal marked with yellow or orange. The species flowers in July, and favours rocky sandstone slopes. Narrow-leaved forms of *F. caryophyllacea* (previously treated as *F. elimensis*), notably those from limestone ridges around Bredasdorp and coastal rock outcrops around Hermanus, have fewer, lanceolate leaves that are rather abruptly acute, tunics which are mostly more wiry, and flower earlier, in April and May.

History: the species was described by N.L. Burman in 1768 from plants cultivated in Europe but the original collector and date of collection are not recorded. The Burman specimen is extremely fragmentary, consisting of a detached flowering stem and two separated leaves. The acute tips of the leaves and the lack of any indication of the stature of the plant prevented British botanist N.E. Brown from associating this plant with the species as we know it today and he accordingly described *Freesia parva* in 1935 to accommodate the small, blunt-leaved plants that we associate with *F. caryophyllacea* today. *Gladiolus xanthospilus*, described in 1807, and transferred by Klatt in 1866 to *Freesia*, was based on a painting by the French artist Redouté from a plant cultivated at the Royal Gardens at Malmaison. The identity of this species remained uncertain until Goldblatt (1982) suggested that



PLATE 14.—*Freesia praecox*

it was either *F. alba* or more likely *F. caryophyllacea*, grown lax in cultivation. The recognition of axillary cormels as a defining character of *F. alba* (now *F. leichtlinii* subsp. *alba*) makes it clear that *F. xanthospila*, which lacks these, is correctly identified with *F. caryophyllacea* and it is accordingly placed into synonymy here.

14. ***Freesia praecox*** J.C.Manning & Goldblatt, sp. nov.

Freesiae leichtlinii subsp. *albae* similis sed plantae 60–300 mm altae, caule sine cormelis axillaribus, foliis 4–10(–14) mm latis, tubo perianthii (15–)20–30 mm longo, filamentis 15–20 mm longis, antheris 4–6 mm longis, seminibus perverrucosis.

TYPE.—Western Cape, 3419 (Caledon): Riviersonderend, hill north of town, (–BB), 15 June 2004, Manning 2921 (NBG, holo.; K, MO, PRE, iso.).

Plants 60–300 mm high; corm conic, 10–20 mm diam., tunics pale, of medium-textured fibres, accumulating with age but not forming neck around base of stem; stem flexed outward above uppermost sheath and then suberect, minutely puberulous, sometimes with one or two branches. *Leaves* 6–9(–11), prostrate or suberect, usually slightly longer than stem, narrowly lanceolate, 50–200(–250) × 4–10(–14) mm, tapering-attenuate. *Spike* lightly flexed to horizontal, 3–8-flowered. *Bracts* herbaceous, green with hyaline margins, obovate, 5–10(–12) mm long, acute or lower weakly tridentate, inner slightly shorter. *Flowers* (30–)35–45 mm long, white, usually flushed dull purple on reverse of tepals, base of lower median tepal (rarely lower laterals also) marked yellow-orange, lower tepals, especially laterals, with purple or mauve veins in basal half, strongly violet-scented; perianth tube (15–)20–30 mm long with basal narrow part 5–9 mm long, widening abruptly into wider, flared upper portion; tepals unequal, dorsal largest, suberect, oblong-elliptic, 13–22 × 6–10 mm, upper laterals slightly narrower, oblong, lower tepals recurved, lower laterals oblong-elliptic, 15–20 × 6–8 mm, lower median oblong, 12–20 × 5–7 mm. *Filaments* arcuate, 15–20 mm long, inserted at base of widened upper portion of tube, included; anthers 4–6 mm long. *Style* dividing at

or slightly beyond anther apices. *Capsules* ovoid, 3-lobed, 11–12 × 8–9 mm, papillate-verrucose. *Seeds* obliquely globose with inflated chalaza and raphe, 2.0–3.0 mm diam., finely wrinkled, glossy reddish brown. *Flowering time*: mid-June to mid-July. Plates 14; 18G; Figure 7.

Distribution and ecology: a highly localized species, so far known with certainty only from the lower end of Olifantskloof, which cuts into the eastern end of the Riviersonderend Mountains at the town of Riviersonderend in the southwestern Cape (Figure 20). Plants grow in loamy soils in sandstone outcrops with their corms wedged between the rocks. Suitable cracks and crevices are often packed with dozens of plants. In exposed sites the leaves are prostrate and relatively short, while in more sheltered situations, in the lee of overhangs or in deeper clefts, plants are taller with erect or somewhat falcate leaves. Flowering is profuse after a fire has removed shrubs and overgrowth. The flowers are strongly scented during the day.

Diagnosis and relationships: *Freesia praecox* is a poorly defined species that is morphologically intermediate between *F. leichtlinii* subsp. *alba* and *F. caryophyllacea*. As a consequence, its specific status has not been recognized until now, principally through a more intimate knowledge of the species in the field. It has the finely fibrous corm tunics and numerous, relatively narrow, tapered leaves of *F. leichtlinii* subsp. *alba*, along with similar flowers in which usually just the lower median tepal (rarely the laterals also) is marked with yellow. Early collections were consequently first referred to that taxon. However, it lacks the axillary cormels that are now recognized to be diagnostic of *F. leichtlinii*, and it also flowers several months earlier, in June and July rather than August and September. The two species are geographically and ecologically separated, with *F. leichtlinii* restricted to the coastal plain of the southern Cape, and *F. praecox* found inland along the foot of the Riviersonderend Mountains.

Freesia praecox is most likely to be confused with narrow-leaved forms of *F. caryophyllacea* but tends to have more numerous leaves, usually 6–9 and up to 11, with gradually tapering, narrowly lanceolate-attenuate blades that are distinctly longer than the flowering stem. *Freesia*

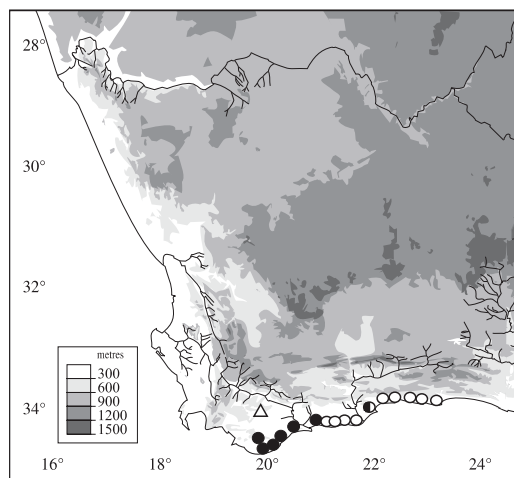


FIGURE 20.—Known distribution of *Freesia praecox*, Δ ; *F. leichtlinii* subsp. *leichtlinii*, $\bullet$; *F. leichtlinii* subsp. *alba*, $\circ$.

caryophyllacea generally has fewer leaves, 5–7(–9), with lanceolate to oblong-lanceolate, more abruptly tapered, subacute or obtuse blades that are shorter than or as long as the spike. The flowers in *F. caryophyllacea* mostly have yellow markings on all three lower tepals, although plants from Bredasdorp and Hermanus typically have just the lower median tepal marked. In addition, *F. praecox* appears to be restricted to rocky sandstone outcrops, rather than the shale flats or loamy pockets along limestone outcrops that are favoured by *F. caryophyllacea*. We have collected typical *F. caryophyllacea*, with characteristic broad, blunt leaves and a prostrate flower spike in renosterveld shrubland on shale soils along the foothills of the Riviersonderend Mountains, within sight of *F. praecox*. Flowering in these plants takes place in April or May and they are in fruit by the time *F. praecox* flowers on the slopes above them.

History: the species seems to have been first collected by local farmer N. Neetling near Riviersonderend in June 1931 on the family farm, Esperance, which lies at the foot of the Riviersonderend Mountains a few kilometres west of the town. This collection plus another made by the Cape Town botanist and specialist in Iridaceae, G.J. Lewis, in June 1951, probably at or near the

type locality in Olifantskloof near Riviersonderend, attracted little botanical attention. A third collection from 1974 (Goldblatt 2053) was referred at the time to *F. muirii*, a name that was then applied to *F. leichtlinii* subsp. *alba*, and was subsequently included in *F. alba* by Goldblatt (1982). Recent field studies led us to conclude that *F. alba* (here treated as *F. leichtlinii* subsp. *alba*) is exclusively a coastal taxon that flowers in late August and September, and is characterized by the development of prominent axillary cormels along the lower stem. This raised doubt as to the identity of the Riviersonderend plants and caused us to revisit the area in 2004. A healthy population of plants was located in full flower following a burn the previous summer. We conclude that these plants cannot be included in either *F. leichtlinii* subsp. *alba* or *F. caryophyllacea*, and are thus best regarded as a separate species.

Additional specimens examined

WESTERN CAPE.—3419 (Caledon): Riviersonderend, (–BB), June 1931, Neethling s.n. (BOL); Riviersonderend Mtns, among stones on lower slopes, (–BB), 27 June 1951, Lewis 2321 (SAM); Riviersonderend, rocky places (–BB), 14 June 1974, Goldblatt 2053 (MO, NBG); pipe bridge over Riviersonderend River, (–BB), 20 July 2004, Volk s.n. [photograph only] (NBG).

15. ***Freesia leichtlinii*** Klatt in Regel, *Gartenflora* 23: 289 (1874). *Nymanina leichtlinii* (Klatt) Kuntze: 701 (1891). *Freesia xanthospila* var. *leichtlinii* (Klatt) N.E.Br.: 22 (1935). Type: illustration in *Gartenflora* 23: plate 808 (Regel 1874).

Freesia muirii N.E.Br.: 467 (1932). Type: South Africa, [Western Cape], Mossel Bay Division, without exact locality or date, *F. Muir* 4849 (K, syn.), 4849A (K, PRE!, syn.).

Freesia middlemostii W.F.Barker: 112 (1933). Type: South Africa, [Western Cape], Bredasdorp, August 1932, A.J. Middlemost s.n. (BOL, holo.!).

Freesia gentilis N.E.Br.: 20 (1935), syn. nov. Type: South Africa, cultivated at the Botanical Gardens, Cape Town, from corms said to have been collected by G. Alston at Vanwyksvlei, SAM20966 (SAM, holo.!).

Plants 60–250 mm high (rarely up to 500 mm under bushes), producing cormels along stem in lower leaf axils and later at base of corm; corm conical, 10–15(–20) mm diam., sometimes deeply buried, tunics pale, of fine- to medium-

textured fibres; stem erect or flexed upwards above uppermost sheath and then suberect, minutely papillate, at least towards base, usually unbranched, rarely with one or two branches. *Leaves* 5–9, inclined to suberect or rarely prostrate, less than half as long to $\pm$ as long as stem, narrowly lanceolate to linear-lanceolate, 40–140(–300) $\times$ (3–)6–12 mm, acute. *Spike* deflexed or horizontal, (2–)4–9-flowered. *Bracts* herbaceous and firm-textured, green with hyaline margins, obovate, 4–7(–12) mm long, inner bracts slightly shorter. *Flowers* (25–)30–45 mm long, white to cream-coloured or pale yellow, usually $\pm$ flushed dull purple on reverse of tepals, base of all three lower tepals or only lower median tepal marked yellow to orange, strongly violet-scented; perianth tube funnel-shaped, (15–)20–25(–40) mm long with basal tubular portion (5–)6–9(–20) mm long, widening $\pm$ abruptly into flared upper portion; tepals subequal or unequal with dorsal largest, suberect, ovate, 13–18 $\times$ 8–14 mm, upper laterals slightly narrower, lower tepals recurved, 12–14 $\times$ 6–12 mm. *Filaments* arcuate, (12–)15–18(–22) mm long, inserted at base of wider upper portion, included; anthers 6–9 mm long. *Style* dividing at or slightly beyond anther apices. *Capsules* oblong, 3-lobed, 10–12 $\times$ 8–10 mm, papillate or rugulose. *Seeds* obliquely subglobose with inflated chalaza and raphe, 2.5–3.0 mm diam, wrinkled or smooth, glossy reddish brown. *Flowering time*: early August to late September. Plates 15; 18.

Etymology: named for the German horticulturist and plantsman Max Leichtlin.

Distribution and ecology: *Freesia leichtlinii* is a coastal species that has been recorded along the southern Cape from south of Bredasdorp eastwards to Plettenberg Bay (Figure 20). It favours lime-enriched sands or calcareous loam and is found in coastal bush, thicket or restioid fynbos. The species is readily seen at Cape Agulhas, where it grows on rocky outcrops in the shadow of the Agulhas lighthouse, west of Still Bay, and in the Robberg Nature Reserve near Plettenberg Bay.

Diagnosis and relationships: *Freesia leichtlinii* is distinguished by its deeply buried corms with fine-textured corm fibres, suberect, acute leaves with the lower always bearing cormels in their axils along the subterranean portion of the stem, and the white to pale yellow flowers, produced

in spring, mainly between August and late September. In the revised circumscription of the species followed here, *F. leichtlinii* comprises two sets of populations that are treated as subspecies. The typical form, subsp. *leichtlinii*, occurs in the west of the range, from Cape Agulhas to Cape Infanta, and has pale yellow flowers with a perianth tube (15–)20–25 mm long, the lower portion always fairly short, 5–9 mm. Populations from east of Cape Infanta, treated as subsp. *alba*, have white or cream-coloured flowers, sometimes without the usual dull purple flush on the reverse of the outer tepals, and a perianth tube (15–)20–40 mm long, with the lower portion varying in length from 5–20 mm. Until now these two populations were treated as independent species under the respective names *F. leichtlinii* (plants with 2-lipped, yellow flowers with darker markings on all three lower tepals) and *F. alba* (characterized by almost regular white flowers with a yellow mark only on the lower median tepal). These floral differences apply strictly only to the populations from the extreme west and east of the range respectively, and western plants of *F. alba* have 2-lipped flowers that are variably marked on all three or just the lower median tepal, thus differing from *F. leichtlinii* only in their white or cream-coloured vs yellow perianth.

A feature of both taxa that appears to us to be of much greater taxonomic significance than flower colour is the development of cormels in the axils of the lower leaves along the subterranean portion of the stem. Apart from the incomplete tendency to different floral coloration and markings, there are no other evident differences between the two sets of populations and we have no hesitation in uniting them. We treat the two as subspecies in recognition of the $\pm$ geographically consistent difference in flower colour between them and because of the historical significance that the two colour forms have played in the development of cultivars in the genus.

Plants from near Mossel Bay, notably near Great Brak River, including the type of *Freesia muirii* (which consists of both pale yellow- and white-flowered plants), fall within the geographical range of subsp. *alba* but have the pale yellow flowers characteristic of subsp. *leichtlinii* and are evidently intermediate between the two subspecies. Goldblatt (1982), who maintained the two taxa as separate species, speculated that



PLATE 15.—*Freesia leichtlinii*; a, subsp. *leichtlinii*; b, subsp. *alba*.

the type collection of *F. muirii* from near Mossel Bay (here regarded as a synonym of *F. leichtlinii*), represented a mixed collection comprising pale yellow-flowered plants of *F. leichtlinii* (now subsp. *leichtlinii*) and white-flowered plants of *F. alba* (now subsp. *alba*), and therefore rejected *F. muirii* on the basis that the collection was a mixture of two species. Similar mixed yellow- and cream-flowered plants occur in populations of *F. leichtlinii* subsp. *leichtlinii* around Bredasdorp. Detailed cytogenetic study is required to determine whether the yellow-flowered plants in the Mossel Bay and Great Brak River areas represent an independent evolution or expression of yellow pigmentation in subsp. *alba* or whether they are the result of dispersal from western yellow-flowered subsp. *leichtlinii*.

Freesia leichtlinii is naturalized along roadsides and on waste ground, and also locally in native vegetation, in the winter rainfall parts of Australia, namely in southwestern Western Australia, southern South Australia, around Sydney in New South Wales, and in southern Victoria (Cooke 1986). Although some specimens are referable to either subsp. *alba* or subsp. *leichtlinii*, most fall within a continuum between the two colour forms and the Australian plants are thus treated as a single entity, either under the name *Freesia* hybrid (Cooke 1986) or more specifically as *F. leichtlinii* subsp. *alba* × subsp. *leichtlinii*. It remains to be established if they represent a single or multiple introductions of *F. leichtlinii* to the continent. Plants matching the typical subspecies are also recorded as naturalized north of Nice in France.

History: the botanical history of this species illustrates the almost incomprehensible facility with which South African plants have found their way into European gardens. The species was named in 1874 by F.W. Klatt in honour of the German plantsman, Max Leichtlin, who came across plants in a neglected part of the Botanical Gardens in Padua in Italy in 1872 or 1873. Digging out some corms, Leichtlin returned to Germany and set about increasing the stock and disseminating the surplus. The plant described by Klatt in 1874 originated from Leichtlin's garden. It is not known how the species came to be cultivated at Padua but it was acquired by the Botanical Gardens in 1842 under the name *Freesia refracta*. Herbarium specimens of the species

were certainly collected in the 1820s and 1830s by both Ecklon & Zeyher and by J.F. Drège, but none of these collectors are known to have sent seeds or living plant material to Europe. *Freesia leichtlinii* subsp. *leichtlinii* remained in cultivation in Europe for some time and contributed to the production of new cultivars.

The history of the better known *Freesia leichtlinii* subsp. *alba* is equally uncertain. Plants were widely known and cultivated in Europe in the late nineteenth century, when they were first offered for sale by the New Plants and Bulb Co. of Colchester in England in 1878 under the name *Freesia refracta* 'alba', the trinomial representing nothing more than a horticultural variety. The plant was subsequently formally named *F. refracta* var. *alba* by G.L. Meyer in the first issue of the Swiss publication *Zeitschrift des Schweizerischen Gartenbauvereins*, which appeared in early February 1881, and almost simultaneously by W. Robinson in the English journal *The Garden*, published a few days later on 19 February 1881. From the shape of the beautifully illustrated flowers, it is fairly certain that the original plants came from the eastern part of its range, possibly from Plettenberg Bay itself, and it is this form that is in cultivation today. Although it is evident that the species was brought to England from the Cape sometime before 1878, the exact date and collector are unknown. The taxon was later treated as *F. sparrmanii* var. *alba* (Brown 1921) and although this combination was attributed to both E. Phillips and N.E. Brown by Goldblatt (1982) it is clearly attributed to Brown alone in the protologue. This pure-white form was treated under the illegitimate name *F. lactea* by N.E. Brown (1935).

