Systematics and biology of

Lapeirousia, Codonorhiza, Psilosiphon & Schizorhiza

in southern Africa

Peter Goldblatt & John C. Manning

STRELITZIA 35

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STRELITZIA

This series has replaced *Memoirs of the Botanical Survey of South Africa* and *Annals of the Kirstenbosch Botanic Gardens*, which the South African National Biodiversity Institute (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 SANBI is partly 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 SANBI to champion the exploration, conservation, sustainable use, appreciation and enjoyment of South Africa's exceptionally rich biodiversity for all people.

Peter Goldblatt
B.A. Krukoff Curator of African Botany, Missouri Botanical Garden, St. Louis; Research Centre for Plant Growth and Development, School of Biological and Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg, Private Bag X01, Scottsville 3209, South Africa

John C. Manning
Compton Herbarium, South African National Biodiversity Institute, Cape Town; Research Centre for Plant Growth and Development, School of Biological and Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg, Private Bag X01, Scottsville 3209, South Africa

EDITOR:	Yolande Steenkamp
PROOFREADER:	Alicia Grobler
COVER DESIGN & LAYOUT:	Elizma Fouché
COVER PHOTOGRAPHS:	John C. Manning

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Abstract

Plastid and nuclear DNA sequence analyses show that the sub-Saharan African genus *Lapeirousia* Pourr. is paraphyletic as presently circumscribed. Species of *Lapeirousia* are retrieved as a clade in which are nested the tropical African genera *Cyanixia* Goldblatt & J.C.Manning and *Savannosiphon* Goldblatt & Marais as sister to *Lapeirousia* sect. *Paniculatae* Goldblatt plus the taxonomically isolated *L. neglecta* Goldblatt. To preserve taxonomic monophyly we dismember *Lapeirousia*, recognising the new genera **Codonorhiza** Goldblatt & J.C.Manning for *L.* sect. *Fastigiatae* Goldblatt (7 spp.) and **Schizorhiza** Goldblatt & J.C.Manning (1 sp.) for *L. neglecta,* both from the Cape Floristic Region, as well as **Psilosiphon** Welw. ex Goldblatt & J.C.Manning (15 spp.) for *L.* sect. *Paniculatae*, all from tropical and eastern southern Africa. This leaves *Lapeirousia* (27 species) centred in western southern Africa, but also represented in south tropical Africa. All four genera have derived corms with a flat base, each with distinctive and different corm tunics and sometimes corm shapes that are correlated with fundamental differences in leaf morphology and anatomy, floral bracts, and seed shape and surface sculpturing. *Codonorhiza* and *Schizorhiza* also have apomorphic, 1-banded pollen apertures. We revise the infrageneric taxonomy of *Lapeirousia* in light of the molecular phylogeny, recognising sect. **Chasmatocallis** (R.C.Foster) Goldblatt & J.C.Manning, sect. *Lapeirousia* and sect. **Sophronia** (Licht. ex Roem. & Schult.) Goldblatt & J.C.Manning. We provide dichotomous keys to the four genera in southern Africa and full revisions of all four genera. We recognise the following six new species: *C.* **elandsmontana** Goldblatt & J.C.Manning and *C.* **pillansii** Goldblatt & J.C.Manning from Western Cape, South Africa; *L.* **purpurea** Goldblatt & J.C.Manning from Western Cape; *L.* **kalahariensis** Goldblatt & J.C.Manning from southern Namibia and Northern Cape; *L.* **kamiesmontana** Goldblatt & J.C.Manning, a local endemic of the Kamiesberg of Northern Cape; and *P.* **erongoensis** Goldblatt & J.C.Manning from central Namibia. We also raise *L. dolomitica* subsp. *lewisiana* (B.Nord.) Goldblatt and *L. littoralis* subsp. *caudata* (Schinz) Goldblatt to species rank as *L.* **lewisiana** B.Nord. and *L.* **caudata** Schinz respectively, and recognise *L.* **angustifolia** Schltr., currently included in *L. pyramidalis* (Lam.) Goldblatt. We describe two new subspecies in the South African *L. fabricii* (D.Delaroche) Ker Gawl.; subsp. **compressa** Goldblatt & J.C.Manning and subsp. **purpurascens** Goldblatt & J.C.Manning; the new subsp. **foliosa** Goldblatt & J.C.Manning of *L. plicata* (Jacq.) Diels; and the new *P. sandersonii* subsp. **limpopoensis** Goldblatt & J.C.Manning.

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INTRODUCTION

Phylogenetic analysis of plastid and nuclear DNA sequences (Forest et al. 2014) shows that the sub-Saharan African genus *Lapeirousia* Pourr. (± 45 species) is paraphyletic as presently circumscribed (e.g. Goldblatt 1990a; Goldblatt & Manning 2008). Three tropical African genera of tribe Watsonieae Klatt (subfamily Crocoideae Burnett) (Goldblatt et al. 2006), *Cyanixia* Goldblatt & J.C.Manning (1 sp.), *Savannosiphon* Goldblatt & Marais (1 sp.) (and by inference *Zygotritonia* Mildbr., 6 spp.) nest within the genus, where they are retrieved as sister to the largely tropical and eastern southern African *L.* sect. *Paniculatae* Goldblatt, excluding *L. neglecta* Goldblatt. This clade is in turn sister to the largely southern but also south tropical African subg. *Lapeirousia*, with this combined clade sister to *L. neglecta* and then with *L.* sect. *Fastigiatae* Goldblatt from the Cape Floristic Region (Figure 1). The characters used to unite *Lapeirousia* in the past were a flat-based, ± bell-shaped corm (unique in Watsonieae but also present in several other genera of Crocoideae), and often a strongly asymmetric karyotype (Goldblatt & Takei 1993). Most species also have deeply divided style branches, a character ancestral in Watsonieae but lacking in *Cyanixia*, *Zygotritonia* and the Cape endemic *Pillansia* L.Bolus as well as in some species of *Lapeirousia* sect. *Paniculatae*.

Options for circumscribing genera in Watsonieae as monophyletic based on the molecular phylogeny are either to unite *Cyanixia*, *Savannosiphon* and *Zygotritonia* in an expanded and, in practice, morphologically indefinable *Lapeirousia*, or to treat *L.* sect. *Paniculatae*, *L. neglecta* and sect. *Fastigiatae* as separate genera. We select the latter option, transferring the tropical and eastern southern African species of sect. *Paniculatae* to the new genus *Psilosiphon* (naked or smooth tube) and those of sect. *Fastigiatae* to a second new genus *Codonorhiza* (bell-shaped root). We treat the phylogenetically isolated and morphologically intermediate *L. neglecta* as the new genus *Schizorhiza*. In this revised generic taxonomy all genera in the *Lapeirousia* clade are evidently monophyletic and readily distinguished by macro- and micro-morphological features, including leaf anatomy, pollen and seed morphology, and chromosome cytology.

The inference to be drawn from the phylogenetic analysis is that flat-based, ± bell-shaped corms are ancestral to the greater *Lapeirousia* clade and were either lost by reversal in *Cyanixia*, *Savannosiphon* and *Zygotritonia* or were acquired independently in *Psilosiphon* and *Codonorhiza* plus *Lapeirousia* and *Schizorhiza*. Woody corm tunics of brown colour characterise *Lapeirousia*, and tunics of blackish, compressed fibres are unique to *Codonorhiza* (sect. *Fastigiatae*). *Psilosiphon* has pale or dark brown, fibrous tunics, usually becoming loosely fibrous with age, and *Schizorhiza* has pale, corky tunics and ± ellipsoid rather than bell-shaped corms with a flat base; the diameter of the base smaller than the middle of the corm. These differences make the latter hypothesis seem reasonable. Associated with the corm differences are smooth, round seeds in *Psilosiphon*, *Schizorhiza* and most species of *Lapeirousia* (in which *L. caudata* Schinz, *L. littoralis* and all members of sect. *Sophronia* have a sculptured seed surface). In contrast, *Codonorhiza* has unusually small, ellipsoid seeds with reticulate sculpturing and a prominent funicular collar. Differences in the floral bracts among the four genera correlate closely with the corm tunic, seed and leaf features and are consistent with separate generic status for the three clades.

The molecular phylogeny renders the available taxonomic accounts of the *Lapeirousia* complex out of date and in need of substantial revision. This account presents a full revision of *Codonorhiza*, *Lapeirousia*, *Schizorhiza* and the

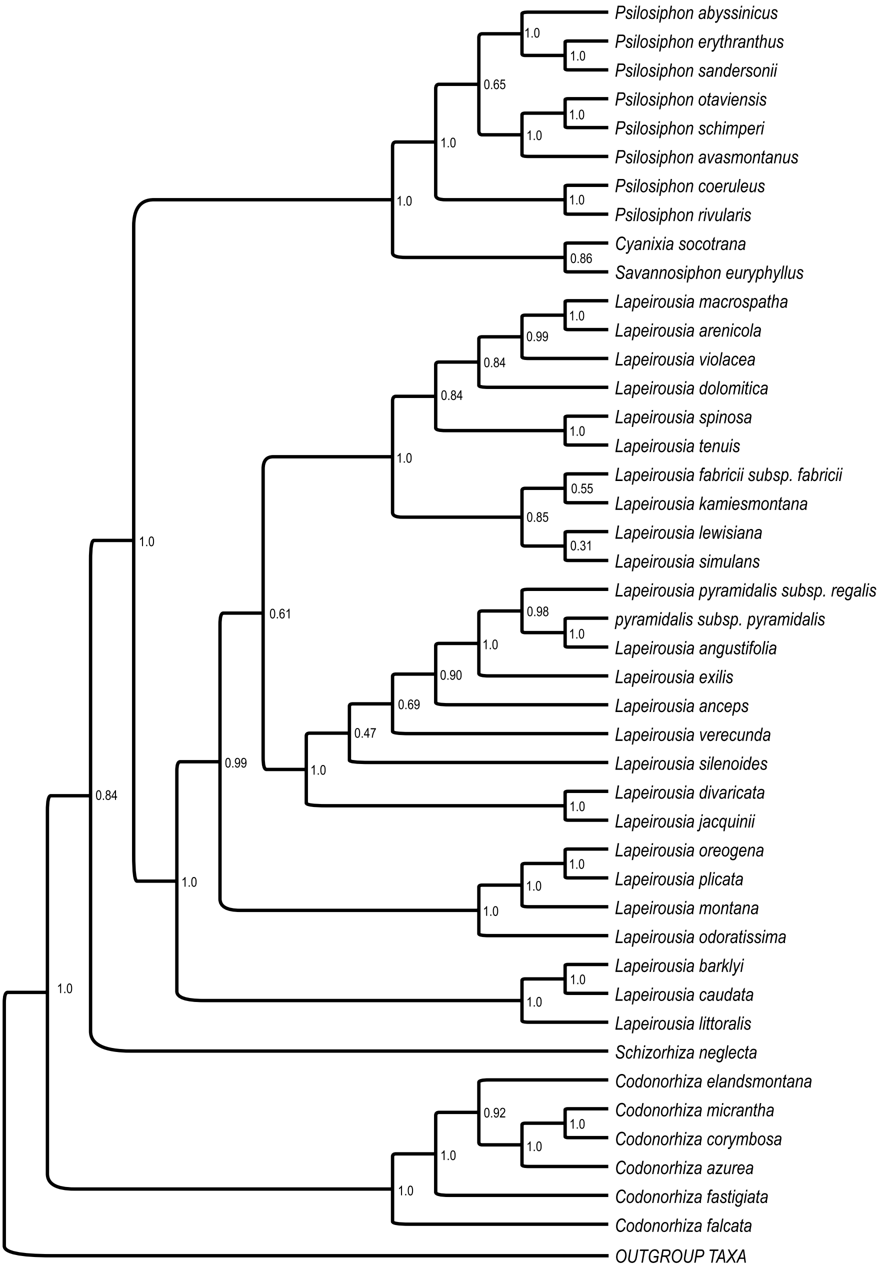


FIGURE 1.—Phylogenetic relationships in *Lapeirousia* and allied genera based on ten plastid regions (matK, rpl16, trnQ-rps16, trnL, trnL-trnF, ndhJ, ycf5, ndhf-rpl32, rpl32-trnL, ACCD-psa1) and one nuclear marker (RPB2) and obtained using the Bayesian inference implemented in MrBayes. Posterior probabilities are indicated on nodes (modified from Forest *et al*. 2014).

southern African species of *Psilosiphon*, thus bringing together the results of a series of papers in systematics, chromosome cytology, floral biology and phylogeny and speciation published after a revision of *Lapeirousia* in the southern African winter-rainfall zone (Goldblatt 1972) and later for tropical Africa (Goldblatt 1990a). In this treatment, we recognise seven species in *Codonorhiza*, 27 species in three sections in *Lapeirousia*, 15 species in *Psilosiphon* and one in *Schizorhiza*. Four species of *Psilosiphon* occur exclusively in tropical Africa and we do not deal with them in detail here, providing only the new combinations in *Psilosiphon*.

Six new species are included in the account, *C. elandsmontana*, *C. pillansii*, *L. kalahariensis*, *L. kamiesmontana*, *L. purpurea* and *P. erongoensis*, as well as new subspecies in *L. fabricii* and *L. plicata*. In addition, we recognise *L. lewisiana* B.Nord., which Goldblatt (1972) treated as subsp. *lewisiana* of *L. dolomitica*; *L. caudata*, currently treated as a subspecies of *L. littoralis*; and *L. angustifolia* Schltr., included by Goldblatt (1972) in *L. pyramidalis*.

TAXONOMIC HISTORY

The genus *Lapeirousia* was described in 1788 by French naturalist, Pierre André Pourret for the single species *L. compressa*, which he believed to have been collected in Isle de France, now Mauritius. Pourret was unaware that several species corresponding to his genus had already been described but assigned to *Gladiolus* L. (species with zygomorphic flowers) or to *Ixia* L. and even *Galaxia* Thunb. (both genera for species with radially symmetric flowers). John Ker Gawler (1804) adopted *Lapeirousia* in his then novel treatment of southern African Iridaceae in which he described the new genera *Anomatheca* Ker Gawl., *Babiana* Ker Gawl., *Geissorhiza* Ker Gawl., *Hesperantha* Ker Gawl. and *Tritonia* Ker Gawl., while also recognising *Gladiolus* and *Ixia*. Ker Gawler's *Lapeirousia* included just seven species, three of them now referred to *Codonorhiza*.

Shortly thereafter K.P. Sprengel (1817) erected the genus *Ovieda* to replace *Lapeirousia* without providing any reason for his action and the name was adopted for a short time despite the fact that it was not only a later synonym, thus superfluous and illegitimate, but also a later homonym for *Ovieda* L. (Verbenaceae). In the same year Roemer & Schultes (1817) described *Sophronia* for the acaulescent species, *S. caespitosa*, which had already been illustrated by Jacquin (1795) under the name *Galaxia plicata* (now *L. plicata* (Jacq.) Diels). In the *Dictionaire des Sciences Naturelles*, Poiret (1826) used the name *Peyrousia* for species of *Lapeirousia*, a name perhaps intended as a grammatical correction rather than a new genus since the circumscription of *Peyrousia* corresponded exactly to that of *Lapeirousia*. Then, for no evident reason, A. Dietrich (1833) transferred all the known species of *Lapeirousia* to a new genus *Meristostigma* A.Dietr., now regarded as an illegitimate, superfluous name. *L. falcata* (L.f.) Ker Gawl., *L. fastigiata* (Lam.) Ker Gawl. and *L. corymbosa* (L.) Ker Gawl., all described before 1800 in *Gladiolus* or *Ixia*, were included without question in *Lapeirousia*, then distinguished by the combination of bell-shaped corms and divided style branches. These three species form the core of the new genus *Codonorhiza*.

The first species of *Psilosiphon* was discovered in Ethiopia by Henry Salt on his 1809–1810 expedition to Abyssinia (Salt 1814). His collections were referred by Robert Brown in the report of the expedition to *Geissorhiza* as *G. abyssinica*, without description. Over 25 years later in the 1840s, the French explorers Quartin-Dillon and Petit again collected *P. abyssinica*; their collections being described as *Montbretia abyssinica* by A. Richard (1850). The species was later transferred to *Lapeirousia* by J.G. Baker in 1877. Quartin-Dillon and Petit also collected *P. schimperi* (Aschers. & Klatt) Goldblatt & J.C.Manning, as did the Austrian, Georg W. Schimper, who spent the years 1837–1878 in Ethiopia. The species was first referred to *Tritonia* (Klatt 1866b), then to *Acidanthera* Hochst. because the white flower and elongate perianth tube corresponded to the circumscription of that genus. Only in 1934 was *T. schimperi* Aschers. & Klatt transferred to *Lapeirousia*. Then in the 1860s another Austrian, Friedrich Welwitsch, living in Angola, collected different populations of what we now regard as the same species, to which he gave the manuscript names *P. cyanescens* and *P. fragrans*. Welwitsch also discovered *L. odoratissima* Welw. ex Baker, naming his collections *Psilosiphon odoratissima*. J.G. Baker (1878) referred all Welwitsch's provisional *Psilosiphon* species to *Lapeirousia*. At the time *Psilosiphon* remained without formal description.

Species of both *Codonorhiza* and *Psilosiphon* were included in *Lapeirousia* together with Ker Gawler's new genus *Anomatheca* (now included in *Freesia* Klatt) by Baker in his accounts of the Iridaceae for *Flora capensis* (Baker 1896) and *Flora of tropical Africa* (Baker 1898), evidently on the basis of their long-tubed flowers with divided style branches. Foster (1939) described the genus *Chasmatocallis* for the florally distinctive *L. divaricata* Baker, an action that was largely ignored by the botanical community. Baker's circumscription of *Lapeirousia* was revised by Goldblatt (1972), who recognised *Anomatheca* as a separate genus more closely allied to *Freesia* Klatt (1866a) than *Lapeirousia*. Goldblatt's (1972, 1990a) accounts of *Lapeirousia* for the southern African winter rainfall region and for tropical and summer rainfall southern Africa collectively admitted 34 species to the genus. Additional species were added in the years that followed (Goldblatt & Manning 1992, 1994) with the result that in 2010 *Lapeirousia* included over 40 species.

A subgeneric classification based on corm and leaf morphology, proposed by Goldblatt & Manning (1990), recognised two subgenera, subg. *Lapeirousia* and subg. *Paniculatae* [as *Paniculata*], the latter with sect. *Paniculatae* (now *Psilosiphon*) and sect. *Fastigiatae* [as *Fastigiata*] (now *Codonorhiza*). Apomorphic features for subg. *Lapeirousia* are the prominently ridged leaves without a central vein, large outer floral bracts, leathery or succulent in texture, an inner bract much smaller than the outer, and particularly hard, woody corm tunics. For subg. *Paniculatae* the derived features are primarily the hard but ± fibrous corm tunics, and an inflorescence that is (usually) a false panicle of few-flowered spikes. The floral bracts are ± equal in length in both sections of subg. *Paniculatae* but in sect. *Fastigiatae* the bracts are leathery, green and obtuse to ± truncate vs. of softer texture, acute and becoming dry apically in sect. *Paniculatae*.

Although first collected in 1943 by R.H. Compton, *Schizorhiza neglecta* was only described in 1972 as subsp. *alta* Goldblatt of *Lapeirousia corymbosa* and later treated as the separate species *L. neglecta* (Goldblatt & Manning 1992) and referred to sect. *Paniculatae*.

Molecular phylogenetic studies in the Iridaceae (Goldblatt et al. 2006; Goldblatt & Manning 2008) showed that *Lapeirousia* in the broad sense falls in a clade that retrieves *Watsonia* Mill., *Micranthus* (Pers.) Eckl., *Pillansia* L.Bolus and *Thereianthus* G.J.Lewis as sister to *Lapeirousia* plus *Savannosiphon* and *Cyanixia*. The tropical African *Zygotritonia* was inferred to belong here as well, but was not included in these studies. This assemblage of genera currently constitutes the tribe Watsonieae of subfam. Crocoideae.

MORPHOLOGY

Corm: although the corms of all three genera are bell-shaped to broadly obconic (triangular in outline), the corm tunics differ markedly among them (Figure 2). Tunics of *Codonorhiza* are dark grey and composed of concentric layers of compacted fibres with a broad basal lip. Those of *Lapeirousia* are dark brown to reddish brown and woody with a crenate to finely toothed or spiny basal margin. In *Psilosiphon* the tunics are usually light brown and of a hard, fibrous to leathery texture and lack marginal decoration (Table 1). Somewhat unusual for the entire *Lapeirousia* clade, *Schizorhiza* produces multiple cormlets at the subterranean and lower aerial nodes of the stem. The genus is also unusual in that several new corms replace the parent at the end of the growing season instead of the usual single new main corm.

Stem: usually aerial and branched, stems are rounded to somewhat compressed in cross section. Branching is pronounced in *Codonorhiza*, with the branches arranged in corymbose fashion forming a compound, flat-topped inflorescence. Stems of most species of *Psilosiphon* have a similar branching pattern, especially prominently branched in *P. coeruleus*, *P. erythranthus* and *P. sandersonii*, whereas branching in *P. gracilis* and *P. schimperi* is limited, resulting in a rather different appearance. Aerial stems of *Lapeirousia* are more strongly flattened and branches bear multiple flowers in spikes. In species of *L.* sect. *Sophronia* the stem is subterranean and strongly contracted so that plants form low tufts at ground level with flowers crowded together.

Leaves: leaf anatomy, especially the leaf margins, is typically consistent in genera of Crocoideae (Rudall 1995; Goldblatt et al. 2006) and is, as far as known, consistent in all genera of Watsonieae. Leaf margins in the *Lapeirousia* group of genera are of two types: simple and without an associated marginal vein or subepidermal strand of sclerenchyma; or with a well-developed marginal vein present with ± prominent sclerenchyma cap (Figure 3). *Codonorhiza* (*C. corymbosa* examined: Rudall 1995) and *Schizorhiza* have simple margins of the first type, lacking marginal veins or a sclerenchyma strand. In contrast, *Lapeirousia* (*L. anceps*, *L. divaricata* and *L. odoratissima* examined) and *Psilosiphon* (*P. avasmontanus*, *P. bainesii*, *P. coeruleus*, *P. erythranthus* examined) (Table 1) have margins

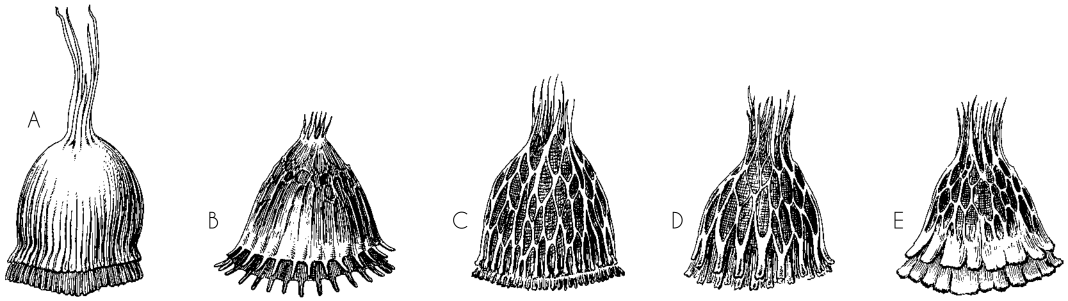


FIGURE 2.—Corm morphology in *Lapeirousia* and allied genera. A, *Lapeirousia plicata*; B, *L. dolomitica*; C, *Psilosiphon bainesii*; D, *Psilosiphon coeruleus*; E, *Codonorhiza micrantha*. Artist: John Manning.

TABLE 1.—Comparison of taxonomically significant vegetative characters in the *Lapeirousia* clade

Taxon	**Corm shape**	**Corm tunics**	**Foliage leaves**	**Leaf marginal vein**	**Vascular bundles**	**Leaf surface**
Codonorhiza	bell, base flat	compacted fibres, grey-black	1 or 2, lower largest	absent	opposite; sheath complete	plane
Lapeirousia	bell to obconic, base flat	woody, brown	few, lower largest	present	alternate; sheath incomplete	corrugately ribbed
Psilosiphon	± bell, base flat	leathery or compacted fibres, brown	2–several in basal fan	present	± opposite; sheath incomplete	plane
Schizorhiza	± ellipsoid with flat base	cork-like, light brown	few in basal fan	absent	alternate; sheath complete	slightly pleated
Cyanixia	globose	fibrous, red-brown	2 or 3 in basal fan	present	alternate; sheath incomplete	pleated
Savannosiphon	globose	fibrous, red-brown	several in basal fan	present	opposite; sheath complete	pleated
Zygotritonia	globose	fibrous, red-brown	1 or 2, lower largest	present	n/a	pleated

of the second type, with a prominent marginal vein with sclerenchyma cap (Rudall & Goldblatt 1991; Goldblatt & Manning 1990).

Codonorhiza and *Psilosiphon* have plane leaves with a visible and sometimes prominent main vein ± centrally placed to form a pseudo-midrib, and with the primary and secondary vascular bundles ± opposite. In *Lapeirousia* at least the basal leaf is prominently closely plicate (corrugate) with the angles of the folds thickened and ribbed, without a pseudo-midrib, and with the major vascular bundles alternate (Goldblatt & Manning 1990). *Schizorhiza* has a distinctive leaf anatomy in which the main vascular bundles near the centre are ± alternate and surrounded by a complete sclerenchyma bundle sheath, also characteristic of *Codonorhiza*. The latter is unusual in having falcate, ± obtuse leaves with the margins often undulate to crisped. In both *Codonorhiza* and *Lapeirousia* the basal leaf is largest and is sometimes the only foliage leaf, whereas *Psilosiphon* and *Schizorhiza* have a fan of a few to several basal leaves. The differences in leaf anatomy and morphology among the four genera (Table 1) are congruent with the molecular phylogeny.

Inflorescence: one of the reasons in the past for maintaining a broad circumscription of *Lapeirousia* has been the trend for inflorescences to form flat- or round-topped false panicles – sometimes called corymbs (Table 2). Usually some flowers in ultimate branches are sessile as in a spike, the ancestral inflorescence type in the tribe and subfamily. Such false panicles are universal in *Psilosiphon* and *Schizorhiza* and almost so in *Codonorhiza* (the exception, *C. falcata* has a spike). All *Lapeirousia* species with aerial stems have spicate inflorescences. Because *C. falcata* is retrieved as sister to the remaining species of that genus, a spike may be inferred as ancestral in *Codonorhiza* as well as for *Lapeirousia*. It follows that the false panicles in *Codonorhiza*, *Psilosiphon* and *Schizorhiza* may be independently derived. That interpretation is again congruent with the molecular phylogeny.

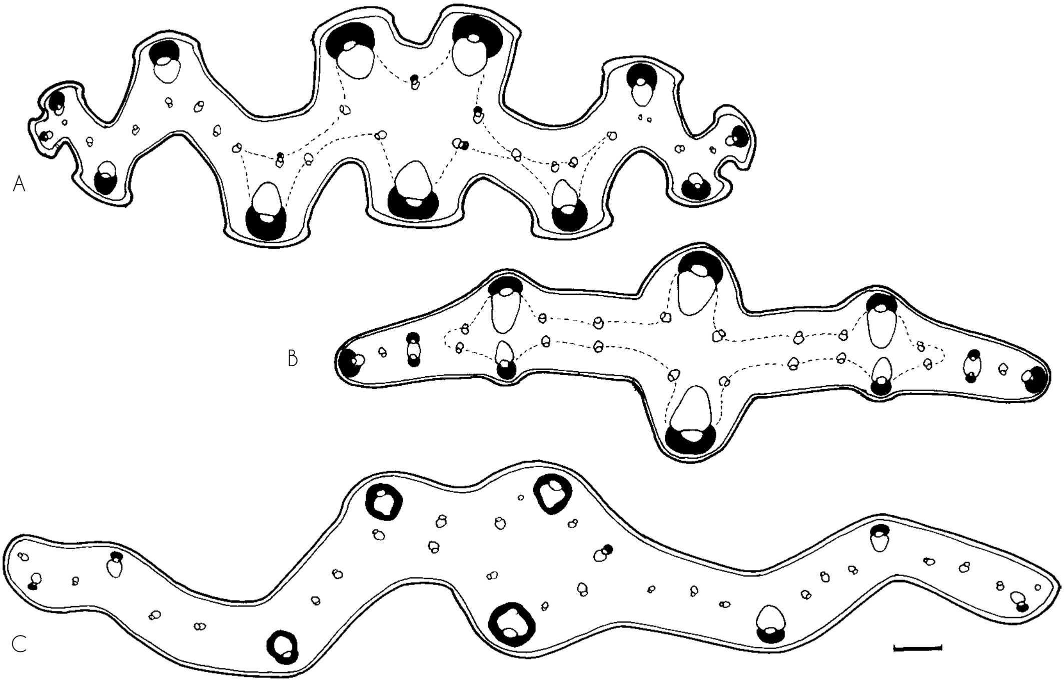


FIGURE 3.—Leaf anatomy in *Lapeirousia* and allied genera. A, *Lapeirousia odoratissima*; B, *Psilosiphon bainesii*; C, *Schizorhiza neglecta*. Scale bar: 200 μm. Artist: John Manning.

Floral bracts likewise, are consistent with the phylogeny in texture and morphology. In *Lapeirousia* the large, fleshy to succulent outer bract is usually twice as long as the membranous, 2-keeled inner bract. This contrasts with the leathery, green, subequal outer and inner bracts of *Codonorhiza* and *Schizorhiza*. In *Codonorhiza* the inner bracts are ± obtuse and not 2-keeled or forked apically although sometimes emarginate. Bracts of *Psilosiphon* represent a third type, relatively soft-textured, often becoming dry from the tips at anthesis, the outer only slightly longer than the inner or sometimes slightly shorter.

Flowers: remarkably diverse in form, size and colour, flowers of *Lapeirousia* and *Psilosiphon* reflect their adaptation to a range of pollinators. All species have a well-developed perianth tube, shortest in white-flowered *L. divaricata* and *L. spinosa* (7–12 mm long) and in some species of *Psilosiphon*. In species with tubes exceeding 30 mm, the tube is narrow almost throughout. Long-tubed species have one of two predominant colours. One group, exemplified by *L. silenoides* and *L. lewisiana*, has flowers intensely pigmented in shades of purple, red or violet, often with white markings on the lower tepals or, in species with radially symmetric flowers, on all tepals. The second group, exemplified by *L. anceps* and *L. fabricii*, has a white to beige perianth with red markings on the lower tepals and often pink or red outside, which gives otherwise white flowers a pink cast. The flowers in both of these long-tubed groups are unscented. A third group of long-tubed species, including *L. pyramidalis* subsp. *pyramidalis* and *L. odoratissima*, has white or pale pink to dull yellow (or sometimes dull maroon) flowers usually without markings on the tepals but often intensely scented. The three groups represent the main pollination groups in the genus: long-proboscid flies of the genus *Prosoeca*; long-proboscid flies in the genera *Moegistorhynchus* and *Philoliche*; and moths. In *Psilosiphon*, *P. bainesii* and *P. schimperi* have flowers

TABLE 2.—Summary of inflorescence, floral and pollen grain differences among genera of the *Lapeirousia* clade

Taxon	Inflorescence	Bracts	Style branches	Pollen grains
Codonorhiza	spike or flat-topped false panicle	leathery, subequal, inner entire	deeply divided	monosulcate, operculum band 1
Lapeirousia	spike (or basal rosette)	fleshy, inner smaller, forked at tip	deeply divided (entire)	monosulcate, operculum bands 2
Psilosiphon	flat- or round-topped false panicle	soft (leathery), subequal, inner forked at tip	deeply divided or entire	monosulcate, operculum bands 2
Schizorhiza	flat- or round-topped false panicle	firm to leathery, subequal, inner entire	deeply divided	monosulcate, operculum band 1
Cyanixia	spike	soft, green, inner smaller, forked at tip	entire	trisulcate
Savannosiphon	spike	leathery, subequal, inner entire	deeply divided	polyaperturate
Zygotritonia	spike	firm to leathery, short, becoming dry, inner forked at tip or not	style undivided or branches short, undivided	trisulcate

of the third group, pollinated by moths. Shorter-tubed species of *Psilosiphon* and *Schizorhiza* with darkly pigmented (or white) flowers, including *P. erythranthus* and *P. sandersonii*, exhibit no such specialised pollination systems and evidently have a generalist pollination strategy.

Flowers are typically bilaterally symmetric (zygomorphic), most likely the ancestral condition, with unilateral stamens held erect or arched beneath the dorsal tepal and the style parallel to or arching over the stamens. All species of the acaulescent sect. *Sophronia* have radially symmetric (actinomorphic) flowers, sometimes with either relatively short or exceptionally long tubes (*Lapeirousia oreogena* and *L. odoratissima*, up to 140 mm long in the latter). Two species of *Psilosiphon*, *P. avasmontanus* and *P. coeruleus*, have radially symmetric flowers but their different vegetative morphology and cytology indicate that they are not immediately related. In *Codonorhiza*, *C. coeruleus* and *C. fastigiata* have radially symmetric flowers, again the derived condition, and possibly shared in the two (the molecular data are ambiguous). Radial floral symmetry has thus evolved at least four times in the four genera and also in the related genus *Cyanixia* (Goldblatt et al. 2004a). The lability of floral symmetry, perianth pigmentation and perianth tube length is typical of many African genera of Crocoideae (Goldblatt & Manning 2006). We discuss floral longevity under the chapter on Floral Biology (pg. 16).

Apart from their orientation, the stamens offer few useful taxonomic characters. Anther and pollen colour is however, variable. Yellow anthers and pollen are most common, but in long-tubed species with white or beige flowers the anthers are often blue or purple, particularly noticeable in *Lapeirousia fabricii*. The unusual pollen colour may serve as orientation guides for visiting pollinators or as camouflage to deter pollen foraging by bees.

In the gynoecium, the level of division of the style is often important, as is the nature of the style branches, either deeply divided or entire (Table 2). Parsimony suggests that deeply divided style branches are ancestral in the *Lapeirousia* clade and in Watsonieae. Thus ± entire style branches in *L. plicata* subsp. *effurcata* and several species of *Psilosiphon* are reversals of ancestral states. The style itself may divide below, opposite, or beyond the anther apices. The level of division thus may allow for direct contact of the pollen-bearing anthers and permits selfing in self-compatible species when pollination by outside agents fails. Most species with style branches in contact with pollen have been experimentally shown to be facultatively autogamous (see discussion of Floral Biology, pg. 16).

Capsules and seeds: capsules of the *Lapeirousia* clade offer few characters of taxonomic significance: they are ± globose to broadly ovoid, somewhat 3-lobed and contain relatively few seeds, the outlines of which are often evident as slight bulging of the capsule walls. Several species of *Lapeirousia* sect. *Chasmatocallis*, however, have unusual capsules with prominent locular ridges on the lateral walls, and in *L. silenoides, L. verecunda* and a few other species, the ridges continue distally as ear-like lobes.

Rarely collected, seeds have virtually no practical value for species identification. Nevertheless, seed shape, size and surface features provide valuable information about generic and species relationships (Table 2, 3). Seeds are typically ± globose in *Psilosiphon*, *Schizorhiza* and most species of *Lapeirousia*, with a smooth (rarely slightly wrinkled) surface of domed (colliculate) epidermal cells (exceptionally tuberculate in *L. pyramidalis*). In *Lapeirousia*, all members of sect. *Sophronia* and two of sect. *Lapeirousia* (*L. caudata* and *L. littoralis*) have seeds with a reticulate or rugulose surface and plane outer epidermal cells walls.

In contrast, seeds of *Codonorhiza* are smaller and ellipsoid with rounded ends and a prominent funicular collar at the micropylar end (Goldblatt & Manning 1992). Seeds are mostly 0.8–1.0 mm long in *Codonorhiza* but up to 1.6 mm long in *C. micrantha*. In *Lapeirousia* and *Psilosiphon*, seeds are typically larger than 1.3 mm diam. and up to 2 mm diam. in *L. odoratissima* and the *L. dolomitica* group (Table 3). Most species of sect. *Sophronia* have unusually large seeds, 1.7–2.3 mm diam., but *L. plicata* has smaller seeds than are typical of the section, 1.0–1.5 mm diam. Among the largest in the clade, seeds of *Schizorhiza* are 2.0–2.5 mm diam.

Most species of the *Lapeirousia* group of genera show no adaptations for dispersal in their

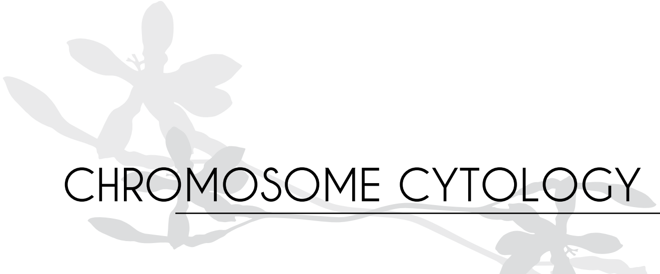
TABLE 3.—Comparison of seed characteristics for genera and sections of the *Lapeirousia* clade. Seed length is measured from micropyle to chalaza

Taxon	**Seed shape**	**Length (mm)**	**Sculpturing**	**Surface cell outline and orientation**
Codonorhiza	ovoid, collar prominent	mostly 0.8–1.3	rugulo-reticulate or reticulate	flat, not organised
Lapeirousia				
Sect. *Chasmatocallis*	globose	mostly 1.5–2.0	smooth	usually ± domed (rarely tuberculate to areolate), scalariform
Series Sophronia	globose	mostly 1–2	rugose to reticulate	flat, not organised
Sect. *Lapeirousia*	globose	1.3–1.4	smooth (reticulate in 2 spp.)	domed, scalariform
Psilosiphon	globose (± angled by pressure)	mostly 1.5–2.5	rugulose to smooth	flat or domed, not organised
Schizorhiza	± globose	2.0–2.5	rugulose	flat, not organised
Savannosiphon	± globose	1.7–2.2	rugulose	± domed
Cyanixia	± globose	± 2.0 × 1.8	rugulose	± domed, not organised
Zygotritonia	globose-ellipsoid	± 2	smooth	flat–foveate

seeds or capsules, but dispersal by wind of the entire plant when dry is important in species of arid areas. In *Psilosiphon bainesii*, dry plants bearing mature, intact capsules may be blown significant distances across open veld. Similarly, in acaulescent species like *L. exilis*, *L. montana*, *L. oreogena*, *L. plicata* and even *L. kalahariensis* and *L. oreogena*, the dry plants detach from the corm and blow across the veld for some distance, shedding their seeds as the capsules break open on rough ground.

Pollen grains: species of *Lapeirousia* and *Psilosiphon* (Table 2) have the ancestral type pollen grains for subfamily Crocoideae, ellipsoid in shape with a single broad sulcus in which lies a pair of longitudinal exine bands, the operculum (Goldblatt et al. 1991). In contrast, species of *Codonorhiza* have pollen grains with a single opercular band, as do both the diploid and tetraploid populations of *Schizorhiza neglecta*. The one-banded condition is an occasional character state in subfamily Crocoideae, consistent only in *Ixia* and *Xenoscapa* (Goldblatt) Goldblatt & J.C.Manning and found in one or more species of *Freesia*, *Romulea* Maratti and *Thereianthus* (Goldblatt & Manning 2009).

The closely related genera *Cyanixia* and *Zygotritonia* have trisulculate grains (Goldblatt et al. 2004a). Other pollen apertures also occur in the family and are reviewed by Goldblatt & Manning (2009). Pollen grains are always shed singly, and the exine sculpturing is uniformly perforate-scabrate, the ancestral and most common condition for Crocoideae (Schulze 1971).



CHROMOSOME CYTOLOGY

Cytology has played an important role in our understanding of the systematics and evolution of *Lapeirousia* and the segregates, *Codonorhiza* and *Psilosiphon*. Early counts (Goldblatt 1971, 1972) revealed little of the variation now evident because the highly asymmetric and bimodal karyotypes include B chromosomes that obscured the base numbers in some species counted. Later work (Goldblatt 1990b) and especially by Goldblatt & Takei (1993) resolved much of the confusion and allowed a reinterpretation of earlier counts, here assembled in Table 4. The patterns we now perceive still need further clarification but correlate reasonably well with some morphological characters and are consistent with our taxonomy.

Codonorhiza consistently has $2n = 20$ (not including B chromosomes) and a karyotype of one long and nine much shorter chromosome pairs, thus $x = 10$. Basic chromosome number in *Schizorhiza* is $x = 6$ and that in *Lapeirousia* $x = 9$ and 8, and the karyotypes are also asymmetric with one long chromosome pair. This pattern characterises sect. *Chasmatocallis* except for *L. divaricata*, the two counts for which are $2n = 20$, possibly representing 18 + 2B. Sect. *Lapeirousia* and sect. *Sophronia* have derived karyotypes with $2n = 16$ (again excluding B chromosomes) (Table 4). The chromosome numbers are interpreted here as a descending series because related genera of the tribe have a basic chromosome number of $x = 10$ (*Micranthus*, *Pillansia*, *Thereianthus*) or 9 (*Watsonia*) and we infer $x = 10$ for the entire tribe. Ancestral base number for *Lapeirousia* is evidently $x = 9$ and the base of $x = 8$ is secondary, possibly derived independently at least twice, once in sect. *Sophronia* and once in sect. *Lapeirousia*.

Psilosiphon has a wide range of diploid chromosome numbers, the highest recorded, $2n = 16$ in *P. avasmontanus*, and the lowest $2n = 6$ in some populations of *P. bainesii* (others $2n = 10$). Karyotypes of most species are also strongly asymmetric with one long and the remaining much smaller chromosome pairs. Chromosome rearrangement is evident in *P. erythranthus* and its immediate allies (Table 4), $2n = 8$, which have a relatively symmetric karyotype without gross size differences (Goldblatt & Takei 1993). Neopolyploidy is present in *P. erythranthus*, some populations of which have $2n = 14$ or 12 (hypopolyploid on the base of $2n = 8$), and hypopolyploid karyotypes characterise *P. bainesii*, *P. otaviensis* and *P. schimperi* ($2n = 10$); *P. bainesii* also has derived populations in central Namibia with $2n = 6$.

Ancestral karyotypes in *Psilosiphon* and *Schizorhiza* are distinctive in consisting of one long chromosome pair, 4.1–6.5 μm long. In most species the remaining smaller pairs are 1–2 μm long. Because of the constant presence of the large chromosome pair and a constancy in chromosome length (which is correlated with quantity of DNA), species of all four genera with high base numbers of 10, 9, 8 or 6 must be regarded as palaeodiploid, as are some lower base numbers. *Codonorhiza* and *Lapeirousia* are also palaeodiploid. The northern population of *S. neglecta* is exceptional in its diploid number of $2n = 24$ (tetraploid); one of the two southern populations examined for chromosome number has $2n = 12$.

A descending dysploid series is a striking feature of *Psilosiphon*: *P. avasmontanus* ($2n = 16$), *P. gracilis* ($2n = 12$) and *P. sandersonii* ($2n = 10$) maintain the putatively ancestral pattern of one large and the remainder small chromosome pairs, as is the total quantity of DNA per cell (Table 4). *P. abyssinicus*, *P. coeruleus*, *P. setifolius* and the southern populations of *P. erythranthus* have $2n = 8$, but *P. erythranthus* in Zambia and Malawi, the northern part of its range, has $2n = 14$ or 12, with the latter cytotypes having twice as

TABLE 4.—Chromosome numbers, mean total length of the chromosome complement and number of opercular bands in the pollen grain aperture in *Codonorhiza, Lapeirousia*, *Schizorhiza* and *Psilosiphon* (from Goldblatt 1971; Goldblatt 1990b; Goldblatt & Takei 1993). Karyotype measurements were made from photographs or camera lucida drawings of karyotypes of estimated comparable degree of contraction; all at the same magnification. The asterisk (*) indicates readings corrected for measurements made using a different cytological method by Goldblatt & Manning (1992). New counts are indicated in bold type and voucher data are as follows: *C. azurea* 2*n* = 20 +2B (*Goldblatt 8016*, Malmesbury commonage, NBG); *Schizorhiza neglecta* 2*n* = 24 (*Goldblatt & Manning 10122*, Bains Kloof, NBG). Genome sizes where known are from Goldblatt & Takei 1993)

Taxon	**Diploid number 2*n***	**Total chromosome length (inferred ploidy level, *x*)**	**Genome size (μm), pg**	**Number of opercular bands in aperture**
Codonorhiza (7 spp.; *C. elandsmontana*, *C. pillansii* not counted)				
C. azurea	20, **20 + 2B**	–	–	1
C. corymbosa	20	31.5 (2*x*)	–	1
C. falcata	20	–	–	1
C. fastigiata	20	–	–	1
C. micrantha	20	28.7* (2*x*)	–	1
Psilosiphon (16 spp.; *P. erongomontanus*, *P. masukuensis, L. teretifolius, P. zambesiacus* not counted)				
P. abyssinicus	8	28.3* (2*x*)	–	2
P. avasmontanus	16	28.0* (2*x*)	–	2
P. bainesii	10	–	2	
	6	46.5* (4*x*)	–	2
P. coeruleus	8	27.6 (2*x*)	–	2
P. erythranthus	8	24.5 (2*x*)	2.7	2
	14	– (4*x*)	–	2
	12, 12 + 0–3B	54.1 (4*x*)	5.8	2
P. gracilis	12	26.2 (2*x*)	2.4	2
P. otaviensis	10	47.8 (4*x*)	5.1	2
P. rivularis	12	47.2 (4*x*)	–	2
P. sandersonii	10	28.6 (2*x*)	–	2
P. schimperi	10	47.1 (4*x*)	5.1	2
P. setifolius	8	25.4 (2*x*)	–	2
Schizorhiza (1 sp.)				
S. neglecta	12	26.2 (2*x*)	–	1
	24	– (4*x*)	–	1
Lapeirousia (27 spp.)				
Sect. *Chasmatocallis* (8 spp.)				
L. anceps	18, 18 + 2B	30.1* (2*x*)	–	2
L. angustifolia	18	–	–	2
L. divaricata	20 (?18 + 2B)	–	–	2

TABLE 4 (cont.).—Chromosome numbers, mean total length of the chromosome complement and number of opercular bands in the pollen grain aperture in *Codonorhiza*, *Lapeirousia*, *Schizorhiza* and *Psilosiphon* (from Goldblatt 1971; Goldblatt 1990b; Goldblatt & Takei 1993). Karyotype measurements were made from photographs or camera lucida drawings of karyotypes of estimated comparable degree of contraction; all at the same magnification. The asterisk (*) indicates readings corrected for measurements made using a different cytological method by Goldblatt & Manning (1992). New counts are indicated in bold type and voucher data are as follows: *C. azurea* 2*n* = 20 +2B (*Goldblatt 8016*, Malmesbury commonage, NBG); *Schizorhiza neglecta* 2*n* = 24 (*Goldblatt & Manning 10122*, Bains Kloof, NBG). Genome sizes where known are from Goldblatt & Takei 1993)

Taxon	**Diploid number 2*n***	**Total chromosome length (inferred ploidy level, *x*)**	**Genome size (μm), pg**	**Number of opercular bands in aperture**
L. jacquinii	18, 18 + 2B	25.7 (2*x*)	–	2
L. exilis	18 + 0–2B	29.8 (2*x*)	–	2
L. pyramidalis				
subsp. *pyramidalis*	18	33.1 (2*x*)	–	2
subsp. *regalis*	18	–	–	2
L. silenoides	18, 18 + 0–2B	27.1 (2*x*)	–	2
L. verecunda	18	–	2	
Sect. *Sophronia* (5 spp.; *L. kalahariensis, L. montana* not counted)				
L. odoratissima	16	31.4 (2*x*)	–	2
L. oreogena	16, 16 + 0–2B	28.8 (2*x*)	–	2
L. plicata	16	31.1 (2*x*)	–	2
Sect. *Lapeirousia* (14 spp.; *L. kamiesmontana, L. macrospatha, L. purpurea, L. simulans, L. tenuis* not counted)				
L. arenicola	16	26.4 (2*x*)	–	2
L. barklyi	16	–	–	2
L. caudata	16	32.0 (2*x*)	–	2
L. dolomitica	16, 16 + 0–2B	–	–	2
L. fabricii	16 + 1B	–	–	2
L. lewisiana	16	34.8 (2*x*)	–	2
L. littoralis	16	30.8* (2*x*)	–	–
L. spinosa	16	–	–	2
L. violacea	16	–	–	2

much DNA per cell as those with 2*n* = 8 (Goldblatt 1990b). They must, therefore, be regarded as hypopolyploid (perhaps derived from a hypothetical 2*n* = 16, so far not found in the wild). *P. rivularis* (one Zambian population counted) also has 2*n* = 12, but *P. otaviensis* and *P. schimperi* have 2*n* = 10 and *P. bainesii* has cytotypes with 2*n* = 10 and 6 (the latter recorded for two Namibian populations and the lowest chromosome number recorded in the Iridaceae). All four species have genomes with total chromosome length and, where known, DNA quantity per cell that marks them as polyploid, but with radically reorganised karyotypes. They are in fact polyploid but with lower chromosome numbers than their ancestral stock. The most parsimonious explanation is that the latter four species share a common polyploid ancestor. Our molecular phylogeny is not informative on this issue as too few species of *Psilosiphon* have been sequenced.

Among the genera of Watsonieae believed to be most closely related to the *Lapeirousia* group of genera, *Cyanixia* has $x = 10$ and *Zygotritonia* $x = 8$, both with strongly bimodal karyotypes consisting of one large pair and the remaining pairs much smaller, thus consistent with the ancestral pattern for the entire *Lapeirousia* clade (Goldblatt 1989, Goldblatt et al. 2004a). *Savannosiphon* has $x = 7$ but a very different karyotype of large, medium and small chromosomes (Goldblatt & Marais 1979), without strong bimodality. The pattern of chromosome evolution, viewed in the light of the DNA-based phylogeny, is consistent with the scenario outlined above in which $x = 10$ and a bimodal karyotype are ancestral.

Additional counts will help clarify the patterns already evident. The variability in number, even within some species of *Psilosiphon*, indicates that the genus is not adequately sampled. It would be particularly useful to determine the chromosome number of the Namibian populations of *P. rivularis* in light of the counts for the Zambian populations, which have $2n = 12$. Counts are also needed for additional populations of *P. sandersonii* and *P. gracilis* while *P. erongoensis* remains uncounted.

FLORAL BIOLOGY

Reproductive compatibility: compatibility relations in *Lapeirousia*, although inadequately known, are informative: at least one or more populations of *L. anceps*, *L. arenicola*, *L. fabricii*, *L. jacquinii*, *L. oreogena*, *L. simulans* and *L. violacea* have been determined to be self-compatible and facultatively autogamous using pollinator exclusion experiments (Goldblatt et al. 1995; Manning & Goldblatt 1997; Pauw et al. 2008). Notably, all of these species are either known or inferred to be specialised for long-proboscid fly pollination. Similar studies of bee pollinated *L. barklyi* and *L. spinosa*, long-proboscid fly pollinated *L. lewisiana*, *L. pyramidalis* subsp. *regalis* and *L. silenoides*, and moth pollinated *L. pyramidalis* subsp. *pyramidalis* show these species to be self-incompatible and unable to set seed even when self-pollen is transferred by hand to receptive stigmas in those species in which the stigmatic surfaces are not normally in contact with anthers and pollen. The association of self-compatibility and often autogamy (facultative when species have regular pollinator visits) with specialist pollination strategies is not uncommon in the southern African Iridaceae (Goldblatt & Manning 2006) and is documented, for example in *Babiana* (Anderson et al. 2005; Goldblatt & Manning 2007; De Waal et al. 2011) and *Sparaxis* (Goldblatt et al. 2000; Goldblatt & Manning 2013). The phenomenon evidently represents a failsafe mechanism when pollinators are absent or visits are rare or unreliable. We suspect that *L. arenicola* and *L. simulans* may be truly autogamous. No pollinators have ever been recorded on flowers of either of these long-tubed species and both have flowers with a shorter tube and smaller tepals than typical fly pollinated taxa. Moreover, they flower earlier in the season than the long-proboscid flies, which are inferred to be their pollinators, are on the wing.

Floral longevity: like most Crocoideae, flowers of the *Lapeirousia* group of genera are long-lived, lasting at least three and up to five days (Goldblatt et al. 1995). Known exceptions are *L. odoratissima* and *P. bainesii*, both of which have scented, pale-coloured flowers and are known or inferred to be pollinated by sphinx moths. The tepals of both species unfold in the late afternoon, at which stage the flowers produce a strong fragrance, and remain open all night but begin to wilt early to mid-morning. Flowers lasting at most 24 hours are unusual in Crocoideae and we know of only two comparable situations in the subfamily in the Namibian *Gladiolus diluvialis* Goldblatt & J.C.Manning and *Savannosiphon euryphyllus*, both also evidently sphinx moth-pollinated (Manning et al. 2011; R.E. Gereau, pers. comm. 2013). Flowers of other sphinx moth-pollinated Crocoideae, notably *Lapeirousia pyramidalis* subsp. *pyramidalis* and *Gladiolus tristis* L., last at least three days. Flowers of those species examined for the character are protandrous. The anthers dehisce first, two to four hours after tepals unfold, but pollen remains in place on the anther surface until removed by insect activity, either passive or active, or is washed away by rain. The style branches, at first appressed to one another, only curve outward on the following days, exposing glistening, ciliate surfaces.

Pollination: among the genera of the *Lapeirousia* clade, only the pollination systems of *Lapeirousia* have been extensively studied. As suggested by the remarkable floral variation in the genus, it exhibits a diversity of pollination strategies, ranging from generalist systems that rely on a mix of different bee families, butterflies, and even settling moths and bee-flies, to specialist systems using only pollinators of a single class, viz. sphinx moths or long-proboscid flies, or even a single species of pollinator (Goldblatt et al. 1995; Manning & Goldblatt 1996). The reward for most pollinators is nectar, retained within the perianth tube and secreted from septal nectaries, the pores of which open at the apex of the ovary at the base of the style. Nectar is sucrose rich or sucrose dominant (Goldblatt et al. 1995), irrespective of pollination system, and nectar quantity correlates closely with perianth tube length.

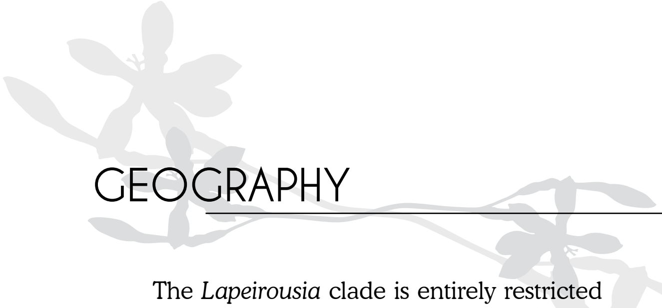
Most striking in *Lapeirousia* are the long-tubed species with purple, violet or cerise to magenta tepals with white markings on a dark background. These species, including *L. jacquinii*, *L. dolomitica*, *L. oreogena*, *L. pyramidalis* subsp. *regalis*, *L. silenoides* and *L. violacea*, are pollinated by two species of *Prosoeca* (Nemestrinidae), *P. peringueyi* in Namaqualand and northwestern Western Cape, and a second, unnamed *Prosoeca* species in the Bokkeveld Mtns and Plateau (Goldblatt et al. 1995). These flies, with probosces (15–)25–45 mm long, feed on nectar held within perianth tubes 20–50 mm long. Pollen is deposited on the frons or dorsum. We infer that *L. fabricii* subsp. *violacea*, *L. lewisiana* and *L. purpurea* also belong to this pollination guild in light of their early flowering, floral morphology and pigmentation.

A second group of long-tubed species in *Lapeirousia* with white to pale yellow flowers marked with pink or red near the tepal bases is pollinated by a second series of long-proboscid flies, including *Moegistorhynchus longirostris* (Nemestrinidae) and *Philoliche gulosa* (Tabanidae). Species with this pollination system include *L. anceps*, *L. fabricii* and by inference because of similarly shaped and coloured flowers, *L. kamiesmontana*, *L. macrospatha* and *L. verecunda*. Flies of both these pollination groups sometimes hover while feeding but more often grasp the tepals, especially the lower three, as they forage. In *Psilosiphon*, the northern Namibian *P. otaviensis* is a likely candidate for long-proboscid fly pollination but this pollination strategy has not been documented within its range to date. Fly mouthparts may be up to 95 mm in *M. longirostris* and up to 35 mm in *P. gulosa* and *P. rostrata* (Goldblatt & Manning 2000).

Moth pollination is likely for long-tubed species with white flowers that are open and strongly scented at night, the most striking examples of which are *Lapeirousia odoratissima* (sect. *Sophronia*) and *Psilosiphon schimperi*, which have perianth tubes 100–150 mm long. The night blooming cycle in *L. odoratissima* adds support to the inference of moth pollination. *Psilosiphon bainesii* most likely has a similar pollination system and we have seen but not captured sphinx moths visiting its flowers in Namibia. In *Lapeirousia* moth pollination also occurs in *L. pyramidalis* subsp. *pyramidalis* and is likely for *L. caudata*, *L. kalahariensis* and *L. littoralis*. Hawk moths are the likely pollinators. *Codonorhiza micrantha*, which has small, dull-coloured flowers, but a strong, clove-like scent at night, is almost certainly also pollinated by moths, specifically settling moths (e.g. Noctuidae) because of the small size of the flowers and relatively short, narrow perianth tube that are consistent with these pollinators (Goldblatt et al. 2004b).

The remaining species appear to have less specialised pollination strategies. The short-tubed, open flowers of species such as *Psilosiphon erythranthus* and its allies, *P. sandersonii* and the *Codonorhiza corymbosa* group have a range of visitors including butterflies, female bees of several families, worker honey bees and even wasps, but the recorded pollinators of *C. azurea* are anthophorine bees (*Anthophora*) and hopliine beetles. *L. divaricata* and *L. spinosa*, which have short-tubed, gullet flowers, are known to be pollinated by large-bodied anthophorine bees and honey bees and in the late afternoon by noctuid moths (Goldblatt et al. 1995), possibly a bimodal system sensu Manning & Goldblatt (2005). In our study population of *P. coeruleus*, which has secondarily radially symmetric flowers, the only pollinator captured was a small bee (family unknown), which nestles in the flowers (which lack nectar) and presumably forages for pollen.

While much research remains to be done to determine the pollination systems of several species, especially of *Psilosiphon* in summer rainfall southern and tropical Africa, it is clear that pollination systems in the *Lapeirousia* clade are even more labile than they are in most other genera of African Iridaceae (Goldblatt & Manning 2006). Matching the pollination system to the phylogeny (Figure 1) shows that the *Prosoeca peringueyi* pollination system evolved five or possibly six times (if ancestral in the genus), and the *Moegistorhynchus–Philoliche* pollination system three times. Hawk moth pollination evidently evolved independently in *L. odoratissima*, *L. pyramidalis* and *L. caudata–L. littoralis* (and possibly also in *L. kalahariensis*) in *Lapeirousia* as well as in *Psilosiphon bainesii* and *P. schimperi* (or their common ancestor). Long-proboscid fly pollination is not recorded in *Psilosiphon* but seems likely in *P. masukuensis* (perianth tube length 15–25 mm). This lability of pollination system in *Lapeirousia* was first noted by Goldblatt & Manning (1996) and has been calculated as one shift in strategy for every 1.5 species by Forest et al. (2014), a level of lability unprecedented in Iridaceae and among all flowering plants. In *Gladiolus* and *Babiana* (Iridaceae), one pollination shift has been inferred for every five to six species (Goldblatt & Manning 2006), an estimate later confirmed for *Gladiolus* by Valente et al. (2012). Shifts in pollination system in *Lapeirousia* are closely associated with speciation events, but whether they are the direct cause of these events or are reproductive reinforcement following geographic isolation or edaphic shifts remains uncertain.



GEOGRAPHY

The *Lapeirousia* clade is entirely restricted to mainland sub-Saharan Africa and is centred in southern Africa. The range of *Codonorhiza* is exclusively in the Cape Floristic Region (CFR), with *C. micrantha* the most widespread species in the genus, extending through the Cape Fold Mountains from the Gifberg in the north to the Langeberg in the southeast. The remaining species are restricted to the southwest of the CFR, mostly on the coastal lowlands and lower slopes of the mountains although *C. falcata* is essentially montane. Only *C. corymbosa* and *C. pillansii* occur on the Cape Peninsula. The monospecific *Schizorhiza* is also restricted to the CFR, known from just three populations in the extreme southwest of Western Cape.

Lapeirousia, largely a genus of the southern African winter rainfall zone, has a far wider range. Centred in central Namaqualand in Northern Cape, South Africa, several species extend south through the Cederberg to the Western Cape coastal plain, but only *L. anceps* reaches the Cape Peninsula, extending along the southern coast to near Mossel Bay. Several species extend to the north of Namaqualand into the winter rainfall belt of southwestern Namibia, and *L. plicata* ranges from interior Western Cape through the Great and Upper Karoo to southern Namibia. *L. plicata* subsp. *effurcata* is surprising in occurring in the southern Cape limestone country south of Riversdale as well as in the western Little Karoo. The remaining *L. caudata*, *L. kalahariensis* and *L. odoratissima* are species of the southern African summer rainfall area, the latter species extending from central Namibia to Angola, Zambia, Malawi and Tanzania. The range of *L. caudata* broadly corresponds to that of *L. odoratissima* but reaches further south into Gordonia, the margins of Bushmanland and Limpopo in South Africa, with isolated populations in southern Mozambique, an exceptional disjunction for sub-Saharan Iridaceae.

Psilosiphon is exclusively a genus of summer rainfall sub-Saharan Africa, its range virtually complementing those of *Codonorhiza, Lapeirousia* and *Schizorhiza*. Species extend from central Namibia and the northern provinces of South Africa across south tropical Africa. The most widespread species of *Psilosiphon*, the variable *P. erythranthus*, crosses the equator into northern Nigeria. Almost as widespread, *P. schimperi* extends in suitable, seasonally moist habitats from central Namibia and Botswana to Ethiopia, Somalia and possibly Yemen. *P. abyssinicus* is restricted to the Ethiopian highlands, *P. setifolius* to Malawi and southwestern Tanzania, *P. teretifolius* to Congo, and *P. zambeziacus* to western Zambia and adjacent Angola.