Freesia gentilis was described by N.E. Brown (1935) from cultivated plants, grown from corms ostensibly sent to Cape Town by G. Alston of Vanwyksvlei, the type locality of *F. andersoniae*. No such plants are known in the wild from this region and the species was accordingly identified as a horticultural form by Goldblatt (1982) and the name excluded. Examination of the type shows the fine-textured corm tunics and, critically, the presence of an axillary cormel, both features that are diagnostic of *F. leichtlinii*. The flower colour was described by Brown (1935) as creamy or pale yellow on the inside but flushed purple on the reverse, and we accordingly synonymize

it under the typical form of *F. leichtlinii*. *Freesia picta* N.E.Br. is another species described from cultivated plants, this time from Beaufort West. The name was excluded by Goldblatt (1982) as based on a cultivar of *F. alba* (here *F. leichtlinii* subsp. *alba*), and the presence of axillary cormels in the type confirms this identification. The large, long-tubed, white flowers leave no doubt that the plants represent the large-flowered form from the eastern part of the range of the species that have been in cultivation for over a century and we have no hesitation in synonymizing the name under subsp. *alba*.

Key to subspecies

- 1a Flowers pale yellow or cream-coloured, lightly flushed purple outside, with base of lower three tepals marked deep yellow to orange; perianth tube (15–)20–25 mm long with basal narrow part 5–9 mm long; plants from Agulhas to St Sebastian Bay 15a. subsp. *leichtlinii*
- 1b Flowers uniformly white, or white to cream-coloured, flushed purple outside, usually with base of only lower median tepal marked yellow to orange; perianth tube (15–)20–40 mm long with basal narrow part 5–20 mm long; plants from Still Bay to Plettenberg Bay 15b. subsp. *alba*

15a. subsp. *leichtlinii*

Plants mostly 100–200 mm high. *Leaves* usually prostrate or inclined and $\pm$ half as long as flowering stem. *Flowers* cream-coloured or pale yellow, usually lightly flushed dull purple on reverse of tepals, base of lower three tepals marked deep yellow to orange; perianth tube (15–)20–25 mm long with basal narrow part (5–)6–9 mm long; tepals unequal, dorsal largest, 13–18 $\times$ 8–14 mm, lower tepals 12–14 $\times$ 8–12 mm. *Seeds* wrinkled. *Flowering time*: early August to late September. Plate 18H.

Distribution and ecology: subsp. *leichtlinii* is scattered along a short stretch of the southern Cape coast, from Agulhas eastwards to St Sebastian Bay (Figure 20), and favours sandy or calcareous loam in open scrub or coastal thicket.

Freesia leichtlinii subsp. *leichtlinii* is most likely to be confused with *F. fergusoniae*, the other yellow-flowered species in sect. *Viridibractea*. The two are distinguished by habitat, foliage, texture of corm tunics, and by the presence or absence

of axillary cormels. *Freesia fergusoniae* grows in heavier, clay soils and the leaves are often prostrate and obtuse, and typically much shorter than the flowering stem. The shallowly buried corm is covered with coarse, wiry outer tunics, and the short underground stem does not bear cormels in the axils of the lower leaves. *Freesia leichtlinii*, in contrast, grows in friable, sandy or calcareous loam along the coast and the leaves are usually acute, the corm tunics are finely fibrous, and the corms themselves are more deeply buried, usually with a significant length of underground stem, along which axillary cormels develop.

Freesia leichtlinii subsp. *leichtlinii* co-occurs with white-flowered *F. caryophyllacea* in parts of its range, most notably south of Bredasdorp, where both species grow together along the lower slopes of limestone ridges at Die Poort. *Freesia caryophyllacea* is an early-flowering species, invariably in fruit by the time *F. leichtlinii* comes into bloom, and no sign of hybridization has been observed.

15b. subsp. *alba* (G.L.Mey.) J.C.Manning & Goldblatt, stat. et comb. nov.

Freesia refracta var. *alba* G.L.Mey. in Zeitschrift des Schweizerischen Gartenbauvereins: 37 (1881). *Freesia alba* (G.L.Mey.) Gumb.: 392 (1896). *Freesia sparrmannii* [as 'sparmannii'] var. *alba*. (G.L.Mey.) N.E.Br.: t. 11 (1921). Type: illustration in Zeitschrift des Schweizerischen Gartenbauvereins 1, t. 3 (Meyer 1881).

Freesia picta N.E.Br.: 21 (1935), syn. nov. Type: South Africa, [Western Cape], Beaufort West, August 1933, *Black s.n. NBG1558/13* (BOL, holo.!).

Freesia lactea Fenzl ex N.E.Br. [as Fenzl ex Klatt]: 23 (1935), illegitimate name, without Latin description.

Plants mostly 200–500 mm high. *Leaves* usually inclined or suberect and $\pm$ as long as flowering stem. *Flowers* white to cream-coloured and flushed dull purple on reverse of tepals, or pure white, usually only lower median tepal marked with yellow to orange; perianth tube (15–)20–40 mm long, basal narrow part 5–20 mm long; tepals subequal or unequal then dorsal largest, 13–18 $\times$ 8–12 mm, lower tepals 12–14 $\times$ 6–10 mm. *Seeds* smooth or slightly wrinkled. *Flowering time*: late July to early October. Plate 18I; Figure 4H, I.

Etymology: Latin *albus*, white, referring to the pure white flowers of the type illustration.

Distribution and ecology: subsp. *alba* occurs along the southern Cape coast from just west of Still Bay to Plettenberg Bay in the east (Figure 20). Plants grow in coarse sandy soils derived from Cape sandstone or in limestone, usually in stony situations, often in crevices in rocky outcrops, or in light shade along the margins of coastal scrub or forest patches. South of Riversdale, plants also grow in deep, lime-enriched sands, usually among small shrubs or restios, where the corms are protected from predation.

The finest form of the species occurs on the Robberg Peninsula at Plettenberg Bay, where plants have large, pure white flowers 50 mm long with subequal tepals and the lower part of the perianth tube 15–20 mm long. This is the form associated with the species in cultivation. Plants west of this have smaller flowers, 35–40 mm long with the outer surfaces of the tepals more or less flushed with purple and a shorter lower portion of the perianth tube, 5–10 mm long.

Spring-flowering subsp. *alba* resembles *Freesia caryophyllacea* in its white flowers flushed purple on the outside, and the two have been confused in the past. *Freesia leichtlinii* subsp. *alba* is strictly a coastal taxon, growing in sandy soils derived from sandstone or limestone, and in this respect differs from *F. caryophyllacea*, which favours clay, shale or loamy substrates and flowers in the winter months between May and July. The corm tunics of *F. caryophyllacea* are moderately to coarsely fibrous and the corm develops sessile or shortly stoloniferous cormels from its base, never from the leaf axils as in *F. leichtlinii*. In addition, the flowers of *F. caryophyllacea* usually have deep yellow markings on all three lower tepals, rather than just the lower median one. The species typically has broader leaves than subsp. *alba* although plants with narrower, suberect leaves occur around Bredasdorp. These can be distinguished from subsp. *alba* by their shorter, strongly inclined spikes and early flowering.

The name *Freesia elimensis* was applied to plants from coastal limestones near Bredasdorp that had the early-flowering habit of *F. caryophyllacea* but the erect, acute leaves of *F. leichtlinii* subsp. *alba*. Although thought to be the product of hybridization between these two taxa (Goldblatt 1982), we now consider these populations and others along the coast at Hermanus and On-

rus to be a local form of *F. caryophyllacea* (Goldblatt & Manning 2000).

Freesia fucata is another early-flowering species that approaches subsp. *alba* in its narrow leaves. This species, which is known only from clay soils in the Worcester basin, has rather firmer, glaucous green leaves, tricuspidate floral bracts, and basal cormels.

Superficially similar plants with the narrow, pointed leaves and erect stems of *Freesia leichtlinii* subsp. *alba* but flowering in June or July, have been collected along the foothills of the Rivier-sonderend Mountains, growing on the edge of forest patches in rocky soils at the transition between clay and sandstone. Although initially included in *F. alba* (Goldblatt 1982), these plants are anomalous in subsp. *alba* in their ecology and geography, and in lacking the axillary cormels that characterizes *F. leichtlinii*, and we recognize them here as a separate species, *F. praecox*.

16. ***Freesia fergusoniae* L.Bolus** in South African Gardening and Country Life 17: 337 (1927). Type: South Africa, [Western Cape], Riversdale, August 1926, *E. Ferguson* s.n. (BOL, holo.).

Plants 60–200(–300) mm high; corm conical, 15–20 mm diam., tunics of pale, coarse-textured fibres, accumulating; stem erect or flexed upwards above uppermost sheath and then suberect, minutely papillate at least towards base, usually unbranched, rarely with one or two branches. *Leaves* (5–)7–13, prostrate to inclined, oblong to lanceolate, usually less than half as long as stem, 40–140(–200) × 6–16 mm, obtuse to subacute. *Spike* deflexed or horizontal, (2–)4–8(–12)-flowered. *Bracts* herbaceous and firm-textured, green with hyaline margins, obovate, 4–7(–10) mm long, inner bracts slightly shorter. *Flowers* (25–)30–45 mm long, pale yellow to cream-coloured, rarely whitish, ± flushed dull purple on reverse of tepals, base of lower tepals marked orange, strongly violet-scented; perianth tube funnel-shaped, (15–)20–25 mm long with basal tubular portion 5–9 mm long, widening ± abruptly into flared upper portion; tepals unequal, dorsal largest, suberect, ovate, 13–18 × 8–14 mm, upper laterals slightly narrower, lower tepals recurved, 12–14 × 8–12 mm. *Filaments* ar-



PLATE 16.—*Freesia fergusoniae*.

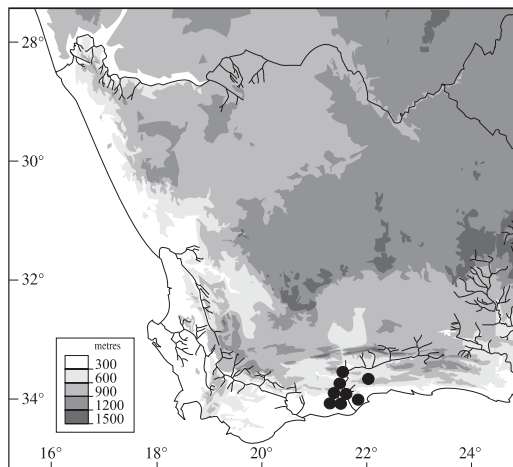


FIGURE 21.—Known distribution of *Freesia fergusoniae*.

cuate, 14–20 mm long, inserted at base of widened upper portion, included; anthers 6–8 mm long. Style dividing at or slightly beyond anther apices. Capsules oblong, 3-lobed, 10–12 × 8–10 mm, papillate. Seeds obliquely subglobose with inflated chalaza and raphe, 2.5–3.0 mm diam., wrinkled, glossy reddish brown. Flowering time: late July to middle August, rarely as early as late June. Plates 16; 18J; Figure 4G.

Etymology: named for Emily Ferguson of Riversdale, naturalist and correspondent of H.M.L. Bolus.

Distribution and ecology: an attractive species, *Freesia fergusoniae* is well known along the southern foothills of the Langeberg, where it is locally common between Heidelberg and Riversdale (Figure 21). Its distribution extends inland along the Gourits River where it cuts through the Langeberg, and the species just enters the Little Karoo, where it has been recorded from the Rooiberg and the northern end of Robinson's Pass. *Freesia fergusoniae* is invariably found on clay soils in renosterveld, flowering best in cleared or burned sites but not in thick growth.

Diagnosis and relationships: *Freesia fergusoniae* was regarded by Goldblatt (1982) as one of the most attractive species in the genus, and our experience with plants growing wild near Heidelberg supports this claim. The species produ-

ces fragrant, good-sized, pale yellow flowers with prominent orange markings on the lower tepals, borne on spikes held well above the leaves. The leaves are typically prostrate and obtuse but in some populations may be suberect and acute. Erect-leaved plants of *F. fergusoniae* are most likely to be confused with *F. leichtlinii* subsp. *leichtlinii*, which also produces pale yellow flowers but *F. leichtlinii* is restricted to coastal sands or sandy loam and has a deeply buried corm with fine- to medium-textured tunics that do not accumulate, and the subterranean portion of the stem produces axillary cormels. In *F. fergusoniae* the stems never have a significant subterranean portion and cormels are produced only at the base of the parent corm, which is covered with an accumulation of coarse-textured tunics. Flowering in *F. fergusoniae* is also slightly earlier than in *F. leichtlinii*, with a short period of overlap in late August.

Freesia fergusoniae resembles white-flowered *F. caryophyllacea* in its coarse-textured corm tunics and prostrate, obtuse leaves. This species, which is widespread west of Swellendam, is also most commonly found on clay soils in renosterveld but flowers before *F. fergusoniae*, between April and mid-June. It is typically shorter, rarely more than 100 mm tall, and the mostly simple stems are usually prostrate in the lower half and inclined above rather than erect as often in *F. fergusoniae*. Populations of plants from Soetmelksrivier, southeast of Riversdale, with cream-coloured or white flowers and a prostrate flower spike are easily confused with *F. caryophyllacea*. In cultivation, however, they develop the erect stems that are typical of *F. fergusoniae*, which they also match in their very coarse corm tunics, more numerous leaves (9–12 vs 5–7) and later flowering (middle to late July), and we accordingly assign them to *F. fergusoniae* despite their pale flowers.

History: *Freesia fergusoniae* was discovered in the 1920s by Mrs Emily Ferguson of Riversdale, and plants sent by her to Cape Town botanist Louisa Bolus were described in 1927. The relatively distinctive appearance of the species, combining prostrate, obtuse leaves and yellow flowers on erect stems, ensured that it did not suffer from the identity crises that bedevilled some of the other species in sect. *Viridibractea*.



PLATE 17.—A, *Freesia laxa* subsp. *laxa*; B, *F. grandiflora* subsp. *grandiflora*; C, *F. andersoniae*; D, *F. speciosa*; E, *F. verrucosa*; F, *Freesia corymbosa* (yellow colour form); G, *F. corymbosa* (pink colour form 'Armstrongii'); H, *F. refracta* and I, *F. occidentalis*.



PLATE 18.—A, *Freesia viridis* subsp. *viridis*; B, *F. viridis* subsp. *crispifolia*; C, *F. sparrmanii*; D, *F. fucata*; E, *F. marginata*; F, *Freesia caryophyllacea*; G, *F. praecox*; H, *F. leichtlinii* subsp. *leichtlinii*; I, *F. leichtlinii* subsp. *alba*; J, *F. fergusoniae*.



ADDITIONAL MATERIAL SEEN

Acocks 12065, 23272, 23849 (6) PRE; 14519 (9a) PRE; 19289, 19300 (9b) PRE; 20548, 20575 (7) PRE; 20594 (5) BOL, PRE; 21340 (15a) BOL, NBG, PRE; 22349 (15a) PRE; 22360 (16) PRE; 23682 (8) PRE; 24041 (7) NBG, PRE; 703 (3) PRE; 9168 (1a) PRE. Adams 149 (3) PRE. Agnew 427 (2) MAL. Albertyn 438 (13) NBG. Alston s.n. (3) SAM. Anderson A130 (1a) PRE. Anderson sub Marloth 6455b (3) PRE. Andrews sub E.E. Galpin 4692 (6) PRE. Atkinson 20 (1a) NU.

Balkwill 191 (1b) NU. Balkwill & Cadman 1728 (1b) NU. Balkwill et al. 1015 (1a) NU. Bally & Hardy 10725 (1a) G, K. Bamps, Symoens & van den Berghen 903 (2) BR, SRGH. Barbosa 7626 (1b) K, LMA. Barker 684, 1307, 3565 (1a) NBG; 10638 (16) NBG; 1976 (4) NBG; 2691 (15b) NBG; 4569 (13) BOL; 4663, 5391, 5428, 8024, 10699 (7) NBG; 6314, 6549 (9b) NBG; 6928, 7013 (6) NBG; 7382, 9268 (13) NBG. Bayer T26 (1b) NU. Bayliss 2525 (1a) NBG; 7689 (6) NBG. Behr 703 (2) PRE. Bidgood 75 (1a) K. Bidgood & Vollesen 2189 (1a) K. Bidgood, Abdallah & Vollesen 1963 (2) K. Biegel 1783 (2) K, SRGH. Blackburn s.n. (4) BOL. Bohnen 3881 (15a) PRE; 7586 (16) NBG, PRE; 8232 (7) NBG, PRE. Bolnick 71 (2) NBG. Bolus 1751, 10311 (1a) BOL. Bond 1300 (1a) NBG. Bos 1190 (2) NBG, PRE. Botha 5637 (6) PRE. Boucher 1569 (7) NBG; 6728 (9b) NBG. Braun 903 (1a) PRE. Brayshaw 138 (1a) NU. Bredenkamp 1333 (1a) PRE. Brent 9 (1a) PRE; 17 (2) NBG. Broadhurst-Hill 2 (1a) K. Bruce 7 (1a) PRE. Brummitt 8853 (2) BR, K, EA, MAL, SRGH. Bruyns 3201, 8867 (9b) NBG; 8410 (6) NBG. Bryant J324 (3) PRE. Buchanan 176 (2) SAM. Buitendag 391 (1a) NBG, PRE; 398 (2) NBG, PRE. Burgers 1090, 2194 (15b) PRE; 2194 (15b) NBG; 2878 (13) NBG. Burgoyne 3933 (1a) PRE; 7309 (9b) PRE. Burrows 2087 (3) PRE. Burt-Davy 1496 (2) PRE. Buthelezi 548 (1b) PRE.

Carney 31 (1a) PRE. Cassidy 233 (1a) BOL, NBG. Chapman 1169 (2) K, MAL, SRGH. Chase 1911 (2) K. Codd 2944 (1a) PRE. Codd & De Winter 5164 (2) PRE. Codd & Dyer 9098 (2) PRE. Coetzee 107, 854 (2) PRE. Collins 9886 (2) PRE. Compton 3733 (8) BOL, NBG; 5408 (8) NBG; 7293 (6) NBG; 9011 (15b) BOL, NBG; 15896 (9a) NBG; 16973 (15a) NBG; 17669 (1a) NBG; 20521 (7) NBG; 29488 (1a) PRE; 27306, 32242, 78329 (1a) NBG, PRE. Correia 408 (2) LISC. Correia & Marques 2194 (1b) LMU, WAG; 2282 (2) BR, LMU, MO, WAG.

Dahlstrand 2414 (7) PRE; 2684 (1a) NBG, PRE. De Koning & Hiemstra 8933 (1b) BR, LMU, MO, SRGH; 9007 (1b) LMU, MO. De Lemos & Balsinhas 136 (1b) K, LISC; 252 (2) K, LMA, SRGH. De Vos 2213 (5) NBG. Denman 31 (15a) NBG. Desmet 283 (9b) NBG; 1049 (9a) NBG. Devenish 1353 (1a) PRE. Dieperink 68 (2) PRE. Du Toit 1241 (1b) PRE.

Ecklon & Zeyher 1618 (9b) PRE, SAM; 4027 (10) G, K, P. Eggeling 5983 (1a) K. Ellery 56 (1a) NU. Esterhuysen 2984, 23226 (15b) BOL; 10377 (10) BOL, K; 13285 (1a) BOL. Eyless 1134 (2) SRGH.

Fairall 97 (1a) NBG. Fanshawe 5370, 5379 (1a) BR, K, NDO. Feinauer s.n. (3) NBG, PRE. Ferguson BOL18589 (15a) BOL. Flanagan 434 (1a) PRE; 21030 (1a) SAM. Fock KMG8209 (3) PRE. Fouche 30 (9b) NBG. Fourcade 1659, 4035 (5) BOL, NBG, PRE; 3122 (6) NBG; 4626 (6) BOL, NBG. Fourie s.n. (3) PRE. Fries, Norlindh & Weimarck 1182 (6) PRE, SAM. Fuller s.n. (3) BOL, PRE.

Galpin 330 (2) PRE; 1014, 10885, 12107 (1a) PRE. Giess & Müller 14384 (9b) MO. Geldenhuys 809 (1a) NBG. Germishuizen 1208, 1220, 1674, 5026, 5871, 7210, 9081 (1a) PRE. Gerstner 5035 (1a) NBG; 5905, 6029 (2) PRE; 6593 (2) NBG. Giess 14633 (9b) MO, PRE. Gilfillan sub Galpin 5577 (3) PRE. Gillett 1599 (5) NBG, PRE. Glass 558 (6) SAM. Glen 84 (1a) PRE. Goldblatt 253 (7) BOL; 451 (5) BOL; 585 (9a) BOL; 602 (2) BOL; 2053 (14) MO, NBG; 2335 (9a) MO, PRE; 2933 (5) NBG; 3742 (16) PRE; 4069 (8) NBG; 4864 (15b) NBG, PRE; 4935 (6) NBG, PRE; 4959 (10) BR, C, E, K, MO, NBG, PRE, S, US, WAG; 5542, 5602 (13) PRE; 5632 (13) NBG; 7576 (2) MO. Goldblatt & Manning 9215 (9a) MO, PRE; 9890 (9b) MO, PRE; 9599, 12257 (15a) MO, NBG; 12252 (16) NBG. Goldblatt & Nänni 11069 (9a) MO, PRE. Goldblatt & Porter 11787, 12076, 12108 (9b) MO, NBG; 11840, 12183, 12286 (5) MO, NBG; 12043 (7) MO, NBG; 12065, 12267 (7) NBG; 12114 (9a) MO, NBG; 12274 (6) MO, NBG; 12379 (10) MO, NBG. Goldblatt, Porter & Manning 12177 (4) MO, NBG. Goldsmith 53/58 (2) BR, K, SRGH. Grant 3107 (1a) PRE. Grout 272 (2) K, NDO. Guthrie 3440 (6) NBG. Gwynne-Evans 385 (7) NBG; 19.05.10/10 (2) NBG.

Hall 286 (8) NBG; 706, 904, 4214 (9b) NBG. Hanekom 2417 (8) PRE; 2429 (3) PRE. Hardy 252 (13) PRE; 5027, 5045 (9b) PRE. Harrower 2116 (9a) NBG; 2281 (6) NBG; 2293 (5) NBG. Higinbotham 14, 129 (13) NBG. Heinecken

- 12 (15a) PRE. *Helme* 1787, 2506 (7) NBG. *Herman* 743 (2) PRE. *Hiemstra* 344, 351 (15a) NBG; 369 (7) NBG; 419 (8) NBG. *Hildyard* 58 (1a) PRE. *Hilliard & Burr* 4645, 6306 (2) NU. *Hilner* 71 (1a) PRE. *Hofmeyr* 186 (2) PRE. *Hofmeyer Davison* 8 (1a) PRE. *Holt* 144 (2) PRE. *Horler* 218 (1a) PRE. *Horrocks* (15a) NBG. *Hugo* 1394a (6) NBG; 1481 (5) NBG. *Hunter* 20 (3) PRE. *Hurling & Neil s.n.* (13) BOL. *Hutchings* 615 (1a) NU. *Hutchings & Hutchings* 2601 (1a) NU; 3016, 3017, 3019 (1b) MO. *Hutton* 599 (1a) PRE.
- Jacobsen* 1404, 2558 (1a) PRE; 5002 (1b) PRE; 5437 (2) NBG. *James* (1a) K. *Jansen & Boane* 7879 (2) K, LMU, MO. *Jooste* 179 (7) NBG.
- Keet* 1042 (15a) PRE. *Kemp* 1151 (1a) PRE. *Kies* 246 (3) PRE. *Killick* 259 (1a) PRE. *Kluge* 1172, 1499, 1569 (1a) PRE; 2531 (1b) PRE. *Kurzweil* 1677 (2) NBG; 1820 (1a) NBG.
- Le Maitre* 335A (9b) PRE. *Le Roux* 343 (9a) NBG; 2112 (9b) NBG. *Leach & Bayliss* 10644 (2) PRE. *Leendertz* 698 (2) BOL; 4061 (1a) PRE. *Leipoldt* 161 (9b) BOL, NBG, PRE; 3466 (9a) BOL. *Leistner & Joynt* 2700 (3) PRE. *Levy* 4283 (15a) BOL; 1029 (9a) SAM; 2296 (9b) SAM; 2327 (9b) PRE, SAM; 4432 (7) SAM; 5629 (15a) NBG; 5880 (8) NBG; 5911, 6133 (13) NBG; 5970, 6048 (7) NBG; 5978, 5990 (9a) NBG, PRE; 6006, 6189, 6190 (16) NBG; 6151, 6178 (1a) NBG. *Linder* 1223 (1a) PRE; 2461 (9a) BOL. *Long* 1349 (6) PRE. *Lotter* 816 (1a) PRE. *Loubser* 908 (6) NBG; 999, 2118 (7) NBG; 2017 (15b) NBG; 2035 (9a) NBG. *Louw* 3181 (1a) NBG. *Low* 7004, 7838, 7947 (8) NBG. *Lucas* 188 (1a) K.
- MacOwan* 90 (6) SAM; 378 (1a) SAM. *Mainwaring* 2673 (1a) K. *Malaisse* 4889 (1a) BR, K; 13868 (1a) BR. *Manning* 1076, 2810, 2812 (13) NBG; 2657 (1a) NBG; 2760 (8) NBG; 2883 (7) NBG; 2884 (4) NBG; 2885 (6) NBG; 2934 (3) NBG. *Markötter* 8664 (1a) NBG. *Marloth* 67 (1a) PRE; 7494 (3) PRE; 10429, 12815 (8) NBG, PRE; 14192 (13) PRE. *Martin* 177, 178 (1a) NBG; 374 (15a) BOL, NBG. *Martindale* 19 (1a) NU. *Matthews* 1070 (7) NBG, PRE; 1986 (16) NBG. *Mauve* 4758 (7) NBG, PRE; 4781 (7) PRE. *Mauve & Oliver* 226 (7) NBG, PRE. *McDonald* 458 (1a) NU; 1193 (10) NBG. *Medley Wood* 4896 (1a) NBG, PRE. *Merxmüller & Giess* 28592 (9b) MO. *Middelmost* 1684 (13) NBG; 2148 (9b) NBG; SAM61716 (15a) SAM. *Miller* 2652 (2) K, LISC, SRGH. *Milne-Redhead & Taylor* 9272 (2) K. *Mogg* 13847 (1a) PRE; 15877 (2) PRE. *Moll* 1976 (1a) PRE. *Mucina* 6436/7 (15a) PRE. *Muir* 383 (15a) SAM; 5570 (16) PRE. *Muller* 1013 (3) PRE. *Myre & Carvalho* 2571 (1a) LMA. *Myre & Macedo* 4344 (1b) LMU.
- Neethling s.n.* (14) BOL. *Netshiungani* 842 (2) PRE. *Nicholas* 1467 (1b) NH. *Nordenstam & Lundgren* 1148 (7) NBG. *Norlindh & Weimarck* 4223 (2) SAM.
- Obermeyer* 2770 (2) PRE. *Oliver* 3557, 4636 (5) NBG; 3596 (6) NBG, PRE; 3658 (6) NBG; 7705, 9472 (9b) NBG; 9448 (13) NBG; 9579 (8) NBG, PRE; 10797 (16) NBG. *Oliver, Tölken & Venter* 439 (9b) PRE. *Orpen* 280 (3) SAM.
- Pamphlett* 77 (9a) NBG. *Papendorf* 265 (2) PRE. *Paterson-Jones* 540 (15b) NBG; 855, 855A, 860 (11) NBG. *Pawek* 9161 (1a) K, MAL, MO, SRGH. *Pegler* 858 (1a) PRE. *Pentz* 56 (1a) PRE. *Pereira, Marques & Balsinhas* 469 (1b) LMU. *Perry* 118 (13) NBG; 2018 (2) NBG. *Phelan* 742 (1a) NU, PRE. *Phillipson* 3196 (1b) MO, RUH. *Pienaar* 1202 (2) PRE. *Plowes* 6085 (1a) PRE. *Pole-Evans* 3554 (1a) PRE. *Pole-Evans & Smith* 1811 (3) PRE; *Polhill & Paulo* 1382A (1a) B, BR, K, LISC, SRGH. *Pooley* 1868, 1869 (1a) NU; 1870, 2146 (1b) NU; 473 (2) E, NU. *Pope & Müller* 1520 (2) SRGH. *Pott* 5463 (1a) PRE; 12779 (2) PRE. *Prosser* 1829 (2) PRE.
- Raal & Raal* 1154 (1a) PRE. *Raitt* 0519 (10) NBG. *Reid* 1101 (2) PRE; 1497 (8) NBG, PRE. *Rens* 10 (2) BOL. *Repton* 1189 (1a) PRE; 1591, 3892 (2) PRE. *Retief* 224A (1a) PRE. *Reyneke* 220 (1a) PRE. *Richards* 8724, 12110, 12295 (1a) K; 15005 (1a) K, MO, SRGH. *Robinson* 2007 (2) K, SRGH. *Robson* 1428 (2) K, LISC, MAL, SRGH. *Rodin* 1320 (15a) BOL; 3898 (2) PRE; 4695 (1b) PRE. *Rogers* 4146 (15a) PRE. *Ross* 1 (2) PRE; 2223 (1a) PRE. *Roussouw* 225 (2) PRE. *Rudatis* 79 (2) NBG. *Rycroft* 3084 (15a) NBG.
- Salter* 4819 (15b) BOL. *Sanane* 145 (1a) B, K. *Schäfer* 6640 (1a) LMU, WAG. *Schajies* 2256 (1a) K; 3286 (2) BR. *Scharf* 1416 (6) PRE; 1582 (6) NBG. *Scheepers* 136 (2) PRE. *Schlechter* 3109 (1a) BOL, PRE; 8019 (9b) PRE; 12150 (2) BOL. *Schlieben* 9159a (3) PRE. *Schutte-Vlok* 854, 858 (16) NBG. *Scully* 112 (1a) SAM. *Sim* 715 (1a) NU; 4083 (6) NU; 19892 (6) NU, PRE; 19902 (1a) PRE; 19904 (1a) NU, PRE. *Simão* 339 (2) LMA. *Singh & Baijnath* 258 (1a) PRE. *Smart* 22794 (15a) PRE. *Smith* 385 (3) PRE; 1664 (2) PRE; 3045 (15b) PRE. *Smuts* 2328 (1a) PRE. *Smuts & Gillett* 2197, 2489 (1a) NBG; 2346 (1a) NBG, PRE. *Snijman* 123 (13) NBG; 327, 360 (6) NBG; 1894 (8) NBG; 1986 (9b) NBG. *Stalmans* 409, 1100, 1258 (2) PRE. *Stanton* 9 (1a) NU. *Stayner* 49 (1a) PRE. *Steiner* 1713 (9b) NBG. *Steyl* 2 (1a) NBG. *Steyn* 348 (13) NBG. *Stirton* 10783b (6) NBG. *Strey* 6815, 10446 (1b) PRE. *Strydom* 215 (2) PRE. *Styles* 158 (1a) NU. *Swanepoel* 51 (1a) NU. *Swierstra* 7412 (2) PRE. *Synnott* 1024 (1a) K.
- Taylor* 12 (1b) NU; 2039 (1a) PRE; 3002 (13) NBG; 3633 (6) NBG. *Teague* 338 (2) BOL. *Theron* 862 (3) PRE; 2117 (1a) PRE. *Thode* 6498 (1a) NBG; A1265 (1a) PRE; A2763 (6) PRE. *Thomas* 1959 (1a) K. *Thompson* 1345 (5) NBG; 1888 (6) PRE; 1950 (6) NBG. *Thorncroft* 22 (1a) PRE. *Torre* 8046 (1b) LISC. *Torre, Carvalho & Ladeira* 18812 (2) LISC.
- Ubbink* 1214 (2) PRE.
- Vahrmeijer & Tölken* 912 (1b) PRE. *Van Dam* 23286, 25684 (2) PRE. *Van der Linden* 23 (1a) NU. *Van der Merwe* 2981 (7) PRE. *Van der Schijff* 113 (2) PRE; 5969 (1a) BOL. *Van Jaarsveld* 10984 (6) NBG. *Van Maanen s.n.* (3) NBG. *Van Niekerk* 75, 482 (7) BOL, PRE; 443 (16) BOL; 577 (7) BOL; 10255 (2) PRE. *Van Vuuren* 381 (2) PRE. *Van Wijk* 163 (2) PRE; 1961 (15b) NBG. *Venter* 9214 (1a) PRE. *Verdoorn* 628 (1a) PRE; 781 (2) PRE. *Victor* 296 (15a) PRE; 2400 (1a)

PRE. *Vimpany* s.n. (3) BOL. *Viviers* 279, 385 (13) NBG, PRE; 310 (13) NBG. *Vlok* 329 (5) NBG. *Volk* s.n. (14). *Vos* 161 (1a) NU.

Walters 144 (9b) NBG; 467, 505, 2469 (7) NBG; 157 (11) NBG. *Ward* 5, 440 (1b) NU; 452, 3301 (1a) PRE; 3112 (2) PRE; 8653 (1b) NU, PRE. *Werdermann & Oberdieck* 2172 (1a) PRE. *West* 995 (1a) PRE. *Willemse* 649 (15a) NBG. *Williamson*

3526, 3528, 3531 (9b) NBG. *Wisura* 1201 (2) NBG. *Wragg* 718 (1b) NU. *Wurts* 1432 (4) NBG; 1556, 2236 (15a) NBG.

Young 56 (1a) PRE.

Zambatis 312 (1a) PRE. *Zantouska* 93 (5) PRE. *Zeyher* 88.10 (6) PRE; 286 (6) NBG, PRE, SAM; 1618 (9b) BOL; 4026 (6) SAM. *Zinn* s.n. (5) SAM.



A decorative illustration in orange ink, featuring a central horizontal line with several stylized flowers and leaves branching out from it, positioned above the 'EXCLUDED SPECIES' header.

EXCLUDED SPECIES

Freesia angolensis (Baker) Klatt in Dur. & Schinz., *Conspectus florae africae* 5: 187 (1894); *Anomatheca angolensis* Baker: 337 (1876). This is a synonym of *Lapeirousia schimperi* (Asch. & Klatt) Milne-Redh. (Goldblatt 1990).

Freesia curvifolia Klatt in Dur. & Schinz., *Conspectus florae africae* 5: 187 (1894). This is a name without description, thus illegitimate. Its identity is unknown.





FLORAL SCENT CHEMISTRY OF FREESIA SPECIES

by R. Kaiser

The attractive scent of *Freesia* flowers, praised by poets and prized by perfumers, has made the genus one of the most important ornamentals in the flower trade, particularly in Europe and Japan, where the appearance of the blooms in florists' shops is welcomed as a harbinger of spring. Despite the wide appeal of their scent, however, the fact that the delicate flowers generate disturbing olfactory artefacts during extraction which render the final product worthless, has meant that no commercial extracts in the form of essential oils or absolutes are available.

Among the many cultivated varieties of *Freesia* that have been produced, it is the highly scented, pure white, creamy-white, and yellow forms that are especially popular (Table 8). The scent composition (Figure 22: the number of the structural illustration of the chemical in Figure 22 is indicated by a number in bold type in brackets in the text) of commercial freesias is dominated by linalool (**1**), α -terpineol (**2**) and the ionones (**3**, **4**) (Harada & Mihara 1984; Mookherjee *et al.* 1988). Individually, all of these molecules are common and widespread components of floral volatiles in flowering plants, emphasizing the importance of particular combinations of compounds rather than the presence of novel chemicals in producing distinct scent accords. Among the 2 800 fragrant plant species that have been investigated over the past 30 years in the Givaudan Laboratory, linalool (**1**) occurs in 76 % of the species, α -terpineol (**2**) in 30 %, β -ionone (**3**) in 21 %, and dihydro- β -ionone (**4**) in 11 %.

The scent of commercial *Freesia* hybrids has been the subject of several investigations (Harada & Mihara 1984; Mookherjee *et al.* 1988) but far less is known about the wild species. The most comprehensive study to date, an investigation of nine species and 16 cultivars (Wongchao-

chant *et al.* 2005), is at least partially misleading because only gas chromatography (GC) retention times were used as an identification tool, resulting in the misidentification of some important compounds. There is also no indication as to the origin of the material analysed, and the correct application of names is a primary consideration in the genus given past nomenclatural confusion. Another recent study of the floral volatiles of *F. refracta* and six cultivars by Fu *et al.* (2007) used a combination of gas chromatography and mass spectrometry to identify the presence of 75 compounds but unfortunately most of these compounds cannot be considered as being of genuine origin or even of having been correctly identified.

The present study analysed the scent composition of 13 wild taxa (11 species plus two subspecies) out of a potential 15 found to be fragrant to the human nose (Table 4; Appendix).