The clade sister to *Psilosiphon* comprises the Socotran endemic, *Cyanixia socotrana*, and the south tropical African *Savannosiphon euryphyllus*. *Zygotritonia*, which has yet to be sequenced, is almost certainly immediately allied to these two genera: it shares with the tribe axillary corm development, with *Cyanixia* and *Savannosiphon* corms rounded at base and shaggy, brown fibrous tunics, plicate leaves, and with *Cyanixia* trisulcate pollen grains, unique in Crocoideae. The six species of *Zygotritonia* extend from West Africa to Ethiopia and south to Tanzania, Malawi and Zambia (Goldblatt 1989; Demissew et al. 2003; Goldblatt et al. 2015).

Genera immediately related to the *Lapeirousia* clade (tribe Watsonieae) are all southern African, either restricted to the Cape Floristic Region or with their centre here. *Codonorhiza*, sister to the remaining members of the *Lapeirousia* clade is also a Cape genus. The origins of the *Lapeirousia* clade thus lie to the south, a pattern repeated in the few genera of Crocoideae that extend outside the Cape area.

ETHNOBOTANY

As early as the 17th century, European explorers in southern Africa noted the use of corms of *Lapeirousia* and its allies as a food, for example in the manuscript *Codex Witsenii* (Wijnands et al. 1996), where the Khoisan vernacular names *cabong* and *chabi* were used for the relatively common *L. jacquinii* and *L. fabricii*. It was only in the early 20th century that the first published documentation appeared when, in 1912, Kurt Dinter reported that corms of *Lapeirousia* and *Psilosiphon* species were used as a food for humans. Dinter mentioned specifically that corms of *L. caudata*, *L. odoratissima* (as *L. juttae*), *P. coeruleus* (as *L. coeruleus*) and *P. schimperi* (as *L. uliginosa*) were valued foods eaten after roasting in hot ashes. Dinter provided vernacular names *onduvi* (*ozonduvi* pl.) (Herero) and *garib* (Khoi) for these species. Dinter's observation has been confirmed repeatedly by plant collectors and ethnobotanists, notably R. Story for the !Kung Bushmen (*P. coeruleus – Story 6121* and *L. caudata – Story 6162*). Story also noted that corms of *P. coeruleus* were a staple, eaten after roasting in hot ash. In addition, a collection of *P. gracilis* (*Seydel 3419*) documents the edibility of this species. The !Kung Bushmen are also reported to eat the corms of *L. odoratissima* for their water content (Marshall 1976), which seems unlikely, and to eat corms of *P. bainesii* after baking, or to pound the cooked corms into a meal, which is then eaten as a gruel with water (Fox & Young 1982).

The ethnobotanist R. Rodin (1985) reported that corms of *Psilosiphon coeruleus*, *P. bainesii* (as *Lapeirousia vaupeliana*) and *P. schimperi* (as *L. cyanescens*) were eaten both raw and roasted by the Kwanyama Ovambo in northern Namibia. Leffers (2003) confirms the use of three species by the Jul'hoansi subgroup of the San in north-eastern Namibia, *P. bainesii*, *P. coeruleus* and *P. schimperi*, with the vernacular names g‖*xàrú*, g≠*àrì* and g!*úíh* respectively. Corms are shucked and then roasted in hot ash and either consumed directly or pounded and stewed with water or more recently, milk, usually without the addition of other ingredients.

Lapeirousia and *Psilosiphon* appear to have little value to human communities outside Namibia and presumably adjacent Angola and Botswana. There are, however, isolated reports that corms of *P. erythranthus* are eaten in the Shire Highlands of southern Malawi 'in time of great famine' (*Buchanan 426*). Collection notes (*Simpathu 60*) from Victoria Falls, Zimbabwe, also indicate that corms of *P. erythranthus* are eaten raw.

In the light of the amply documented use of the corms of several Namibian species of *Lapeirousia* and *Psilosiphon* as food, the report cited, without source, by Watt & Breyer-Brandwijk (1962) that *P. coeruleus* is poisonous, must be regarded as doubtful at best, particularly as tests performed on a frog for cardiac glycoside action proved negative.

PHYLOGENY AND SUBGENERIC CLASSIFICATION

Analyses of DNA sequences of 10 plastid regions and one nuclear gene (Forest et al. 2014) have provided surprising and unanticipated insights into phylogenetic relationships among the *Lapeirousia* clade, prompting us to radically dismember *Lapeirousia* sensu Goldblatt (1972) in order to maintain monophyly of the genera. Results (e.g. Figure 1; Forest et al. 2014) show that two genera *Cyanixia* and *Savannosiphon* are nested in *Lapeirousia* s. lat. where they are retrieved together as sister to *Lapeirousia* sect. *Paniculatae* (one of two sections of subg. *Paniculatae*) [following the classification of Goldblatt & Manning 1990]. Sect. *Fastigiatae* of subg. *Paniculatae* is retrieved as sister to the remainder of the entire *Lapeirousia* clade, with subg. *Lapeirousia* placed as sister to sect. *Paniculatae* plus *Cyanixia* and *Savannosiphon*. Our preferred solution to restoring monophyly is the recognition at generic rank of both sect. *Paniculatae* and sect. *Fastigiatae*. As already outlined in the foregoing text, sect. *Paniculatae* is here recognised as the new genus *Psilosiphon*, sect. *Fastigiatae* as *Codonorhiza*, and the phylogenetically isolated *L. neglecta* as the monospecific *Schizorhiza*. This solution is absolutely congruent with morphology. Although the corms of these three new genera plus *Lapeirousia* s. str. have a flat base (the primary justification for their initial treatment as a single genus), corm tunic structure differs in all four genera, as do the floral bracts. Seeds of *Codonorhiza* are unique in Watsonieae and the pollen grains of *Codonorhiza* and *Schizorhiza*, which have a single banded operculum, differ from the 2-banded operculum in *Lapeirousia* and *Psilosiphon*. Chromosome cytology likewise differs in all three genera.

Species relationships in *Codonorhiza* are well resolved and supported (Figure 1). *Codonorhiza falcata* is consistently retrieved as sister to the remaining species, a relationship that accords with its spicate inflorescence, the plesiomorphic condition in Watsonieae – the remaining species have derived, round- or flat-topped, false panicles composed of multiple branches each bearing just one or two flowers. The two species *C. corymbosa* and *C. fastigiata* have (evidently independently) derived radially symmetric flowers, and *C. micrantha* is nested within the otherwise blue-flowered *C. corymbosa* group of species and sister to *C. corymbosa*. Only *C. pillansii* was unavailable for inclusion in our molecular analyses.

Lapeirousia in its restricted sense is strongly supported as monophyletic (1.0 PP), and comprises three main clades or species groups. The first, the *L. silenoides* clade with eight species, includes *L. angustifolia* and the two subspecies of *L. pyramidalis* in a strongly supported subclade that is characterised morphologically by unique, retuse floral bracts. A close association of the long-tubed *L. jacquinii* with short-tubed *L. divaricata* (1.0 PP) is the only surprise here. Flowers of the latter closely resemble those of *L. spinosa* – evidently convergent as their corms are very different. Corms with margins bearing minute teeth and unusual transparent windows in the floral bracts are the only evident morphological features linking *L. jacquinii* and *L. divaricata*.

A second major clade (1.0 PP) in *Lapeirousia* comprises the four acaulescent species included in the study: *L. oreogena, L. plicata, L. montana* and *L. odoratissima* (one additional species, *L. kalahariensis*, was not available). Within this clade, the tropical African and hyper long-tubed *L. odoratissima* is retrieved as sister to the shorter-tubed southern African species. The acaulescent species all have a radially symmetric flower and seeds with a sculptured surface, both derived characters.

The third major clade includes the remaining species. Surprisingly, *L. caudata*, *L. littoralis* and *L. barklyi* are retrieved as sister to the remaining species of *Lapeirousia* in the combined analysis, a result that receives no support from morphology or chromosome cytology and defies explanation. In contrast, the association of white-flowered and short-tubed *L. spinosa* and *L. tenuis* (1.0 PP) is congruent with corm and floral morphology, as is that of *L. arenicola* and *L. macrospatha* (1.0 PP).

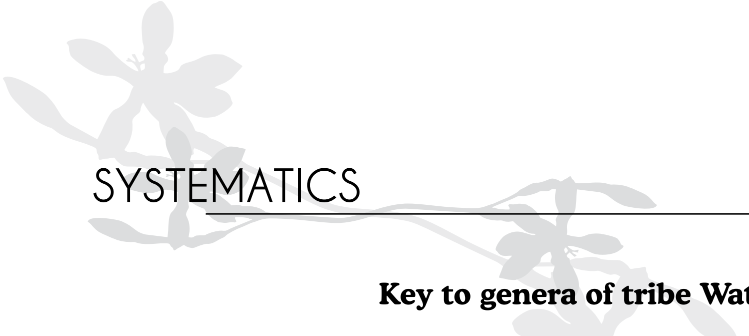
We are somewhat surprised that the molecular analyses do not show a close relationship between *L. dolomitica* and *L. lewisiana*, the latter until now treated as a subspecies of the former, nor with *L. kamiesmontana*, until now regarded as merely a white-flowered race of subsp. *lewisiana*. We accept the results of the molecular analyses as support for the recognition of the three sets of populations as separate species. In the taxonomic account, however, we group the species in sequence for they are linked by specialised corm tunics and a long perianth tube, and *L. lewisiana* and *L. kamiesmontana* are further linked by unique, sparsely hairy leaves. The weak association of *L. lewisiana* and *L. simulans* in the molecular analysis (0.31 PP) is not supported by morphology – the corms of *L. simulans* lack the specialised spines present in *L. lewisiana*. An association between *L. fabricii* and *L. kamiesmontana* is likewise weakly supported (0.55 PP), but in this case the two species share similar corms, suggesting a reflection of true relationship.

Lastly, the species of *Lapeirousia* here segregated as *Psilosiphon* comprise a clade (1.0 PP) sister to *Cyanixia* plus *Savannosiphon* (0.85 PP). Relatively few species of *Psilosiphon* were included in our study (8 out of 15) but notably the hypopolyploid *L. otaviensis* and *L. schimperi* (both $2n = 10$) are retrieved as sisters (1.0 PP) in all analyses. The two species with radially symmetric flowers, *P. avasmontanus* and *P. coeruleus*, are retrieved as only distantly related within the genus, a result congruent with their very different corm tunics and branching patterns.

Undoubtedly one of the most surprising results of the molecular analysis is the position of *Lapeirousia neglecta* (now the monospecific genus *Schizorhiza*). This taxon, from the southern African winter-rainfall region and until now included in the otherwise tropical and summer rainfall southern Africa sect. *Paniculatae*, is retrieved with moderate support (0.84 PP) as sister to *Lapeirousia* + *Psilosiphon* + *Cyanixia* + *Savannosiphon*. Re-examination of its morphology, leaf anatomy, and pollen grains provides grounds for accepting this result. The corm shape, ellipsoid with a small flat base, and corky tunics are unique and are discordant with *Psilosiphon*, as are the simple leaf margins and the single-banded pollen operculum. Its chromosome base number, $x = 6$, which is shared in *Psilosiphon* with *P. gracilis*, must be seen as convergent.

We propose the following infrageneric classification for *Lapeirousia*, based on the high level of congruence among the molecular phylogeny, morphology and cytology. The *L. silenoides* clade (1.0 PP) merits sectional rank, as sect. *Chasmatocallis*, and we likewise treat the clade (1.0 PP) of acaulescent species with radially symmetric flowers as sect. *Sophronia*. We treat the remaining species as sect. *Lapeirousia* despite their being retrieved as two separate clades, the *L. littoralis* clade (1.9 PP) and the *L. fabricii* clade (1.0 PP). We see no morphological or anatomical reason for their separation taxonomically and both have the derived basic chromosome number $x = 8$. Additional sampling of these species may resolve the current incongruence of morphology and molecular data.

Codonorhiza is too small a genus for an infrageneric classification to be useful, and until more species of *Psilosiphon* are obtained for sequencing, establishing an infrageneric classification of the genus is premature. We continue to recognise the remaining genera of the *Lapeirousia* clade of Watsonieae, *Cyanixia*, *Savannosiphon* and *Zygotritonia*.



SYSTEMATICS

Key to genera of tribe Watsonieae

1a Corm bell-shaped, ellipsoid or obconic (triangular in outline), with flat base and roots emerging from margin of base:

2a Corm ± ellipsoid, diameter of flat base narrower than midline; lower axils of stem bearing multiple cormlets; inflorescence a many-branched false panicle . . . . *Schizorhiza*

2b Corm bell-shaped or obconic, widest at base; lower axils of stem with a single cormlet or without cormlets; inflorescence a spike or a false panicle:

3a Corm tunic layers woody, base sometimes serrated to spiny; leaves corrugate (plicately ridged); inflorescence a spike or a crowded rosette when plants lack aerial stem; floral bracts large, fleshy, the inner significantly smaller than outer; seeds globose . . . . *Lapeirousia*

3b Corm tunic layers not woody, composed of compressed fibres, the outer layers often becoming loosely fibrous with age, base never serrated to spiny; leaves plane or terete; inflorescence a spike or a many-branched false panicle, the individual flowers always sessile (subtended by a pair of opposed bracts at base of ovary); floral bracts subequal, the inner slightly shorter or slightly longer than outer; seeds ovoid or globose:

4a Floral bracts green, firm and ± leathery, apices ± rounded or emarginate; seeds ovoid with surface reticulate to rugose; pollen with 1-banded operculum . . . . *Codonorhiza*

4b Floral bracts green to dry, soft-textured, often becoming membranous, apices acute; seeds globose with smooth surface; pollen with 2-banded operculum . . . . *Psilosiphon*

1b Corms globose to obconic with rounded base and roots emerging from lower half of the corm:

5a Style branches deeply divided:

6a Leaves ± clustered in a basal fan, with thickened, hyaline margins; flowers medium to large, usually at least 20 mm long, never blue; bracts usually green, sometimes becoming dry *Watsonia*

6b Leaves superposed, only lowermost basal, without thickened, hyaline margins; flowers small to medium, mostly less than 30 mm long, blue or mauve to white; bracts ± dry:

7a Spikes distichous; flowers small, < 12 mm long, crowded in dense spikes; bracts solid below with broad membranous margins . . . . *Micranthus*

7b Spikes spiral; flowers > 15 mm long, with a ± straight perianth tube; bracts without broad membranous margins . . . . *Thereianthus*

5b Style branches undivided or at most notched apically:

8a Inflorescence a panicle, individual flowers always pedunculate; flowers radially symmetric; perianth bright orange; leaves firm, leathery, plane; plants of the southwestern Cape. . *Pillansia*

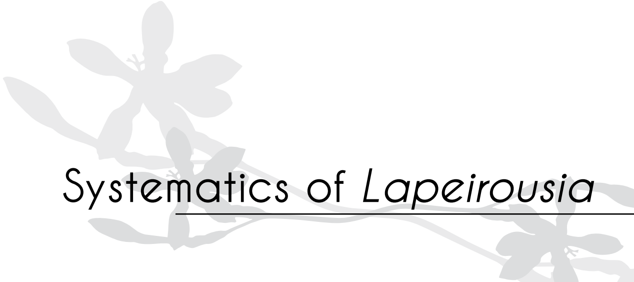
8b Inflorescence a simple or branched spike and individual flowers sessile, rarely inflorescence reduced to a single flower; flowers actinomorphic or zygomorphic; perianth variously coloured; leaves shallowly pleated and relatively soft-textured:

9a Flowers radially symmetric; perianth pale blue; plants of Socotra . . . . *Cyanixia*

9b Flowers zygomorphic; perianth shades of red to purple or white:

10a Style undivided or with short, entire branches; flowers relatively small and perianth tube shorter than dorsal tepal; perianth shades or red to purple or partly white; plants of tropical Africa . . . . *Zygotritonia*

10b Style 3-branches, each branch deeply divided; flowers large and perianth tube much longer than dorsal tepal; perianth white . . . . *Savannosiphon*



Systematics of *Lapeirousia*

Lapeirousia *Pourr.* in Histoire et Mémoires de l'Académie Royale des Sciences, Toulouse 3: 79 (1788). *Ovieda* Spreng.: 258 (1817), illegitimate homonym and superfluous name, not *Ovieda* L. (1753). *Meristostigma* A.Dietr.: 593 (1833), superfluous name. *Peyrousia* Poir.: 363 (1826), possible orthographic variant of *Lapeirousia* (also spelled *Lapeyrousia*), or superfluous name. Type: *L. compressa* Pourr. (= *L. fabricii* (D.Delaroche) Ker Gawl.).

Sophronia Licht. ex Roem. & Schult.: 482 (1817). Type: *S. caespitosa* Licht. ex Roem. & Schult. (= *Lapeirousia plicata* (Jacq.) Diels).

Chasmatocallis R.C.Foster: 40 (1939). Type: *C. macowanii* R.C.Foster (= *Lapeirousia divaricata* Baker).

Named in honour of the Compte de la Peyrouse, 18th century patron of French science and contemporary of the Abbe Pourret, who described the genus.

Deciduous geophytes. *Corms* bell-shaped with flat base, rooting from lower edges; axillary in origin; tunics of hard, woody layers, sometimes spiny at base. *Foliage leaves* few, lowermost linear to sword-shaped, inserted on stem near ground level, closely corrugate, upper leaves progressively smaller. *Stem* aerial or sometimes subterranean, compressed, often angled, angles sometimes winged, simple or branched. *Inflorescence* a spike or when acaulescent, a dense rosette; bracts paired and opposed, outer green and firm to ± succulent, sometimes ridged, keeled, crisped or toothed; inner much shorter, usually hidden by outer, 2-keeled and often partly membranous, forked at apex. *Flowers* zygomorphic or actinomorphic in acaulescent species, often salver-shaped, blue, purple, red, pink or white, lower or all tepals usually with contrasting darker or lighter markings, sometimes sweetly scented; perianth tube cylindric or obliquely funnel-shaped, short to extremely long; tepals subequal or unequal, with dorsal largest. *Stamens* unilateral and arcuate or symmetrically disposed; filaments slender, free; anthers linear, splitting longitudinally. *Ovary* ± ovoid; *style* filiform, 3-branched, style branches usually forked for ± $^{1}/_{2}$ their length, occasionally not divided. *Capsules* ovoid to oblong, cartilaginous, often showing outline of seeds. *Seeds* globose, flattened at chalazal end, either smooth with surface cells domed (rarely tuberculate) or rugulo-reticulate or reticulate with surface cell walls flat. *Basic chromosome number* $x = 9$; diploid numbers $2n = 18$, 16.

Species 27; mainly of winter-rainfall, western South Africa and southwestern Namibia, also central South Africa and south tropical Africa, mainly in sandy soils or rock outcrops.

Key to sections

Notes: All measurements are from living plants; floral parts may shrink up to 20% depending on care taken with pressing specimens. Measure corm diameter at corm base, bract length in middle of spike if there is considerable variation along a spike. Seeds may decrease in size with age through desiccation; dimensions are for capsule-matured seeds no more than a year old.

Measure perianth tube from base to point of separation of tepals, thus including narrow and wide parts of tube; tepal length is from point of separation from tube to tepal tip.

1a Corm bell-shaped, basal margin bluntly ridged to crenate or minutely spiny with fine teeth directed downward (not with laterally directed spines or teeth); flowers radially symmetric or zygomorphic:
  2a Plants with aerial stems (unless depauperate); flowers zygomorphic . . . . . . 1. sect. *Chasmatocallis*
  2b Plants acaulescent; flowers radially symmetric . . . . 2. sect. *Sophronia*
1b Corm bell-shaped to obconic, thus ± triangular in profile, basal margin serrated to spiny and bearing short to long teeth; flowers zygomorphic . . . . 3. sect. *Lapeirousia*

Key to species

1a Plants tufted, ± acaulescent with axis contracted above ground level and inflorescence congested; flowers radially symmetric:

2a. Floral bracts 60–150 mm long; perianth tube 100–140 mm long .... 13. *L. odoratissima*

2b. Floral bracts 40–50 mm long; perianth tube 12–60 mm long:

3a. Flowers violet, lower $^{1}/_{3}$ of tepals dark violet to black with wedge-shaped white mark in centre of dark zone; perianth tube 50–60 mm long .... 11. *L. oreogena*

3b. Flowers whitish or pale blue, sometimes with dark blue to purple mark near base of tepals; perianth tube 12–50 mm long:

4a. Perianth tube 12–30 mm long; tepals 7–9 mm long; anthers 1.8–3.0 mm long, blue or whitish .... 9. *L. plicata*

4b. Perianth tube (33–)35–60 mm long; tepals 10–12 mm long; anthers 3–4 mm long, white or pale yellow:

5a. Flowers ± white; leafy upper parts of floral bracts ± straight, channelled to apex, not ribbed .... 12. *L. kalahariensis*

5b. Flowers white or pale blue; leafy upper parts of floral bracts falcate, unifacial above and strongly ribbed. .... 10. *L. montana*

1b Plants with aerial stems unless depauperate (e.g. *L. exilis*, *L. arenicola*); flowers zygomorphic with stamens unilateral:

6a Flowers predominantly white to creamy white, often flushed pink outside; perianth tube 7–15 mm long:

7a Corm bell-shaped, basal rim minutely serrated or entire and lobed:

8a Perianth tube 7–10 mm long, obliquely funnel-shaped; corm margin with short fine teeth directed downward; plants of the Cederberg, Gifberg and Bokkeveld Mtns. . . . 1. *L. divaricata*

8b Perianth tube 13–15 mm long, ± slender throughout; corm margins entire; plants of the Knersvlakte .... 7. *L. angustifolia*

7b Corm obconic (triangular in profile), basal rim bearing prominent, spreading spines:

9a Dorsal tepal 18–23 × 5–8 mm .... 21. *L. spinosa*

9b Dorsal tepal 9–11 × 2–3 mm .... 20. *L. tenuis*

6b Flowers variously coloured; perianth tube 20–70 mm long:

10a Corm bell-shaped, basal rim bluntly ridged to crenate or minutely serrate with teeth directed downward:

11a Outer floral bracts obtuse to retuse when opened flat .... 8. *L. pyramidalis*

11b Outer floral bracts tapering to an acute apex:

12a Flowers deep violet or cherry-red to magenta, lower tepals with white to yellow markings near base:

13a Floral bracts with median keel, without white patches; flowers cherry-red to magenta; perianth tube 40–55 mm long .... 3. *L. silenoides*

13b Most or all floral bracts 2-keeled, fenestrate with white patches; flowers violet to purple, lower tepals streaked with white; perianth tube 30–40 mm long . . . 2. *L. jacquinii*

12b Flowers not as above:

14a Outer floral bracts mostly 6–10 mm long; lower tepals ± linear to narrowly lanceolate with a short, filiform tooth near base .... 5. *L. anceps*

14b Outer floral bracts (10–)12–25 mm long; lower tepals broadly lanceolate to ovate, with or without teeth:

15a Perianth white to pink, pale blue or maroon-brown; not marked with red on lower tepals:

16a Perianth tube slender below, ± abruptly expanded to wider upper part; tepals ascending below to form part of floral cup, spreading distally; tepals predominantly pink to lilac with yellow nectar guides on lower tepals; style dividing opposite or beyond anther tips . . . . 14. *L. barklyi*

16b Perianth tube slender ± throughout, slightly wider distally; tepals spreading from base; tepals predominantly white to ivory or pale blue; style dividing between base and middle of anthers:

17a Plants slender, less than 60 mm high, often unbranched; flowers pale blue (rarely ± white) with violet streaks on lower tepals . . . . 6. *L. exilis*

17b Plants usually > 100 mm high, usually repeatedly branched from base; flowers white, pale yellow, yellow-brown or dull maroon, usually without contrasting markings on lower tepals:

18a Perianth tube 28–35 mm long; tepals 13–15 × 2–3 mm; bracts (12–)15 –20(–25) mm long . . . . 15. *L. littoralis*

18b Perianth tube (25–)30–45(–70) mm long; tepals 18–30 × 1.3–2 mm; bracts 10–18(–23) mm long . . . . 16. *L. caudata*

15b Perianth white to pink or creamy beige, lower tepals always marked with red to brown near base:

19a Perianth tube 40–55 mm long; corm with basal margins entire to crenately lobed . . . . 4. *L. verecunda*

19b Perianth tube (10–)12– 35 mm long; corm with basal margins minutely serrated:

20a Lower tepals ± 13 × 5 mm . . . . 17. *L. macrospatha*

20b Lower tepals 8–11 × 3–4 mm:

21a Corm relatively shallowly buried, and underground part of stem not bearing cormlets at nodes; perianth tube mostly 15–25 mm long . . . . 18. *L. arenicola*

21b Corm relatively deeply seated, with underground part of stem bearing cormlets at nodes; perianth tube mostly 27–35 mm long . . . . 19. *L. simulans*

10b Corm obconic (triangular in profile) with margins bearing prominent, spreading spines:

22a Flowers white to beige or blue-mauve (rarely pink), usually with red markings on lower tepals:

23a Perianth tube slender below, expanded in upper 5–10 mm into a wider gullet; style dividing opposite base to upper $^{1}/_{3}$ of anthers; basal leaf smooth . . . . 27. *L. fabricii*

23b Perianth tube slender, ± uniformly wide throughout; tepals spreading from base; lower tepals not bearing a tooth at base; style dividing opposite or above anther tepals; basal leaf sparsely hairy . . . . 26. *L. kamiesmontana*

22b Flowers predominantly blue, violet, purple or magenta, variously marked on lower tepals:

24a All or only median lower tepal with tooth-like projection near base:

25a Only lower median tepal with tooth near base; upper lateral tepals strongly recurved; lower tepals with white V-shaped mark near base on darker violet background . . . . 23. *L. purpurea*

25b All three lower tepals with tooth near base; upper lateral tepals not obviously recurved; lower tepals white near base with large red to purple blotch in centre . . . . . 22. *L. violacea*

24b All lower tepals without tooth-like projections:

26a Basal leaf smooth or minutely papillate along edges of ribs; perianth tube (25–)35–45 mm long; perianth pale to deep blue to violet, lower tepals white(–pale yellow) at base . . . . 24. *L. dolomitica*

26b Basal leaf sparsely hairy; perianth tube 40–50 mm long; perianth deep magenta to purple marked with white lines on lower margins and darker magenta in lower midline . . . . 25. *L. lewisiana*

In the descriptions that follow, we have tried to be as concise as possible. Stem characters are included in the opening sentence beginning 'Plants'. Cataphylls offer no taxonomic insight and are mentioned only in the generic description. The ovary provides minimal information, always ± ovoid-oblong and its size changes rapidly after fertilisation, even before flowers fade so that dimensions are of little utility and we do not include information about the ovary. We do provide descriptions of capsules, which are variable, even though plants with well-developed capsules are rarely collected.

A. Sect. *Chasmatocallis* (Spp. 1–8)

A. Sect. **Chasmatocallis** *(R.C.Foster) Goldblatt & J.C.Manning*, comb. et stat. nov. *Chasmatocallis* R.C.Foster: 40 (1939). Type: *C. macowanii* R.C.Foster (= *Lapeirousia divaricata* Baker).

Corm bell-shaped; tunics with basal rim bluntly lobed or minutely denticulate with minute teeth directed downward. *Stem* mostly aerial (sometimes ± subterranean in *L. exilis* and *L. silenoides*) and often branched, stems compressed with angles often crisped. Inflorescence a spike. *Flowers* bilaterally symmetric, lower tepals usually with nectar guides of contrasting colour; variously coloured and perianth tube short to elongate, cylindric or funnel-shaped. *Capsules* often with auriculate lobes and locular ridges. *Seeds* smooth (scarcely wrinkled) with surface cells domed or tuberculate (*L. pyramidalis*). Basic chromosome number $x = 9$ (or 10).

1. **Lapeirousia divaricata** *Baker* in Journal of Botany (London) 14: 337 (1876). Goldblatt: 64 (1972), including *L. spinosa* and *L. tenuis* as varieties. Type: South Africa, [Northern Cape], without precise locality or date, *Thom s.n.* (K, holo!).

Gladiolus setifolius L.f.: 96 (1782 [as 1781]). *Lapeirousia setifolia* (L.f.) N.E.Br.: 30 (1928), hom. illegit. non Harms (1901). Type: South Africa, without precise locality, probably in 1774, *Thunberg s.n. UPS-THUNB1067* (UPS-THUNB, holo.!).

Chasmatocallis macowanii R.C.Foster: 40 (1939). Type: South Africa, [Western Cape], Pakhuis Pass, Oct. 1897, *MacOwan 1975* (GH, holo.!; G!, SAM!, iso.).

Plants 120–250 mm high, with axillary cormlets below ground, stem simple or more often branched and then mostly well above ground, terete. *Corm* bell-shaped, ± 10 mm diam.; tunics dark brown, often glossy, basal margin finely serrated, teeth directed downward. *Leaves* 3–6 (or more), lowermost usually exceeding others, linear, suberect or falcate, 2.0–3.5 mm wide, strongly ribbed, generally longer than stem, up to 350 mm long, upper cauline leaves shorter, sometimes resembling bracts and not ribbed, usually subtending branches. *Inflorescences* 5–12-flowered spikes, usually crowded; outer bracts green or flushed reddish, often white to semi-transparent below, firm, 8.5–12.0 mm long, obtuse or acute, usually folded in midline or channelled, margins hyaline, inner bracts $^1/_2$ to $^2/_3$ as long. *Flowers* zygomorphic, white or sometimes flushed with pink to lilac (aging pink), lower tepals often with pink to purple streak in midline and bearing tooth-like ridge in lower midline; perianth tube short, 7–10 mm long, narrow below, curved and widening toward apex; *tepals* unequal, lanceolate, acute, dorsal 14–16 mm long, erect, separating from tube below lower tepals, margins undulate, remaining tepals joined for ± 4 mm, upper lateral tepals sharply reflexed shortly above base, lower 3 tepals united for additional 2–3 mm, ± 12 mm long, bent at right angles shortly above base, directed downward distally. *Stamens* unilateral and arcuate; filaments ± 6 mm long, exserted 4 mm from tube; anthers ± 4 mm long, white; pollen white. *Style* dividing opposite anther tips; branches forked for ± $^2/_3$ their length, recurved. *Capsules* obovoid, 4.5–7.0 mm long, apices of locules forming auriculate lobes decurrent on low locular ridges. *Seeds* ± globose, flattened at chalazal end, 1.0–1.2 mm diam., light brown. *Chromosome number* $2n = 20$ (?18 + 2B). *Flowering time*: mainly late August to late September, but October at higher elevations.

Distribution and biology: *Lapeirousia divaricata* has a restricted distribution from Citrusdal in the Olifants River Valley north through the valleys of the Cederberg to the Gifberg and Bokkeveld Mtns (Figure 4). It occurs exclusively in sandy ground in soils derived from Cape sandstones, in valley bottoms, seeps or poorly drained flats where the ground remains moist for some time.