The yellow-flowered *Freesia leichtlinii* subsp. *leichtlinii* and *F. fergusoniae* most closely resemble the commercial cultivars in their scent profile. The strong ionone-floral scent of these taxa, generated by β -ionone (**3**) (Figure 22) and dihydro- β -ionone (**4**) and blended with the typical pine-needle/floral note of α -terpineol (**2**) or the mild floral-woody note of linalool (**1**), epitomizes the scent that is popularly associated with the genus. Two other marker chemicals of low concentration and minor olfactory importance, 2-methylbutyraldoxime (E+Z) and α -selinene, also characteristic of these two species, are also found in the yellow-flowered cultivars. Commercial white *Freesia* cultivars show a stronger similarity in their fragrance profile to *Freesia corymbosa*. Significant marker compounds, all derived from the main compound linalool (**1**), are 2-methyl-2-vinyltetrahydrofuran-5-ol, 2,6-dimethylocta-3,7-

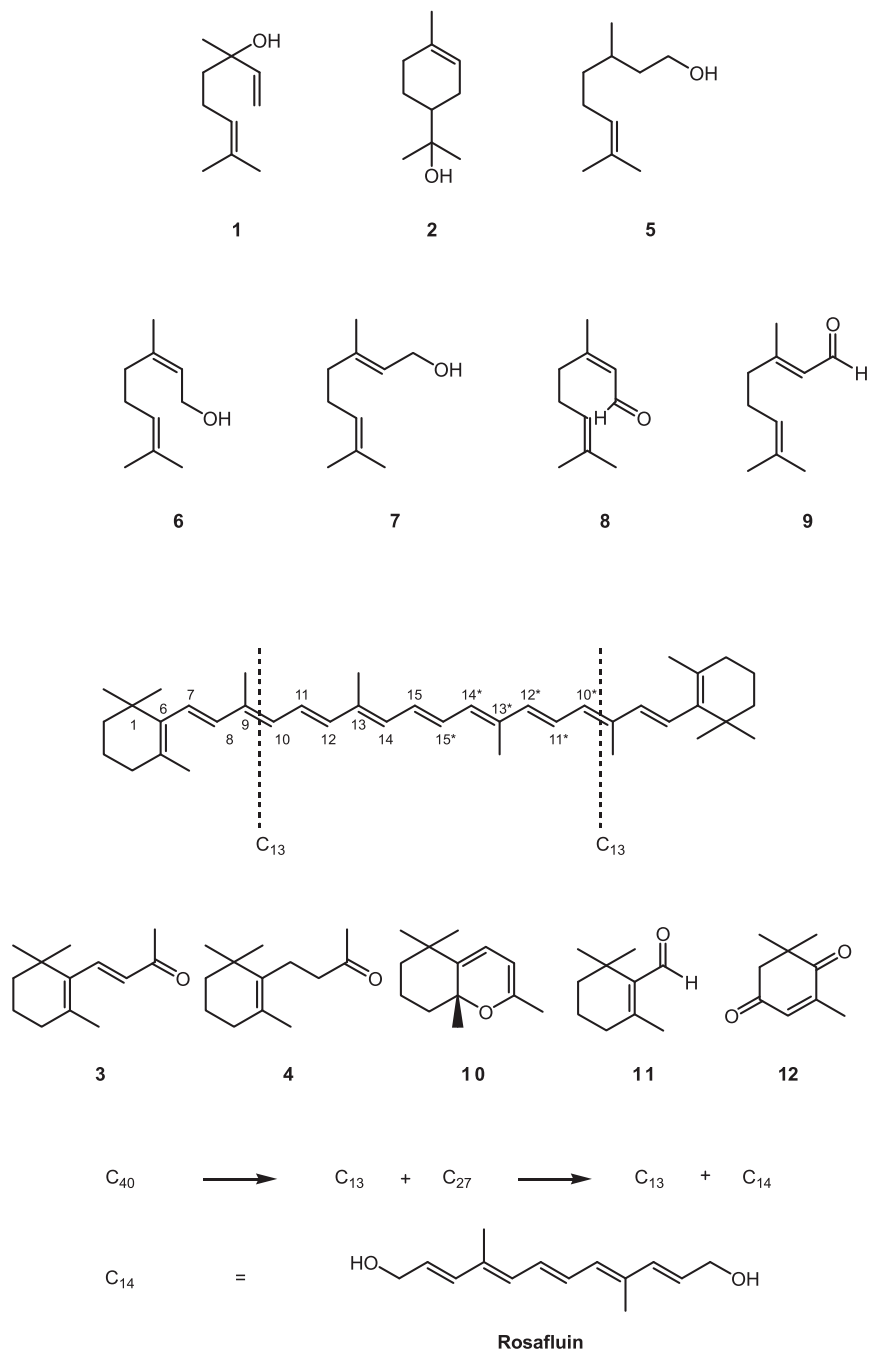


FIGURE 22.—Carotenoid-derived compounds in *Freesia* scents.

dien-2,6-diol and 2,6-dimethylocta-1,7-dien-3,6-diol. The presence of 2-methylbutyraldoxime, α -terpineol and β -ionone in these white cultivars reflects the involvement of *Freesia leichtlinii* subsp. *leichtlinii* in their parentage.

Other species, however, deviate significantly from this scent accord, in particular *Freesia refracta* and the two subspecies of *Freesia viridis*, all of which emit a strong and deep rosy-floral scent due to citronellol (**5**), nerol (**6**) and geraniol (**7**) together with a lemony shade caused by neral (**8**) and geranial (**9**). The mixture of the latter two isomers is also known as citral, the key compound for the lemon scent in many essential oils. Adding an adequate amount of 2-phenylethyl alcohol to this rosy-floral freesia scent would result in the classical scent of *Rosa centifolia* or *Rosa damascene* (Kaiser 2006). The rosy-floral concepts of *Freesia refracta* and *F. viridis* merge in *F. caryophyllacea* with the mild floral-woody note of linalool (**1**) (which dominates the scent of *F. andersoniae*, *F. corymbosa* and *F. speciosa*) and the pine-needle/floral note of α -terpineol (**2**) (co-occurring with the violet-related notes of the ionones (**3**, **4**) in *F. leichtlinii* and *F. fergusoniae*), to produce a wonderful freesia scent that is not well known to the public through the commercial cultivars.

Linalool (**1**) is present in the scents given off by many night-blooming species but it is most unusual to find it in concentrations of $\pm 80\%$ or more, as produced by *Freesia andersoniae* and *F. speciosa*. Similar high concentrations of linalool have been found in *Gladiolus maculatus* (Iridaceae) (Goldblatt & Manning 2002), and in *Citrus medica* (Rutaceae), *Asplundia ewanii* (Cyclanthaceae) and *Catasetum vinaceum* (Orchidaceae) (Kaiser unpublished obs.). *F. speciosa* also includes an appreciable concentration of methyl benzoate in its scent profile, a compound not found in other species of *Freesia*.

The ionones, β -ionone (**3**) and dihydro- β -ionone (**4**) are present in the scent profiles of all fragrant species in sect. *Viridibractea* that have been analysed, and are also present in small amounts in some populations of *Freesia viridis*, but are absent in all species in subgen. *Freesia* (Table 4). They appear, therefore, to be a phylogenetic marker, providing corroborative bio-

chemical evidence for the relationship between *F. viridis* and the gullet-flowered species in sect. *Viridibractea* suggested by DNA sequence data and bract texture. These ionones and their derivatives have found an enormous appreciation in perfumery during the past three decades and many of the famous fragrances contain high amounts of **3** and **4**, often in ratios similar to those found in nature (Kaiser 2006). This is due to their attractive olfactory profile, their potential to form new fragrance accords with other products, and their low odour thresholds. The term 'ionone-floral' has even become a descriptor of natural scents as well as fragrances (Kaiser 1993a, b).

These ionones are most likely the product of enzymatic cleavage of the carotenoids present as pigments in the flower, which accords with our localization of the dark yellow or orange markings on the lower tepals of *Freesia leichtlinii* subsp. *alba* as the primary sites for the production of fragrance in the flowers. Eugster & Märki-Fischer (1991) found that the postulated Car (9,10:9',10') dioxygenase is not specific to the carotenoid end groups but also causes eccentric cleavage leading to the corresponding C₁₃ catabolite and the C₂₇ alcohol. In many cases the latter may be transformed into the C₁₄ diol rosaflurin and a second C₁₃ compound. As discussed and reviewed by Winterhalter (1996) and Kaiser (2002), not only the C(9/9')=C(10/10') bond but also the C(7/7')=C(8/8') or, after isomerization and/or other steps, the C(6/6')=C(7/7') bond, may be attacked by dioxygenesis, leading finally to a great variety of carotenoid-derived volatiles. Thus the flower scent of *F. caryophyllacea* includes β -cyclocitral (**11**) and that of *F. leichtlinii* subsp. *leichtlinii* 2,2,6-trimethylcyclohex-2-en-1,4-dione (**12**) as minor components. The scent of both species also contains the photocyclization product of β -ionone, the so-called cyclic- β -ionone (**10**), as well as additional examples of this type of compound. This illustrates that such primarily formed volatiles can be additionally transformed, in this case by exposure to sunlight.

Minor differences in the fragrance profile between samples are evident in all species in which multiple populations were investigated, suggesting that quantitative and qualitative variation in floral scents is a normal characteristic of biologi-

TABLE 4.—Olfactory descriptions of floral fragrance in *Freesia*

Taxon	Olfactory description	Voucher
<i>F. andersoniae</i>	mild floral-woody scent typical of linalool with slightly sour note	Free State, Windsorton, Manning 2934 (NBG)
<i>F. caryophyllacea</i> 1	ionone-floral with typical rosy-floral note generated by combination of geraniol and geranyl acetate and note of α -terpineol	Western Cape, Napier, no voucher
<i>F. caryophyllacea</i> 2	ionone-floral scent with typical rosy-floral note of geraniol and notes of α -terpineol and linalool	Western Cape, Onrus, Manning 2810 (NBG)
<i>F. corymbosa</i> 'Armstrongii'	mild floral-woody, typical of linalool with slightly sour, bitter note	Western Cape, Joubertina, ex hort. NBG141/85
<i>F. fergusoniae</i>	strong ionone-floral scent with pine-needle/floral note of α -terpineol	Western Cape, Heidelberg, Goldblatt & Manning 12252 (NBG)
<i>F. fucata</i>	ionone-floral scent with mild floral-woody note of linalool	Western Cape, Villiersdorp, Manning 2271 (NBG)
<i>F. grandiflora</i>	no detectible fragrance	ex hort. Kirstenbosch Garden, no voucher
<i>F. laxa</i> subsp. <i>laxa</i>	no detectible fragrance	KwaZulu-Natal, Drummond, Manning 2657 (NBG)
<i>F. leichtlinii</i> subsp. <i>alba</i> 1	ionone-floral with pine-needle/floral note of α -terpineol and shade of floral-woody note of linalool	Western Cape, Blombos, Goldblatt & Manning 12257 (MO, NBG)
<i>F. leichtlinii</i> subsp. <i>alba</i> 2	ionone-floral scent with mild floral-woody note of linalool and shade of pine-needle/floral note of α -terpineol	Western Cape, Plettenberg Bay, ex hort. NBG796/71, Hiemstra 344
<i>F. leichtlinii</i> subsp. <i>leichtlinii</i>	strong ionone-floral scent generated by β -ionone and dihydro- β -ionone with typical pine-needle/floral note of α -terpineol	Western Cape, Agulhas, ex hort. Kirstenbosch, Duncan 534a
<i>F. occidentalis</i>	faint slightly rosy-floral with lemony shade	Western Cape, Karooport, Manning 2760 (NBG)
<i>F. praecox</i>	ionone-floral scent based on pine-floral note of α -terpineol and tender-floral note of linalool, with violet-related notes of β -ionone and dihydro- β -ionone	Western Cape, Riviersonderend, Manning 2921 (NBG)
<i>F. refracta</i>	strong and deep rosy-floral with lemony shade	Western Cape, Worcester, no voucher
<i>F. sparmanii</i>	no detectible fragrance	Western Cape, Grootvadersbos, Goldblatt & Porter 12379 (MO, NBG)
<i>F. speciosa</i>	mild floral-woody and somewhat lemony with lily-related aspects. Sour/bitter hint present during day but not at night.	Western Cape, Calitzdorp, Manning 2884 (NBG)
<i>F. verrucosa</i>	no detectible fragrance [other populations recorded as lightly scented]	ex hort., no voucher
<i>F. viridis</i> subsp. <i>crispifolia</i>	strong rosy-floral, typical of combination of citronellol, nerol and geraniol with lemony shade generated by neral and geraniol	Western Cape, Trawal, no voucher
<i>F. viridis</i> subsp. <i>viridis</i>	rosy-floral, typical of combination of citronellol, nerol and geraniol with lemony shade generated by neral and geraniol	Western Cape, Langebaan, Goldblatt & Manning 9215 (MO, PRE)

cal systems. Careful analysis of the apparent differences is necessary to fully appreciate their significance. The quantitative difference between *Freesia viridis* subsp. *viridis* and *F. viridis* subsp. *crispifolia* appears rather obvious, especially regarding limonene, although the scent concept remains the same in both samples (Table 5). The difference is significantly reduced, however, by recalculating the quantitative data that were measured in the gas phase to the hypothetical liquid phase necessary to reproduce these headspace concentrations. In order to generate 26 % of limonene in the gas phase of such a mixture, only 0.3 to 0.4 % of limonene is required in the corresponding liquid phase, whereas over 30 % of geraniol is necessary to get a headspace concentration of 11.8 %. This reflects the relatively high volatility and high vapour pressure of limonene compared to the comparatively low volatility and vapour pressure of geraniol.

A more significant infraspecific difference is shown by the quantitative variation in linalool

and α -terpineol in the two populations of *Freesia leichtlinii* subsp. *alba*, one from either end of the range of the subspecies (Table 6). The significance of these differences is reduced by the somewhat intermediate nature of the single sample of *F. leichtlinii* subsp. *leichtlinii*. There are also quantitative differences in the scent composition of the two samples of *Freesia caryophyllacea*, especially in the relative levels of geraniol (7) and its acetate, although the scent concept for both specimens remains the same.

The identification of ionone-negative and ionone-positive groups in the genus raises the exciting possibility of developing distinct fragrance-lineages in *Freesia*. The potential for this was effectively removed from current breeding programmes by the very early crossing of *F. leichtlinii* with *F. corymbosa*. Our new understanding of relationships among the species opens up the opportunity for selective breeding within each of the two fragrance-groups to derive fragrance-cultivars that can only enhance our enjoyment

TABLE 5.—Primary olfactory components and olfactory perception of scent in *Freesia* subgen. *Freesia* (% composition)

Compound	Olfactory perception	<i>F. andersoniae</i>	<i>F. speciosa</i>	<i>F. corymbosa</i>	<i>F. refracta</i>	<i>F. occidentalis</i>
Limonene	bright, fresh base note of citrus peel	0.40	0.20	0.20	1.4	0.60
Eucalyptol	fresh cool-camphoraceous		0.02		0.02	
(E)-ocimene	diffuse, clean 'floral-woody' terpenic	0.02	0.03		0.10	
Linalool	attractive soft floral-woody	92.0	79.0	66.5	1.1	1.1
Methyl benzoate	heavy-sweet, deep aromatic-floral, somewhat pungent		16.10			
2-methyl-2-vinyltetrahydrofuran-5-ol		0.1	1.20	12.6		
α -terpineol	floral, sweet with pine-needle undertones			0.20	0.20	
Neral	zesty, green, lemon-peel				2.2	2.0
Geranial	zesty, fruity, lemon-peel				2.3	2.3
Citronellol	fresh, diffuse, rose-petal				19.4	
Nerol	fresh rose-like with citrus undertones				57.5	77.8
Geraniol	deep, floral rose				8.9	0.30
Dihydro- β -ionone	unique floral and woody					
β -ionone	unique floral-woody, reminiscent of freesia and violet					

of this wonderful genus. It is a great pity, for instance, that *F. caryophyllaceae* has never been involved in breeding programmes. Combining this species to the existing mix of olfactory characteristics from *F. leichtlinii* subsp. *leichtlinii* and

F. corymbosa would add rosy-floral notes via geraniol and nerol including derivatives. This aspect could also be introduced more selectively through *F. refracta*, which is extremely rich in these rose compounds.

TABLE 6.—Primary olfactory components of scent in *Freesia* subgen. *Viridibractea* (% composition; see Table 5 for olfactory perception of individual compounds)

Compound	<i>F. viridis</i>		<i>F. fucata</i>	<i>F. leichtlinii</i>			<i>F. caryophyllaceae</i>		<i>F. praecox</i>	<i>F. fergusoniae</i>
	subsp. <i>viridis</i>	subsp. <i>crispifolia</i>		subsp. <i>leichtlinii</i>	subsp. <i>alba</i> 1	subsp. <i>alba</i> 2	1	2		
Limonene	26.0	0.04	0.3		0.2	7.9	3.5	2.3	19.5	8.2
Eucalyptol	0.50			3.0	0.4	9.5	4.8	2.6	3.7	6.7
(E)-ocimene			54.0	16.8	0.2	12.5	10.2	26.9	0.5	2.6
2-methylbutyraldoxime			0.6							0.1
Linalool	0.2	0.04		2.2	86.4	4.3	13.4	0.7	19.7	8.8
α -terpineol				29.3	1.7	35.8	34.0	23.5	25.0	23.2
α -selinene				0.2		0.3				0.8
Neral	0.80	0.90					0.2	0.05		
Geranial	1.0	1.30					0.5	0.3		
Citronellol	6.5	23.5		0.05					0.05	
Nerol	27.7	41.5		0.05			0.6			
Geranyl acetate		0.03					0.1	9.9		
Geraniol	11.8	27.0		0.05			12.8	3.2		
Dihydro- β -ionone			1.8	2.4	0.5	1.2	1.2	0.3	0.8	2.3
β -ionone		0.06	23.0	27.5	1.6	2	4.2	2.9	1.5	19.1





POLLINATION BIOLOGY

Almost nothing is known about pollination in *Freesia*, a striking contrast to many other genera of Crocoideae, which have been well studied in this regard (Goldblatt & Manning 2006). Specialist pollination systems dominate among the southern African Iridaceae and several distinct pollination syndromes have been identified, making it possible to predict the likely pollinators of most species of *Freesia* despite our scant knowledge of pollination in the genus.