The flowers of *Lapeirousia divaricata* remain open at night, unlike most species of the

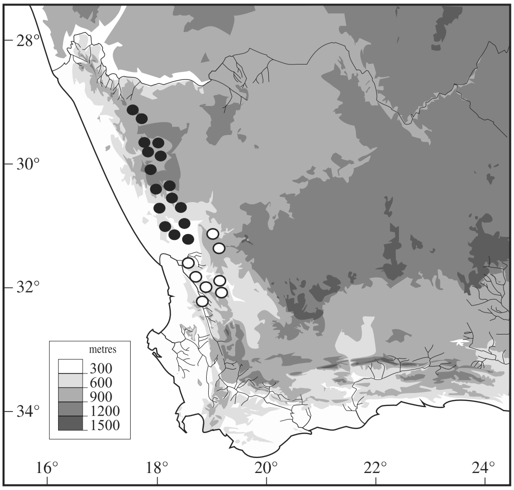


FIGURE 4.—Distribution of *Lapeirousia divaricata*, ○; *L. silenoides*, ●.

genus, and are visited by a range of large bees including four species of *Anthophora* (*A. braunsii*, *A. diversipes*, *A. krugeri* and *A. schulzei*), *Amegilla grisella*, and a species of Megachilidae from midmorning until sunset, and in the later afternoon and early evening by settling moths *Heliothis* (Noctuidae) (Goldblatt et al. 1995). Both bees and moths forage for nectar, present in small quantities, and are probably effective pollinators of *L. divaricata*. Sometimes present in large numbers, the moths make a striking evening sight, fluttering from plant to plant. We regard *L. divaricata* as having a bimodal pollination system. The flowers are self-compatible and readily self-pollinate as the style branches remain in contact with the anthers during anthesis.

Diagnosis and relationships: *Lapeirousia divaricata*, named for its uneven and wide-angled (divaricate) branching pattern, is readily recognised by its short-tubed white to pale pink flower, a stem normally branched well above the ground, and short floral bracts that are white to translucent on the sides. The lower tepals bear a conspicuous tooth-like ridge in the lower midline, a feature shared by only a few other species of *Lapeirousia*. The bell-shaped corm has finely toothed margins, the teeth directed downward. The relatively small capsules of *L. divaricata* are ridged with apically auriculate locules, a feature consistent with several other species of sect. *Chasmatocallis*.

Lapeirousia spinosa, treated by Goldblatt (1972) as subsp. *spinosa* of *L. divaricata*, has similar, short tubed white flowers but a very different corm, triangular in profile with the basal rim bearing prominent spreading spines. A second subspecies of *L. divaricata*, subsp. *tenuis*, also now a separate species, has corms of the same type as *L. spinosa* and both taxa are now believed to be only distantly related to *L. divaricata*. The DNA-based molecular phylogeny (Figure 1) places the two in sect. *Lapeirousia*. The floral similarity in the three species is evidently convergent. The sister relationship of *L. divaricata* with *L. jacquinii* retrieved in the molecular phylogeny is unexpected as the flowers of the two are very different. They do, however, share virtually identical corms and distinctive fenestrate floral bracts with white or semi-transparent patches.

History: *Lapeirousia divaricata* was first recorded by C.P. Thunberg, whose collection, most likely made in 1774, formed the basis for *Gladiolus setifolius*, described by the younger Linnaeus in 1782. The species was not transferred to *Lapeirousia* when this genus was understood to be distinct from *Gladiolus* and continued to be known as *G. setifolius* throughout the 19th century. After examining the Iridaceae in the Thunberg Herbarium in Uppsala, Sweden, N.E. Brown transferred the species to *Lapeirousia* in 1928. Unfortunately, by this time a tropical African species had been named *L. setifolia* (Harms 1901) (now *Psilosiphon setifolius*), and unknown to Brown, his combination was an illegitimate homonym. A second collection of the species was described in 1876 as *L. divaricata* by J.G. Baker. The American botanist, R.C. Foster named a third collection of the species *Chasmatocallis macowanii* in 1939, the epithet honouring Peter MacOwan, who made the type collection. Foster seems to have been unaware that his new genus *Chasmatocallis* differed in no significant way from either *G. setifolius* or *L. divaricata*.

Representative specimens

SOUTH AFRICA. NORTHERN CAPE.—**3119** (Calvinia): sandy ground near Grasberg, west of Nieuwoudtville, (–AC), 18 Sept. 1980, *Goldblatt 5839* (MO, PRE); Farm Driefontein, 18 km south of Nieuwoudtville, (–AC), 9 Oct. 1991, *Manning 1043* (MO, NBG); Lokenburg, ± 700 m, (–CA), 26 Sept. 1953, *Acocks 17252* (PRE).

WESTERN CAPE.—**3118** (Vanrhynsdorp): Gifberg plateau, (–DC), 21 Sept. 1948, *Acocks 14904* (PRE), Sept. 1911, *Phillips 7617* (NBG, PRE), *7508* (NBG); Nardouw, (–DC), Sept. 1941, *Stokoe s.n.* (NBG). **3119** (Calvinia): Doornbos, (–CC), 4 Sept. 1948, *Compton 20908* (NBG). **3218** (Clanwilliam): deep sand at old campsite, Clanwilliam, (–BB), 24 Sept. 1974, *Goldblatt 2754* (MO, PRE). **3219** (Wuppertal): Biedouw Valley, (–AA), 14 Sept. 1976, *Thompson 2922* (MO, PRE, STE), 7 Sept. 1953, *Compton 24230* (NBG), 21 Sept. 1952, *Lewis s.n.* (PRE, SAM); Brandewyn River, (–AA), 20 Sept. 1933, *Barker 254* (NBG), 2 Oct. 1940, *Bond 615* (NBG), 8 Sept. 1974, *Goldblatt 2538* (MO, PRE); Pakhuis Mtns [as Pakenberg], (–AA), Oct. 1897, *MacOwan 3300* (G, PRE); Diamond Drift, Bidouw River, (–AA), Aug. 1939, *Leipoldt s.n.* (NBG 61341, PRE); Hoek, 27 Aug. 1896, (–AB), *Schlechter 8712* (E, G, MO, PH, PRE); Koudeberg near Wuppertal, ± 900 m, (–AC), 4 Oct. 1897. *H. Bolus 9100* (NBG, PRE).

2. **Lapeirousia jacquinii** *N.E.Br.* in Journal of the Linnean Society, Botany 48: 20 (1928); Goldblatt: 56 (1972). Type: South Africa, Cape, without precise locality, illustration in Jacquin: t. 269 (1794) (specimens believed to have been destroyed).

Plants 80–120(–200) mm high, stem often ± prostrate below for a short distance, erect above, often branched from close to ground, compressed and triangular in cross section, one side narrower than other two, angles strongly winged, wings undulate and usually slightly denticulate. *Corm* bell-shaped, 7–9 mm diam.; tunics light to dark brown, basal rim minutely serrate, teeth directed downward. *Leaves* 3–5, ± crowded at ground level, lowermost longest, ascending or arcuate, often quite short, lanceolate to falcate, 50–200 × 4–12 mm, strongly ribbed, remaining leaves smaller, weakly ribbed, progressively bract-like above. *Inflorescences* 2–5(–10)-flowered spikes; outer bracts green-glaucous, often ± translucent on sides, (10–)15–20 mm long, margins narrowly hyaline, prominently 2-keeled or lowermost sometimes 1-keeled, keels undulate to crisped, minutely denticulate, inner bracts ± $^{2}/_{3}$ as long, membranous and translucent with two prominent green keels, forked apically for 2–3 mm. *Flowers* zygomorphic, violet (rarely white), lower 3 tepals darker violet or reddish in lower midline with margins white to pale yellow in proximal half, scentless; perianth tube cylindric, 30–40 mm long, widening and weakly curved near apex; *tepals* unequal, dorsal largest, 8–10 × 4–5 mm, oblanceolate, initially erect but usually reflexed when fully open, then held in same plane as lower; upper lateral tepals spreading at right angles to tube, weakly spooned, apices curved upward, lower 3 tepals directed forward with upcurved tips, 7–8 × ± 2 mm. *Stamens* unilateral, ± erect; filaments ± 7 mm long, exserted 4–5 mm; anthers parallel, ± 3 mm long, violet; pollen usually blue-violet. *Style* dividing near base of anthers, style branches deeply forked and recurved. *Capsules* oblong, 7–9 mm long, apices of locules forming auriculate lobes decurrent on weakly developed locular ridges; *seeds* globose, 1.1–1.5 mm diam., dark brown. *Chromosome number* $2n = 18$. *Flowering time*: (late July) August to mid-September.

Distribution and biology: one of the most common species of the genus, *Lapeirousia jacquinii* extends from Cape Town along the West Coast as far north as Garies in southern Namaqualand, extending inland through the Breede River valley east of Worcester as far as Overhex and Aan de Doorns, and into the western valleys of the Cederberg and Bokkeveld Mtns (Figure 5). It is especially common in the Olifants River valley in sandy, often disturbed, places. Plants flower fairly early in the season and are some-

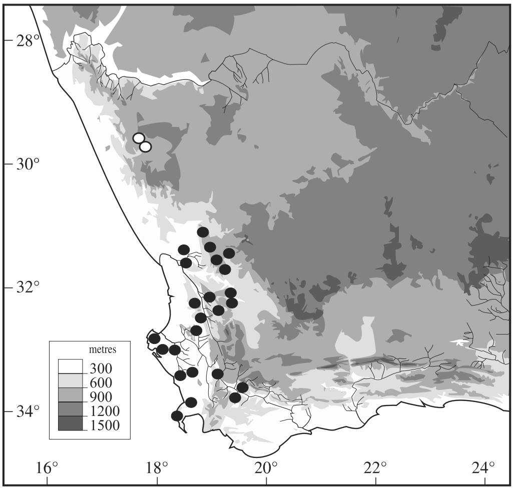


FIGURE 5.—Distribution of *Lapeirousia jacquinii*, ●; *L. verecunda*, ○.

times so common that they form sheets carpeting the ground under sparse low shrubs, notably in the Bokkeveld Mtns. Records indicate that *L. jacquinii* once occurred on the Cape Peninsula near Salt River and on the slopes of Lion's Head. Urbanisation around Salt River has long since eliminated native plants but *L. jacquinii* probably persists on Lion's Head (Lewis 1950).

Lapeirousia jacquinii is self-compatible and facultatively autogamous, and reproduces very readily from seed, thus rapidly colonising new habitats. It is also often cross-pollinated in the parts of its range where long-proboscid flies are active. In the Bokkeveld Mtns plants are regularly visited by two species of *Prosoeca*, *P. peringueyi* and *P.* sp. (Nemestrinidae), and elsewhere only by *P. peringueyi*. Both insects are effective pollinators while foraging for nectar (Goldblatt et al. 1995). East of Pakhuis Pass and at the southern end of the Bokkeveld Mtns and in Biedouw Valley *L. jacquinii* frequently co-occurs with the florally similar *L. violacea*, also pollinated by *Prosoeca peringueyi*. Although flies visit flowers of both species, no hybrids between them are known.

Diagnosis and relationships: *Lapeirousia jacquinii* is most easily recognised by the prominently 2-keeled outer floral bracts (occasionally 1-keeled, especially the lowermost) and even in fruit the species can be recognised by this feature. The stems are conspicuously 3-angled and the angles winged and undulate and sometimes minutely toothed. The long-tubed flowers are deep violet (rarely white) with darker violet or red makings outlined in white on the lower tepals, a colour combination very similar to that in *L. violacea*, with which it is sometimes sympatric. This last species has quite different corms, triangular in profile and bearing long spines radiating from the base, unlike the bell-shaped corm of *L. jacquinii*, the basal rim of which bears minute, downward-directed teeth. The outer bracts of the two species also differ, those in *L. violacea* being folded or keeled and the keels minutely crisped. The remarkable similarity in shape, tube length and colouration of the flowers in the two species is evidently due to convergence for the same long-proboscid fly pollinators.

The immediate relationships of *Lapeirousia jacquinii* are uncertain, but the basic chromosome number, $x = 9$, is consistent with sect. *Chasmatocallis* and most species have similar, if not identical, bell-shaped corms either with crenate or minutely serrate margins. The plastid DNA sequence-based phylogeny consistently shows *L. jacquinii* to be most closely related to *L. divaricata*, which is very different in its short-tubed, white to palest pink flowers, and short, 1-keeled floral bracts. The corms of the two are, however, identical and they also share unique, fenestrate outer bracts with pale, almost translucent sides.

History: although common, *Lapeirousia jacquinii* is poorly represented in older herbarium collections. It was first recorded in the *Codex Witsenii*, a collection of illustrations of plants encountered on Simon van der Stel's 1685–1686 expedition to the Copper Mountains of Namaqualand. The painting, a very poor likeness, was copied in Jan Commelin's manuscript account of the Cape Flora, written between 1687 and 1692 (Wijnands et al. 1996), and called therein 'branching *Sisyrinchium aethyopicum* with helmeted purple flower'. The name appears never to have been adopted in the botanical literature: the first post-Linnaean record is evidently the plant figured by N.J. Jacquin in 1794, presumably collected north of Cape Town a few years earlier. Jacquin confused the species with *Gladiolus* (*Lapeirousia*) *anceps* of Linnaeus fil. and in doing so initiated the confusion that long surrounded these two very distinct, but long-tubed species. Ker Gawler (1804) perpetuated the error, and *L. jacquinii* continued to be considered conspecific with *L. anceps* (e.g. Sprengel 1824; Poiret 1826; Dietrich 1833) and was so treated by J.G. Baker in 1896 in *Flora capensis*. The situation was only clarified in 1928 by N.E. Brown, who then formally described *L. jacquinii*, naming it in honour of Jacquin.

Representative specimens

SOUTH AFRICA. NORTHERN CAPE.—**3017** (Hondeklipbaai): ± 71 km west of Garies to Hondeklip Bay, dune ridges, (–AD), 18 Sept. (fr.), *Goldblatt & Manning 9998* (MO); hills above Garies on road to Hondeklip Bay, (–DB), 20 Aug. 2001, *Goldblatt & Porter 11717* (MO), 27 Aug. 1991, *Goldblatt & Manning 9135* (MO, NBG). **3119** (Calvinia): Bokkeveld Mtns, Farm Avontuur, (–AA), 28 Aug. 2008, *Goldblatt & Manning 13052A* (MO); top of Vanrhyns Pass, (–AC), 6 Sept. 1963, *Nordenstam 2990* (MO, S); Farm Driefontein, southwest of Calvinia, (–CA), 8 Sept. 1992, *Goldblatt & Manning 9412* (MO); top of Botterkloof Pass (growing with *L. violacea*), (–DD), 3 Sept. 1994, *Goldblatt & Manning 9966* (MO).

WESTERN CAPE.—**3118** (Vanrhynsdorp): Biedouw River, Vanrhynsdorp, (–DA), 21 Aug. 1954, *Barker 8599* (NBG), *Lewis 1407* (SAM); hills north of Klawer, (–DC), 5 Aug. 1974, *Goldblatt 2266* (MO); Windhoek, (–DC), 30 July 1896, *Schlechter 8340* (MO). **3217** (Vredenburg): Stompneus, (–DB), 23 Aug. 1953, *Hall 735* (NBG); Olifantskop, Langebaan, (–DD), 15 Aug. 1976, *Goldblatt 2328* (MO). **3218** (Clanwilliam): east of Graafwater, on pass, (–BA), *Booysen 48* (NBG); north of Piketberg, flats at foot of Zebrakop, (–DB), 1 Sept. 1981, *Goldblatt 6128* (MO); Piekenierskloof, *Schlechter 4916* (BOL). **3219** (Wuppertal): Pakhuis Pass, (–AA), *Barker 1309* (NBG), *Lewis 1854* (SAM); Cederberg, 2 km from Algeria to Clanwilliam, (–AC), 13 Aug. 1986, *Van Wyk 2564* (MO, PRE); Citrusdal, (–CA), 24 Sept. 1928, *Grant s.n.* (MO). **3318** (Cape Town): near Hopefield, (–AB), *H. Bolus 12852* (BOL); Darling Flower Reserve, (–AD), 11 Aug. 1960, *Barker 9182* (NBG); west slope of Lions Head, (–CD), *MacOwan 24609* (BM, BOL, K, SAM); 13 miles [18.5 km] from Cape Town to Kalbaskraal, (–DC), *Hutchinson 174* (BOL, K, PRE). **3319** (Worcester): below Tulbagh Falls, deep sand, (–AC), 29 Aug. 1978, *Goldblatt 4759* (MO); rocky flats between Worcester and Overhex, (–CA), 1 Sept. 1992, *Goldblatt & Manning 9371* (MO); Aan de Doorns, Farm Reiersrus, (–CB), *Walters 2163* (NBG).

3. **Lapeirousia silenoides** *(Jacq.) Ker Gawl.* in König & Sims Annals of Botany 1: 238 (1804); Goldblatt: 36 (1972). *Gladiolus silenoides* Jacq.: 168 (1792). *Ovieda silenoides* (Jacq.) Spreng.: 147 (1824); *Peyrousia silenoides* (Jacq.) Poir.: 365 (1826). *Meristostigma silenoides* (Jacq.) A.Dietr.: 596 (1833). Type: South Africa without precise locality or collector, illustration in Jacq.: t. 270 (1794) (herbarium specimens believed destroyed).

Lapeirousia speciosa Schltr.: 105 (1900). Type: South Africa, [Western Cape], Kareebergen, 17 July 1896, *Schlechter 8187* (B, holo.!; BM!, BOL!, COI!, E!, G!, GRA!, K!, PH!, PRE!, iso.).

Plants 50–150(–200) mm, taller in sheltered or shaded sites, ± acaulescent in exposed sites or in seasons of low rainfall, stem aerial often branched close to base, compressed, 2-angled, often 2-winged below first flower, wings often minutely serrate. *Corm* bell-shaped, 8–10 mm diam.; tunics light brown, basal rim ridged (minutely serrate in plants from Spektakel Mtns). *Leaves* few, lowermost longer than others, lanceolate to linear, ribbed or corrugate, ± as long as or longer than stem, 1.5–5.5 mm wide; remaining leaves shorter and broader, progressively bract-like above. *Inflorescence* usually a crowded to lax spike, or a head-like cluster at ground level, up to 12-flowered, initially 2-ranked, spiral with age; outer bracts linear to lanceolate, sometimes very broad at base, occasionally ± succulent, outer 15–20 mm long, unifacial for distal 2–4 mm, acute and curving upward, folded or lightly keeled below, keels usually minutely serrate, margins membranous; inner bracts ± $^{1}/_{2}$ as long, with broad transparent margins. *Flowers* zygomorphic, bright cerise to dark magenta (rarely white), lower 3 tepals each with creamy white markings near base, limbs with large central blotch of dark red or purple, scentless; perianth tube cylindric, slender, ± erect, 40–55 mm long, curved outward near apex; tepals subequal, ± broadly obovate, obtuse, limbs concave, 10–12 × ± 5 mm, dorsal erect or sometimes slightly inclined toward stamens, upper lateral tepals reflexed, lower 3 united basally for ± 1 mm, inclined at ± 45° to horizontal. *Stamens* unilateral, ± erect; filaments 7–8 mm long, exserted ± 4 mm from tube; anthers 3–4 mm long, blue violet; pollen white or pale blue to mauve. *Style* erect, dividing close to or just beyond anther tips, ultimately exceeding them; branches 1.0–1.5 mm long, forked for ± $^{1}/_{2}$ their length, recurved. *Capsules* obovoid to oblong, trigonous, 10–15 × 5–7 mm, usually with well-developed wing-like locular ridges in distal half. *Seeds* globose, light brown, variable in size even on same plant, 1.2–2.2 mm diam. *Chromosome number* $2n = 18$. *Flowering time*: (July) August to mid-September.

Distribution and biology: widespread in Namaqualand, *Lapeirousia silenoides* extends from near Nuwerus in the south to the Anenous Mtns west of Steinkopf in the north (Figure 4). It is restricted to granitic soils, and may grow either in deep, coarse granitic sand where plants tend to be robust in years of adequate rainfall or in granite outcrops where the corms are usually wedged in rock cracks, in little or no soil. On rocks, plants tend to be fairly dwarfed but in years of ample rainfall the main stem branches repeatedly at the base, producing a cushion-like form. In years of poor rainfall, plants can be virtually acaulescent with the flowers produced close to ground level. Similarly, at higher elevations in the Kamiesberg, the aerial stem is often hardly or not at all produced above the ground, and plants assume a low, tufted growth habit.

Self-incompatible, *Lapeirousia silenoides* often has relatively low seed set in the wild, and in cultivation does not produce capsules unless actively cross pollinated even though the recurved style branches do come into contact with pollen. Pollination studies show that the species is regularly visited by the long-proboscid nemestrinid fly, *Prosoeca peringueyi*, which appears to be its only legitimate pollinator (Goldblatt et al. 1995). Plants produce up to 3.6 ml of nectar of moderate sugar concentration (mean 26.5% sucrose equivalents). Plants reproduce very successfully by seed and *L. silenoides* can be seen flowering along roadsides in masses, the seed having fallen from parent plants growing on banks and slopes above the road.

Diagnosis and relationships: the bright magenta to cerise flower with darker colour in the centres of the lower tepals and cream streaks or blotches on the lower tepal bases instantly identify *Lapeirousia silenoides* in Namaqualand. To the south, in the Vanrhynsdorp and Clanwilliam districts, *L. pyramidalis* may be similarly coloured, though more often purple to violet, but the two species can be separated by their different bracts; narrow to fairly broad and acute with an upturned apex in *L. silenoides*, broad and often retuse with the apex curving downward in *L. pyramidalis*. The two are undoubtedly related as is evidenced not only by their similarly marked and sometimes almost identically coloured flowers but by the similar, red-brown corms and capsules with wing-like locular ridges, a character shared by relatively few other species of *Lapeirousia*. When dry, *L. silenoides* can easily be confused with red-flowered *L. pyramidalis* subsp. *regalis* unless the bracts are carefully compared.

Bract shape is fairly variable in *Lapeirousia silenoides*. In the centre of its range, in the Kamieskroon area, the bracts are narrow and often quite long. In this area too, the plants are often tallest and are occasionally slender. This form resembles the type illustration of Jacquin (1794). Both south and north of this area the plants are smaller, and generally less robust, with the bracts shorter and broader. Plants with particularly broad-based bracts occur in the south of its range, notably in the vicinity of Bitterfontein. This variant, named *L. speciosa* by Schlechter (1900), has flowers identical with those of plants from further north and although the difference in the shape of the bracts in Schlechter's type material is striking, the presence of populations intermediate for bract shape and the consequent difficulty in placing these makes an infrageneric classification seem unnecessary.

History: as far as we have been able to determine, *Lapeirousia silenoides* was first collected by the French explorer, François le Vaillant, during his expedition to Namaqualand in 1783 (Gunn & Codd 1981). Although Le Vaillant collected few plant specimens, one attributed to him in the Lamarck Herbarium in Paris attests to his discovery of the species. *L. silenoides* was, however, described (as *Gladiolus*) by N.J. Jacquin whose painting in *Icones plantarum rariorum* (1794) of a plant cultivated and flowered in Vienna is regarded as the type of the species. The source of Jacquin's plant must have been Franz Boos and Georg Scholl who collected bulbs, corms and seeds for Jacquin in the period 1786 to 1788, just a few years after Le Vaillant visited Namaqualand. The species was not recorded by the 1665–1666 Simon van der Stel expedition to the 'copper mountains' of Namaqualand, probably because they only reached Namaqualand proper in late September (Wijnands et al. 1996) when *L. silenoides* would no longer have been in bloom.

Representative specimens

SOUTH AFRICA. NORTHERN CAPE.—**2917** (Springbok): between Steinkopf and Klipfontein, (–BA), 17 Sept. 1929, *Herre s.n.* (*BOL30710*, PRE); Klipfontein, (–BA), Aug. 1883, *H. Bolus 696* (BM, BOL, G, GRA, SAM); Anenous Pass, (–BA), 23 Aug. 1983, *Van Wyk 6168* (PRE); top of Anenous Pass, (–BA), 27 Aug. 2008, *Goldblatt & Manning 13032* (MO, NBG); ± 11 km northeast of Nigramoep, (–BC), *Acocks 19351* (PRE); 12 km north of Komaggas, (–CD), 20 July 1970, *Wisura 1692* (NBG); top of Spektakel Pass, west of Springbok, (–DA), 17 Aug. 1974, *Goldblatt 2365* (MO); hill west of Springbok, (–DB), 24 Aug. 1992, *Goldblatt & Manning 9322* (MO, NBG); Droëdap, (–DD), 27 Aug. 1941, *Barker 1306* (NBG). **3017** (Hondeklipbaai): Grootvlei, (–BB), 18 July 1961, *Middlemost* 1636 (NBG), *Lewis 1637* (SAM); hills between Garies and Kamieskroon near microwave tower, (–BD), 21 Aug. 1992, *Goldblatt & Manning 9278* (MO), 16 Sept. 1992 (fr.), *Goldblatt & Manning 9467* (MO); hills at Brakdam, (–BD), 4 Sept. 1945, *Compton 17205* (BOL); 24 July 1941, *Esterhuysen 5442* (BOL), *Leighton 1140* (BOL), 8 Sept. 1897, *Schlechter 11122* '*L. montana* Schltr.' (BM, COI, E, GRA, K, MO, PH, SAM);

Darter's Grave, (–BD), 7 Sept. 1950, *Barker 6611* (NBG), 18 July 1961, *Middlemost 2156* (NBG); Karkams, Kamiesberg, (–BD), 11 Sept. 1911, *Pearson 6661* (BOL, SAM); 6 km north of Garies, (–DB), *Schlechter 1400* (BM, BOL); 13.7 km from Kotzesrus to Garies, along seasonal stream, (–DD), 3 Sept. 2001, *Goldblatt & Porter 11817* (MO). **3018** (Kamiesberg): top of Kamiesberg Pass at Farm Bo-Tuin, (–AA), 9 Sept. 1980, *Goldblatt 5762A* (MO); Twee Rivieren, Kamiesberg, (–AC), 13 Sept. 1911, *Pearson 6478* (BOL, SAM); Kamiesberg, Damsland Kloof, northern approach to Rooiberg, (–AC), 19 Sept. 1991, *Goldblatt 9259* (MO); ± 16 km south of Garies, (–CA), *Barker 7330* (NBG); 10 km south of Garies, (–CA), 29 Aug. 1991, *Goldblatt & Manning 9202* (MO); Kamiesberg, road between Karas and Farm Naartjiesdam, (–CA), 1 Sept. 2002, *Goldblatt 12134* (MO).

WESTERN CAPE.—**3118** (Vanrhynsdorp): 6.5 km west-northwest of Bitterfontein, (–AA), 26 Aug. 2008, *Goldblatt & Manning 13029* (MO, NBG); Mierenkasteel, (–AA), *Drège 2642* (MO, SAM); Bitterfontein (–AB), 23 July 1941, *Bond 1091* (NBG); 23 July 1941, *Esterhuysen 5407* (BOL); 10 km northeast of Bitterfontein toward Kliprand, (–AB), 22 Aug. 1974, *Nordenstam & Lundgren 1456* (MO, NBG, S); 8 km north of Nuwerus, (–AB), 18 July 1948, *Compton 20565* (NBG).

4. **Lapeirousia verecunda** *Goldblatt* in Contributions from the Bolus Herbarium 4: 38 (1972). Type: South Africa, [Northern Cape], Namaqualand, upper east slopes of Spektakel Pass, 24 Aug. 1970, *Goldblatt 573* (BOL, holo.!; K!, MO!, NBG!, PRE!, iso.).

Plants 80–150 mm high, stem simple or with 1–3 branches from base, slightly compressed and 2-angled, one or both angles winged, wings decurrent on leaves or bracts. *Corm* bell-shaped, 10–13 mm diam.; tunics red-brown, slightly rugose, basal rim slightly lobed. *Leaves* 5–7 (more when stem branched), lowermost longest, linear, ascending to falcate, closely ribbed, 70–100 × 3.5–5.0 mm, seldom exceeding stem; upper leaves < $^1/_2$ as long as lowermost, progressively shorter and bract-like distally. *Inflorescences* 9–12-flowered, 2-ranked, spikes; outer bracts green, firm, narrowly lanceolate, acute, often recurved at tips, 10–20 mm long, margins membranous, channelled or folded in midline; inner bracts ± $^1/_2$ as long, notched at tips. *Flowers* zygomorphic, white, tube and reverse of tepals copper-pink, lowermost or all 3 lower tepals with red, heart-shaped mark in lower midline; perianth tube cylindric, slender, 40–50(–55) mm long, slightly curved forward distally; tepals subequal, ovate-elliptic, slightly narrowed at base, sub-acute or obtuse, 10–12 × 5.5–6.0 mm, dorsal erect, lower 3 tepals ± horizontal. *Stamens* unilateral, erect; filaments ± 6 mm long, exserted ± 3 mm; anthers parallel, contiguous, ± 3 mm long, purple; pollen purple. *Style* dividing opposite anther tips, branches ± 2 mm long, divided for $^1/_2$ their length, recurved. *Capsules* obovoid-trigonous, ± 10–13 × 7 mm, with prominent wing-like locular ridges in distal half. *Seeds* ± globose, smooth, dark brown, 1.6–1.9 mm diam. *Chromosome number* $2n = 18$. *Flowering time*: late August to the end of September, rarely early October.

Distribution and biology: a narrow endemic of the Spektakel Mtns west of Springbok, *Lapeirousia verecunda* was thought, when first described in 1972, to consist of a single extended population on the eastern slopes of Spektakel Pass, at elevations of 700–800 m. Now also recorded near Nigramoep, some 20 km to the north in the same mountain complex (Figure 5), the species is largely restricted to stony shale slopes (Nama Shale Formation), which has a scattered distribution in Namaqualand. Toward the eastern summit of Spektakel Pass where the shale merges with the surrounding granite, *L. verecunda* grows together with cerise-flowered *L. silenoides*. The latter, which is widespread in Namaqualand, always grows in granite derived soils or in crevices in granite outcrops. We have found hybrids between the two species on the farm Naries on Spektakel Pass where the ranges of the two species converge (*Goldblatt & Manning 9969*). The flower colour, white with red markings, and the long perianth tube of *L. verecunda* are stereotypical adaptations for the *Moegistorhynchus longirostris* long-proboscid fly pollination system, but to date no pollinators have been seen visiting *L. verecunda*. Hybrids are likely the result of the pollinator of *L. silenoides*, *Prosoeca peringueyi* visiting both species.

Diagnosis and relationships: this attractive plant is easily recognised by its odourless, long-tubed white flowers with red, round to heart-shaped marks on one or more of the three lower tepals, and the red colour on the reverse of the tepals and tube. Aside from colour, the floral tube, usually 50–55 mm long, plane tepals, and fairly long and comparatively narrow bracts with deflexed apices are distinctive. *L. verecunda* belongs to the group of species in sect. *Chasmatocallis* with bell-shaped corms with tunics that are ridged or regularly lobed on the basal rim rather than being serrated. In its long perianth tube and fairly broad, ovate-elliptic tepals the flowers of *L. verecunda* most closely resembles those of *L. silenoides*, but because of the colour differences of the flowers the two are unlikely to be confused. The cerise flowers of *L. silenoides* with spoon-shaped lower tepals are rather different from the white perianth with flat lower tepals of *L. verecunda*. The species is named for its rarity (Latin *verecunda* = shy) and for the pale flowers with a slight blush from the pink colour on the reverse of the tepals.