The narrow-tubed flowers of *Freesia grandiflora*, *F. laxa*, *F. viridis* and *F. verrucosa* ensure that floral visitors remain outside the perianth while foraging for nectar. Three floral syndromes can be identified among these species. The narrowly funnel-shaped flowers of *F. verrucosa*, with a moderately long perianth tube, 15–20 mm long, are pink with small red and yellow markings on the lower tepals and either unscented or lightly scented during the day. They are typical of flowers pollinated by long-tongued, nectar-collecting bees, and we have observed anthophorine bees visiting the species in the wild. A second pollination syndrome is evident in *F. laxa* and *F. grandiflora*, which produce unscented, salver-shaped, scarlet (rarely pink or mauve) flowers with dark red markings at the mouth of a long, $\pm$ straight floral tube, 20–40 mm long. These flowers are probably pollinated by day-flying butterflies (or possibly by tangle-veined flies in the case of *F. laxa* subsp. *azurea*) but no visits have been observed. A third syndrome is demonstrated by *F. viridis*, which has unique, green or brown flowers with the tube curved sharply downwards at the tip so that the flowers face the ground. The tepals are sharply recurved or somewhat twisted at the tips and the anthers are included within the upper portion of the tube. The dull coloration, attenuate tepals, and included stamens are all characteristics of flowers adapted for pollination by night-flying settling moths, especially noctuids, and the sweet or sometimes spicy fragrance that

is produced at night by the species, reinforces this conclusion. Again, observations are lacking.

The gullet-shaped flowers that characterize the remaining species are structured such that floral visitors may crawl into the broad upper part of the flower tube in order to reach the nectar contained in the narrow lower portion. The flowers are white to pale or deep yellow (rarely pink), often flushed purple on the outside, with bright yellow or orange markings and often dark streaks on some or all of the lower tepals, and are moderately or strongly sweetly scented (unscented in *Freesia sparrmanii*). Excision experiments that we have carried out on flowers of *F. leichtlinii* subsp. *alba* show the primary site of fragrance production to be the yellow or orange patches on the lower tepals. The funnel-shaped perianth tube has a basal narrow portion 5–15(–20) mm long. Superficially similar flowers are widespread among Crocoideae and are adapted to pollination by long-tongued, nectar-collecting bees, primarily in the Apidae: Anthophorinae. We have observed visits to *F. refracta* by species of *Amegilla* (Apidae: Anthophorinae) and *Andrena* (Andrenidae), and visits to *F. fucata* by *Amegilla*, which confirm that long-tongued, nectar-collecting bees are very likely the primary pollinators in the subgenus. Although the flowers in this group typically cease scent production at night, those of *F. andersoniae* and *F. speciosa* remain strongly fragrant throughout the day and night, raising the possibility that these species are at least partially pollinated by moths. This is strengthened by the scent chemistry of the flowers (Table 5; Appendix), which is dominated by linalool, a common component in the scent profile of many moth-pollinated Iridaceae (Goldblatt & Manning 2002, 2006).

Flowers of *Freesia*, like those of the majority of Crocoideae, remain fresh for several days, typically $\pm$ three days. The flowers of most spe-

cies appear to show more or less marked circadian rhythms in perianth closure and/or scent production. Nastic movements are most marked in *F. verrucosa*, in which the flowers close up tightly at night. This behaviour is unique in the genus and contrasts sharply with the other tubular-flowered species, *F. grandiflora*, *F. laxa* and *F. viridis*, which show no closing movements. Species with gullet-flowers similarly show no or at most only slight closing movements at night or in cold weather but observations are largely lacking. The timing of scent production, in contrast, is much more strictly regulated. Scent production in the fragrant species with gullet-flowers is highest during the day and diminishes markedly or ceases entirely at night. The flowers of *F. andersoniae* are exceptional in remaining open and strongly fragrant throughout the day and night. *Freesia viridis* is unique in the genus in having flowers that are unscented during the day but become strongly fragrant at dusk.

Freesia flowers in the six species that we have examined for nectar (standing crop) show modest quantities by volume, in the range 1.0–2.0 μ l. Among the putatively bee-pollinated species, *F. refracta* has the highest nectar volume of any species we have examined (2.6–3.8 μ l), and nectar sugar concentrations in these species are relatively high (35–45 % sucrose equivalents) compared to other known bee-pollinated species of Iridaceae. The putatively moth-pollinated *F. viridis*, in contrast, has the lowest nectar volume (< 1.0 μ l) with slightly lower nectar sugar concentration (35–38 % sucrose equivalents).

All populations of *Freesia laxa* and *F. viridis* tested for self-pollination in the greenhouse have proved to set seed autogamously and this appears to be a characteristic of these two species. Other species will not self-pollinate.





ECOLOGY

Freesia is largely confined to the southern African winter rainfall region, where the species are concentrated in the southern and south-western coastal regions (Figure 23). The genus is best represented in areas of low or moderate, seasonal rainfall. Among the winter-growing species, *F. viridis* extends furthest north, into southern Namibia but most of the remaining species occur exclusively in South Africa. Exceptions to this pattern are *F. andersoniae*, which although winter-growing, is widespread through the semi-arid interior of South Africa, and the two normally summer-growing species *F. grandiflora* and *F. laxa*, which are restricted to the summer rainfall region, ranging from southeastern South Africa northward into tropical Africa. Species occur from sea level to over 1 000 m but none are strictly montane. In tropical Africa, *F. grandiflora* occurs from near sea level to about 2 000 m on the African central plateau and *F. laxa* occupies montane habitats in East Africa and Sudan but in southern Africa it occurs along the coast from near sea level to well inland.

Most *Freesia* species favour open scrubland, usually renosterveld or Succulent Karoo but also fynbos and coastal thicket (Table 7). Exceptions are *F. grandiflora* and *F. laxa*, found in subtropical savanna, woodland and forest; *F. andersoniae*, from arid savanna and Nama Karoo; and *F. sparrmanii*, which is restricted to the margins of afrotemperate forest. Despite their prevalence in the Cape Floristic Region (Goldblatt & Manning 2000), few freesias are true fynbos elements, i.e. restricted to the acidic, nutrient-poor soils associated with this vegetation type. Only *F. praecox* appears to be restricted to fynbos, although a few other species spread into fynbos habitats. These include *F.*

occidentalis, which extends from mountain renosterveld into marginal fynbos in sandstone soils in the Swartruggens and eastern Cedarberg Mountains; *F. caryophyllacea*, which occurs in fynbos on limestone soils around Bredasdorp but is restricted to renosterveld across the greater part of its range; and *F. leichtlinii*, found in coastal fynbos as well as thicket vegetation.

Freesia species favour medium-textured, moderately fertile, loamy or clay soils, and *Freesia leichtlinii* is unique in preferring limestone or lime-enriched sands along the coast. Unlike many other Iridaceae of the Cape Floristic Region, most species of *Freesia* are not strict edaphic endemics, usually occurring on a variety of soil types. *Freesia viridis*, for instance, has been collected on granite, limestone, sandstone and clay; *F. corymbosa*, *F. occidentalis* and *F. refracta* on sandstone and clay; *F. caryophyllacea* on limestone and clay; and *F. leichtlinii* on pure limestone as well as lime-enriched sands.

Species vary greatly in the extent of their distribution (Table 7). At one extreme are highly localized endemics such as *Freesia praecox*, known only from the southern foothills of the Riversonderend Mountains; *F. fucata* and *F. marginata*, restricted to small parts of the Breede River Valley; and *F. sparrmanii*, found only on the margins of the Grootvadersbos forest in the Langeberg foothills near Heidelberg in the southern Cape. In contrast, *F. grandiflora* is widely distributed through eastern subtropical and tropical Africa, and *F. laxa* ranges from southeastern South Africa to southern Sudan. The remaining species fall somewhere between these two extremes, and have relatively circumscribed ranges.



FIGURE 23.—Distribution of *Freesia*, showing numbers of species in the areas of occurrence.

TABLE 7.—Distribution and ecology of *Freesia* species

Subgen. <i>Freesia</i>	Distribution	Habitat	Flowering time
1. <i>F. laxa</i>	South Africa: Eastern Cape to Mpumalanga; Swaziland, Mozambique, Malawi, Tanzania, Kenya, Uganda, Sudan	Woodland, forest margins, coastal dunes	Mainly June–Jan.
2. <i>F. grandiflora</i>	South Africa: KwaZulu-Natal to Mpumalanga; Swaziland, Mozambique, Malawi, Tanzania, Zambia	Savanna, woodland, forest	Mainly Jan.–Apr.
3. <i>F. andersoniae</i>	South Africa: North-West Province and Northern Cape	Savanna and Nama Karoo shrubland	(May) Aug.–Oct.
4. <i>F. speciosa</i>	South Africa: Western Cape (western Little Karoo)	Succulent Karoo shrubland	Aug.–Sept.
5. <i>F. corymbosa</i>	South Africa: Eastern Cape (De Rust to Butterworth)	Renosterveld, Succulent Karoo shrubland, arid fynbos	(May) Aug.–Oct.
6. <i>F. refracta</i>	South Africa: Western Cape (Worcester to Oudtshoorn)	Renosterveld, Succulent Karoo shrubland, arid fynbos	July–Sept.
7. <i>F. occidentalis</i>	South Africa: Western Cape (Swart-ruggens, eastern Cedarberg and Ceres Karoo)	Renosterveld, Succulent Karoo shrubland, arid fynbos	Aug.–Sept.
8. <i>F. verrucosa</i>	South Africa: Western and Eastern Cape (Ladismith to Willowmore and Langkloof)	Renosterveld	Aug.–Oct.
Subgen. <i>Viridibractea</i>			
Sect. <i>Alatae</i>			
9. <i>F. viridis</i>	Namibia and South Africa: Northern and Western Cape (Richtersveld to Mamre)	Succulent Karoo shrubland, arid fynbos, coastal thicket	May–Aug. (Oct.)
Sect. <i>Viridibractea</i>			
10. <i>F. sparrmanii</i>	South Africa: Western Cape (Langeberg foothills near Heidelberg)	Afrotemperate forest margin	Sept.–Oct.
11. <i>F. fucata</i>	South Africa: Western Cape (Hoeks River Valley south of Worcester)	Renosterveld	July
12. <i>F. marginata</i>	South Africa: Western Cape (Breede River Valley near Robertson)	Succulent Karoo	May–June
13. <i>F. caryophyllacea</i>	South Africa: Western Cape (Botrivier to Swellendam)	Renosterveld, limestone fynbos	Apr.–June
14. <i>F. praecox</i>	South Africa: Western Cape (southern foothills of Riviersonderend Mtns)	Fynbos	June–July
15. <i>F. leichtlinii</i>	South Africa: Western Cape (Cape Agulhas to Plettenberg Bay).	Coastal thicket, coastal fynbos	(July) Aug.–Sept. (Oct.)
16. <i>F. fergusoniae</i>	South Africa: Western Cape (Riversdale District)	Renosterveld	(June) July–Aug.

A decorative illustration of a flowering branch with several small, five-petaled flowers and leaves, rendered in a light orange or tan color. It arches over the 'BIOGEOGRAPHY' section header.

BIOGEOGRAPHY

Endemic to continental Africa south of the Sahara, *Freesia* is among the more widely distributed genera of subfamily Crocoideae, ranging from southern Namibia and southwestern South Africa through the eastern parts of the country into Mozambique and northwards to east tropical Africa as far north as southern Sudan (Figure 23; Table 7). This wide range conceals a very uneven occurrence of species, as the distribution of the great majority of species of *Freesia* is tightly focused on the southwestern and southern Cape, with just four species extending beyond the subregion. Four separate and essentially complementary distribution areas are evident, based on climate and ecology. The centre of diversity of the genus is clearly in the temperate southern and central parts of the southwestern Cape, where 12 of the

16 species are endemic, including all members of sect. *Viridibractea*. To the northwest, *F. viridis* (sect. *Alatae*) is distributed along the summer-arid west coast of South Africa into southern Namibia; to the north, *Freesia andersoniae* occupies the semi-arid interior of South Africa, where rainfall is concentrated in autumn; and to the northeast, *F. grandiflora* and *F. laxa* extend along the southeastern and eastern seaboard and near interior of the subcontinent through tropical East Africa to southern Sudan, with rainfall predominantly in the summer months. The biogeographic pattern shown by the genus thus comprises a small, highly circumscribed centre of diversity in the southwestern Cape, with three independent, peripheral areas of occupation, each containing a single or a pair of closely allied species.

A decorative illustration of a flowering branch with several small, five-petaled flowers and leaves, rendered in a light orange or tan color. It arches over the 'SPECIATION PATTERNS' section header.

SPECIATION PATTERNS

Speciation patterns are clearest at present in subgen. *Viridibractea*. Here, species appear to have arisen primarily through geographic or microgeographic speciation, without any shift in floral morphology and pollination system. These small-scale geographical patterns are compounded by local shifts in soil preferences between fine-grained clay, coarse-grained sandstone, and lime-enriched sands, combined in some instances with differences in flowering time (Table 7). Similarly intricate patterns have been identified in the genus *Lapeirousia* (Goldblatt & Manning 1996) but in that genus speciation events are usually associated with shifts in pollination system.

In subgen. *Freesia*, the sister pair *F. laxa* and *F. grandiflora* have diverged through adaptation to slightly different habitats, reinforced by a shift in flowering time: *F. laxa* favours a temperate or maritime climate and flowers mainly between June and January, whereas *F. grandiflora* is essentially tropical or subtropical and flowers mainly from January to April (Table 7). The marked difference in filament length in the two species is certainly associated with a difference in the placement of pollen on visiting butterflies but this has not been studied. The relationships among the remaining species in the subgenus are not clear enough to permit an assessment of speciation patterns.



HORTICULTURAL HISTORY

The horticultural history of *Freesia* is more poorly known than for most plant groups of comparable economic importance. Although the origin of the early cultivars has been documented, the literature is scattered (Goldblatt 1982) and much that has been written appears confusing and contradictory, owing both to the frequent misapplication of specific names and to the vastly different taxonomic interpretations of the genus that have been in use over the last one hundred and fifty years. The history as outlined by Chittenden (1951), Morgan (1929, 1930), Brown (1935), Zeilinga (1971), Goemans (1980), and others, varies in detail and accuracy, and we relate the history here following Goldblatt's (1982) conclusions, giving original sources wherever possible.

Available records indicate that *Freesia* was first grown in Europe in the Netherlands in the mid-eighteenth century. The type collections of both *F. caryophyllacea* and *F. corymbosa* were cultivated there and were described by N.L. Burman in 1768. *Freesia refracta* was grown in Vienna later in the century and was figured in a 1795 publication. None of these early introductions concerns the horticultural history of the genus; however, as the plants do not appear to have been widely grown nor, except for *F. corymbosa*, were they used in the breeding programmes of the later nineteenth century. *Freesia caryophyllacea* evidently did not persist in cultivation but *F. corymbosa* and *F. refracta* either continued to be grown, possibly only by specialist collectors, or were reintroduced from the wild. *Freesia refracta* was occasionally figured in botanical and horticultural publications, notably in Pierre Redouté's, *Les Liliacées* (1813: t. 419) and in Sydenham Edwards's, *The botanical register* (1816: t. 135) in the nineteenth century. *Freesia corymbosa* was illustrated under the name *Tritonia odorata* in Charles Loddiges' *The botanical cabinet* (1832: t. 1820), and was very likely reintroduced at about

this period. Loddiges' name lacks an adequate description and we regard it as illegitimate.

The history of modern *Freesia* cultivation really begins with the discovery in 1872, by the remarkable gardener-plantsman Max Leichtlin, of yellow-flowered plants in the Botanic Gardens at Padua in Italy (Jacob 1909). Leichtlin obtained some specimens for his own garden and proceeded to distribute material widely. The German botanist, F.W. Klatt, was only one of several people who received plants, and in 1874 described the species, naming it *F. leichtlinii* in Leichtlin's honour. *Freesia leichtlinii* was figured repeatedly in horticultural journals in the following decade, evidence that it was a popular ornamental container plant freely available in the nursery trade. How *F. leichtlinii* ever reached Padua will probably remain a mystery but it was received there under the name *F. refracta* as early as 1842, and persisted at Padua for over 30 years (Minelli 1995). Evidence suggests that the species was first discovered in South Africa in the 1820s by C.F. Ecklon and by J.-F. Drège, and either of them may have been responsible for its introduction into Europe, although the period during which these two collectors were active does not quite coincide with the date of its receipt at Padua.

The next introduction of importance was the white-flowered, sweet-scented plant called *Freesia refracta* 'alba', which appeared in the English nursery trade in 1878. This is now *F. leichtlinii* subsp. *alba* and is known today to be native to the southern Cape coast of South Africa, where wild plants most closely matching the introduction occur on coastal rock outcrops near Knysna and Plettenberg Bay. Shortly after its appearance in Great Britain, *F. leichtlinii* subsp. *alba* spread to continental Europe and then to North America. It was figured in numerous horticultural publications over the following decades, generally as

F. refracta 'alba' or *F. refracta* var. *alba*, the use of varietal status here being best understood as meaning what we now call a cultivar, not a taxonomic variety. Its initial treatment as simply a variant of *F. refracta* was most unfortunate because that error has persisted, and still today the cultivated *Freesia* is often called *F. refracta*, even in otherwise reliable publications. Likewise, references to *F. refracta* in the parentage of the cultivated *Freesia* (Bryan 1995) actually apply to *F. leichtlinii* subsp. *alba*.

There is no record of how *Freesia leichtlinii* subsp. *alba* reached England and it may have been a casual introduction. The Cape botanist, Peter MacOwan (1888) hints in a brief note that this species may have been cultivated at the Cape by Ecklon in the 1820s and grown on there continuously. He also suggests that the pure white form was the result of deliberate selection over sixty years but Brown (1935: 25), in his revision of *Freesia* doubted this strongly and Goldblatt (1982) concurred, for there is no evidence supporting this statement. Indeed, the lack of herbarium specimens of *F. leichtlinii* collected by either Ecklon, or others, during the early to mid-nineteenth century, refutes MacOwan's assumption. The southern Cape coast where *Freesia leichtlinii* subsp. *alba* grows is off the main travel routes from Cape Town to the east, and neither Ecklon's colleague Zeyher nor Drège collected along that seaboard, which was then largely covered with forest and dense bush, preferring instead the inland route through the Little Karoo and Langkloof. Both collectors did, however, come across *F. corymbosa* there, where it is common, and Zeyher's collection, *Ecklon & Zeyher Irid no. 108*, distributed to European herbaria under the manuscript name *Freesea* [sic] *odorata*, became the type collection of Klatt's *Freesia odorata*.