History: when described in 1972, *Lapeirousia verecunda* was thought to have been discovered only in August 1970, a year of ample rainfall in Namaqualand that encouraged collecting in the region. Later, we learned that there were at least three earlier records of the species. The first of these is was found in the personal herbarium of the American botanist, A.L. Grant, whose South African plant collection was bequeathed to the University of California, Los Angeles, and was later incorporated into the Missouri Botanical Garden Herbarium, St. Louis, in 1972. The specimens were collected by Harry Bolus, founder of the Bolus Herbarium at the University of Cape Town. Bolus collected in the Spektakel Mtns in September 1883, on his single expedition to Namaqualand. The collection, undated but accompanied by labels, some bearing the numbers 38 and 42, was provisionally identified as *L. anceps* (a name then misapplied to *L. fabricii*). Bolus's field register (University of Cape Town Archives) records *L. anceps*, number 36, collected on the Spektakelberg (not Kommagas Kloof as one of the labels indicates). It seems clear that Bolus did indeed make the first gathering of *L. verecunda*, but through a quirk of circumstance, the entire collection was acquired by the Missouri Botanical Garden, evidently because it was thought to be yet another collection of a common Namaqualand species and considered not worth retaining in the Bolus Herbarium collection. Later collections of *L. verecunda* were made by B.E. Martin in 1950 and J.P.H. Acocks in 1957.

Representative specimens

SOUTH AFRICA. NORTHERN CAPE.—**2917** (Springbok): west-facing slope south of Nigramoep, 800 m, (–BC), 4 Sept. 1983, *Oliver 8033* (NBG, PRE); ± 23 km south-southwest of Springbok, 25 Aug. 1957, (–DA), *Acocks 19432* (PRE); Eselsfontein (Spektakelberg), (–DA), 8 Sept. 1950, *Martin 515* (NBG); upper eastern slopes of Spektakel Pass, (–DA), 7 Sept. 1980, *Goldblatt 5710* (MO, NBG), 23 Sept. 1977, *Perry 383* (NBG), Sept. 1970, *Thompson 1021* (NBG), 28 Aug. 1991, *Goldblatt & Manning 9144* (MO); Naries, Spektakel Mtns., (–DA), undated [probably Sept. 1883], *H. Bolus 38 & 42* (BOL, MO); Spektakel Mtns, at top of Pass, (–DA), 26 Sept 1974, *Goldblatt 2789* (MO, NBG), 28 Aug. 9144, *Goldblatt & Manning 9144* (MO); Kommagas Kloof, (–DA), but perhaps Spektakelberg intended, without date [1883?], *H. Bolus s.n.* (MO).

5. **Lapeirousia anceps** *(L.f.) Ker Gawl.* in König & Sims Annals of Botany 1: 238 (1804); Goldblatt: 33 (1972). *Gladiolus anceps* L.f.: 94 (1782). *Ovieda anceps* (L.f.) Spreng.: 147 (1824). *Peyrousia anceps* (L.f.) Poir.: 363 (1826). *Meristostigma anceps* (L.f.) A.Dietr.: 596 (1833). Type: South Africa, without precise locality, *Sparrman 192* (59/19–LINN, holo!.).

Lapeirousia pentheri Baker: 27 (1906). Type: South Africa, [Western Cape], Breede River, *Penther 728* (BOL!, BM!, K!, syn.).

[*anceps* – 'two-edged' referring to the compressed, usually two-angled stem.]

Plants 100–300 mm high; stem usually repeatedly divaricately branched, compressed and elliptic in cross section, 2- or 3-angled, angles slightly winged, wings weakly denticulate. *Corm* bell-shaped, red-brown, 8–10 mm diam.; tunics lightly ridged, rim bluntly lobed. *Leaves* 5–7, lowermost usually somewhat longer and wider than others, (40–)80–200 × 3–15 mm, ascending to falcate, lanceolate, ribbed, remaining leaves shorter, mostly crowded near base, becoming increasing bract-like above. *Inflorescences* (2–)4–8-flowered spikes, at first 2-ranked, ultimately spiral; outer bracts grey-green, (5–)6–10 mm long, apices and margins often tinged red, channelled, folded along upper midline, acute in profile; inner 3–5 mm long, transparent with two green keels. *Flowers* zygomorphic, white to beige or faintly flushed pink, reverse of tepals and tube pink, lower 3 tepals each with red mark in lower midline, and usually with small, claw-like cusp near base; perianth tube narrow and cylindric, weakly arched distally, (20–) 40–80 mm long (3–6 times as long as tepals); tepals narrowly lanceolate to ± linear, acute, dorsal largest, 12–14 × 4–5 mm, erect or recurved when fully open, upper lateral 12–14 × ± 3 mm, widely separated from dorsal, lower tepals united basally for 2–3 mm, free parts 12–14 mm long, extended horizontally. *Stamens* unilateral, ± erect; filaments ± 6 mm long, exserted ± 4 mm from tube; anthers parallel, ± 2.5 mm long, pollen grey-blue or white. *Style* arching adaxial to anthers, dividing between base and middle of anthers; branches 2–3 mm long, divided for $^1/_2$ their length and recurved. *Capsules* ± barrel-shaped, 9–10 × ± 7 mm. *Seeds* red-brown, globose, smooth, somewhat flattened at chalazal end, ± 1.5 mm diam. *Chromosome number* 2*n* = 18. *Flowering time*: (late September–)October, to late November at higher elevations and in the south. Figure 6.

Distribution and biology: with one of the widest distribution ranges of the southern African species of *Lapeirousia*, *L. anceps* extends from the sandy coastal plain of central Namaqualand near Hondeklip Bay in the north through the mountains and coastal plain of Western Cape to near Mossel Bay in the east (Figure 7). Over this wide range, plants almost always occur in deep sandy soils, sometimes growing among tufts of Restionaceae. Like many geophytes of sandstone soils, *L. anceps* shows a pattern of profuse flowering following fires the previous season. Along the Cape west coast this is not, however, the rule but even here flowering is promoted by disturbance of the native, largely shrubby vegetation. Plants are typically scattered, but sometimes grow in masses, when the slender flowers then make a notable display.

Pollination studies have shown that *Lapeirousia anceps* is pollinated by long-proboscid flies, either the nemestrinid *Moegistorhynchus longirostris* or the horseflies *Philoliche gulosa* and *P. rostrata* (Goldblatt et al. 1995; Manning & Goldblatt 1997; Pauw et al. 2008). The remarkable range of perianth tube length in different populations is closely correlated with variation in proboscis length in the pollinators, shorter-tubed populations being pollinated by flies with correspondingly shorter probosces (Pauw et al. 2008). Over much of its range *L. anceps* has a tube 25–40 mm long, corresponding to the proboscis of *P. gulosa*, 30–34 mm. In the southern Cape the tube tends to be shorter, sometimes only 20 mm long (e.g. *Woodvine 91* from Hermanus and *Bohnen 7863* from Riversdale). In the west, along the coastal plain and at sites in the Olifants River Mtns, some populations have tubes as long as 70–80 mm. Both this very long-tubed form and the southern populations are pollinated largely by *Moegistorhynchus*, some morphs of which have the longest probosces of any fly in southern Africa.

Diagnosis and relationships: *Lapeirousia anceps* is readily recognised by the combination of short floral bracts and white to ivory flowers, pink on the outside of the tepals and tube, and usually relatively long perianth tube, mostly 50–80 mm but occasionally only 20–40 mm, and narrow tepals 3–4 mm wide (sometimes the dorsal up to 5 mm). The lower tepals usually have a claw-like projection just above the base. The bell-shaped corms have either bluntly lobed or minutely serrated basal rims. The species has no close allies within the section and the short floral bracts of *L. anceps*, 5–10 mm long, are particularly surprising in view of its long perianth tube.

History: the background to the protologue of *Lapeirousia anceps* was outlined in some detail by Goldblatt (1972) and we briefly summarise its history here. The draft description of the species was penned by Linnaeus senior, who called it *Gladiolus decurrens*, based on a collection of Anders Sparrman. The younger Linnaeus deleted that name in the amanuensis draft of Linnaeus's account and replaced the species epithet with the name *anceps*, which he copied from a draft description by C.P. Thunberg of a second species, now *L. fabricii*, which at the time was thought to be the same species. Thunberg (1800) and later authors, among them John Ker Gawler, included *L. anceps*, *L. fabricii* as well as a third species (now *L. jacquinii*) under one name, *L. fabricii*, described by D. Delaroche in 1766. Baker (1896) also confused the three species and in *Flora capensis* he treated them under the name *L. anceps*, distinguishing what we now know as *L. fabricii* as *L. anceps* var. *aculeata*. N.E. Brown (1928) was the first to establish that *L. anceps*, *L. fabricii* and *L. jacquinii* are in fact separate species. We now believe that *L. anceps* with its bell-shaped corm and *L. fabricii* with an obconic corm with prominent teeth are not closely related and that their floral similarities are due to convergence for long-proboscid fly pollination.

Representative specimens

SOUTH AFRICA. NORTHERN CAPE.—**3017** (Hondeklipbaai): sandy flats west of Wallekraal, (–AD), Sept. (in bud), *Goldblatt & Manning s.n.* (sight record). **3119** (Calvinia): Lokenburg, sandstone hills (–CA), *Story 4330* (GRA).

FIGURE 6.—*Lapeirousia anceps*, *Goldblatt & Manning 10347*. Scale bar: 10 mm. Artist: John Manning.

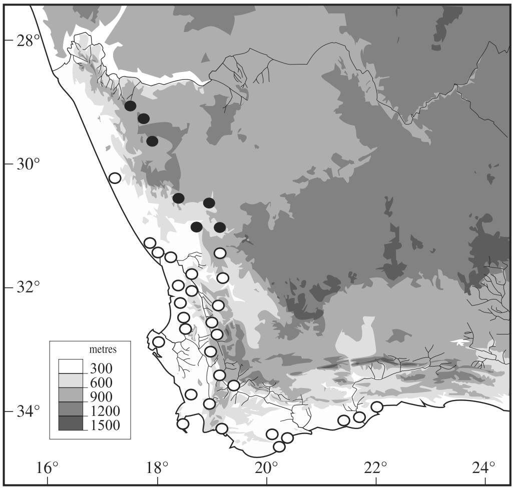


FIGURE 7.—Distribution of *Lapeirousia anceps*, ○; *L. exilis*, ●.

WESTERN CAPE.—**3118** (Vanrhynsdorp): 3 km north of Vredendal, (–DA), 30 Sept. 1972, *Bremer 234* (MO, S); near Klawer turnoff on road to Clanwilliam, (–DC), 4 Sept. 1980, *Goldblatt 5664* (MO). **3217** (Vredenburg)**:** Witklip Farm, 1 mile [1.5 km] south of Vredenburg, (–DD), 16 Oct. 1975, *Thompson 2657* (PRE). **3218** (Clanwilliam): Nortier Experimental Farm, Lambert's Bay, (–AB), 6 Nov. 1974, *Boucher 2579* (PRE); 11 km west of Clanwilliam toward Graafwater, (–BB), 13 Oct. 1976, *Hugo 660* (PRE); 10 km from Clanwilliam on road to Graafwater, Farm Ysterfontein, (–BB), 10 Oct. 1995, *Goldblatt & Manning 10347* (MO, NBG);Verloren Vlei, Piketberg District, (–DA), 29 Sept. 1943, *Barker 2617* (BOL, MO, NBG). **3219** (Wuppertal): Vleikraal, southeast of Klawer (–AB), Sept. 1979, *Walters 50* (PRE); Cederberg, 3 km west of Algeria on Clanwilliam road, burnt sandy slope, 16 Nov. 1979, *Goldblatt 5147* (MO); 1 mile [1.5 km] south of The Baths, Farm Latjeskloof (–CC), 24 Oct. 1977, *Emdon 103* (MO, PRE); Keerom, Olifants River Valley, (–CC), *Esterhuysen 17868* (BOL). **3318** (Cape Town): Bloubergstrand turnoff from Malmesbury road, (–DC), 18 Nov. 1981, *Snijman 578* (NBG, PRE); Jonkershoek, Farm Waterval, (–DD), 5 Nov. 1975, *Oliver 6200* (PRE). **3319** (Worcester): Saron, 800 ft [244 m], (–AA), Oct. 1896, *Schlechter 10634* (GRA, K, MO); near Tulbagh Falls, (–AC), *MacOwan 2157* (E); Nuwe Kloof near Tulbagh, *Drège 8507a* (BM, K, MO); Botha Station, (–CB), *Compton 18692* (NBG); Wemmershoek Mtns, (–CC), *Esterhuysen s.n.* (*BOL30327*). **3418** (Simonstown): Kommetjie, stony hillside near Ocean View Village, (–AB), 7 Nov. 1982, *Goldblatt 6720* (MO); Kommetjie, (–AB), *Galpin 4692* (GRA, K); Buffels Bay, Cape Point Reserve, (–AD), *Salter 1843* (BM, BOL). **3419** (Caledon): Hermanus, Fernkloof Nature Reserve, (–AD), 11 Nov. 1981, *Woodvine 91* (MO); Riviersonderend, (–BA), *Schlechter 5635* (BM, GRA, K, SAM). **3420** (Bredasdorp): De Hoop, Melkkamer, (–AD), 17 Oct. 1984, *Fellingham 830* (NBG, PRE); near Struisbaai, (–CA), *Leipoldt 2595* (BOL). **3421** (Riversdale): Farm Klein Jongensfontein, Riversdale, (–AD), 1 Oct. 1980, *Bohnen 7863* (PRE); sandy dunes, Riversdale, (–AB), *Ferguson s.n.* (BOL); Albertinia commonage, (–BA), *Muir 1139* (BOL). **3422** (Mossel Bay): between the Great and Little Brak rivers, deep sand on north-facing slope, (–AB), 28 Oct. 1988, *Vlok 2035* (MO, NBG).

6. **Lapeirousia exilis** *Goldblatt* in Contributions from the Bolus Herbarium 4: 44 (1972). Type: South Africa, [Northern Cape], Namaqualand, Ratelpoort, ± 25 km north of Springbok, 6 July 1970, *Tölken 3238* (BOL, holo.!; K!, MO!, NBG!, iso.).

Plants small, usually 30–50 mm high, rarely taller, usually unbranched, stem subterranean or produced shortly above ground. *Corm* ± 8 mm diam., light brown, bell-shaped, ridged at base, margin slightly lobed (not serrated). *Leaves* usually 2, basal longest, falcate or ± trailing, 80–160 × 1–2 mm, ribbed, second leaf much shorter, often only slightly longer than floral bracts, 2–3 mm wide, channelled in lower half. *Inflorescence* a congested spike, sometimes ± a basal rosette, 6–13-flowered, 2-ranked in bud, becoming spiral as flowers open; outer bract 15–25 mm long, lowermost longest, with unifacial apices, upper leaves channelled, apices rounded without unifacial tips, not keeled, translucent over veins, margins pale, membranous; inner bract ± $^{1}/_{3}$ as long as outer, transparent with two green keels. *Flowers* zygomorphic, white to pale blue with proximal 1–2 mm fading to ± white, lower 3 tepals with a dark blue median streak in lower midline (fading in dried material), strongly and sweetly scented; perianth tube slender, erect, curved and widening at apex, 20–25 mm long; tepals subequal, ± 8 mm long, spreading, dorsal suberect at anthesis, later spreading, lower 3 tepals slightly smaller broadly to narrowly ovate, obtuse, narrowed at base and ± clawed. *Stamens* unilateral, ± erect; filaments ± 4 mm long, inserted close to top of tube, ± fully exserted; anthers ± 3 mm long, pale blue; pollen ± white. *Style* arching adaxial to stamens, dividing opposite anther bases, style branches forked for $^{1}/_{2}$ their length and recurved. *Capsules* broadly ovoid, trigonous, 8–11 × ± 6.5 mm. *Seeds* globose, smooth, flattened at chalazal end, ± 1.3 mm diam., light brown. *Chromosome number* 2*n* =

18. *Flowering time*: mid-June to mid-August. Figure 8.

Distribution and biology: *Lapeirousia exilis* has a scattered range across Namaqualand from Steinkopf north of Springbok southward to the rugged northern edge of the Bokkeveld Escarpment northeast of Nieuwoudtville (Figure 7). Plants grow in stony ground in granitic gravel, sand, or occasionally clay. Pollination studies show the species to be pollinated by large bodied bees and bombyliid flies (Goldblatt et al. 1995). The fairly long perianth tube appears to indicate a pollinator with long mouthparts, but we have found that nectar is held fairly high in the tube and within reach of long-tongued bees and bombyliids.

Diagnosis and relationships: although known since at least 1898 when it was collected by Maximilian Schlechter, *Lapeirousia exilis* was included in *L. plicata* (sometimes as *L. caespitosa*), often only tentatively, until 1972 when it was recognised as a separate species (Goldblatt 1972). When pressed, the plant and its flowers can appear similar to *L. plicata* and may be difficult to distinguish from that species. The similarity to *L. plicata*, which is acaulescent and has radially symmetric flowers, is superficial. In *L. exilis* the stem in well-grown plants is short but produced above the ground and the flower is zygomorphic. The stamens are unilateral and the lower tepals bear markings only on the horizontal lower tepals. The branches, when produced, are short, but the internodes are not as severely contracted as in *L. plicata* except in the most depauperate plants with only a few flowers. *L. exilis* has floral bracts typical of *Lapeirousia* and not like those found in *L. plicata*, which have elongated leaf-like tips above the sheathing bases. The seeds (Table 3) accord with sect. *Chasmatocallis* in their smooth surface and domed surface cells, thus quite unlike the sculptured, ± reticulate to rugose surface and flat surface cells of *L. plicata* and its acaulescent allies. Molecular data support the fundamental differences in flower, bract and seed morphology in allying *L. exilis* with sect. *Chasmatocallis* rather than to *L. plicata* (sect. *Sophronia*).

Representative specimens

SOUTH AFRICA. NORTHERN CAPE.—**2917** (Springbok): 2 km west of Steinkopf, shale hillside, (–BA), 16 July 1981, *Goldblatt 6004* (MO); Sabies [Zabies], (–BC), 16

FIGURE 8.—*Lapeirousia exilis*, *Goldblatt 6004*. Scale bar: 10 mm. Artist: John Manning.

June 1898, *M. Schlechter 99* (BOL, GRA); 11 km north of Concordia, (–DB), 30 June 1935, *Salter 5540* (BM, BOL); north of Okiep, (–DB), *Barker 9170* (NBG), *Esterhuysen 32474* (BOL). **2918** (Gamoep): Goegap (Hester Malan) Nature Reserve, gravel pit along Pofadder road, (–CA), 1 July 1975, *Rosch & Le Roux 1160* (PRE); ± 28 km east of Springbok toward Pofadder, sandy plains, (–CA), 23 Aug. 1993 (fr.), *Goldblatt & Manning 9650* (MO, NBG). **3018** (Kamiesberg): Farm Klein Lieslap, ± 14 km southwest of Kliprand, exposed granite sheets, (–DA), 17 May 1993, *Snijman 1313* (NBG). **3019** (Loeriesfontein): Taaiboskloof, north slopes of Langberg, (–CA), 4 July 1970, *Oliver 9501* (NBG). **3119** (Calvinia): 17.6 km along Rondekop road off R27, Soetlandsfontein River, (–AD), 6 June 2005, *Manning 2948* (NBG); 10 July 2008, *Manning s.n.* (NBG).

WESTERN CAPE.—**3118** (Vanrhynsdorp): Knersvlakte, Farm Kalkgat, (–BB), 16 June 1987, *Boucher 5137* (NBG); 2 July 1998, *Orthen s.n.* (NBG).

7. **Lapeirousia angustifolia** *Schltr*. in Botanische Jahrbucher für Systematik 27: 105 (1900). Type: South Africa, [Western Cape], Zoutrivier, 15 July 1896, *Schlechter 8144* (B, holo.!; BOL!, BM!, COI!, F, G!, GRA!, K!, PH!, PRE!, iso.). [Schlechter's handwritten collection number has also been misread as 8149 or 8188]

Plants 30–140(–180) mm high, stem simple or sometimes 1 or 2 branched from base, slightly compressed. *Corm* bell-shaped, 7–10 mm diam.; tunics brown, surface lightly ridged, basal rim smooth or bluntly lobed. *Leaves* few, lowermost longest, linear, ascending, usually exceeding stem, to 100(–180) mm long, ribbed, cauline leaves broader and shorter than basal, ± bract-like. *Inflorescence* a 6–15-flowered spike, spiral in flower; outer bracts green, firm, 8–13 mm long, oblong to broadly ovate, channelled, obtuse (retuse when opened), apex deflexed in profile, margins hyaline; inner bracts ± ${}^{1}/_{2}$ as long, transparent with two green keels. *Flowers* zygomorphic, white to pale lilac or mauve, lower 3 tepals pale yellow at base and with violet median streak, tube pink on reverse, lower tepals each with small claw-like tooth in lower midline, with light sweet scent; *perianth tube* 13–15 mm long, slender below, ± abruptly curved and expanded in upper 5–6 mm; *tepals* unequal, dorsal erect or slightly arched over anthers, 7–9 × 4 mm, oblanceolate, upper lateral tepals outspread, lower 3 united basally for ± 2 mm, 7–9 mm long, directed downward 35–40°. *Stamens* unilateral, suberect; filaments 7–8 mm long, exserted 3.0–3.5 mm; anthers parallel, 2.5–3.0 mm long, lilac; pollen ± white. *Style* dividing opposite middle ${}^{1}/_{3}$ of anthers, style branches ± 2.5 mm long, forked for slightly > ${}^{1}/_{2}$ their length. *Capsules* obovoid-trigonous, 5–8 mm long, without locular ridges. *Seeds* globose, somewhat flattened to irregularly lobed at chalazal end, 1.0–1.2 mm diam., brown, smooth with outer epidermal walls lightly colliculate. *Chromosome number* unknown. *Flowering time*: early July to late August.

Distribution and biology: restricted to the Knersvlakte of southern Namaqualand (Figure 9), *Lapeirousia angustifolia* grows in sandy or light clay soils, sometimes in areas with a surface of quartz pebbles. Its appearance, size and exact flowering is very unpredictable from season to season in this area of low and unreliable rainfall. Pollination of the pale, faintly scented flowers is unknown but is likely to be by long-tongued bees. Records from central and northern Namaqualand (e.g. *Marloth 6730* PRE, Aug. 1925, Garies-Okiep), are evidently incorrect given the absence of any recent collections from this relatively well-botanised area.

Diagnosis and relationships: evidently first collected by the German botanist Rudolf

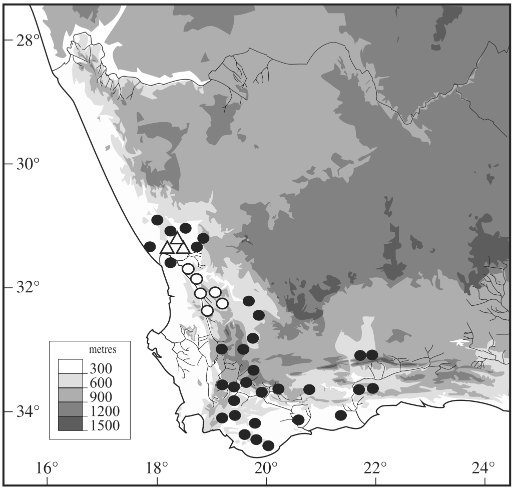


FIGURE 9.—Distribution of *Lapeirousia angustifolia*, Δ; *L. pyramidalis* subsp. *pyramidalis*, ●; *L. pyramidalis* subsp. *regalis*, ○.

Schlechter in 1896 and described by him in 1900, *Lapeirousia angustifolia* has been inextricably confused with the widespread and fairly common *L. pyramidalis*. These two species are alike in general appearance and share derived, obtuse floral bracts, and were treated as synonymous by Goldblatt (1972). Recent field work, including pollination biology, suggests that Schlechter was correct in regarding *L. angustifolia* as a separate species. The flowers, like those of *L. pyramidalis* subsp. *pyramidalis*, are white to pale lilac in colour and also pleasantly, if not as strongly sweet scented, but are readily distinguished by the shorter perianth tube, 13–15 mm long vs. 25–40 mm, the claw-like cusps on the lower tepals, and the small capsules lacking the wing-like locular ridges characteristic of *L. pyramidalis*. The small seeds, 0.9–1.3 mm diam., and slightly wrinkled with colliculate epidermal cells also differ from the slightly larger seeds of *L. pyramidalis* subsp. *pyramidalis*, 1.5–1.9 mm diam., which have derived, tuberculate epidermal cells (hedgehog-like under the microscope). The molecular phylogeny (Figure 1) confirms the very close relationship of the two taxa.

Until more is known about *Lapeirousia angustifolia*, it is more consistent to treat it as separate from *L. pyramidalis*, not merely a short-tubed local variant. Differences in capsule and seed morphology are significant in determining relationships in *Lapeirousia* and in the case of *L. angustifolia* and *L. pyramidalis* suggest that the two should be regarded as separate, closely allied species. This conclusion is supported by the co-occurrence of both taxa near Hol River north of Vredendal, without evidence of hybridisation or introgression between them.

Representative specimens

SOUTH AFRICA. WESTERN CAPE.—**3118** (Vanrhynsdorp): Knersvlakte, Quaggaskop reserve, (–BC), 27 Aug. 1991, *Goldblatt & Manning 9127* (MO, NBG); Knersvlakte, road to Quaggaskop from N7, (–BC), 25 Aug. 2008, *Goldblatt & Manning 13027* (MO, NBG); 7 miles [11.2 km] north of Vredendal, Farm Liebendal, (–CB), 22 July 1970, *Hall 3663* (NBG); 4 miles [6.4 km] north of Hol River Station, near Moedverloor, (–CB), 10 Aug, 1962, *Nordenstam 900* (NBG, S); 6 miles [9.6 km] north of Klawer, (–DA), 22 Aug. 1950, *Lewis 2347* (NBG, SAM); Farm Varschrivier, (–DA), 11 July 2001, *Boucher 6724* (NBG); north of Vredendal, deep red soil, (–DA), 3 Aug. 2007, *Van der Niet 451* (NBG); between Vanrhynsdorp and Vredendal, (–DA), 24 Aug. 2007, *Goldblatt, Manning & Porter 12859* (MO, NBG); near Olifants River, without date, *Drège 8508* (SAM); Farm Troe-troe, 3 km from Vanrhynsdorp on Nieuwoudtville road, (–DB), 3 Aug. 1977, *Le Roux 2010* (NBG); Vanrhynsdorp, Mauwerskop, (–DB), 2 July 1990, *Oliver 9450* (NBG).

8. **Lapeirousia pyramidalis** *(Lam.) Goldblatt* in Contributions from the Bolus Herbarium 4: 41 (1972). *Ixia pyramidalis* Lam.: 334 (1789). *Witsenia pyramidalis* (Lam.) Pers.: 42 (1805). Type: said to be from Isle de France [Mauritius], but certainly from western South Africa, said to be collected by *Commerson* but probably by *P. Sonnerat s.n.* (P-Herb. Jussieu, holo.!).

[See additional synonymy under subsp. *pyramidalis*.]

Plants (50–)80–140 mm high, stem simple or 1–few-branched from near base, slightly compressed. *Corm* bell-shaped, ± 10 mm diam.; tunics light red-brown, lightly ridged, basal margin entire or bluntly lobed. *Leaves* 4 or 5, lowermost much longer than others, up to 160 mm long, linear to lanceolate, 2–6 mm wide, strongly ribbed, upper leaves shorter and broader, becoming progressively bract-like above. *Inflorescences* 6–20-flowered spikes, initially 2-ranked, later becoming spiral; outer bracts green, firm, ± succulent, 10–20 mm long, channelled, ovate when flattened, obtuse in side view (deltoid and retuse when unfolded), apex deflexed in profile, margins hyaline; inner bracts $^1/_3$ to $^1/_2$ as long, transparent with 2 green keels. *Flowers* zygomorphic, either white to pale mauve, pale blue or pale pink, lower tepals each with a small triangular to diamond-shaped median mark in lower half (subsp. *pyramidalis*) or violet, purple or dark carmine, lower tepals each with white or cream markings near base and a central zone of darker pigment (subsp. *regalis*), either intensely sweet scented day and night (subsp. *pyramidalis*) or evidently scentless (subsp. *regalis*); perianth tube 25–55 mm long, slender, straight or widening slightly in upper 5 mm; tepals subequal, narrowly to broadly ovate, narrowed into claw-like base ± 1.5 mm long, lower tepals each occasionally with a small claw-like cusp near base, dorsal tepal 9–15 × 6–7 mm, erect, held apart from others, upper lateral tepals slightly reflexed, lower 3 tepals usually held closely together and at right angles to tube, 8 × 5 mm. *Stamens* unilateral, ±

erect to ascending; filaments 5–6 mm long, exserted ± 3.5 mm; anthers ± 3 mm long, usually pale yellow to white; pollen ± white. *Style* dividing between base and apex of anthers or slightly beyond; branches ± 2.5 mm long, forked for $^1/_2$ their length, often becoming tangled in anthers. *Capsules* obovoid, 8–10 mm long, with wing-like locular ridges in distal half. *Seeds* ± globose to ovoid, usually somewhat flattened at chalazal end, 1.3–1.5 × 1.4–1.9 mm, epidermal cells tuberculate. *Chromosome number* 2*n* = 18. *Flowering time*: July to September.

Distribution and biology: *Lapeirousia pyramidalis*, one of the more widespread species of *Lapeirousia*, extends from the southern edge of Namaqualand though dry areas of the northwestern Cape to the Little Karoo and southern Cape (Goldblatt 1972) (Figure 9). Over much of its range it has a fairly consistent appearance. Plants are compact with broadly obtuse floral bracts, and the flowers are white to pale blue or pale pink to lilac with a perianth tube 25–35 mm long, slightly curved and wider in the upper 5–7 mm, and always strongly scented, both during the day and in the evening. In the west of its range, in the Olifants and Biedouw River valleys, and at Karoo Poort to the south, plants segregated as subsp. *regalis* are distinguished by bright red, purple, or dark violet flowers with a long, nearly straight perianth tube, 35–55 mm long, and have no discernible odour. We considered the two sets of populations too similar to be treated as separate species (Goldblatt & Manning 1994). As far as we know, the two forms never grow sympatrically and their ranges are more or less complementary. They also favour different habitats: subsp. *pyramidalis* normally grows on shale and clay soils, but subsp. *regalis* has only been recorded on stony sandstone ground.