Breeding of *Freesia* began almost as soon as *F. leichtlinii* subsp. *alba* came on the market. Corms of subsp. *alba*, together with subsp. *leichtlinii*, were acquired in 1878 by Rodolfo Ragionieri, head gardener of the Marquis Corsi-Salviati, who lived near Florence. The plants flowered in the same year (Ragionieri 1884) and were crossed to produce the hybrids later named *Freesia* 'Giardino Corsi-Salviati'.

There is a lapse in the records of *Freesia* breeding until the introduction in 1897 of the pink-flowered form of *F. corymbosa* 'Armstrongii' but some degree of selective breeding evidently took place during this period, as evidenced by the introduction by Suttons Nursery in England of *F. leichtlinii* 'Major' sometime before 1896 (Gumbleton 1896) and of a few other named forms. Morgan (1929, 1930) gives an indication of *Freesia* growing in North America and mentions Richard Bragg who had been hybridizing *Freesia* there since 1885, although this work seems to have been of no lasting importance.

The pink-flowered *Freesia corymbosa* 'Armstrongii' was the plant that really provided the stimulus to *Freesia* breeding. Watson (1898) records that the original plants were sent to Kew by a Mr Armstrong of Port Elizabeth, who found them growing wild on a farm near Humansdorp. A half-dozen specimens bloomed at Kew in 1898, when the plant was named *F. armstrongii*. Stocks were increased and a good display was recorded in 1901 in *The Garden* 59: 374. The hybrid known as *F. × kewensis* dates from this time, and records indicate that it was the offspring of an unintended cross between *F. leichtlinii* subsp. *leichtlinii* and the pink-flowered *F. corymbosa* (= *F. armstrongii*) that arose at Kew Gardens.

The Dutch nursery firm of Van Tubergen soon acquired *Freesia armstrongii* and this material, crossed with *F. leichtlinii* subsp. *alba*, yielded the rose-coloured hybrid marketed in 1905 as *F. tubergenii*. Van Tubergen continued breeding with the species and hybrids then available (Hoog 1909) to produce a range of tall *Freesias* with colours ranging from blue, mauve, shades of rose, yellow and white. Attilio Ragionieri, the son of Rodolfo, also acquired *F. armstrongii* and bred a strain called *Freesia* 'Ragionieri' (Grignan 1907) by crossing it first with *F. leichtlinii* subsp. *alba* and then with subsp. *leichtlinii*, continuing to breed the offspring of these hybrids.

Another important development in the early history of cultivated freesias concerns the so-called Chapman freesias, raised by F. Herbert Chapman. According to Jacob (1909), Chapman crossed *F. leichtlinii* subsp. *alba* (as *F. refracta* var. *alba*) with a plant called *F. aurea*, and then crossed the resulting F1 hybrids back to *F. leichtlinii* subsp. *alba* to produce a range of tall,

pale to deep yellow forms, the finest of which became known as *Freesia* 'Chapmanii'. *Freesia aurea* was a name used in horticulture only, and is evidently a deep yellow-flowered form of *F. corymbosa* (Brown 1935). Michael Foster (1888), who knew the *Freesia* cultivars then in cultivation in England well, mentions *F. aurea* as being similar to *F. refracta* but with rich bright yellow flowers and less scarious bracts. This is supported by observations by Gumbleton (1896), who describes *F. aurea* as deep golden, late blooming and very like *F. refracta* (by which he meant *F. leichtlinii* subsp. *alba*) in other respects. *Freesia aurea* is thus a second form of *F. corymbosa* to play a role in the history of cultivated *Freesia*, the first being *F. armstrongii*. It was also the fourth wild genome that entered the gene pool of horticultural stocks.

The transfer of the Ragionieri *Freesia* stocks to C. Bruggemann in southern France is recorded by Grignani (1907) but this strain was evidently lost during World War I (Morgan 1929; Zeilinga 1971). Van Tubergen and several other European and American breeders continued to produce new varieties, with the first polyploid, *Freesia* 'Buttercup', making its appearance in 1911. Today most registered cultivars are polyploid (Mohr 1958; Zeilinga 1971), with diploid strains important mainly in areas where plants are grown every season from seed (Sparnaaij *et al.* 1968). Plants of *Freesia leichtlinii* subsp. *alba* (under the name *Freesia refracta*) were first introduced into Japan in the 1910s, and have since been followed by numerous further introductions from America and Europe. The story of *Freesia* breeding after 1920 has been described in some detail by Goemans (1980), a breeder whose knowledge of *Freesia* in cultivation is unparalleled.

Several of the horticultural forms raised in the late nineteenth and early twentieth centuries received names, some of them formally published but others merely listed in seed catalogues or horticultural journals (Gumbleton 1896). Many are treated by Brown (1935) but we do not discuss them here as their identity is uncertain and they are, in any event, of no nomenclatural or taxonomic significance.

Holland is currently the leading producer of freesias, with 215 ha of greenhouses stocked

with the plants in 2001 and Japan ranking second, with about 60 ha of plants. The estimated production in England and the USA in the same year was less than 10 ha each.

Despite the large number of *Freesia* cultivars that have been produced over the past century, all are apparently derived from crosses and selections of just the two original parent species, *F. corymbosa* (including pink and dark yellow forms) and *F. leichtlinii* (both yellow-flowered subsp. *leichtlinii* and white-flowered subsp. *alba*). These complex hybrids between *F. corymbosa* and *F. leichtlinii* are known collectively as *F. × hybrida* and all available evidence indicates that no further wild species have been involved. *Freesia* breeding is in fact a continuous round of relatively minor variations, with persistent viral infections and to some extent changes in fashion determining the release of a succession of named selections.

Breeding of *Freesia* continues today and varieties, including double-flowered types, are being produced that bear less and less resemblance to the wild species from which their stock originally stemmed. The cultivars range in height from 100–300 mm, in habit from neat and tufted to tall and graceful, in inflorescence from short and semi-erect to long, sparsely branched and horizontal, and produce scarcely to strongly fragrant flowers in almost every conceivable colour (Bryan 1995). Although famous for its fragrant flowers, which are typically described as 'sweet-smelling', very few *Freesia* cultivars have been developed primarily for their fragrance, and many commercial varieties have lost their scent during the breeding and selection processes, a cause for special concern among Chinese and Japanese growers (Wongchaohant *et al.* 2005; Fu *et al.* 2007). The favoured colours by far in both Holland and Japan are yellow, followed by white, and it is probably no coincidence that these are typically the most fragrant.

It is remarkable that this variety derives from such limited parentage. There is nevertheless a sameness about the cultivars that belies the diversity to be found among the wild species and which compares poorly with the wide range of flower forms that has been developed in the related genus *Crocasmia* (Goldblatt *et al.* 2004), in

which many more wild species have contributed to breeding programmes.

The foundation of the cultivated stock on the two species indigenous to the southern Cape, which experiences more or less year-round rainfall, has certainly contributed to its success in cultivation but there are certainly other valuable characteristics to be derived from introducing additional, more seasonal members into the mix. Novel flower forms can be expected from involving the tubular-flowered species, larger flowers from *Freesia speciosa*, an extended flowering season from early-blooming species such as *F. caryophyllacea* and *F. fucata*, and possibly even frost- and drought-tolerance from *F. andersoniae*.

The discovery that there are two different scent profiles among the gullet-flowered species in the genus raises the exciting possibility of developing distinct fragrance-lineages with typical freesia-type flowers, based respectively on members of subgen. *Viridibractea* (with ionone) and subgen. *Freesia* (without ionone). The very early crossing of *F. leichtlinii* (subgen. *Viridibractea*) with *F. corymbosa* (subgen. *Freesia*) has effectively removed this potential from current breeding programmes.

It is very evident that precious little of the natural variation available in *Freesia* has actually been utilized in the development of today's commercial cultivars.





CULTIVATION AND PROPAGATION OF FREESIA SPECIES

by G.D. Duncan

Cultivation

The only species of *Freesia* produced to any commercial extent is *F. laxa*, available in limited numbers for sale in garden centres in the United Kingdom. In South Africa, the home of *Freesia*, corms of *F. leichtlinii* subsp. *alba*, *F. laxa* and *F. refracta* are sometimes offered for sale, but only by specialist nurseries, and the number of species available as seeds in this country is not much greater. In contrast, *Freesia* cultivars are produced by the million in The Netherlands, Japan and the Channel Islands, and to a lesser extent in England and California, with smaller numbers grown in Israel, Denmark and South Africa. Unfortunately, in the development of cultivars with larger, more intensely coloured flowers, much of the strong sweet scent that characterizes many of the species has been lost. *Freesia* species and cultivars can be grown outdoors in mild parts of the northern hemisphere such as the Channel Islands, in Cornwall and South Devon in the southwestern part of England, and on the southwestern Japanese islands of Okinoerabu and Hachijo, which are essentially frost-free (Imanishi 1993). In colder climates they require the protection of the cool glasshouse.

Growth cycle

With the exception of summer-growing *Freesia grandiflora* and *F. laxa*, most *Freesia* species are winter-growing in the wild, responding to cool temperatures of not more than 15°C to initiate rooting and vegetative growth in autumn. Flowering in the winter-growing members follows within four weeks to six months of the start of vegetative growth, depending on the species. This is followed by a dormant phase of approximately five months that coincides with the hot, dry summers that characterize the southwestern

Cape. With temperature manipulation, growth and development of *Freesia* cultivars can be controlled to produce cut flowers or flowering plants almost all year round. Sturdy vegetative growth, although slow, can only be achieved by keeping the temperature low, with 5–10°C being the ideal range for winter days. Rapid, soft growth is disadvantageous to the formation of strong stems with high quality flowers and also places the plants at greater risk of attack by pests and disease. *Freesia grandiflora* and *F. laxa* are unusual among other summer-growing bulbs in cultivation as they readily adapt to a winter growth regime, their seeds germinating easily whether sown in autumn or spring. *Freesia andersoniae*, which is distributed across the mainly summer rainfall zone of the interior of South Africa, receives most of its rain in the wild during late summer and autumn, and follows a winter growth cycle with a pronounced summer dormant period.

Without intervention, the corms of *Freesia* species and cultivars naturally remain dormant in summer, but their dormant phase can be shortened by temperature manipulation, smoke treatment, or application of a growth regulator such as ethylene. Photoperiodism has a limited influence on the development of *Freesia* compared with temperature. In their early stages, flower initiation and development is promoted by short days, with later stages only slightly promoted by long days. Flower initiation and development is delayed by low light intensity, which has the effect of producing fewer flowers per spike (Mansour 1968).

Aspect

Freesias perform best when grown under cool temperatures with high light intensity. When grown outdoors in mild climates, most freesias

will only flower well in positions receiving at least full morning sun with afternoon shade but *Freesia leichtlinii* subsp. *alba*, *F. grandiflora* and *F. laxa* flower fairly well in positions receiving light shade throughout the day. *Freesia* species and cultivars grown as spring-flowering crops in glasshouse conditions and in tunnels in the northern hemisphere, where a minimum temperature of 10 °C can be maintained during the worst winter weather, need bright light for as much of the day as possible. Corms that have been specially cold-treated for planting in spring (April and May) can be grown outdoors as summer bedding plants or indoors on south-facing window sills in cold climates of the northern hemisphere. In the southern hemisphere, a north-facing, well-ventilated aspect is best for all species and cultivars. When grown in excessive shade the plants easily fall over and may not flower at all.

Growing medium

Freesia cultivars and most species require a light, loamy soil containing well-decomposed compost or leaf mould that is well drained but retains sufficient moisture. Highly acidic soils must be avoided as the plants prefer only slightly acidic to neutral or slightly alkaline soils, with pH for most species and cultivars ideally ranging between 6.3–7.5 (McKenzie 1957), whereas *F. andersoniae* needs an alkaline soil to do well. *Freesias* do not require heavy fertilization and are especially sensitive to high salt concentrations that result in root burn and poor leaf development. A suggested medium for cultivars and easily grown species such as *F. grandiflora*, *F. laxa* and *F. leichtlinii* is John Innes Potting Compost no. 2 that equates to 7 parts loam, 3 parts peat and 2 parts coarse sand, while for less easily grown species such as *F. andersoniae* and *F. speciosa*, the amount of loam should be reduced drastically to just one part.

Planting

In the southern hemisphere, the winter-growing *freesias* are planted in autumn, late March and April being the most suitable time. *Freesia grandiflora* and *F. laxa* can be grown in winter or in summer, and if the latter, should be planted in early September. In northern hemisphere countries with cool summers, such as The Netherlands, commercial growers stagger their plant-

ing for cut flower production in order to have flowers available throughout the year, but for corm production, planting from April to July is best as larger corms are produced from longer day length and better light quality at that time of year, and cormlet development (which occurs directly after flowering) is encouraged by short days and relatively low temperatures (Mansour 1968). For large-scale production of cut flowers in glasshouses, the growing medium should be steam-sterilized or treated with chloropicrin before planting, or the corms can be soaked in benomyl (e.g. Benlate) or captab (e.g. Kaptan).

The conical corms of *freesias* are planted with the point facing upwards, with 20–30 mm of growing medium above the top of the corm. When planted in summer or in sandy soils, the corms should be planted 30 mm deep. To prevent flower stems from falling over, the plants need support and for this purpose a layer of plastic mesh is placed above the plants.

Production of cultivar corms and cormlets in the northern hemisphere usually takes place outdoors in mild climates in places such as California, the Channel Islands, and the southwestern islands of Japan. They are planted in autumn (September to October) in treated open beds and the flowers are removed to allow for greater corm and cormlet development.

Garden and container cultivation

In mild climates, *Freesia* cultivars and some of the species (*F. caryophyllacea*, *F. laxa*, *F. leichtlinii* subsp. *alba* and subsp. *leichtlinii*, *F. refracta* and *F. occidentalis*) are ideal subjects for rock garden pockets, herbaceous borders, window boxes, troughs and large terracotta containers. *F. leichtlinii* subsp. *alba* is especially useful to gardeners as it tolerates irrigation during its summer-dormant period. In cold climate parts of the southern hemisphere, *freesias* can be planted in sheltered positions under overhanging branches of deciduous trees, or against north-facing walls. They can also be grown in smaller, deep pots to be taken into the home where the flowers and scent can be enjoyed at close range, and the flowers last longer this way, not having to be cut. Ideal sizes for the latter purpose are 20 or 25 cm diam. pots, with ten corms planted to a 20 cm pot and 15 to 20 corms to a 25 cm pot. All *Freesia* species

are suitable for cultivation in pots. Amongst the best for this purpose are *F. leichtlinii* subsp. *alba* (strongly scented, can be grown in semi-shade or full sun), *F. corymbosa* (the pink form is especially attractive), *F. caryophyllacea* (early-flowering, heavily scented), *F. grandiflora* (large, bright red flowers, suitable for full sun or light shade), *F. laxa* (bright red or white flowers, blooms in 5–6 months from seed, naturalizes easily, flowers are partially self-fertile), *F. leichtlinii* subsp. *leichtlinii* (heavily scented, flowers light yellow with broad orange bands across lower tepals, likes alkaline soils), *F. refracta* (early-flowering, good forms have bright orange bands across lower tepals, spicy-scented) and *F. sparrmanii* (dainty, small-flowered species). When more has been learned regarding the successful cultivation of *F. speciosa*, this large-flowered, pale yellow-flowered plant with dark yellow bands across its lower tepals promises to be a great horticultural addition.

Watering

Once planting has been completed, the corms should receive a heavy drench and then not again until the young leaf shoots appear after about two weeks, following which heavy drenches can be given about twice a week depending on local climatic conditions. The plants need plenty of water during the growing period but the soil should never become waterlogged. Watering directly onto the leaves should be avoided and rather be done onto the ground around the base of the plant to minimize the incidence of fungal attack. The plants need more water as the buds are forming and when in flower, but watering must be gradually reduced as leaves begin to die off and be terminated completely just before the leaves have completely desiccated.

Species from arid and semi-arid habitats such as *Freesia andersoniae* and *F. refracta* require much less water, not more than one drench per week, allowing the medium to dry out almost to the point of desiccation before the next drench is given.

Forcing

In order to be able to produce *Freesia* cut flowers year-round, it is necessary to reduce the dormancy period of the corms, and this is achieved by temperature manipulation in stor-

age. In The Netherlands it has been found that when corms are stored at 30°C for six weeks, then brought down to 20°C, root emergence is promoted, making it possible to bring the planting date forward. The corms develop shoots within two weeks, thus reducing the dormancy period by up to 30 % or one month, without any loss in flower quality (Berghoef *et al.* 1986). To promote earlier flower initiation together with excellent flower development, it is necessary to maintain a soil temperature of 13°C for a period of seven weeks directly after planting. By this method, production of flowers can be achieved year-round.

Corms should be harvested just before the leaves have completely dried to minimize cormlet loss, as the cormlets readily become detached if corms are harvested too late.

Feeding

Freesias are highly sensitive to excess soluble salts in the soil, usually the result of consecutive annual applications of high sulphate fertilizers to greenhouse soils, without regular drenching with water during the growing period. Under such conditions, soils become much too acidic. The plants are also sensitive to excessive nitrogen as this causes thickening and eventual splitting of the scapes. Excessive salt concentration is often seen as a brown or white crust on the soil surface and around the inside perimeter of containers.

Hardiness

Most *Freesia* species are cold tender but can withstand temperatures down to just above freezing for short periods of a day or two. Although not particularly showy, *F. andersoniae* is almost certainly hardy, occurring in the central parts of South Africa where night temperatures regularly drop to below freezing in winter. This species might be a useful addition for incorporation into breeding programmes for hardier cultivars. In mild parts of the northern hemisphere such as in southern England, *F. laxa* grows well outdoors and will often become naturalized in gardens (Fenwick 2004). Due to its ability to reach flowering size from seed within five to six months, it is grown as a summer annual in very cold climates such as in Canada.

Cultivars

More than 340 *Freesia* cultivars have been listed and described in the *International checklist for hyacinths and miscellaneous bulbs* (Van Scheepen 1991) and since then, many more have come onto the market (Plate 19). The corms of cultivars usually lose their vigour about seven years after introduction, necessitating their replacement with new cultivars of the same colour and type every seven years. This results in a profusion of cultivar names, yet the number of cultivars actually being produced at any time is relatively small (Table 8). In the selection of new cultivars, breeders have to attend to a number of aspects including tolerance or resistance to current diseases, stem length and lasting ability for cut flowers or as container plants, vigour of lateral stems, flower fragrance and the number of cormlets produced (Imanishi 1993).

Propagation

Freesias can be propagated by seed, cormlets and tissue culture. The species are usually propagated sexually and asexually (seed and cormlets) but cultivars are mostly propagated asexually (cormlets, and to a much lesser extent, tissue culture) in order to preserve the particular genetic make-up that constitutes each cultivar.

Seed

In the southern hemisphere, seeds of all *Freesia* species should be sown in autumn (April–late May) once cool weather has definitely set in. *Freesia grandiflora* and *F. laxa* are exceptional in that they can also be sown in spring, depending on whether one requires a spring- or summer-flowering display. In mild parts of the northern hemisphere such as the Channel Islands, southern and southwestern United Kingdom and southern Europe, seeds can be sown outdoors (for corm production) or in cool glasshouses (for cut flower production) in autumn (September–October). In regions where summer temperatures are generally cool, including The Netherlands and the colder parts of the United Kingdom, seeds can also be sown from early spring to early summer (mid-March–early June), for flowering in October and November. The optimum temperature for germination of *Freesia* seeds sown in spring

in the United Kingdom and Europe is 20°C, although they will also germinate at lower and higher temperatures (McKenzie 1957).

Each grower will discover the ideal sowing medium suited to local conditions but in general, the growing medium should be light and well aerated, with perfect drainage. For cultivars and the more easily grown species such as *Freesia caryophyllacea* and *F. leichtlinii*, a John Innes

TABLE 8.—Top-ranked *Freesia* cultivars in The Netherlands (compiled by Joop Doorduyn)

Ranking*	Cultivar	Colour	S or D	Flowering time	Plant size	Fragrance
1	Yvonne	yellow	D	I	dw/M	Ex
2	Ambassador	white	S	I	M	G
3	Argenta	white	S	E	S/M	G
4	Dukaat	yellow	S	I	M	G
5	Blue Moon	blue	S	I	M/T	F
6	Volante	white	D	I	dw/M	Ex
7	Purple Rain	purple	D	I	M	F
8	Versailles					
	Ricaille	white	D	I	dw/M	G
9	Gold River	yellow	S	I	M	Ex
10	Alderney	yellow	S	L	M/T	G
11	Santorini	red	S	I	M	G
12	Avila	blue	S	E	M	F
13	Aladin	yellow	S	I/L	M	Ex
14	Blue Bayou	blue	D	L	M	F
15	Cote d'Azure	blue	S	I	M	P
16	Grace					
	Vacredu	yellow	semi-D	I	M	G
17	Blue River	blue	S	E	dw/M	F
18	Bergamo	white	S	I/L	M	G
19	Bellina	white	S	E/I	M	G
20	Troubadour	dark pink	semi-D	E	G	G
21	Aleide	pink	S	I/L	M	F
22	Saffier	blue	S	I	M/T	F
23	Castor					
	Ricastor	blue	S	E	M	P
24	Cassis Ricassis	pink	D	E	M	F
25	Elegance	white	E	I/L	dw/M	G

* Van Pouderoijen (2005); S, single flowers; D, double flowers; E, early; I, intermediate; L, late; dw, dwarf; M, medium; T, tall; Ex, excellent; G, good; F, fair; P, poor.



Athene



Beethoven



Escapade



Tchikowsky



Mozart

Auricol Butter

seed compost can be used, whereas for less easily grown species, including *F. andersoniae* and *F. speciosa*, a medium with less loam and more grit or sand should be used. A slightly acid, neutral or slightly alkaline medium is preferred by cultivars and most species, but the medium for *F. andersoniae* definitely needs to be on the alkaline side. When sowing large numbers of seeds, it is advisable to dust them with a fungicide powder such as captab prior to sowing. Sowing depth should be two to three times the diameter of the seeds and they should be sown thinly in order to reduce the incidence of damping-off fungi, notably *Pythium* species. Seedbeds should be kept moist but not constantly wet, and germination of fresh seeds (six months old) takes place within two to four weeks. Under ideal conditions, *F. laxa* can be brought into flower within five or six months from seed, and a number of other species from naturally sandy soils including *F. caryophyllacea*, *F. grandiflora*, *F. leichtlinii* subsp. *alba*, *F. leichtlinii* subsp. *leichtlinii* and *F. sparrmanii*, can flower within eight months. Most species usually flower for the first time in the spring of their second year, but *F. speciosa* probably takes a third season before flowering.

Cormlets

Asexual propagation by cormlets is the method most widely used by commercial growers for increasing stocks of cultivars, as it is the fastest way of producing large numbers of corms that will flower true to cultivar type. If the mother corms have been well grown, the cormlets reach maturity by the time they enter their first summer dormant period and will flower the following season. Cormlets start to form directly after flowering has taken place, so the longer the mother corms can be kept in green leaf, the larger the cormlets will be. Most *Freesia* species reproduce by this method although *F. andersoniae* and *F. speciosa* appear to produce fewer cormlets than the other species and reproduce naturally mainly by seed. Cormlets form in a ring around the base of the mother corm, or along the subterranean portion of the stem, especially in *F. leichtlinii*. *Freesia grandiflora* is the only member of the genus that produces cormlets at the tips of subterranean, scaly rhizomes, produced from the base of the corms, and it also occasionally produces aerial cormlets in the axils of its leaves. A single cormlet is produced at the tip of each

rhizome. Well-developed cormlets of *Freesia* cultivars and species usually flower during the following season.

Tissue culture

Propagation by this method is relatively expensive and is used mainly to obtain virus-free material when stocks of particularly desirable cultivars have become infected or dwindled to dangerously low levels as a result of attack by pests or disease. It is also used to build up stocks of new cultivars. Once healthy new material has become available, the corms can then be further propagated by the conventional method of cormlet production.

Pests and diseases

In combating the pests and diseases that free-sias are susceptible to, it is always preferable to take action immediately they are noticed or suspected, before their effects result in excessive losses. Growers may need to use a combination of cultural, chemical and biological control measures to manage severe outbreaks of insect populations, and pesticides should be rotated to avoid resistance. Wherever possible, biological control is a recommended alternative to pesticide use, as resistance complications do not arise, spray damage to the plants is avoided and the environment is spared.

Pests

Aphids: the mouthparts of aphids or 'greenfly', as they are also known, suck the sap of developing *Freesia* inflorescences, and to a lesser extent, their leaves. They multiply extremely rapidly and should be controlled as soon as an infestation is noticed, as they transmit viral disease (to which free-sias are highly susceptible) through the transfer of infected sap from one plant to another. The insects can be washed off the plants by spraying them with a strong jet of water from a spray-can, or can be smothered by spraying them with a mineral oil such as Oleum, that is partially environmentally compatible. Alternatively, an aerosol insecticide containing tetramethrin and phenothrin (e.g. Wonder Garden Gun) can be used for rapid treatment of small numbers of plants.

Mealy bugs: these oval-shaped, soft-bodied insects attack the corms and leaf bases of freesias by sucking the sap. They have filamentous projections around their perimeters and attach themselves to the plant parts and secrete a powdery waxy layer that protects them while feeding. Mealy bugs are sexually dimorphic. The females are wingless but have legs, whereas the males are winged and undergo complete metamorphosis, changing from nymphs to flying, gnat-like adults. Mature male mealy bugs are short-lived and do not feed, their only purpose being to fertilize the females. Once fertilized, large numbers of offspring are produced directly from the females. Mealy bugs like the warm, protected conditions of greenhouses and breed especially rapidly in early autumn, just as freesias are beginning their winter growth cycle. They cause weakening and stunting of plants and transmit viral disease from one plant to another and can become a very serious pest where Argentine ants are prevalent, as the latter protect them from predators and parasites. In return, the ants feed on honeydew secreted by the mealy bugs. Controlling ants effectively should be a first step in reducing mealy bug populations, and can be achieved by pouring neat Jeyes Fluid down ant holes, then washing it down with water, a process that should be repeated several times. Biological control is possible by introduction of predatory ladybird beetles, released at 2–3 week intervals. Alternatively the soil can be drenched with the systemic insecticide imidacloprid (e.g. Kohinor 350 SC), that provides protection for one year.

Red spider mites: these minute reddish arachnids infest the leaf surfaces of the two summer-growing species, *Freesia grandiflora* and *F. laxa*, spinning protective silky webs and feeding on the sap by puncturing the leaf surfaces. They are prevalent under protected, warm dry conditions such as those developed in greenhouses in spring and early summer. Control is by predatory insects such as lady beetles (e.g. *Stethorus* species), predatory mites (such as *Phytoseiulus persimilis*) that feed on the eggs and active stages, and chemical control. Red spider mites rapidly develop resistance to continued application of the same pesticide and require rotational application for effective control. Suggested formulations include mineral oil (e.g. Oleum) and the pyrethroids, tetramethrin and phenothrin.

Thrips: adult thrips are recognized as small, elongated, brown- or yellow-bodied insects. They are attracted to pollen but both the adults and nymphs feed mainly on the developing flower buds and foliage of freesias and are prevalent as temperatures rise in late spring and summer. Thrips feed by rasping tissue surfaces to extract the fluids, resulting in silvery stippling across leaf surfaces and browning and disfigurement of developing flowers. They have a very rapid life cycle of about ten days and it is essential that they are controlled preventatively where cut flower crops are being produced, as even mild attacks result in blemished flowers that cannot be sold. Thrips are also transmitters of viral disease, for which there is no cure. Eradication of thrips is difficult, requiring a combination of cultural, chemical and biological methods. Cultural control in greenhouses or tunnels includes fitting fine mesh to vents to exclude thrips, but vents must be large enough as fine mesh reduces the rate of ventilation. Eradication of weeds inside and immediately surrounding greenhouses is essential as they often harbour thrips. For biological control, use of microbial insecticides such as the fungal pathogen *Beauveria bassiana* (e.g. Botani-Guard) is suggested. Chemical control can be achieved with the pyrethroids, tetramethrin and phenothrin.

Rodents: in South Africa, *Freesia* corms are relished by porcupines and mole rats. The latter can be excluded by planting corms into sunken wire baskets covered on all sides, but porcupines are very difficult to control in an environmentally friendly manner as they are able to scale fences and dig underneath them, and can pull corms through the holes of wire baskets. Suggested measures of control are to plant numbers of one of their favourite foods, *Zantedeschia aethiopica* tubers, some distance away from areas where freesias are being grown, or alternatively to actively feed porcupines alternative foods such as pumpkins and potatoes in the hope that their appetites will be satisfied and that *Freesia* corms will be ignored.

Diseases

Botrytis blight: this is a fungal disease mainly affecting the flowers, stems and especially the leaves of freesias. It is prevalent during wet or humid weather and is seen as a grey or black

sooty mould. Prevention is achieved by ensuring adequate ventilation around the plants, allowing rapid evaporation of moisture off the plant surfaces, and by maintaining excellent hygiene by removal of any blighted plant parts as soon as possible. Corms are also subject to *Botrytis* blight when stored under warm, poorly ventilated conditions, and can be avoided by dusting with equal parts of captab and iprodione prior to storage and maintaining a cool, dry atmosphere.

Fusarium corm rot: *Freesia* corms are highly susceptible to attack by the *Fusarium* fungus (*Fusarium oxysporum*), causing the corm to rot during the active growing period, resulting in wilting of the leaves and eventual death of the plant. Affected corms exhibit spotting that penetrates to the centre of the corm, the leaves turn yellow and the scape is easily pulled out of the corm due to neck rotting of the corm. Susceptibility varies markedly between cultivars, the greatest losses occurring at high soil temperatures. Infected material should immediately be removed, together with its surrounding soil, and destroyed. Preventative measures against the disease are steam sterilization or treatment of the soil with chloropicrin, and disinfection of the corms with benomyl (e.g. Benlate).

Virus: viral infection is a very serious disease in *freesias*. Once a plant has been infected there is usually nothing that can be done to remedy the problem. Most modern cultivars are lightly infected with one virus or another and they cause unsightly streaking or light and dark brown necrosis of the leaves, and stunted, deformed flowers. They may also cause 'colour breaking' of the tepals, resulting in a striped effect as the colours are 'broken' by the virus. *Freesias* are susceptible mainly to the *freesia* mosaic virus (FMV) and the bean yellow mosaic viruses, and both are transmitted by aphids. The best methods of control are by only planting very healthy corms, destroying infected plants as soon as infection is suspected, and controlling aphids, thrips, mealybugs and snails as soon as infestations are noticed. As soon as plants are suspected of being infected by a virus, they should immediately be isolated, treated against aphids and given a balanced fertilizer that includes trace nutrient elements. Should the symptoms persist, viral infection is highly likely and the material should be destroyed before nearby healthy plants become infected (Du Plessis & Duncan 1989). Viruses are not carried within the seeds of *freesias* although they can be carried on the seed coat.





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APPENDIX—Analytical composition of *Freesia* scent

Freesia andersoniae (trapped on Porapak SQ at Kimberley, South Africa, 20.00–08.00, 28 August 2008): α -pinene 0.40 %, camphene 0.20 %, b-pinene 0.10 %, sabinene 0.04 %, myrcene 0.10 %, limonene 0.40 %, (E)-ocimene 0.02 %, p-cymene 0.01 %, octanal 0.01 %, 6-methylhept-5-en-2-one 0.01 %, nonanal 0.05 %, trans-linalool oxide (furanoid) 0.20 %, cis-linalool oxide (furanoid) 0.20 %, campher 0.01 %, linalool 92.00 %, 2-methyl-2-vinyltetrahydrofuran-5-ol 0.08 %, methyl benzoate 5.40 %, 2-methyl-2-vinyltetrahydrofuran-5-one 0.02 %, borneol 0.10 %, trans-linalool oxide (pyranoid) 0.01 %, cis-linalool oxide (pyranoid) 0.02 %, 2,6-dimethylocta-3,7-dien-2,6-diol 0.10 %, (E)-nerolidol 0.01 %, 2,6-dimethylocta-1,7-dien-3,6-diol 0.01 %, nonanoic acid 0.01 %, capric acid 0.02 %.

***Freesia caryophyllacea* 1** (trapped on Porapak SQ at Napier, South Africa, 13.00–16.00, 30 May 2008): α -pinene 1.50 %, camphene 0.20 %, b-pinene 0.60 %, sabinene 1.50 %, myrcene 1.40 %, limonene 2.30 %, eucalyptol 2.60 %, (Z)-ocimene 1.10 %, (E)-ocimene 26.90 %, p-cymene 0.04 %, terpinolene 0.05 %, octanal 0.09 %, (Z)-hex-3-en-1-yl acetate 0.10 %, 6-methylhept-5-en-2-one 0.20 %, hexan-1-ol 0.05 %, nonanal 0.20 %, rosefuran 0.03 %, trans-sabinene hydrate 0.30 %, decanal 0.20 %, benzaldehyde 0.10 %, b-cubebene 0.10 %, cis-sabinene hydrate 0.20 %, linalool 0.70 %, caryophyllene 0.20 %, terpinen-4-ol 0.05 %, cyclic-b-ionone 0.10 %, aromadendrene 0.05 %, acetophenone 0.10 %, neral 0.05 %, α -terpineol 23.50 %, geranial 0.30 %, δ -cadinene 8.90 %, geranyl acetate 9.90 %, dihydro-b-ionone 0.30 %, geraniol 3.20 %, b-ionone 2.90 %, cubebol 0.40 %, b-ionol 0.20 %, caryophyllene epoxide 0.90 %, methyl myristate 0.20 %, (E,E)-farnesol 0.04 %.

***Freesia caryophyllacea* 2** (trapped on Porapak SQ at Kirstenbosch National Botanical Garden, South Africa, 10.00–15.00, 15 June

2007): α -pinene 2.60 %, camphene 0.10 %, b-pinene 0.80 %, sabinene 2.40 %, myrcene 1.70 %, limonene 3.50 %, eucalyptol 4.80 %, (Z)-ocimene 0.50 %, (E)-ocimene 10.20 %, terpinolene 0.10 %, 6-methylhept-5-en-2-one 0.06 %, (Z)-3(4)-epoxy-3,7-dimethylocta-1,6-diene 0.10 %, (E)-3(4)-epoxy-3,7-dimethylocta-1,6-diene 0.30 %, rosefuran 0.04 %, trans-linalool oxide (furanoid) 0.20 %, trans-sabinene hydrate 0.40 %, cis-linalool oxide (furanoid) 0.30 %, cis-sabinene hydrate 0.50 %, linalool 13.40 %, terpinen-4-ol 0.04 %, b-cyclocitral 0.04 %, cyclic-b-ionone 0.20 %, neral 0.20 %, α -terpineol 34.00 %, geranial 0.50 %, geranyl acetate 0.10 %, nerol 0.60 %, dihydro-b-ionone 1.20 %, geraniol 12.80 %, b-ionone 4.20 %, b-ionol 0.20 %, 2,6-dimethylocta-3,7-dien-2,6-diol 0.02 %, dihydro-b-ionol 0.02 %, 6(7)-epoxygeraniol 0.05 %, 2(3)-epoxygeraniol 0.05 %, (E,E)-farnesol 0.02 %.

***Freesia corymbosa* 'Armstrongii'** (trapped on Porapak SQ at Kirstenbosch National Botanical Garden, South Africa, 11.00–16.00, 27 September 2007): limonene 0.20 %, tridecane 1.30 %, 6-methylhept-5-en-2-one 0.40 %, nonanal 0.30 %, tetradecane 1.10 %, trans-linalool oxide (furanoid) 1.60 %, cis-linalool oxide (furanoid) 1.60 %, α -copaene 0.30 %, decanal 0.50 %, linalool 66.50 %, octanal 0.20 %, 2-methyl-2-vinyltetrahydrofuran-5-ol 12.60 %, 2-methyl-2-vinyltetrahydrofuran-5-one 0.40 %, α -terpineol 0.20 %, trans-linalool oxide (pyranoid) 0.10 %, cis-linalool oxide (pyranoid) 0.10 %, tridecan-2-one 0.90 %, 3,5-dimetroxytoluene 0.10 %, 2,6-dimethylocta-3,7-dien-2,6-diol 0.40 %, heptanoic acid 0.20 %, 2,6-dimethylocta-1,7-dien-3,6-diol 0.20 %, nonanoic acid 0.40 %, capric acid 0.20 %.