The floral differences between the two subspecies reflect a shift in pollination strategy (Goldblatt et al. 1995). Strongly scented subsp. *pyramidalis* is thought to be pollinated primarily by sphinx moths (*Hippotion celerio* is the only insect so far identified as a pollinator), which are most active at sunset and at night, whereas subsp. *regalis* is a member of the *Prosoeca peringueyi* pollination guild. This guild also includes *L. silenoides* (Goldblatt et al. 1995), which has flowers very like those of subsp. *regalis*, with a long, nearly straight tube, erect dorsal tepal, and darkly pigmented perianth with contrastingly pale nectar guides. Volume and quality of nectar produced by the two subspecies appears to reflect their different pollination systems: subsp. *pyramidalis* produces up to 3 ml of nectar of 30–34% sucrose equivalents whereas samples of subsp. *regalis* show that it produces up to 4.8 ml of nectar of approximately 28% sucrose equivalents.

Diagnosis and relationships: *Lapeirousia pyramidalis* can always be immediately recognised by the broadly ovate to deltoid bracts with obtuse to retuse apices. In profile the bracts do not taper to a point but curve outward and have blunt tips. The flowers have shortly clawed, subequal tepals with broadly oval to rounded limbs resembling the Namaqualand species, *L. silenoides* and we consider the two to be closely allied. Both also have unusual capsules with prominent ridges on the locules, a feature shared with the local Namaqualand endemic, *L. verecunda*, and also similar red-brown corms with a ridged or lobed basal margin. The tuberculate seeds of *L. pyramidalis* are unusual in *Lapeirousia*, in which most species of sect. *Chasmatocallis*, including those of *L. silenoides* and *L. verecunda*, have epidermal cells with evenly domed (colliculate) outer walls. The difference is often striking, making it possible to distinguish the seeds of *L. pyramidalis* immediately from other species of the genus. There is a marked size difference between the seeds of the two subspecies. Over much of its range subsp. *pyramidalis* has seeds 1.7–2.0 mm diam., but subsp. *regalis* has seeds ± $^1/_2$ this size, 1.0–1.2 mm diam.

Outgroup comparison with related species suggests that the darkly pigmented flowers of *L. pyramidalis* subsp. *regalis* are plesiomorphic. A shift to pollination by sphinx moths is presumably a specialisation in the species, and associated with the dilution and loss of perianth pigmentation and the development of intense, clove-dominated floral scent. This hypothetical scenario is supported by the molecular phylogeny (Figure 1).

History: *Lapeirousia pyramidalis* has a somewhat confused taxonomic history. The species was described by the French biologist, J.P.B. Lamarck (1789), based on a collection attributed to the botanist, Philibert Commerson (1725–1773), who is not known to have ever visited the Cape (Gunn & Codd 1981). More likely his colleague, Pierre Sonnerat, was responsible for the type collection. Sonnerat briefly visited the Cape on his journey to Mauritius, where he worked with Commerson, who had settled there. Plants cultivated in Vienna were described as *Gladiolus fissifolius* by N.J. Jacquin in 1792, and the fine illustration published shortly thereafter (Jacquin 1794) shows this clearly to be the same as Lamarck's species. Ker Gawler (1804) transferred *G. fissifolius* to *Lapeirousia* and the name remained in use for the species until 1972 when it became clear that *Ixia pyramidalis* was an earlier synonym, and that, in addition, *Gladiolus fissifolius* was nomenclaturally illegitimate, being superfluous for *G. anceps*, now *L. anceps*. The species was collected by C.P. Thunberg in the 1770s and later described by him as *G. bracteatus* (Thunberg 1800). *Lapeirousia fissifolia* was renamed *L. homoidea* F.W. Klatt in 1894, but the reason for his action is not clear.

Key to subspecies

1a Flowers whitish to pale blue (occasionally pale pink to mauve), strongly scented; perianth tube 25–40 mm long, cylindric below but expanded and curved outward in distal 5 mm . . . . 8a. subsp. *pyramidalis*
1b Flowers dark purple, violet-blue or red, not scented; perianth tube (35–)40–55 mm long, ± cylindric throughout . . . . 8b. subsp. *regalis*

8a. subsp. **pyramidalis**

Gladiolus fissifolius Jacq. in Collecteanea 4: 164 (1792) nom. illegit. superfl. pro *G. anceps* L.f. (= *Lapeirousia anceps* (L.f.) Ker Gawl.). *Lapeirousia fissifolia* Ker Gawl.: 238 (1804), as nom. nov. pro *G. fissifolius* Jacq. nom. illegit.; Baker: 92 (1896). *Ovieda fissifolia* (Ker Gawl.) Spreng.: 147 (1824). *Peyrousia fissifolia* (Ker Gawl.) Poir.: 364 (1826). *Meristostigma fissifolium* (Ker Gawl.) A.Dietr.: 595 (1833). *L. homoidea* Klatt: 191 (1895) as nom. nov. pro *Gladiolus fissifolius* Jacq., nom. illegit. Type: South Africa, without precise locality or collector, illustration in Jacq.: t. 268 (1794).

Gladiolus bracteatus Thunb.: 186 (1800). *Lapeirousia bracteata* (Thunb.) Ker Gawl.: sub. t. 1246 (1810). *Ovieda bracteata* (Thunb.) Spreng.: 147 (1824). *Peyrousia bracteata* (Thunb.) Sweet: 499 (1830a). *Meristostigma bracteatum* (Thunb.) A.Dietr.: 597 (1833). Type: South Africa, without precise locality, *Thunberg s.n.* (UPS-THUNB *1008*, holo.!).

Flowers whitish to pale bluish, or flushed with pale pink, lower tepals cream at base with small basal median streak of purple and larger median purple mark, intensely sweetly scented night and day; perianth tube 25–40 mm long, narrow and cylindric below, broadened and curving outward in upper 4–5 mm; tepals subequal, dorsal ± erect, 9–12 × 6–7 mm, upper laterals spreading to reflexed, lower 3 directed downward, with short claw ± 1.5 × 2.0 mm, limbs abruptly expanded, broadly oval, 7.5–8.0 × 6 mm. *Stamens* unilateral, ± erect; filaments 5–6 mm long, exserted ± 3.5 mm; anthers ± 3 mm long, cream or light purple; pollen yellowish to white. *Style* usually dividing shortly above anther bases, style branches becoming tangled in anthers. *Seeds* 1.5–1.9 mm diam. *Flowering time*: late July to September.

Distribution and biology: fairly widespread across the southern African winter rainfall zone, subsp. *pyramidalis* extends from Worcester and Grabouw in the southwest through the Little Karoo and the Overberg to Riversdale in the east and northward into the arid Tanqua Karoo, and dry sites along the interior Cederberg and Bokkeveld Mtns as far north as Loeriesfontein and Nuwerus (Figure 9). Populations in the Tanqua Karoo vary considerably in colour, from white to deep pink but even the darker forms are fragrant, with the perianth tube curved outwards at the end and thus represent the typical subspecies and not subsp. *regalis*. Plants are usually found on heavier soils and are mostly encountered on clays and shales of the Bokkeveld and Malmesbury Systems. Plants also occur in stony alluvial sand but rarely on the poor sandy soils of the Cape Sandstone formation. The closely related *L. angustifolia*, which has smaller flowers with a shorter perianth tube, 13–15 mm long, and faintly scented flowers, is restricted to dry flats of the Knersvlakte west and north of Vanrhynsdorp. Both species have been recorded near Hol River, north of Vredendal.

Representative specimens

SOUTH AFRICA. NORTHERN CAPE.—**3219** (Wuppertal): Stompiesfontein, Calvinia district, (–BA), 26 July 1941, *Compton 11150* (NBG), *Esterhuysen 5361* (BOL); Tankwa National Park, Volmoersfontein, (–BD), 20 July 2006, *Rösch 384* (NBG);

WESTERN CAPE.—**3117** (Lepelfontein): Koekenaap, coast between Olifants River and Brand-se-Baai, (–BD), Aug. 2002, *Desmet 3595* (NBG). **3118** (Vanrhynsdorp):

55.8 km north of Koekenaap on road to Kotzesrus above Sout River, (–AA), 16 Sept. 2001, *Goldblatt & Porter 11890* (MO, NBG); Nieuwerust [Nuwerus], (–AB), 7 Sept. 1945, *Barker 3731* (NBG); 7 km on Kliprand Road east of Nuwerus, (–AB), 9 Sept. 1976 [mainly fruiting], *Thompson 2840* (NBG); 2 miles [3 km] south of Nuwerus, (–AB), *Lewis 1385* (SAM); Hol River, (–AD), 18 Aug. 1970, *Hall 3731* (NBG); Kareeberg, southeast of Bitterfontein, (–BA), 15 Aug. 1997, *Desmet & Ellis 1226* (NBG); Olifants River, 20.8 km from National Road at Rooiberg turn-off, (–BC), 5 August 1977, *Le Roux 2118* (NBG); between Vanrhynsdorp and Pass, (–BD), *Barker 6439* (NBG). **3219** (Wuppertal): 4 km along road to Middelpos from Ceres/Calvinia road, Blaauwboschkolk, (–DA), 31 Aug. 1982, *Snijman 609* (NBG). **3319** (Worcester): Kluitjieskraal, Ceres road (–AC), Aug. 1888, *Tyson 1541* (G, K, SAM). **3319** (Worcester): Karoopoort, (–BA), 30 July 1950, *Hall 282* (NBG), 26 Aug. 1935, *Compton 5409* (BOL, NBG), 6 Aug. 2002, *Manning 2762A* (NBG);between Little and Great Doorn Rivers, (–BB), *Burchell 1213* (K); between Osplaats and Tunnel siding, Hex River Valley, (–BC), without date, *Rogers 16741* (G, K); Riverside, Worcester, 5 Sept. 1963 (-CA), *Walters 187, 590* (NBG); Brandvlei, (–CB), *Hutchinson 134* (K, PRE); Karoo Veldreservaat [Veld Reserve], 29 Aug. 1962, *Olivier 102* (NBG, PRE); Hex River Kloof, (–AD), *Drège s.n.* (K). **3320** (Montagu): near Ashton, (–CC), *Compton 11845* (NBG); 10 miles [15 km] from Montagu to Barrydale, (–CD), *Hurling & Neil s.n.* (BOL 30715); Warmwaterberg, (–DD), 11 July 1948, *Compton 20517* (NBG). **3321** (Ladismith): between Bosluiskloof and Prince Albert (–BC), *Lewis 4435* (SAM). **3322** (Oudtshoorn): near Prince Albert, (–AA), *Krige s.n.* (BOL 10631); Great Doorn River (–CA), *Thorne s.n. SAM51700* (SAM); Moeras River bridge, Robinson Pass road, (–CC), *Van Niekerk 463* (BOL). **3419** (Caledon): roadside near Grabouw, (–AA), *Garside 4496* (K); 8 miles [± 12 km] north of Bot River, *Goldblatt 298* (BOL); Caledon–Villiersdorp road intersection, (–AB), *Barker 26* (BOL), between Houw Hoek and Caledon, (–AB), Oct. 1887, *MacOwan 805* (BOL, G, GRA, K); Appelkraal, Riviersonderend, (–BB), *Zeyher 4025* (G, K, SAM); Fairfield (–BD), *Acocks 15498* (PRE); Napier, *Barker 2510* (BOL, NBG); *Bond 477* (NBG). **3420** (Bredasdorp): Bontebok Park, (–AB), *Acocks 22568* (PRE); Bredasdorp (–CA), *Metelerkamp s.n.* (*NBG6182, 6183*). **3421** (Riversdale): Riversdale, (–AA), *Muir 181* (BOL).

8b. subsp. **regalis** *Goldblatt & J.C.Manning* in Novon 4: 342 (1994). Type: South Africa, [Western Cape], Middelplaas, ± 5 km from Farm Biedouw on road to Wuppertal, 8 July 1941, *Leipoldt 3866* (BOL, holo.!; BOL!, NBG!, iso.).

Flowers red, purple, violet or navy blue, lower tepals with cream markings on claws and darker blue or red markings in centre of limbs, unscented; perianth tube 40–50(–55) mm long, cylindric and ± straight; tepals subequal, 10–12 mm long, dorsal held apart from others when fully open. *Stamens* and *style* as in subsp. *pyramidalis*. *Capsules* oblong-trigonous, locules with prominent ridges, 7–9 mm long. *Seeds* 1.3–1.4 mm diam. *Flowering time*: late July to early September.

Distribution and biology: subspecies *regalis* is restricted to the northwestern corner of Western Cape and occurs in the middle Olifants River Valley between Citrusdal and Klawer, extending inland into the interior valleys of the Cederberg and Pakhuis Mtns (Figure 9). Plants typically grow on light sandy soils, in stony habitats. The flowers are adapted for pollination by the long-proboscid fly, *Prosoeca peringueyi* (Goldblatt et al. 1995; Manning & Goldblatt 1996). Typical of species with this pollination system, the deeply pigmented red to violet flowers have pale markings on the tepals and lack scent.

Representative specimens

SOUTH AFRICA. WESTERN CAPE.—**3118** (Vanrhynsdorp): Olifants River Barrage, (–DD), 22 July 1941, *Esterhuysen 5377* (NBG). **3218** (Clanwilliam): 9 miles [± 14 km] north of Clanwilliam, (–BB), 22 Aug. 1950, *Barker 6420* (NBG); between Nardouwskloof and Bulshoek, 12 Aug. 1976, *Goldblatt 3837* (MO); near Clanwilliam, Aug. 1945, *L. Bolus s.n. BOL23183* (BOL); Olifants River valley south of Clanwilliam, (–BD), *Martin s.n. BOL 30714* (BOL). **3219** (Wuppertal): top of Biedouw valley between Blinkvlei and the Doorn River, (–AB), 23 July 1961, *Lewis 5824* (NBG); 3 miles [4.8 km] from Biedouw on road to Wuppertal, (–AB), 8 July 1941, *Leipoldt 3866* (NBG); 15 km north of Citrusdal, (–CA), *Lewis 2350* (SAM).

B. Sect. *Sophronia* (Spp. 9–13)

B. Sect. **Sophronia** *(Licht. ex Roem. & Schult.) Goldblatt & J.C.Manning* in Annals of the Missouri Botanical Garden 77: 373 (1990). *Sophronia* Licht. ex Roem. & Schult.: 482 (1817). *Lapeirousia* subg. *Sophronia* (Licht. ex Roem. & Schult.) Baker: 482 (1892). Type: *S. caespitosa* Licht. ex Roem. & Schult. (= *Lapeirousia plicata* (Jacq.) Diels).

Corm bell-shaped; tunics with basal rim not produced into teeth or spines. *Stem* subterranean, internodes at ground level crowded. *Inflorescence* a head-like, congested spike. *Flowers* radially symmetric, with perianth tube ± cylindric, short to elongate; stamens symmetrically arranged. *Basic chromosome number x* = 8.

9. **Lapeirousia plicata** *(Jacq.) Diels* in Engler & Prantl, Die naturlichen Pflantzenfamilien ed. 2, 15a: 488 (1930); Goldblatt: 46 (1972). *Galaxia plicata* Jacq.: t. 292 (1795). *Ixia heterophylla* Willd.: 199 (1798), as a new name for *G. plicata* in *Ixia* (not *I. plicata* L.). *Meristostigma heterophyllum* (Willd.) A.Dietr.: 199 (1833). *L. heterophylla* (Willd.) R.C.Foster: 4 (1939). *L. fasciculata* Ker Gawl.: 238 (1804), superfluous name for *Galaxia plicata* Jacq. *Ovieda fasciculata* (Ker Gawl.) Spreng.: 147 (1824). *Peyrousia fasciculata* (Ker Gawl.) Sweet: 499 (1830a). Type: South Africa, without precise locality, illustration in Jacq.: t. 292 (1795) (original specimens, if any existed, believed destroyed). Epitype: South Africa, Western Cape, Matjiesfontein, gravel flats near village, flowers white, 18 July 1974, *Goldblatt 2115* (MO!, NBG!).

   [Additional synonymy under the subspecies.]

Plants small, acaulescent (stem entirely below ground), forming diffuse or compact cushions, seldom > 50 mm high. *Corm* bell-shaped, red-brown, rough-surfaced, basal rim slightly crenate. *Foliage leaves* up to 3, lowermost longest, usually exceeding inflorescence, up to 300 mm long, blades linear, suberect to strongly inclined, closely ribbed, margins of sheaths undulate or often crisped, remaining leaves broader than basal. *Inflorescence* congested, head-like, few- to several -flowered; bracts ovate at base, outer larger than inner, with apex often produced as ribbed leaf-like tip, margins usually crisped especially in basal half. *Flowers* actinomorphic, pale blue, ± white or pale yellow, with blue to violet spot at base of each tepal, scented of cloves or with light, sweet odour; perianth tube 12–30 mm long, ± cylindric, straight; tepals subequal, ± lanceolate, 7–9 mm long, acute, spreading or often slightly deflexed when fully open. *Stamens* symmetrically arranged around style; filaments exserted 1.5–2.0 mm, arching outward later in anthesis; anthers mostly 1.8–3.0 mm long, usually blue (or ± white), initially erect, later ± horizontal. *Style* dividing opposite base to middle of anthers, rarely below anther bases, style branches forked for $^1/_3$ to $^1/_2$ their length or undivided (subsp. *effurcata*). *Capsules* ovoid-oblong, 8–10 mm long. *Seeds* 6–9 per locule, ± globose, with reticulate to rugulose surface, dark brown, 1.0–1.5 mm diam. *Chromosome number* 2*n* = 16 (subsp. *plicata*). *Flowering time*: autumn, winter or spring, mostly June to mid-August, occasionally in May. Figure 10A.

Distribution and biology: widespread in southern Africa, *Lapeirousia plicata* extends from Vanrhynsdorp and Robertson in the southwest, through the Little and Great Karoo to Northern Cape, North West Province, Free State and into southern Namibia (Figure 11). Plants grow in fairly heavy clay soils, less often in light clay or sand, in fairly flat places, as well as on limestone or calcrete, usually where drainage is poor. Flowering is earliest in the north and east of its range, mainly in June but sometimes in May or July; in the west and south flowering usually begins in July lasting into August.

Diagnosis and relationships: smallest of the several acaulescent species of sect. *Sophronia*, the tufts of *Lapeirousia plicata* seldom reach 50 mm including the flowers. The perianth tube ranges from 12 to 20 mm long in southern and western populations to as much as 30 mm in the northeastern populations. A distinctive feature of *L. plicata* is orientation of the stamens, the filaments of which are initially erect but arch outward during anthesis so that the dehisced anthers come to lie in a ± horizontal position. The style typically divides opposite the base to middle of the anthers, but sometimes below the anther bases and rarely slightly beyond the anther tips.

Typification of *Lapeirousia plicata* has never been in doubt: the painting in Jacquin's *Icones plantarum rariorum* (Jacquin 1795), entitled *Galaxia plicata* represents the form of the species with white flowers and a style described as trifid. The type has until now been associated with the form of the species occurring in the western Karoo, as at Calvinia and nearby, but these often have blue flowers and almost always style branches divided for a third to half their length. The name can, however, be applied to white-flowered plants from the Matjiesfontein area of Western Cape, where the species is common and plants have style branches notched apically, the style thus seeming trifid. We designate an

FIGURE 10.—A, *Lapeirousia plicata* subsp. *plicata*, *Goldblatt 6066A*; B, *L. montana*, *Goldblatt & Manning 9672*. Scale bar: 10 mm. Artist: John Manning.

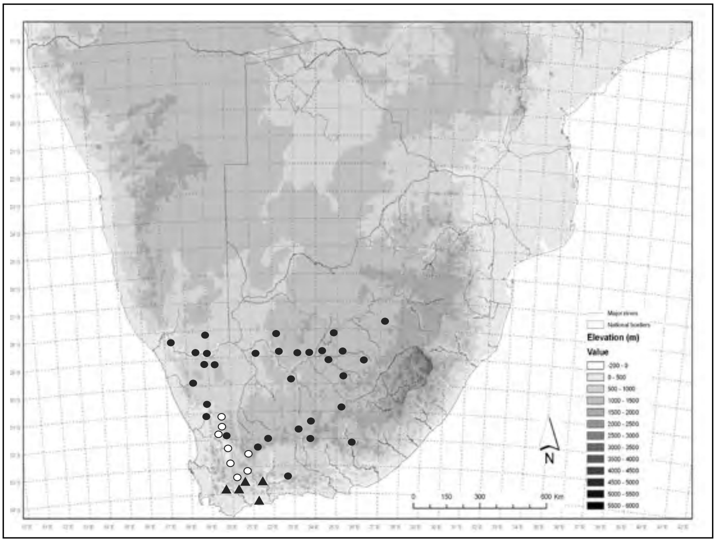


FIGURE 11.—Distribution of *Lapeirousia plicata* subsp. *effurcata*, ▲; subsp. *foliosa*, ●; subsp. *plicata*, ○.

epitype for *L. plicata* stabilising the application of the name, which otherwise might be associated with southern Cape plants, described by Lewis (1952) as *L. effurcata*, which always has white flowers but undivided style branches.

Three subspecies of *Lapeirousia plicata* were recognised by Goldblatt (1972), based on morphological differences and by a moderate degree of geographical discontinuity. One of these, subsp. *longifolia*, is a separate species here described as *L. kalahariensis*. We continue, however, to recognise the other two subspecies, subsp. *effurcata*, which has unusually broad, widely channelled outer floral bracts with undulate margins and consistently white flowers and undivided style branches, whereas subsp. *plicata* has blue or white flowers, with apically notched to deeply divided style branches and somewhat narrower floral bracts, sometimes with short, leafy, ribbed apices. A third series of populations from Bushmanland, the Great and Upper Karoo extending into Free State mostly have white or cream-coloured flowers (sometimes described as pale yellow) but rarely blue and the outer floral bracts have leaf-like, ribbed tips up to 30 mm long, sometimes unifacial towards the tips. These populations are also usually early blooming, often in flower in May and June. We suggest separation at subspecies rank as subsp. *foliosa* for this morph, noting that there are populations intermediate for these features. This subspecies has also been described at species rank as *L. galaxioides* by J.G. Baker (1892), a name that he applied to plants from the Kimberley area, now in Northern Cape.

Key to subspecies

1a Outer floral bracts channelled to apices or with short, ribbed, leafy tips < 10 mm long; perianth tube mostly 12–22 mm long; flowers blue or white with blue to violet mark in lower midline of tepals:
  2a Style branches usually forked for ${}^{1}/_{3}$–${}^{1}/_{2}$ their length, rarely undivided; flowers blue or white . . . . 9a. subsp. *plicata*
  2a Style branches always undivided; flowers white, flushed blue outside 9b. subsp. *effurcata*
1b Outer floral bracts with ribbed, leafy tips up to 30 mm long; perianth tube mostly 19–30 mm long; flowers white to cream (pale yellow), occasionally with a blue to purple spot near tepal bases . . . . 9c. subsp. *foliosa*

9a. subsp. **plicata**

Leaves usually 2 or 3, only lowermost with unifacial blade, ± linear, to 150 × 2–3 mm, suberect, ribbed, usually ciliate or papillate on rib edges, margins plane or undulate, ciliolate. *Bracts* green, outer usually falcate, channelled throughout or with short, ribbed leafy apex up to 10 mm long, margins undulate to slightly crisped, usually ciliate. *Flowers* either blue with white zone at tepal bases and violet or purple triangular mark at distal edge of white zone or white with violet mark near tepal bases; perianth tube mostly 12–22 mm long; tepals 7–8 mm long, spreading or slightly reflexed. *Stamens*: filaments exserted ± 2 mm, diverging; anthers 1.8–3.0 mm long, blue to purple. *Style* dividing below to opposite base (rarely opposite middle) of anthers, style branches usually forked for $^1/_2$ to $^1/_3$ their length or shortly notched at apex, 1.0–1.5 mm long, recurving. *Flowering time*: mainly July and early August. Figure 10A.

Distribution: restricted to the southern African winter rainfall zone, subsp. *plicata* occurs in the Western Karoo from Calvinia and the Bokkeveld Plateau south through the Tanqua Basin to Touws River, Matjiesfontein and Laingsburg where it meets the range of subsp. *foliosa* in the western Little Karoo (Figure 11). Flowers have been reported as pollinated by honey bees (*Apis mellifera*) while foraging for nectar (Goldblatt et al. 1995) in the Calvinia area.

Sophronia (= *Lapeirousia*) *caespitosa* is generally regarded as a synonym of *L. plicata* (Goldblatt 1972), but its typification is problematic. The type, evidently at one time at the Berlin Herbarium, is no longer extant, and we follow the interpretation of the species of past authors, treating it as a synonym of the Jacquin plant (although sometimes under the illegitimate, superfluous names *L. heterophylla* or *L. fasciculata*). Literal reading of the protologue is, however, a source of confusion. Flower colour is described as yellow (*flava*) and the divided style branches (an important consideration) are not mentioned. Nevertheless, the number of stamens (three) leaves no doubt that this is a species of Iridaceae and the radially symmetric flowers and acaulescent (caespitose) habit are consistent with *L. plicata*. Plants of *L. plicata* from near the type locality, Sakrivierspoort, which is southeast of Fraserburg, and near Fraserburg itself, have cream-coloured flowers and otherwise match *L. plicata* vegetatively, thus are reasonably consistent with the current interpretation of the name. We have chosen a neotype for the taxon, one from close to the type locality. It is now subsp. *foliosa* of *L. plicata*.

Representative specimens

SOUTH AFRICA. NORTHERN CAPE.—**3119** (Calvinia): Calvinia, Akkerdam, (–BA), *Lewis 5714* (NBG), 24 July 1981, *Goldblatt 6066A* (MO); Calvinia to Nieuwoudtville, (–BC), *Goldblatt 3892* (MO, NBG); Volstruisvlakte, (–DC), 26 July, *Bond 1169* (NBG). **3220** (Sutherland): Komsberg Nature Reserve, 1 419 m, (–DB), 4 Aug. 2008, *Rosch 175* (NBG).

WESTERN CAPE.—**3320** (Montagu): foot of the Voetpadsberg, 21.5 km east of Touws River, (–AC), *Goldblatt 11411* (MO); Matjiesfontein, gravel flats, (–BA), 26 July 2001, *Burgoyne 8215B* (PRE).

9b. subsp. **effurcata** *(G.J.Lewis) Goldblatt* in Annals of the Bolus Herbarium 4: 51 (1972). *Lapeirousia effurcata* G.J.Lewis: 7 (1952). Type: South Africa, [Western Cape], near Riversdale, Elands Drift, limestone koppies, Aug. 1946, *Ferguson s.n.* (BOL 24923!, SAM!, syn.).

Plants with foliage leaves usually 2 or 3, only lowermost unifacial, ± linear, to 150 × 2–3 mm, suberect to spreading, margins plane. *Bracts* green, outer much exceeding flowers, channelled throughout, margins undulate to slightly crisped. *Flowers* usually white (rarely pale blue) with blue mark in lower midline of tepals; perianth tube mostly 12–20 mm long; tepals ± 7 × 2–3 mm, ± spreading. *Stamens*: filaments exserted ± 3 mm, arching outward; anthers ± 2 mm long, blue. *Style* dividing slightly below to opposite base of anthers, style branches entire, recurved, ± 1 mm long. *Flowering time*: mainly July and August.

Distribution: subsp. *effurcata* occurs on stony flats in the Worcester–Robertson Karoo, the western Little Karoo and locally in the limestone belt of the southern Cape near Riversdale (Figure 11). The Riversdale populations, including the type collection, are from limestone outcrops, a habitat unusual for any species of *Lapeirousia*, but other collections are from stony, sandy or clay ground.

A curious feature of subsp. *effurcata* is that the flowers are reported to be heavily scented toward evening. Flowers of subsp. *plicata* have a light, sweet scent during the day, but we have not noted an increase in scent toward evening.

Representative specimens

SOUTH AFRICA. WESTERN CAPE.—**3319** (Worcester): 10 miles [15 km] west of Worcester to Robertson, (–DA), *Barker 8256* (NBG). **3320** (Montagu): Anysberg Nature Reserve, near Vrede homestead, sandy flats, (–BC), 12 Aug. 1993, *Germishuizen 6732* (PRE); 6 miles [9 km] east of Montagu, (–CC), *Barnard s.n.* (BOL); Montagu Baths (heavily scented toward evening), (–CC) Aug. 1918 & 1920, *Page s.n.* (BOL); Kalkoensnes, Montagu, (–CC), 9 July, *Schonken 263* (NBG). **3321** (Ladismith): Seweweekspoort, southern end, (–AD), *Levyns 7442a* (BOL); Seweweekspoort, middle of pass, (–AD), *Levyns 7442b* (BOL). **3421** (Riversdale): 18 km south of Riversdale, limestone flats at turnoff to Watergat, (–AA), 3 Aug. 1976, *Goldblatt 3744* (MO).

9c. subsp. **foliosa** *Goldblatt & Manning*, subsp. nov.

TYPE.—South Africa, Northern Cape, 3019 (Calvinia): Loeriesfontein Dist., between Graafwater and Donkiedam, (–CC), 4 July 1990, *Oliver 9484* (NBG, holo.).

> *Sophronia caespitosa* Licht. ex Roem. & Schult.: 482 (1817). *Lapeirousia caespitosa* (Licht. ex Roem. & Schult.) Baker: 174 (1892). Type: South Africa, [Northern Cape], Sakrivierspoort, *Lichtenstein s.n.* (probably originally at B, no longer extant). Neotype: South Africa, Northern Cape, 10 km northeast of Fraserburg on Loxton Road, 5 July 2000, *Manning* et al. *2260* (NBG, holo).
>
> *Lapeirousia galaxioides* Baker: 174 (1892). Type: South Africa, [Northern Cape], diamond fields at Klipdrift, without date, *Bowker s.n.* (K, holo!).

Plants often larger in vegetative features than subsp. *plicata*, with foliage leaves 2 or 3, lowermost longest, 150–350 × 2–3 mm, suberect, ribbed, smooth or ciliate to papillate on rib edges, margins usually plane, often ciliate. *Outer bracts* upright below, tapering distally to leaf-like, channelled or unifacial tip mostly 15–30 mm long, linear, straight or falcate. *Flowers* white to cream-coloured (pale yellow), occasionally pale blue, tepals often with purple spot in lower midline, often (?always) scented of cloves; perianth tube mostly 19–30 mm long, well exserted from sheathing part of bracts; tepals 7–9 mm long. *Stamens*: filaments exserted ± 2 mm; anthers 2–3 mm long, blue (often fading white in herbarium specimens). *Style* dividing opposite base to apex of anthers (rarely exceeding anthers); style branches 1.2–2.0 mm long, usually deeply forked. *Flowering time*: mainly May and June.

Distribution: widespread across arid parts of southern Africa, subsp. *foliosa* extends from the Knersvlakte of southern Namaqualand in Western Cape, along the eastern margins of Namaqualand north to southern Namibia and east across Bushmanland to Gordonia, the Kimberley District, western Free State, the Upper Karoo as far east as Colesberg and Murraysburg and with records in Eastern Cape near Cradock (Figure 11).

Diagnosis: subsp. *foliosa* is recognised by the floral bracts with leaf-like, ribbed, unifacial tips at least 12 and up to 40 mm long, versus floral bracts usually channelled to the tips or with short, unifacial tips up to 10 mm long. The distinction is not absolute, hence our rank of subspecies for the plant. Flowers are usually white to cream-coloured, occasionally pale yellow and are strongly clove scented according to notes with several collections. The flowers are sometimes larger than those of subsp. *effurcata* and subsp. *plicata*, with a perianth tube 19–30 mm long.

We include plants from the Roggeveld escarpment in subsp. *foliosa*, evidently the only blue-flowered populations of the subspecies, on account of the floral bracts with leafy tips up to 20 mm long.

Representative specimens

NAMIBIA.—**2818** (Warmbad): Warmbad, Farm Vrede, quartzite hill ‘white, blue anthers fading to white’, (–BD), 16 June 2005, *Bartsch* et al. *1910* (K); Farm Graswater, Warmbad, (–BD), 17 May 1963, *Giess*, *Volk & Bleissner 7041* (WIND); Farm Sperlingsspütz, granietgrobsandfläche, (–CA), 26 May 1972, *Giess & Müller 12275A* (WIND); Farm Eendoorn, in river sand, (–DB), 26 May 1972, *Giess & Müller 12275B* (WIND).

SOUTH AFRICA. EASTERN CAPE.—**3225** (Somerset East): Cradock District, (–BB), May 1904, *Rogers s.n.* (*BOL10551*, MO).

FREE STATE.—**2727** (Kroonstad): Kroonstad, (–CA), *Pont 260* (PRE). **2825** (Boshof): Smitskraal, Boshof, fragrant, (–CA), June 1911, *Burtt Davy 10309* (BOL). **2925** (Jagersfontein): Fauresmith, (–CB), *Henrici 2654* (PRE). **2926** (Bloemfontein): near Bloemfontein, (–AA), *Eyre s.n.* (BOL, MO), *Potts s.n.* (*BOL30761*).

NORTHERN CAPE.—**2817** (Vioolsdrif): Richtersveld, base of Tatasberg, (–AC), *Williams 3543* (NBG). **2820** (Kakamas): ± 20 km west of Augrabies, road to Onseepkans via Nous Wes, scented of cloves, (–CA), 23 June 1999, *Meyer 2117* (PRE). **2821** (Upington): near Upington, (–AC), *Glover 10445* (BOL). **2822** (Glen Lyon): Griekwastad, Farm Elim, banks of spruit above waterfall, (–AA), May 1942, *Cooke 6582A* (KMG); Hay District, Farm Highlands, gravel and sandy ridges, (–AA), May 1942, *Cooke 6582B* (KMG Hay District, Bingap, Van Sittart Mtns, (–CD), 18 June 1938, *Acocks s.n.* (BOL 30737, K). **2823** (Griekwastad): Griquatown, 1 000 m, (–CC), June 1895, *Marloth 2103* (NBG, PRE); dolomite slope, Brakpan near Campbell, (–DB), 5 June 1936, *Acocks 414* (PRE). **2824** (Kimberley): Warrenton, (–BB), *Adams 151* (GRA); Kimberley, (–DB), *Wilman s.n.* (NBG). **2918** (Gamoep): Haramoep near Pofadder, (–BA), *Mauve 4143* (PRE); ± 27 km east of Springbok, sandy plains, (–CA), 2 Aug. 1994, *Goldblatt & Manning 9896* (MO, NBG). **2919** (Pofadder): 30 miles [± 47 km] west of Pofadder, (–AC), 25 May 1961, *Schlieben 8989* (B, BOL, MO, PRE). **2922** (Prieska): Prieska, (–DA), *Bryant 313* (BOL, PRE). **2924** (Hopetown): Modder River, Kimberley, (–BA), *Galpin s.n.* (*BOL30724*). **3018** (Kamiesberg): ± 10 km north of Kliprand, red sand flats, (–DA), 13 Sept. 1993 (fr.), *Goldblatt & Manning 9730* (MO, NBG). **3025** (Colesberg): Colesberg, (–CA), *Shaw s.n.* (K). **3119** (Calvinia): Roggeveld Escarpment, Top of Perdekloof west of Middelpos, (–DD). 3 Aug. 1998, *Goldblatt & Manning 10945* (MO). **3221** (Merweville): between Great Reed River and Stinkfontein, (–AC), *Burchell 1394* (G, K, P). **3122** (Loxton): 36.5 km northeast of Loxton, (–BC), 5 July 2000, *Manning 2266* (NBG); **3124** (Richmond): Vlakplaats [Vlakplaas], Richmond Dist. (–CB), *H. Bolus 3827* (BOL).

WESTERN CAPE.—**3118** (Vanrhynsdorp): Knersvlakte, Douse-the-Glim, (–BB), *Oliver 9497* (NBG); Vars River [Knersvlakte], (–BC), 12 July 1896, *Schlechter 8149* (BOL, GRA, K, MO). **3123** (Victoria West): between Middelkop and Murraysburg, (–DC), June 1879, *Tyson 276* (BOL, GRA, MO, SAM). **3322** (Oudtshoorn): Swartberg near Klaarstroom, (–BC), *Drège 2188* (K, MO, SAM).

10. **Lapeirousia oreogena** *Schltr. ex Goldblatt* in Contributions from the Bolus Herbarium 4: 53 (1972); t. 1670 (1973). Type: South Africa, [Northern Cape], 6 km east of Nieuwoudtville, 14 Sept. 1970, *Goldblatt 541* (BOL, holo.!; K!, MO!, PRE!, iso.).

Plants forming dense tufts at ground level, 50–100 mm high including flowers, stem subterranean, upper internodes contracted. *Corm* bell-shaped, ± 10 mm diam.; tunics light brown, surface lightly rugose. *Foliage leaves* usually solitary, linear, straight, ribbed, 120–200 mm long. *Inflorescence* several- to many-flowered, congested in head-like tuft; outer bracts 30–60 mm long, bifacial and channelled throughout, usually ± falcate, often twisted, margins undulate and crisped, inner up to $^1/_2$ as long, margins often plane. *Flowers* actinomorphic, salverform, dark blue-violet, almost black in centre with white triangular to arrowhead markings close to tepal bases; perianth tube erect, cylindric, 50–60 mm long; tepals subequal, 12–14 mm long, lanceolate, acute, spreading but becoming slightly deflexed with age. *Stamens* symmetrically disposed around style, erect; filaments exserted ± 3 mm; anthers erect, contiguous around style, ± 3.5 mm long. *Style* erect, usually dividing opposite middle $^1/_3$ of anthers, style branches ± 2.5 mm long, deeply forked and recurved. *Capsules* ovoid to oblong, 7–10 mm long, without locular ridges. *Seeds* globose, ± 2 mm diam., red-brown, reticulately sculptured. *Chromosome number* $2n = 16$. *Flowering time*: August to mid-September, rarely late July.

Distribution and biology: restricted to the Calvinia District of Northern Cape, *Lapeirousia oreogena* is common and well known from the rocky, dolerite hills just to the north of Nieuwoudtville, but it extends south at least as far as the Farm Matjesfontein, ± 12 km from Nieuwoudtville, and has also been recorded southeast of Calvinia at Driefontein-se-Berg and northeast of the town in the Agterhantam (Figure 12). Plants typically grow in heavy red, dolerite-derived clay soil, either in open ground or among rocks in shallow soil, but we have also seen plants on stony tillite ground. *L. oreogena* flowers fairly early in the season before the plants are overshadowed by annuals and taller geophytes that reach maturity some weeks later. Although plants are invariably autogamous when grown in the greenhouse, they produce ample nectar and are regularly pollinated by long-proboscid flies of the genus *Prosoeca*. Presumably *L. oreogena* is outcrossed when pollinators are available, but in seasons when pollinators are scarce (or emerge late), self-pollination ensures seed production. This pattern of facultative outcrossing occurs in other nemestrinid-pollinated species of *Lapeirousia*, including *L. jacquinii* and *L. violacea*.

Although *Lapeirousia oreogena* has a very restricted distribution, and on a world scale must be considered a rare species, its survival seems assured by its rocky habitat, unlikely ever to be placed under the plough, and also because parts of its range falls within the Nieuwoudtville Nature Reserve, where it is locally common.

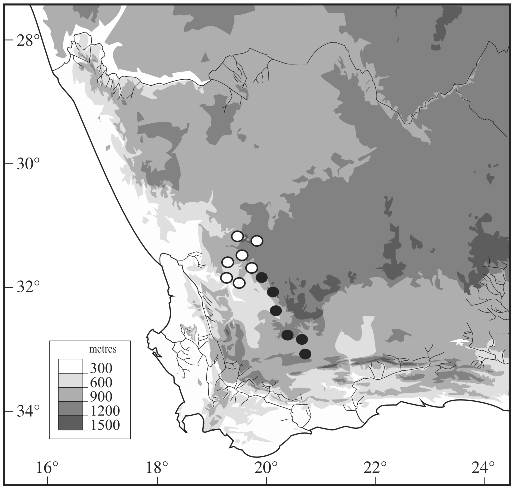


FIGURE 12.—Distribution of *Lapeirousia montana*, ●; *L. oreogena*, ○.

Diagnosis and relationships: the acaulescent *Lapeirousia oreogena* is distinguished from its allies of similar habit by its large dark blue to violet flowers with slightly reflexed tepals and a perianth tube 50–60 mm long. The tepals are almost black at the base with striking white, triangular to arrowhead-shaped marks. The centrally placed, purple anthers form a ring around the style and have dark purple pollen. Like some other acaulescent members of sect. *Sophronia* the leafy outer bracts extend well above the flower buds and have wavy to crisped margins.

The earliest known collection of *Lapeirousia oreogena* was made by Rudolf Schlechter on a visit to the Bokkeveld Plateau in August 1897. Despite its distinctive appearance the species was not formally described until 1972 when Goldblatt revised *Lapeirousia* for the winter rainfall area of southern Africa. Schlechter's collection was widely distributed under the manuscript name *L. oreogena*, the name eventually adopted for the species.

Selected specimens

SOUTH AFRICA. NORTHERN CAPE.—**3119** (Calvinia): Oorlogskloof, hills north of village, (–AC), 27 July 1962, *Nordenstam 742* (MO, S); hill slopes, Nieuwoudtville, (–AC), Sept. 1899, *Leipoldt 827* (BOL, K, SAM); Klipkoppies, Nieuwoudtville, (–AC), *Lewis 5858* (SAM); Wildflower Reserve, Nieuwoudtville, (–AC), Oct. 1983 (fr.), *Snijman s.n.* (MO, NBG); Farm Oorlogskloof south of Nieuwoudtville, (–AC), 10 Aug. 1983, *Van Wyk 1404* (PRE); Matjesfontein hills, (–AD), 20 Aug. 1897, *Schlechter 10924* (B, BM, BOL, COI, E, G, GRA, K, PH, PRE); Agterhantam, 31.5 km from Calvinia to Klipwerf, dolerite clay flats, (–BB), 1 Sept. 2006, *Goldblatt & Porter 12749* (MO); Farm Kareeboomfontein, Calvinia, (–DA), 5 September 1974, *Hanekom 2392* (PRE); southwestern slopes of Driefontein-se-Berg, red clay among dolerite rocks, (–DA), 25 Sept. 2009 (fr.), *Goldblatt, Manning & Porter 13416* (MO, NBG).

11. **Lapeirousia montana** *Klatt* in Abhandlungen der naturforschenden Geselschaft zu Halle 15: 359 (Ergänzungen: 25) (1882). Baker: 93 (1896). Goldblatt: 52 (1972). Type: South Africa, [Northern Cape], without precise locality, as 'Hantams Gebirge,' 1869, *Meyer 10* (B, holo.!).

Plants acaulescent, branched at base, forming compact tufts at ground level, 30–50 mm high including flowers, stem underground. *Corm* bell-shaped, 8–10 mm diam.; tunics light brown, basal rim crenate. *Leaves* 1 or 2, lowermost always longest, linear, 80–180 mm × 2–3 mm, straight or falcate, remaining foliage actually floral bracts, but often resembling leaves and identifiable as bracts only by position. *Inflorescence* of several to many flowers in congested head-like structure borne at ground level, internodes very short but evident on dissection or in fruit; bracts leaf-like, wide and pale below for 15–25 mm, tapering to a green unifacial upper half, resembling leaf blade and 15–40 mm long. *Flowers* actinomorphic, white to pale blue, then with lower third of tepals white, usually with dark blue triangular or diamond-shaped median mark near base, slightly scented of narcissus, lily or carnation; perianth tube cylindric, (25–)32–45(–55) mm long, with filaments decurrent as intrusive ridges dividing tube into 3 compartments and ± blocking tube in lower half; tepals subequal, lanceolate, (10–)12–15 × 4–5 mm, spreading horizontally or deflexed up to 30° below horizontal. *Stamens* symmetrically disposed around style; filaments exserted 2–3 mm from tube; anthers erect, 3–4 mm long, ± white, pollen white to ivory. *Ovary* oblong, 4–5 mm long; *style* straight and erect, usually dividing opposite middle to just below anther tips, style branches divided for $^{1}/_{2}$ their length, 1.8–2.5 mm long. *Capsules* ± ovoid, 8–10 mm long, showing outline of seeds.

Seeds globose, dark brown, ± 2 mm diam., with reticulate sculpturing, *Chromosome number* unknown. *Flowering time*: late August to late September. Figure 10B.

Distribution and biology: a relatively narrow endemic of the western Karoo, *Lapeirousia montana* is centred in the southern Roggeveld of Northern Cape, where it is known from the Roggeveld Escarpment south and west of Sutherland, at sites in the Klein Roggeveld and locally close to the escarpment west of Middelpos (Figure 12). The type is said to be from the Hantam Mtns ('Hantams Gebirge') where the collector, Heinrich Meyer, is known to have collected (Gunn & Codd 1981), but the species has not since been found there. While it would be useful to confirm the type locality we have no doubt Meyer's specimen represents the Roggeveld species. Plants grow in seasonally wet ground in relatively light clay or sandy soil in valley bottoms, around seasonal pools or in shallow soil over rocky pavement. Observations on its pollination indicate that *L. montana* is a generalist despite its long perianth tube. Nectar ascends well up into the tube and is accessible to settling moths, butterflies, bee flies (Bombyliidae) and bees (only *Apis*), all of which have been captured visiting the flowers and found to carry host pollen (Goldblatt et al. 1995). Floral scent is usually strong but unusually variable, sometimes reminiscent of narcissus, lily, carnation or even an unpleasant acrid odour.

Diagnosis and relationships: the acaulescent *Lapeirousia montana* is allied to the widespread *L. plicata*, which it replaces in the southern Roggeveld and is distinguished from that species by the larger flower with longer perianth tube, mostly 32–45 mm long, and tepals 10–15 mm long, always with ± straight margins. The anthers are ± white and 3–4 mm long. *L. plicata* which has smaller flowers with a perianth tube 12–30 mm long, tepals 7–9 mm with undulate margins and anthers usually blue anthers and mostly 1.8–3.0 mm long. The upper leaves and floral bracts are typically crisped in *L. plicata* versus the straight margins of the upper leaves and bracts in *L. montana*.

Representative specimens

SOUTH AFRICA. NORTHERN CAPE.—**3119** (Calvinia) 56 km south of Calvinia on the Blomfontein road to Middelpos, rock sheets, (–DD), *Goldblatt 5811* (MO). **3120** (Williston): Hartebeesfontein, west of Middelpos, (–CC), 5 Sept. 1986, *Oliver 8930* (NBG); entrance to Farm Onderplaas, north of Middelpos, (–CC), 16 Sept. 1999, *Steiner 3379* (NBG). **3220** (Sutherland): top of Gannaga Pass on track to Watervlei, (–AA), 16 Aug. 2007, *Helme 4695* (NBG); Quaggasfontein, Roggeveld, rock outcrop, (–AB), 23 Sept. 1981, *Goldblatt 6352* (MO, NBG, PRE); Ouberg Pass, (–AD), *Helme 4695* (NBG); Roggeveld Escarpment at Farm Blesfontein, (–AD), 24 Sept. 2011, *Goldblatt & Manning 13667* (MO, NBG); Oliviersberg, Farm Tonteldoosfontein, (–DA), 23 Sept. 2007, *Clark & Kelly 182* (NBG); Roggeveld, north of top of Komsberg Pass, 5,269 ft [1 606 m], (–DB), *Goldblatt & Porter 13083* (MO, NBG); 12.5 miles [± 20 km] south-southwest of foot of Komsberg Pass, (–DC), *Acocks 18540* (BOL, PRE); 57 km south of Sutherland, below Komsberg Pass, valley bottom, (–DC), 31 Aug. 1993, *Goldblatt & Manning 9672* (MO, NBG); 1 Oct. 1993 (fr.), *Goldblatt & Manning 9672C* (MO).

12. **Lapeirousia kalahariensis** *Goldblatt & J.C.Manning*, new rank and name for *L. plicata* subsp. *longifolia* Goldblatt in Contributions from the Bolus Herbarium 4: 50 (1972). Type: South Africa, [Northern Cape], Daniels Kuil, in sand, 22 Mar. 1939, *Esterhuysen 1157* (BOL, holo.!).

Plants ± acaulescent or shortly caulescent, 50–100 mm high excluding basal leaves, stem usually reaching 10–40 mm above ground, several-branched, branches crowded to form a compact, stalked rosette. *Corm* bell-shaped, brown, 10–12 mm diam., rough-surfaced, basal rim lightly crenate. *Foliage leaves* ± 5, usually lowermost longest, up to 200 mm long, linear, lightly ribbed, margins of sheathing portion ± straight, remaining leaves shorter than basal, becoming ± bract-like. *Inflorescence* congested, head-like, many-flowered; outer bracts ovate at base, tapering to apex, channelled throughout, often hooked at tips, 50–100 mm long, leaf-like distally, reaching or slightly exceeding flowers, margins undulate to slightly crisped; inner ± $^{1}/_{2}$ as long, transparent with 2 green keels. *Flowers* actinomorphic, evidently uniformly white to cream, ?probably sweetly scented; perianth tube (30–)33–40 mm long, slender, straight; tepals subequal, ± lanceolate, 10–14 × ± 3 mm, acute, held ± at right angles to tube. *Stamens* symmetrically disposed in a ring around style; filaments exserted ± 2 mm, arching outward after anthers split; anthers (3–)4 mm long, white. *Style* dividing opposite middle $^{1}/_{3}$ of anthers, style branches ± 2.3 mm long, recurved, forked for ± $^1/_2$ their length (undivided in *McLea s.n.*). *Capsules* obovoid, ± 5 mm long, concealed in leaf bases, papillate in upper $^1/_3$. *Seeds* probably globose (only immature seen), surface reticulate. *Chromosome number* unknown. *Flowering time*: March, probably also April.

Distribution and biology: with a relatively wide range across the southern edge of the Kalahari, *Lapeirousia kalahariensis* extends from Danielskuil and Kuruman west of Kimberley in Northern Cape, South Africa, to south-central Namibia (Figure 13). Most of the available collections do not describe the habitat except in the broadest terms, but one collection indicates that the species was rare on flats of compacted calcareous sand. Nothing is known about its biology but the relatively long-tubed and white flowers are consistent with pollination by moths.

Diagnosis and relationships: a member of the *Lapeirousia plicata* alliance (sect. *Sophronia*), *L. kalahariensis* was treated by Goldblatt (1972) as subsp. *longifolia* of *L. plicata*. We have examined more material and with a more thorough understanding of the genus, we are now convinced that this is a separate species, which we rename at species rank *L. kalahariensis*. Most significantly, the bracts are channelled throughout and not unifacial distally and, not noted previously, the stem is produced up to 40 mm above the ground. The flowers are recorded as being uniformly white, or in one collection yellowish, always lacking the blue or purple markings of *L. plicata*. The tepals, 10–14 mm long, and tube, 30–40 mm long, are somewhat longer than in *L. plicata*, which has tepals 7–10 mm long and a tube typically 12–20 mm long, rarely up to 35 mm. Significantly, *L. plicata* occurs within the range of *L. kalahariensis* but typically blooms there later in the year, in May and June, sometimes in July. *L. kalahariensis* also shows a resemblance to *L. odoratissima*, which occurs across southern tropical Africa, but that species has much larger flowers, the perianth tube 100–140 mm long, and a well-developed, strongly ribbed basal leaf.

Lapeirousia kalahariensis was first collected in 1875 by J.H. McLea at the vague locality 'Transvaal', presumably north of the Vaal River near Kimberley. Little appears to be known about his travels (Gunn & Codd 1981), but we assume the collection was made while en route from Kimberley to Graaff Reinet where he lived in his later years. When first described, the species was included in *L. plicata* as subsp. *longifolia*.

Representative specimens

NAMIBIA.—**2316** (Nauchas): Rehoboth, Farm Namibgrens, (–CA), 14 Mar. 1953, *Walter 1818* (B, WIND). **2616**

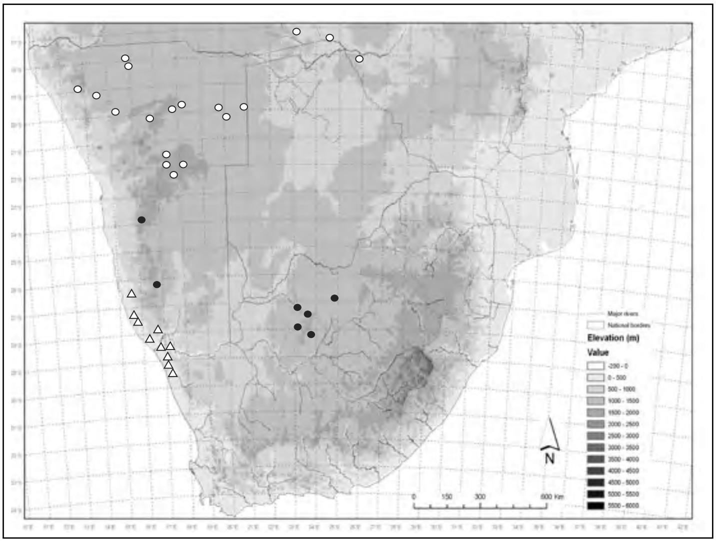


FIGURE 13.—Distribution of *Lapeirousia barklyi*, △; *L. kalahariensis*, ●; *L. odoratissima*, ○ in southern Africa.

(Aus): Luderitz District, Farm Gamochas, on sand, flowers yellowish, (–BA), 2 Apr. 1950, *Kinges 2500* (PRE); between Ausis and Khuias, sandy valley, (–BB), Mar. 1885, *Schenck 1914* (M).

SOUTH AFRICA. NORTH WEST.—**2624** (Vryburg): Vryburg, Armadillo Creek, (–DC), 27 Apr. 1912, *Burtt-Davy s.n.* (PRE 13714). **2723** (Kuruman): Batlharos, open veld, (–AC), Mar. 1921, *E. Silk 248* (K, KMG).

NORTHERN CAPE.—**2822** (Glenlyon): Hay District, Farm Bermolli, (–BD), Feb. 1922, *Wilman s.n.* (KMG 2636); Hay District, Black Ridge, (–DC), Mar. 1934, *Wilman s.n.* (GRA); 8 miles [12 km] west-northwest of west entrance to Farm Padkloof, (–CB), 5 Apr. 1960, *Leistner 1748* (KMG). **2823** (Griekwastad): Danielskuil, (–BA), 25 Mar. 1920, *Pole-Evans 77* (K); Asbestos Hills, Danielskuil, (–BA), 21 March 1939, *Lewis 389* (SAM 53479). Without precise locality: 'Transvaal', 1875, *McLea s.n.* (BOL 5970, K).

13. **Lapeirousia odoratissima** *Welw. ex Baker* in Transactions of the Linnean Society of London, Botany ser. 2, 1: 273 (1878); Sölch: 10 (1969); Geerinck et al.: 344 (1972); Goldblatt: 480 (1990a). Type: Angola, [Huila], sandy woods near Lopollo, *Welwitsch 1551* (BM, lecto.!, so annotated in unknown hand; B!, BM!, C!, G!, K!, iso.).

L. stenoloba Vaupel: 548 (1912). Type: Namibia, Omaheke, 1 300 m, in brown sand, 17 March 1911, *Seiner 329* (B, lecto.!, designated by Sölch on sheet).

L. congesta Rendle: 435 (1895); Baker: 354 (1897). Type: Tanzania, 'between Zanzibar and Uyui' [near Tabora], in 1866, *Taylor s.n.* (BM, holo.!).

L. juttae Dinter: 13 (1912). Type: not cited, unknown.

Plants 100–180(–250) mm high, with condensed aerial axis and then rosette-like, rarely stem partly aerial and up to 100 mm long, with expanded internodes, extending up to 80 mm below ground, rarely 5–10 mm long, simple or with several branches, each subtended by leaves or by leafy bracts. *Corm* bell-shaped, 15–20 mm diam.; tunics woody, brown, outer layers fragmenting irregularly, rarely becoming fibrous by decay. *Leaves* few, often only 2 (hardly distinguishable from the bracts except by position), linear, strongly ridged, lowermost inserted below ground, exceeding bracts and up to twice as long, to 300 × 3–5 mm. *Inflorescence* comprising 1 or more congested spikes, ± umbellate in appearance, flowers 3–6 per branch; *bracts* leafy, outer 60–150 mm long, lanceolate, lightly ridged, inner ± $^{1}/_{3}$ shorter than outer, ± membranous. *Flowers* actinomorphic, salver-shaped, white to ivory, usually strongly scented especially in evenings; perianth tube cylindric, 100–140 mm long; tepals narrowly lanceolate to ± ovate, often attenuate, (25–)5–40(–50) × 3–11 mm, extended horizontally or sometimes slightly drooping. *Stamens* symmetrically arranged in a ring around style; filaments ± 4 mm long, exserted for 1.5–2.0 mm; anthers 6–8 mm long, linear, white; pollen yellow. *Style* usually ultimately reaching to ± apex of anthers, sometimes shorter, style branches 3–4 mm long, forked for ± $^{1}/_{2}$ their length, diverging and recurved. *Capsules* obovoid-oblong, 15–18 mm long, concealed in leaf and bract bases. *Seeds* ± globose, 2.1–2.3 mm diam., with reticulo-rugose sculpturing. *Chromosome number* 2*n* = 16, 16 + 0–2B. *Flowering time*: December to March, occasionally in April. Figure 14.

Distribution and biology: distributed widely across south tropical Africa, *Lapeirousia odoratissima* is apparently common only in Namibia where it occurs most often in sandy flats in the central and northern half of the country. Collections from a number of scattered sites indicate a fairly wide range across south tropical Africa except along the east coast and near interior. It extends from southwestern Angola across Zambia and adjacent Shaba Province of Congo to central and northern Malawi, Zimbabwe, and in locally dry sites in western and central Tanzania (Figure 13). It probably also occurs in Botswana, although to date there are no records from there. Largely a plant of semiarid habitats, *L. odoratissima* also occurs in *Brachystegia* woodland and even in exposed places in montane sites such as the Nyika Plateau in Malawi and the Inyanga Highlands in Zimbabwe, as well as open grassland and *Acacia* savanna.

Little is known about its biology but the large, long-tubed, and usually intensely fragrant flowers are clearly adapted for pollination by hawk moths. Our observations on plants in Namibia indicate that flowers open towards sunset, then with creamy white tepals. By morning the perianth has turned ivory to buff and the tepals droop slightly below the horizontal and wilt by the end of the day. The flowers are most intensely fragrant when they first open and maintain their scent through the following day. Ample nectar is produced in the perianth tube: we measured up

FIGURE 14.—*Lapeirousia odoratissima*, *Goldblatt & Manning 8807*. Scale bar: 10 mm. Artist: John Manning.

to 25 μl in one flower and nectar sugar concentration ranged from 16–25% sucrose equivalents in our study population. Observations made by Jean Pawek in Malawi confirm our phenological studies: she recorded that buds open between 17:30 and 18:00 but have wilted at least by 10:00 the following day (earlier than we recorded in Namibia). Flowers lasting at most 24 hours are unusual in Crocoideae in which flowers usually last at least three days, even when pollinated. We only know of two comparable situations in the subfamily in the Namibian *Gladiolus diluvialis* Goldblatt & J.C.Manning, also evidently moth-pollinated (Manning et al. 2011), and in *Savannosiphon euryphyllus* (R.E. Gereau pers. comm. 2013).

The corms of *Lapeirousia odoratissima* are reported to be edible and to comprise part of the diet of the !Kung Bushmen of Namibia.

Diagnosis and relationships: the tufted or rosette-like growth habit combined with the large white flowers with an exceedingly long perianth tube, 100–140 mm long, set *Lapeirousia odoratissima* well apart in the genus. The other tufted to rosette-forming species of sect. *Sophronia* are all southern African and have smaller flowers, coloured pale blue to violet, or white to pale yellow. The chromosome number, $2n = 16$ ($x = 8$) in *L. odoratissima* and its reticulo-rugose seeds correspond with the southern African species of sect. *Sophronia*. *L. odoratissima* and *L. caudata* are the only tropical African species of the genus. The interior southern African *L. kalahariensis*, which has white flowers and a perianth tube 30–40 mm long, appears to provide a link between *L. odoratissima* and the smaller southern African members of sect. *Sophronia*. These seems no such link between the caulescent *L. caudata*, *L. littoralis* and *L. odoratissima*, although both *L. caudata* and *L. littoralis* have the same basic chromosome number of $x = 8$ and reticulate seed sculpturing, unlike other species of the genus, excepting of course sect. *Sophronia*.

History: *Lapeirousia odoratissima* was discovered by Friedrich Welwitsch in southern Angola in 1859. His collection was distributed widely under the manuscript name *Psilosiphon odoratissima* and formed the basis for J.G. Baker's (1878) *L. odoratissima*. A second early collection made by the Rev. W.E. Taylor in central Tanzania in 1886, was described as *L. congesta* by A.B. Rendle, who distinguished it from *L. odoratissima* on the basis of a more congested habit. Rendle described the plant as having a stem forming a dense sessile head above the first leaf. This is not strictly true although the internodes of the stem and inflorescence axis are shorter than in the type specimens of *L. odoratissima*, which have among the longest internodes found in the species. From the ample material now available it seems clear that the variation between the extremes represented by the two collections is continuous and there is no reason to consider them separate species.

Later collections from the then German South West Africa, made by Kurt Dinter and Franz Seiner, were described as *Lapeirousia stenoloba* by Vaupel (1912). He considered that these Namibian populations constituted a species related to but distinct from *L. odoratissima*, differing by a robust habit and particularly narrow and attenuate tepal apices. Many but not all Namibian specimens of *L. odoratissima* differ from those from tropical Africa in their branched stems and numerous flowers but intra-populational variation is considerable in this species and there are often few- or even unbranched plants in populations of more robust ones with several branches, thus the difference does not seem taxonomically significant.