Freesia fergusoniae (trapped on Porapak SQ at Heidelberg, South Africa, 10.00–16.00, 20 August 2007): α -pinene 5.20 %, α -thujene 0.10 %, camphene 0.20 %, b-pinene 1.20 %,

sabinene 4.60 %, myrcene 3.30 %, limonene 8.20 %, eucalyptol 6.70 %, (Z)-ocimene 0.30 %, γ -terpinene 0.03 %, (E)-ocimene 2.60 %, p-cymene 0.04 %, terpinolene 0.20 %, octanal 0.03 %, (Z)-hex-3-en-1-yl acetate 0.20 %, 6-methylhept-5-en-2-one 0.08 %, α -pinene epoxide 0.03 %, nonanal 0.10 %, tetradecane 0.20 %, 6,7-epoxymyrcene 0.10 %, α -cubebene 0.04 %, trans-sabinene hydrate 0.40 %, trans-linalool oxide (furanoid) 0.04 %, α -copaene 0.20 %, 2-methylbutyraldoxime (E,Z) 0.10 %, decanal 0.04 %, pentadecane 6.40 %, cis-sabinene hydrate 0.40 %, linalool 8.80 %, caryophyllene 0.80 %, terpinen-4-ol 0.03 %, cyclic-b-ionone 1.50 %, humulene 0.03 %, 2,6,6-trimethylcyclohex-2-en-1,4-dione 0.04 %, α -terpineol 23.20 %, α -selinene 0.80 %, germacrene A 0.30 %, (E,E)- α -farnesene 0.05 %, dihydro-b-ionone 2.30 %, p-cymen-8-ol 0.04 %, trans-2-hydroxyeucalyptol 0.02 %, b-ionone 19.10 %, cubebol 0.20 %, b-ionol 0.10 %, 2,6-dimethylocta-3,7-dien-2,6-diol 0.03 %, caryophyllene epoxide 0.10 %, b-ionone epoxide 0.20 %, 2,6-dimethylocta-1,7-dien-3,6-diol 0.03 %, dihydroactinidiolide 0.08 %, indole 0.05 %.

Freesia fucata (trapped on Porapak SQ at Worcester, South Africa, 10.00–15.00, 21 July 2007): α -pinene 0.20 %, b-pinene 0.10 %, myrcene 0.90 %, limonene 0.30 %, (Z)-ocimene 3.80 %, (E)-ocimene 54.00 %, tridecane 0.30 %, (E)-hex-2-en-1-yl acetate 0.30 %, (Z)-3(4)-epoxy-3,7-dimethylocta-1,6-diene 0.30 %, nonanal 0.40 %, (E)-3(4)-epoxy-3,7-dimethylocta-1,6-diene 0.80 %, tetradecane 0.70 %, (Z)-ocimene epoxide 0.10 %, (E)-ocimene epoxide 1.20 %, 2-methylbutyraldoxime (E,Z) 0.60 %, decanal 0.30 %, b-cubebene 0.20 %, caryophyllene 0.10 %, 2,6,6-trimethylcyclohex-2-en-1,4-dione 0.30 %, α -selinene 2.70 %, germacrene A 0.40 %, dihydro-b-ionone 1.80 %, b-ionone 23.00 %, cubebol 0.30 %, b-ionone epoxide 0.30 %, 3,7-dimethylocta-2,6-dien-1,4-diol 0.20 %.

***Freesia leichtlinii* subsp. *alba* 1** (trapped on Porapak SQ at Still Bay, South Africa, 09.00–15.00, 9 September 2007): α -pinene 6.20 %, camphene 0.20 %, b-pinene 1.50 %, sabinene 4.70 %, myrcene 2.40 %, limonene 7.90 %, eucalyptol 9.50 %, (Z)-ocimene 1.00 %, (E)-ocimene 12.50 %, p-cymene 0.04 %, (Z)-hex-3-en-1-yl

acetate 0.02 %, 6-methylhept-5-en-2-one 0.10 %, (Z)-3(4)-epoxy-3,7-dimethylocta-1,6-diene 0.40 %, α -pinene epoxide 0.08 %, nonanal 0.05 %, (E)-3(4)-epoxy-3,7-dimethylocta-1,6-diene 0.70 %, 6,7-epoxymyrcene 0.04 %, 3,10-epoxymyrcene 0.07 %, cis-limonene epoxide 0.30 %, trans-sabinene hydrate 0.60 %, cis-linalool oxide (furanoid) 0.10 %, (Z)-ocimene epoxide 0.10 %, (E)-ocimene epoxide 1.00 %, cis-sabinene hydrate 0.60 %, linalool 4.30 %, caryophyllene 0.30 %, terpinen-4-ol 0.06 %, b-cyclocitral 0.03 %, α -terpineol 35.80 %, α -selinene 0.30 %, germacrene A 0.06 %, dihydro-b-ionone 1.20 %, p-cymen-8-ol 0.03 %, trans-2-hydroxyeucalyptol 0.10 %, benzyl alcohol 0.05 %, b-ionone 2.00 %, cubebol 0.10 %, caryophyllene epoxide 0.20 %, α -terpineol epoxide 0.50 %.

***Freesia leichtlinii* subsp. *alba* 2** (trapped on Porapak SQ at Kirstenbosch National Botanical Garden, South Africa, 11.00–17.00, 30 August 2004): α -thujene 0.15 %, b-pinene 0.04 %, sabinene 0.15 %, myrcene 0.15 %, limonene 0.20 %, eucalyptol 0.40 %, (Z)-ocimene 0.02 %, (E)-ocimene 0.15 %, octanal 0.04 %, nonanal 0.15 %, trans linalool oxide (furanoid) 0.10 %, trans-sabinene hydrate 0.02 %, cis linalool oxide (furanoid) 0.10 %, decanal 0.25 %, benzaldehyde 0.05 %, cis-sabinene hydrate 0.03 %, linalool 86.40 %, α -terpineol 1.70 %, benzyl acetate 0.02 %, dihydro-b-ionone 0.50 %, b-ionone 1.60 %.

Freesia leichtlinii* subsp. *leichtlinii (trapped on Porapak SQ at Kirstenbosch National Botanical Garden, South Africa, 09.00–15.00, 28 July 2005): α -pinene 1.80 %, camphene 0.06 %, b-pinene 0.40 %, sabinene 1.40 %, myrcene 0.90 %, eucalyptol 3.00 %, (Z)-ocimene 0.70 %, (E)-ocimene 16.80 %, p-cymene 0.03 %, terpinolene 0.10 %, (Z)-hex-3-en-1-yl acetate 0.05 %, 6-methylhept-5-en-2-one 0.07 %, (Z)-3(4)-epoxy-3,7-dimethylocta-1,6-diene 0.08 %, nonanal 0.06 %, (E)-3(4)-epoxy-3,7-dimethylocta-1,6-diene 0.20 %, 6,7-epoxymyrcene 0.04 %, cis-limonene epoxide 0.03 %, trans-sabinene hydrate 0.30 %, (E)-ocimene epoxide 0.50 %, 2-methylbutyraldoxime (E,Z) 0.09 %, decanal 0.02 %, cis-sabinene hydrate 0.40 %, linalool 2.20 %, α -fenchol 0.03 %, caryophyllene 1.00 %, terpinen-4-ol 0.05 %, cyclic-b-ionone 0.20 %, humulene 0.06 %, δ -terpineol 0.01 %, 2,6,6-trimethylcyclohex-2-en-1,4-dione

0.04 %, α -terpineol 29.30 %, α -selinene 0.20 %, carvone 0.30 %, benzyl acetate 0.05 %, germacrene A 0.10 %, δ -cadinene 0.70 %, citronellol 0.05 %, nerol 0.05 %, dihydro-b-ionone 2.40 %, (E,E)-2,6-dimethylocta-3,5,7-trien-2-ol 0.06 %, geraniol 0.05 %, 2-phenylethyl alcohol 0.05 %, b-ionone 27.50 %, caryophyllene epoxide 0.50 %, α -terpineol epoxide 0.10 %, b-ionone epoxide 0.30 %, humulenepoxide II 0.04 %, carvonhydrate 0.06 %, 4-oxo-b-ionone 0.08 %.

Freesia occidentalis (trapped on Porapak SQ at Karooport, South Africa, 10.00–14.00, 5 August 2007): limonene 0.60 %, octanal 0.20 %, 6-methylhept-5-en-2-one 1.50 %, nonanal 0.80 %, decanal 0.90 %, linalool 1.10 %, neral 2.00 %, geranial 2.30 %, nerol 77.80 %, geraniol 0.30 %, (E)-geranylacetone 0.40 %, (E)-nerolidol 0.80 %, 2(3)-epoxynerol 0.20 %.

Freesia praecox (trapped on Porapak SQ at Riviersonderend, South Africa, 11.00–16.00, 20 June 2009, 10.00–16.00, 21 June 2009): α -pinene 4.00 %, b-pinene 1.40 %, sabinene 1.10 %, myrcene 1.70 %, limonene 19.50 %, eucalyptol 3.70 %, (Z)-ocimene 0.10 %, (E)-ocimene 0.50 %, (Z)-hex-3-en-1-yl acetate 0.60 %, (E)-hex-2-en-1-yl acetate 0.10 %, 6-methylhept-5-en-2-one 0.10 %, nonanal 0.40 %, tetradecane 0.50 %, trans-linalool oxide (furanoid) 0.10 %, isomenthone 0.10 %, trans-sabinene hydrate 0.30 %, cis-sabinene hydrate 0.30 %, linalool 19.70 %, caryophyllene 2.10 %, humulene 0.70 %, α -terpineol 25.00 %, citronellol 0.05 %, dihydro-b-ionone 0.80 %, (E)-geranylacetone 0.10 %, b-ionone 1.50 %, caryophyllene epoxide 0.05 %, (E)-nerolidol 0.07 %, benzyl benzoate 0.05 %.

Freesia refracta (trapped on Porapak SQ at Worcester, South Africa, 13.00–18.00, 10 July 2006): α -pinene 0.07 %, undecane 0.20 %, b-pinene 0.02 %, sabinene 0.02 %, myrcene 0.20 %, limonene 1.40 %, eucalyptol 0.02 %, b-phellandrene 0.01 %, (Z)-ocimene 0.02 %, γ -terpinene 0.02 %, (E)-ocimene 0.10 %, tridecane 0.40 %, (E)-4,8-dimethylnona-1,3,7-triene 0.08 %, (Z)-hex-3-en-1-yl acetate 0.03 %, 6-methylhept-5-en-2-one 0.02 %, hexan-1-ol 0.02 %, (Z)-hex-3-en-1-ol 0.10 %, nonanal 0.05 %, rosefuran 0.40 %, perillene 0.30 %, cis-linalool oxide (furanoid) 0.02 %, 6-methylhept-5-en-2-ol 0.01 %, citronellal 0.04 %, decanal 0.06 %, pentadecane 0.60 %, linalool 1.10 %, octan-1-ol 0.07 %, caryophyllene 0.07 %, neral 2.20 %, α -terpineol 0.20 %, geranial 2.30 %, citronellol 19.40 %, γ -isogeraniol 0.05 %, nerol 57.50 %, geraniol 8.90 %, dodecan-1-ol 0.70 %, (E,E) farnesal 0.02 %, (E,E) farnesol 0.02 %.

Freesia speciosa (trapped on Porapak SQ at Calitzdorp, South Africa, 10.00–16.00, 1 & 2 August 2009): α -pinene 0.10 %, b-pinene 0.03 %, sabinene 0.03 %, myrcene 0.07 %, limonene 0.20 %, eucalyptol 0.02 %, (Z)-ocimene 0.01 %, (E)-ocimene 0.03 %, p-cymene 0.02 %, octanal 0.01 %, 6-methylhept-5-en-2-one 0.01 %, nonanal 0.03 %, trans-linalool oxide (furanoid) 0.50 %, cis-linalool oxide (furanoid) 0.50 %, decanal 0.04 %, benzaldehyde 0.01 %, linalool 79.00 %, 2-methyl-2-vinyltetrahydrofuran-5-ol 1.20 %, methyl benzoate 16.10 %, 2-methyl-2-vinyltetrahydrofuran-5-one 0.02 %, trans-linalool oxide (pyranoid) 0.05 %, cis-linalool oxide (pyranoid) 0.06 %, caproic acid 0.01 %, benzyl alcohol 0.20 %, 2-phenylethyl alcohol 0.01 %, 2,6-dimethylocta-3,7-dien-2,6-diol 0.30 %, 2,6-dimethylocta-1,7-dien-3,6-diol 0.30 %.

Freesia viridis* subsp. *crispifolia (trapped on Porapak SQ at Trawal, South Africa, 20.00–04.00, 17 July 2007): limonene 0.04 %, (Z)-ocimene 0.03 %, (E)-ocimene 0.70 %, octanal 0.06 %, 6-methylhept-5-en-2-one 0.50 %, nonanal 0.30 %, citronellal 0.04 %, decanal 0.10 %, linalool 0.04 %, caryophyllene 0.10 %, neral 0.90 %, geranial 1.30 %, (E,E)- α -farnesene 0.04 %, geranyl acetate 0.03 %, methyl salicylate 0.03 %, citronellol 23.50 %, nerol 41.50 %, geraniol 27.00 %, b-ionone 0.06 %, 2(3)-epoxynerol 0.20 %, 2(3)-epoxygeraniol 0.10 %, (E)-cinamic alcohol 0.10 %.

Freesia viridis* subsp. *viridis (trapped on Porapak SQ at Langebaan, South Africa, 20.00–08.00, 12 July 2007): α -pinene 2.60 %, b-pinene 2.40 %, sabinene 1.20 %, myrcene 0.70 %, limonene 26.00 %, eucalyptol 0.50 %, octanal 0.30 %, 6-methylhept-5-en-2-one 0.40 %, nonanal 0.90 %, tetradecane 2.30 %, cis-limonene epoxide 0.10 %, trans-limonene epoxide 0.08 %, citronellal 0.04 %, hexadecane 0.60 %, linalool 0.20 %, octan-1-ol 0.20 %, bornyl acetate 0.10 %, neral 0.80 %, geranial 1.00 %, citronellol 6.50 %, nerol 27.70 %, geraniol 11.80 %, caprylic acid 0.30 %, nonanoic acid 0.70 %, lauric acid 0.30 %.

ADDENDUM

2. ***Freesia grandiflora* (Baker) Klatt** in Dur. & Schinz, *Conspectus florae africae* 5: 187 (1894). [see p. 33]

Key to subspecies

- 1a Flowers usually red, rarely pink, always opening fully; filaments 15–25 mm long, exerted 12–20 mm from perianth tube 1a. subsp. *grandiflora*
- 1b Flowers pink, sometimes not opening fully; filaments $\pm$ 6 mm long, exerted $\pm$ 2 mm from perianth tube 1b. subsp. *occulta*

2a. subsp. ***grandiflora***

Flowers usually bright red, rarely salmon pink. Filaments 15–25 mm long, exerted 12–20 mm beyond tube. Style usually dividing between middle and apex of anthers, rarely below anthers. Figure 1A–D.

Distribution and ecology: as for the species.

2b. ***Freesia grandiflora* subsp. *occulta*** J.C.Manning & Goldblatt, subsp. nov.

Freesia grandiflora typica affinis sed flores palide carnei, filamentis brevissimis $\pm$ 6 mm longis $\pm$ 2 mm ex tubo exsertis et stylo brevissimo infra apicem antheris dividenti.

TYPE.—Mozambique, Zambézia Province, near Mocuba, 19 May 2010, *Gwynne-Evans* 90.05.10/10 (NBG, holo.).

Flowers salmon pink, sometimes not opening fully. Filaments $\pm$ 6 mm long, exerted $\pm$ 2 mm. Style dividing just below apex of anthers. Figure 1E.

Etymology: Latin *occultus*, hidden, alluding to the partially included stamens.

Distribution and ecology: subsp. *occulta* is evidently highly localized near Mocuba on the edge of the coastal plain in north-central Mozambique, where it occurs in mid-altitude forest and woodland on granite-derived soils. *Flowering time*: May and June. The typical subspecies has not been recorded around Mocuba.

This distinctive local form was first noted by Goldblatt (1993), based on *Barbosa & Carvalho* 2744. Other collections from surrounding coastal and inland Mozambique, including the type of the species from the mouth of the Luaua River, a tributary of the Zambezi that enters the Indian Ocean some 250 km SSW of Mocuba, have the scarlet perianth and well exerted stamens typical of the species. We were unable to re-examine the original collection from Mocuba but botanist David Gwynne-Evans re-collected this variant on a recent visit to the area (*Gwynne-Evans* 90.05.10/10, NBG). His observations and photographs confirm that all plants are morphologically consistent in their pink perianth and extraordinarily short filaments, $\pm$ 12 mm long and exerted just $\pm$ 2 mm from the perianth tube, thus differing markedly from typical subsp. *grandiflora*, which has well exerted filaments, 12–20 mm long. It appears that the flowers of many of the Mocuba plants fail to open fully. Although the tepals are normal in size and shape, they do not spread out fully and the flowers thus remain funnel-shaped. The anthers and stigmatic branches in these flowers are fully formed, and the plants appear to resemble the typical form in other respects, although we have not been able to check for the development of rhizomes.

It is clear that the Mocuba plants represent a distinctive, geographically localized genotype, and we describe it at subspecific level to highlight this fact.

13. **Freesia caryophyllacea** (Burm.f.) N.E.Br.
(synonymy cont., see p. 60)

Freesia herbertii Klatt ex N.E.Br. in Journal of South African Botany 1: 14 (1935), syn. nov. Type: without locality or original collector, specimen cultivated in Berlin Botanic Garden, May 1848, Kunth s.n. (B, holo., not seen). [Brown took the name from *Sparaxis herbertii*, a name without nomenclatural status that was simply listed in the synonymy of *F. xanthospila* by Klatt (1866), which we regard here as a synonym of *F. caryophyllacea*.]



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Freesias are famous throughout the world for their fragrant flowers but astonishingly, most of the wild species are virtually unknown. The true diversity of the genus is fully explored here for the first time. This important revision covers morphology, anatomy, molecular relationships, floral biology, taxonomy, horticultural history and cultivation of *Freesia*. Each of the 16 wild species is fully described and illustrated in colour, with complete synonymy, notes on ecology, and distribution maps. A new classification is presented, based on molecular and morphological evidence. The floral scent chemistry of most of the species is also reported here for the first time, providing fascinating insights into this poorly studied aspect. A detailed chapter on cultivation makes this an essential guide for anybody interested in growing these lovely plants.



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