Representative specimens

NAMIBIA. Kaokoveld.—**1813** (Ohopoho): Okakura, (–DA), 28 Feb. 1913, *Dinter 3322* (SAM). **1914** (Kamanjab): north of Otjovasandu in red sand, (–BA), 11 Mar. 1976, *Geiss & Loutit 14191* (WIND); Outjo.–Etosha National Park, Kaross, (–B), 9 Apr. 1974 (fr.), *Volk & Le Roux 807* (WIND); between Kaross and Kamanyab, (–BC), *Thorne s.n.* (SAM 313743). **1915** (Okaukuejo) 10 km west of Farm Uitzig, ca. 60 km east-northeast of Otjiwarongo, grassveld on red sandy loam, (–CB), 9 Feb. 1983, *Lavranos & Pehlemann 21059* (MO, WIND). Ovamboland.—**1715** (Ondangua): Ondonga, (–DD), *Barnard 196* (SAM). **1815** (Okahakana): Onolongo–Onambeke, (–BB), Apr. 1923, *Barnard 136* (SAM). Grootfontein.—**1916** (Gobaub): Farm Norabis 387, thornveld, (–DD), 18 Mar. 1988 (fr.), *Goldblatt & Manning 8824* (MO). **1917** (Tsumeb): Auros (Otavi), (–DA), 10 Feb. 1925, *Dinter 5599* (B, G, GH, PRE, SAM, Z). **1918** (Grootfontein): 30 miles [± 42 km] north of Gautscha Pan, (–CA), 10 Feb. 1958, *Story 6460* (PRE); Farm Oliewenhof, sandy flats, (–CB), 8 Mar. 1974 (fr.), *Merxmüller & Giess 30147* (M, WIND). Otjiwarongo.—**2017** (Waterberg): Otjiwarongo, Farm Okosongomingo, (–CA), 4 Mar. 1974, *Merxmüller & Giess 30023* (M, PRE, WAG, WIND). Okahandja.—**2116**

(Okahandja): Omatako View, red sand, (–BA), 4 Mar. 1974, *Woortman 256* (WIND). **2117** (Otjosondu): Okahandja District, Farm Hochveld, brown sandy loam, (–BD), 30 Apr. 1963 (fr.), *Giess et al. 6672* (WIND); Okahandja, (–DD), 22 Feb. 1928, *Bradfield 385* (PRE). Windhoek.—**2117** (Otjosondu): 35 km from Steinhausen to Windhoek on Kapps Farm road, (–DD), 15 Mar. 1988, *Goldblatt & Manning 8807* (MO). **2217** (Windhoek): Farm Bodenhausen, near river, (–BC), 7 Mar. 1959, *Seydel 1771* (M, WIND). Gobabis.—**1920** (Tsumkwe) Grootfontein distr., ± 3 miles ([4.6 km] south of Nama Pan, (–DC), *Story 6275* (M, PRE, WIND). **2020** (Kaukauveld): Kaukauveld, 56 miles north of Eiseb Omuramba towards Kano Vlei, (–AD), 13 Apr. 1967 (fr.), *Giess 9815* (WIND). **2118** (Steinhausen): 15 km from Steinhausen to Windhoek on Kapps Farm road, (–CC), 15 Mar. 1988 (fr.), *Goldblatt & Manning 8803* (MO).

[Exsiccatae for *Lapeirousia odoratissima* from tropical Africa are cited in Goldblatt (1990a)].

C. Sect. *Lapeirousia* (Spp. 14–27)

Corm obconic, ± triangular in outline; tunics with basal rim produced into teeth or long, usually spreading. *Stem* mostly aerial (sometimes ± subterranean in *L. arenicola*) and often branched, stems compressed with angles often crisped. *Inflorescence* a spike. *Flowers* bilaterally symmetric, lower tepals with nectar guides of contrasting colour; perianth tube ± cylindric or funnel-shaped, short to elongate; stamens unilateral. *Capsules* without auriculate lobes or locular ridges. *Seeds* smooth (scarcely wrinkled) with surface cells domed. *Basic chromosome number x* = 8.

14. **Lapeirousia barklyi** *Baker*, Handbook of the Irideae 171 (1892); Goldblatt: 68 (1972) [including *L. macrospatha* Baker]. Type: South Africa, Namaqualand, without precise locality, Sept. 1876, *Barkly s.n.* (K, lecto.!, designated here [not holo. as indicated by Goldblatt, 1972]).

Plants 70–150 mm high, usually branched, sometimes repeatedly, mainly from base; stem compressed and 2-angled to 2-winged, wings often lightly serrated, with cormlet at each of 2 underground nodes. *Corm* bell-shaped, usually 60–90 mm below ground, ± 8 mm diam.; tunics brown, fairly smooth, basal rim lightly serrated, teeth directed downward. *Leaves* 4–6 (or more), lowermost 1 or 2 longest and slightly to about twice as long as stem, linear, ascending to ± falcate, 1.5–2.0 mm wide, corrugately ribbed, upper leaves shorter than stem. *Inflorescences* 2–5-flowered spikes; outer bracts green, veins translucent, lanceolate and acute or acuminate, (10–)20–25 mm long, folded and angular along upper midline, often keeled near apex, margins broadly hyaline; inner bracts ± $^1/_2$ as long as outer, transparent with 2 green keels, forked and turning brown at apex. *Flowers* zygomorphic, light purple-pink to lilac, lower tepals with basal ridge or claw-like tooth near base, marked with median yellow streak edged distally in dark red to purple, odourless; perianth tube obliquely funnel-shaped, (15–)20–25 mm long (often shorter in dry years, or apparently shorter in herbarium material), narrowly cylindric below, abruptly expanded in upper 4–5 mm into wide cylindrical throat; tepals subequal, lanceolate, acute, upper 3 slightly larger, 24–27 × ± 6–7 mm, lower 3 united for 2–3 mm and thus slightly shorter, 18–22 × 5–6 mm, all weakly differentiated below into claws ± 8 mm long, claws forming wide cup, limbs spreading at right-angles to claws, when fully open held ± in one plane. *Stamens* unilateral, arcuate; filaments ± 10 mm long, exserted ± 5 mm from tube but included in cup formed by tepal claws; anthers 5–6 mm long, included in floral cup, shortly apiculate, usually ± white; pollen white. *Style* arching over stamens, dividing close to or 1–2 mm beyond anther tips; branches ± 5 mm long, divided for $^2/_3$ their length, spreading beyond anthers. *Capsules* oblong to ovoid, 8–10 mm long. *Seeds* 1.2–1.3 mm diam., round, smooth. *Chromosome number* $2n = 16$. *Flowering time*: usually mid-September to early October, occasionally in late August.

Distribution and biology: a species of the coastal Namib, *Lapeirousia barklyi* extends along the Atlantic coastal plain and adjacent coastal mountains from near Lüderitz Bay in the north to Lekkersing and Port Nolloth in the south (Figure 13). Where recorded, the soil type is sand. Although first collected in 1876, relatively early for a northern Namaqualand species, and described in 1892 by J.G. Baker, *Lapeirousia barklyi* remained poorly known until the later 20th century. The species was treated as including *L. macrospatha* by Goldblatt (1972), an error only realised later when the development of better roads made travel in the Richtersveld easier and living plants could be compared side-by-side. *Lapeirousia barklyi* was first recorded from Namibia in 1922 by the German botanist and collector, Kurt Dinter, but the widespread occurrence of the species across the southwestern part of the country only became evident after a series of collections were made after the mid-1970s. It is now clear that the larger part of the distribution of *L. barklyi* is in southwestern Namibia and that in South Africa it only occurs in the western Richtersveld.

Diagnosis and relationships: the purple to violet perianth and relatively short-tubed flower combined with a broadly conical corm with well-developed basal teeth serve to distinguish *Lapeirousia barklyi*. The tube 15–25 mm long is normally shorter to about as long as the rest of the flower. This contrasts with *L. macrospatha*, included in *L. barklyi* by Goldblatt (1972), which has a cream to beige perianth flushed pink on the reverse, and a tube 30–35 mm long and half as long again as the rest of the flower.

Goldblatt (1972) suggested that *Lapeirousia barklyi* was probably most closely related to white- to pink- (or pale yellow-) flowered *L. fabricii*, a species of Western Cape and southern to central Namaqualand. The latter has a similar corm with marginal teeth but differs notably in its longer-tubed flower. The two can also easily be distinguished by their bracts, which have an almost plane, smooth margin and keel in *L. barklyi*, but are strongly crisped and serrate in *L. fabricii*.

Representative specimens

NAMIBIA.—**2615** (Lüderitz): Lüderitz District, southern Namib, (–BC), 22 Sept. 1999, *Mannheimer & Mannheimer 269* (WIND). **2715** (Bogenfels): Pomona, (–AB), 1922, *Dinter s.n.* (Z); Sept. 1925, *Schaefer s.n. sub Marloth 6596* (PRE); Klinghardt Mtns, northern slope of quartzite hill (–BC/BD), 18 Aug. 1977, *Merxmüller & Giess 32161* (BR, M, PRE, WIND); Gemsbokstal, Middagskupper, grassy flats south of Bankenberge, (–BD), 17 Aug. 1986 (BD), *Van Berkel 570* (MO, NBG, PRE). **2716** (Witputs): 14 km from Rosh Pinah to Obib Mtn near Spitskop road junction, (–DC), 1 September 1989, *Van Wyk 8909* (PRE). **2816** (Oranjemund): 16 km southwest of Obib-Wasser on road to Orange River (Daberas), (–BA), 17 Sept. 1973, *Giess 13023* (K, M, NBG, PRE, WAG, WIND); red sand flats, road to Obib, Sperrgebiet I, (–BA), 1 Sept. 1963, *Merxmüller & Giess 3413* (BR, M, PRE, WIND); Obib, (–BB), *Merxmüller & Giess 3413* (BR, M, PRE, WIND).

SOUTH AFRICA. NORTHERN CAPE.—**2816** (Oranjemund): gravel flats near Arrisdrif [Arriesdrif], 70 m, (–BC), 21 Aug. 1925, *Marloth 12401* (BOL, PRE); Daberas, sandveld, (–BD), 4 Sept. 1962, *Nordenstam 1264* (MO, NBG, S); Beauvallon, gravel, (–DA), 2 Sept. 1980, *Venter 8201* (PRE); ± 5 km east of Alexander Bay, (–DA), 17 Aug. 1986, *Williamson 3554* (MO, NBG); Grootderm, (–DA), 12 Sept. 1973, *Lavranos 10894* (MO, PRE); 37 km north of Lekkersing, (–DB), 9 October 1991, *Dreyer 182* (PRE). **2817** (Vioolsdrif): sandy flats between Jasper's Werf and Doornpoort, 250 m, (–AC), 26 Aug. 1925, *Marloth 12310* (PRE, STE). **2917** (Springbok): Lekkersing, (–AA), 24 Aug. 1925, *Marloth 12279* (PRE, STE); Anenous plains ± 8 km west of Farm Grasvlakte, in deep red sand, (–AB), 15 Sept. 1992, *Goldblatt & Manning 9460* (MO, NBG, PRE, WAG); near Abbevlakte, (–AD), Aug. 1883, *H. Bolus 6576* (BOL).

15. **Lapeirousia littoralis** *Baker* in Transactions of the Linnean Society, London, Botany ser. 2, 1: 272 (1878). Type: Angola, [Namibe], sandy coastal hills at Praia da Amelia near Villa de Mossamedes, July 1859, *Welwitsch 1546* (BM, holo.! – see discussion of the type specimen).

Lapeirousia burchellii Baker: 171 (1892). *Lapeirousia caudata* subsp. *burchellii* (Baker) Marais & Goldblatt: 30 (1972). Type: South Africa, [?North West], Morokweng, Chooi Desert, (–AC), Oct. 1812, *Burchell 2350* (K, lecto!. designated by Goldblatt (1972: 30); G!, P!, iso.).

Lapeirousia ramosissima Dinter: 255 (1931). Type: Namibia, Lüderitz: dunes near Gründorn, *Dinter 5043* (B, holo.!; BOL!, BR!, G!, K!, PRE!, SAM!, Z!, iso.).

Lapeirousia streyii Suess.: 88 (1951). Type: Namibia, Lüderitz: dunes south of the Kuiseb, *Strey 2587* (M, holo.!; PRE, iso.! [not holo. as cited by Goldblatt, 1972]).

Plants 100–150(–200) mm high, several- to many-branched, branches short, clustered near base, stem ± rounded to weakly angled below nodes. *Corm* bell-shaped, 10–14 mm diam.; tunics woody, brown, outer layers breaking irregularly, rarely becoming ± fibrous, basal rim shortly denticulate. *Leaves* few to several, linear, 2–4 mm wide, slightly corrugately ribbed, lowermost longest, inserted at or just below ground, often as long as inflorescence, rarely slightly longer, ascending to falcate, upper leaves progressively shorter. *Inflorescence* 1 or more short, 4–8-flowered spikes; outer bracts green, succulent, weakly keeled, (12–) 15–20(–25) mm long; inner $^2/_3$ to $^1/_2$ as long, ± membranous with 2 green keels, forked at apex. *Flowers* zygomorphic, white to creamy white, scented or not; perianth tube slender below, curving outwards and expanded above, 28–35 mm long, slightly wider in upper ± 4 mm; tepals subequal, narrowly lanceolate, 13–15 × 2–3 mm, acute, spreading. *Stamens* unilateral, arcuate; filaments 7–8 mm long, exserted 2–3 mm; anthers parallel, 4–5 mm long, ± white; pollen white or yellow. *Style* arching adaxially to stamens, branching between base and middle of anthers, style branches divided in distal $^1/_3$–$^2/_3$, recurved above and usually tangled in anthers. *Capsules* globose, 8–12 mm long. *Seeds* globose, 1.7–2.1 mm diam., dark brown, with reticulate sculpturing. *Chromosome number* $2n = 16$. *Flowering time*: mainly July to October in southern Africa but also at other times, March and April in northern Namibia.

Distribution and biology: relatively widespread, *Lapeirousia littoralis* extends from southwestern Angola and western, largely coastal Namibia to Bushmanland and Gordonia in Northern Cape, South Africa, as far east as Kimberley. In Namibia it extends from near the Brandberg in the central west to the Lüderitz District in the south. There is also a record from southern Botswana adjacent to Northern Cape (Figure 15). *L. littoralis* blooms early in the wet season, usually not long after the first soaking rains have fallen. Thus the Northern Cape and southern Namibian populations usually flower in the spring months (July to October) following the winter rainfall of the southwestern African coast. Elsewhere populations generally bloom in late summer. The species favours sandy, well-drained soils, where we have seen it on red sandy ground. The style branches are tangled with the anthers, suggesting that self-pollination may occur in the absence of pollinator visits.

Diagnosis and relationships: characterised by white to creamy white, uniformly coloured flowers with relatively short, straight tepals, 13–15 mm long, and a long perianth tube, 28–35 mm long, expanded and curving outward distally, *Lapeirousia littoralis* can usually be recognised by its flowers alone. It is sometimes confused with *L. caudata* but this species, from northern Namibia, Zambia, Zimbabwe and Mozambique, has long, relatively lax spikes usually 200–300 mm high, with short bracts, 10–18(–23) mm long. The flowers are creamy-yellow to dull maroon, colours not recorded in *L. littoralis*, and have long, narrow, attenuate, drooping tepals (18–)25–30 mm long and ± 1.3–2.0 mm wide. As the flowers fade and dry the tepals appear virtually filiform.

Plants from arid southwestern Angola, western and southern Namibia, and the spring-flowering populations from Northern Cape in South Africa tend to be shorter, often with the

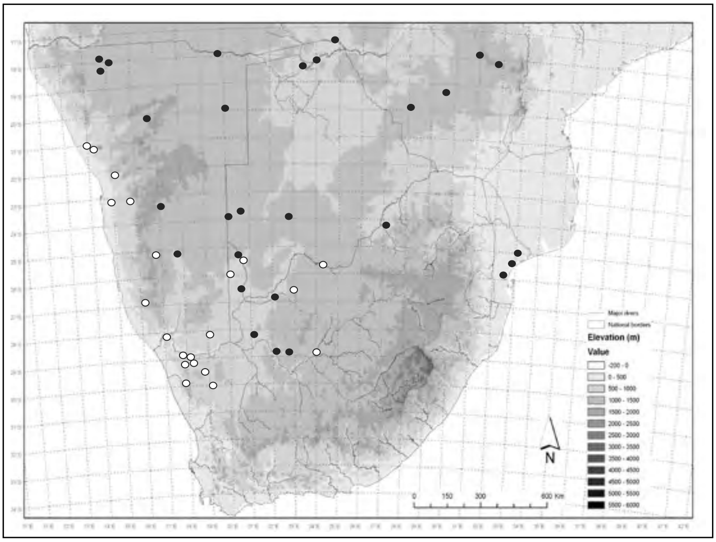


FIGURE 15.—Distribution of *Lapeirousia caudata*, ●; *L. littoralis*, ○ in southern Africa.

branches crowded at the base. In these plants the spikes are shorter, usually 100–150 mm high, and sometimes congested, and the bracts are usually 15–20(–25) mm long. The flowers in these populations have lanceolate, acute tepals ± 20 mm long and 2.0–2.5 mm wide.

With a diploid chromosome number of $2n = 16$, *Lapeirousia littoralis* has the dimorphic karyotype of one very long and seven short chromosome pairs typical of *Lapeirousia*: the base number and karyotype corresponds to that in sects. *Lapeirousia* and *Sophronia*. Molecular phylogenetic studies link the species with the western southern African *L. barklyi* and then to *L. caudata*. Vegetatively the two species are very alike, but the flowers differ sharply, *L. barklyi* having large pink flowers with yellow nectar guides, indicating a different pollination system. The seeds of *L. littoralis* and *L. caudata* are somewhat unusual, having a sculptured, ± reticulate surface, otherwise known only in sect. *Sophronia*. Seeds of *L. barklyi* have a smooth surface characteristic of other species of the genus. The presence of sculptured seeds in *L. littoralis* and *L. caudata* suggests a possible link with sect. *Sophronia* but neither molecular data nor any other morphological features point to a connection with that section.

History: the type collection of *Lapeirousia littoralis* was made by Friedrich Welwitsch in fruit in July 1859, and was described by J.G. Baker in 1878, based on this collection alone. The type locality is near Mossamedes on gravelly hills around Praia da Amelia, in southwestern Angola, now the province of Namibe. The type material is in poor condition and consists of depauperate plants with short branches produced from near the ground, bracts ± 12 mm long, capsules ± 9 mm long, and linear, lightly corrugate leaves. The specimen matches a second collection from southwestern Angola, *Torre 8824*, which was first assigned to *L. caudata*, but the flowers correspond to the South African and southern Namibian *L. burchellii*, which mostly flowers in the spring months. *L. burchellii* was first recorded in October 1812 when the English botanist and explorer William Burchell reached the Kuruman area of Northern Cape and North West. Burchell's collection was only formally described by J.G. Baker in 1892. Goldblatt (1972) considered the taxon to be subsp. *burchellii* of *L. caudata*, the name used until now for *L. littoralis*. *L. ramosissima*, collected near Grundorn in southern Namibia by Dinter and described by him, matches the type collections of *L. burchellii* and *L. littoralis*. A third species, *L. streyii*, from west-central Namibia is close to being intermediate between *L. littoralis* and *L. caudata* from tropical Africa, but has the shorter, slightly broader tepals characteristic of *L. littoralis*.

Selected specimens

ANGOLA.—Near Mossamedes close to Vila Arriaga, 7 Feb. 1956, *Torre 8824* (LISC).

BOTSWANA.—**2525** (Mafekeng): Moropedi ranch, (–CA), 15 Oct.1978, *Hansen 3455* (C, K).

NAMIBIA.—**2114** (Uis): Brandberg, B. W. Mine–Uis Mine road, sand in rocky ground, (–AA), 14 Mar. 1963, *Kers 942* (WIND); Messumberge, foot of mountains, (–AC), 19 Mar. 1967, *Giess 9689* (M, PRE, WIND); Nabab Hill, Brandberg area, (–AB), 4 Mar. 1978, *Craven 715a*, *715b* (WIND). **2215** (Trekkopje): 1 mile [1.5 km] northwest of Farm Bloemhof (AD), *Giess* et al. *5079* (M, WIND). **2315** (Rostock): Namib Park, Tumasberg at campsite, (–BA), *Giess 13550* (M, PRE, WIND). **2516** (Helmeringhausen): Farm Duwisib, (–BC), 17 May 1956, *Volk 12782* (M, MO). **2616** (Aus): dunes 15 miles [~23 km] west of Aus, (–CB), *Giess & Van Vuuren 828* (WIND); 13 miles [± 20 km] west of Aus, coarse sand, *Giess & Van Vuuren 824* (M, WIND).

SOUTH AFRICA. NORTH WEST.—**2623** (Morokweng): Chooi Desert, Giraffe Station, Oct. 1812, (–AD), *Burchell 2341* (K).

NORTHERN CAPE.—**2520** (Mata-Mata): Kalahari Gemsbok Park, between the Nossob and Auob dunes, (–BC), 25 Apr. 1960, *Barnard 807* (PRE); Kalahari Gemsbok Park, 6 miles [± 9 km], southeast of Kafferpan, loose red sand on dune top, (–CC), 22 Apr. 1960, *Leistner 1874* (M, MO, PRE). **2817** (Vioolsdrif): Richtersveld National Park, Ghaapkop near Sandberg, (–AA), 7 July 1993, *Van Jaarsveld 13246J* (PRE); Namaqualand, 15 km south of Vioolsdrif, Koubank River, (–DA), 7 July 1976, *Giess 14536* (M, WIND). **2818** (Warmbad): Goodhouse, (–CD), 27 July 1950, *Barker 6263* (NBG), *Lewis 2272* (SAM). **2824** (Kimberley): 18 miles south-southwest of Schmidtsdrift, red sand, (–CA), 24 Sept. 1961, *Leistner 2866* (B, G, PRE). **2917** (Springbok): 25 miles [± 37 km] north of Okiep on Goodhouse road (old road through Leospoort), (–BD), 25 Aug. 1959, *Lewis 5517* (NBG); Tuinvlak, Goegab (Hester Malan) Nature Reserve, (–DB), 9 Oct. 1974, *Rosch & le Roux 953* (PRE). **2918** (Gamoep): road to Goodhouse (29°13.5' 18°1.73'), sandy soil (–AA), 19 Sept. 1980, *Van Berkel 255* (MO), NBG); Little Bushmanland, Keuzabies, (–AB), 18 June 1973, *M. Schlechter s.n.* or *103* (B, BOL, COI, E, G, MO, P, PRE); Aggenys, Brabees, red sand dunes and plains, (–BB), 15 Aug. 1990, *Dean 1002* (PRE); ± 100 km west of Pofadder to Springbok, (–BC), 13 Sept. 1973, *Coetzee & Werger 1752* (PRE);

Aggenys, 10 miles [± 15 km] west of farmhouse, (–BD, 4 Sept. 1971, *Wisura 2222* (NBG); near Ratelkraal, (–CA), 7 Sept. 1950, *Barker 6755* (BOL, NBG).

16. **Lapeirousia caudata** *Schinz* in Verhandlungen des botanische Vereins der Provinz Brandenburg 31: 213 (1890). *L. littoralis* subsp. *caudata* (Schinz) Goldblatt: 478 (1990a). Type: Namibia, Amboland, Olukonda, *Rautanen 2* (Z, lecto.!, designated by Sölch on sheet; Z, iso.!).

Lapeirousia delagoensis Baker: 171 (1892); Baker: 94 (1896). Type: Mozambique, Delagoa Bay, Lourenço Marques [Maputo], sandy places, *H. Bolus 7618* (K, lecto.!, designated by Goldblatt (1990a: 478); BOL!, G!, SAM!, iso.).

Lapeirousia lacinulata Vaupel: 546 (1912). Type: Zambia, Kantanina Hills, *Kässner 2170* (B, holo.!; BM!, BR!, E!, HBG!, K!, P!, Z!, iso.).

Plants 200–300 mm high, usually with several (rarely up to 12) long branches, produced from near base, stem ± rounded to weakly angled below nodes. *Corm* bell-shaped, 10–14 mm diam.; tunics woody, brown, outer layers breaking irregularly, rarely becoming ± fibrous, basal rim shortly denticulate. *Leaves* few to several, linear, 1.5–4.0 mm wide, lightly corrugately ribbed, lowermost longest, inserted ± at ground level, usually slightly longer than stems, ascending to falcate or trailing, upper leaves progressively shorter. *Inflorescence* comprising (1–)several, relatively lax, 8–12-flowered spikes; outer bract green, succulent, weakly keeled, 10–18(–23) mm long; inner $^2/_3$ to $^1/_2$ as long, ± membranous with 2 green keels, forked at apex. *Flowers* zygomorphic, greenish yellow, light yellow-brown or dull maroon, with strong sweet scent; perianth tube slender below, curving outwards and expanded above, (8–)30–45(–70) mm long, wider upper part ± 6 mm long; tepals subequal, narrowly linear-filiform, (18–)25–30 × 1.3–2.0 mm, attenuate, spreading at right-angles to tube, dorsal ± erect, upper laterals arching backward, lower 3 arching toward ground. *Stamens* unilateral, arcuate; filaments 7–8 mm long, exserted 2–3 mm; anthers parallel, 4–5 mm long, ± white; pollen white or yellow. *Style* arching adaxial to stamens, branching between base and middle of anthers, style branches divided in distal $^1/_3$–$^2/_3$, recurved above and usually tangled in anthers. *Capsules* globose, 6–8(–11) mm long. *Seeds* globose, 1.7–2.1 mm diam., dark brown, with reticulate sculpturing. *Chromosome number* 2*n* = 16. *Flowering time*: mainly January to April (almost any month in Mozambique).

Distribution and biology: occurring in a wide swath across south tropical Africa and northern southern Africa, *Lapeirousia caudata* extends from northern Namibia and Zambia, across Botswana to Zimbabwe and in South Africa to western Limpopo and Northern Cape, and with isolated and surprising populations in southern Mozambique (Figure 15). It blooms late in the wet season, usually after January and sometimes as late as April. In southern Mozambique *L. littoralis* appears to bloom at almost any month, reflecting the non-seasonal rainfall pattern of the southeast coast. The species favours sandy, well-drained soils, sometimes growing on sand dunes. The likely pollinators are moths, in light of the pale coloured, long-tubed flowers and often clove-like fragrance. The style branches are tangled with the anthers, suggesting that self-pollination may occur in the absence of insect-mediated pollen transfer.

Diagnosis and relationships: characterised by uniformly coloured, pale dull yellow, yellow-brown or maroon flowers, usually with a long perianth tube expanded and curving outward distally, *Lapeirousia caudata* can usually be recognised by its flowers alone. The relatively long tepals, 25–30 mm long, are up to 2 mm wide, and as the flowers fade and dry the tepals shrink, then appearing filiform and less than 1 mm wide. The habit is also distinctive: well grown plants have several (up to 12) long branches 200–300 mm high, produced from near the base, and relatively lax spikes with short bracts, 10–18(–23) mm long. In plants we have seen alive the tepals spread outward from the base in somewhat lax fashion with the dorsal tepal ± erect and the lower three arching toward the ground.

Plants from southern Mozambique, mostly from immediately around Maputo, stand out in having particularly long-tubed flowers and in often being very robust. The perianth tube is sometimes up to 70 mm long, compared with the 35–40 mm usual in central African plants. Floral variation is notable in plants from western Zambia, and a collection from Mongu (*Robinson 6749*) has flowers with a perianth tube 8–13 mm long and tepals ± 18 mm long. Such occasional variation, particularly in tube length, also occurs in other species of *Lapeirousia* (see *L. anceps*) and appears to have no taxonomic significance.

Lapeirousia caudata was treated by Goldblatt (1990a) as subsp. *caudata* of *L. littoralis* as collections then available suggested the existence of plants intermediate between the two species, especially for bract and perianth tube length. We have now seen populations of both taxa alive and were impressed by differences between them in overall habit and tepal dimensions and orientation. It seems more useful to recognise two separate, but no doubt closely allied, species. The overlap in perianth tube and bract length in the two species most likely varies independently in each and does not indicate the existence of truly intermediate plants. We include both species in sect. *Lapeirousia*, with which corm morphology and chromosome number accord. *L. caudata* and *L. littoralis* are, however, discordant in the section in having seeds with reticulate to rugose surface sculpturing, a feature otherwise found in *Lapeirousia* only in sect. *Sophronia*.

History: first gathered in December 1885 at the Finnish Mission Station at Olukonda in northern Namibia by Hans Schinz, *Lapeirousia caudata* was described in 1890 by Schinz based on his and the Finnish missionary, Martti Rautanen's ample, but confusingly labelled, collections at the Zurich Herbarium. A sheet collected by Rautanen in 1887 was designated the lectotype by Sölch in 1959 and this choice appears to be as suitable as any other. Corresponding closely with *L. caudata*, although from northern Zambia, plants collected by T. Kässner in 1906 were described by Vaupel in 1912 as *L. lacinulata* on the basis of its slender habit, low stature, and shorter perianth tube, only 25 mm long (actually 25–28 mm), in contrast to the type of *L. caudata* in which the perianth tube is 30–40 (–70) mm long. The distinction now seems minor and insufficient reason for their separation at any taxonomic rank. Several other collections of *L. caudata* have a short perianth tube similar to that in *L. lacinulata*, but not the slender habit. The first of the series of isolated populations near Maputo, Mozambique, were discovered by the Cape Town botanist Harry Bolus in 1886 and his collection was made the type of his new species *L. delagoensis* by J.G. Baker (1892).

Selected specimens

BOTSWANA.—**1823** (Siambiso): sandy floodplain of Kwando River, (–AB), *Smith 2222* (K, PRE, SRGH). **2320** (Ukwi): 120 km west-northwest of Hukuntsi on track to Ncojane, open sandy savanna, (–DC), 13 Mar. 1979, *Skarpe S-333* (K, PRE, SRGH, UCBG). **2322** (Kang): Kang, 320 km west of Gaborone, 3500 ft [1 067 m], (–DD), 20 Sept. 1975, *Mott 772* (SRGH, UCBG).

NAMIBIA.—**1715** (Ondangua): Ondangua, open sandy flats, (–DD), 5 Feb. 1959, *De Winter & Giess 6877* (M, WIND). **1716** (Enana): Oniipa, eroded field, (–CC), 7 Mar. 1967, *Soini 429* (WIND); Olukonda, (–CC), Dec. 1885, *Schinz 15* or *s.n.* (B, Z), 30 Jan. 1887, *Rautanen 2* (Z), Feb. 1894, *Rautanen 170* (B, G, Z). **1719** (Runtu): 10 km east of Runtu, (–DD), Jan. 1956, *Kruger 1* (PRE). **1724** (Katima Mulilo): Mpilila Island, locally common near marsh, 12 Jan. 1959, *Killick & Leistner 3325* (PRE, SRGH, WIND). **1815** (Okahakana): Onambeke–Onolongo, (–?BB), Apr. 1923, *Barnard 141* (SAM), *Barnard 573* (SAM). **1920** (Tsumkwe): 15 km east of Tsumkwe on road to Botswana, (–DA), 10 Jan 1971, *Geiss* et al. *11196* (WIND); Tsumkwe, hard black sand, Oberflachenkalk, (–DA), 13 Jan. 1971, *Giess* et al. *11050* (WIND); Simkue, 157 miles [± 250 km] east of Grootfontein, *Acacia-Combretum* parkland, (–DB), 17 Jan. 1958, *Story 6162* (M, PRE, SRGH, WIND). **2317** (Rehoboth): Farm Arovley, red sand, (–AA), 14 Feb. 1965, *Giess 8401B* (M, WIND). **2517** (Gibeon): sandbodem, Sudkalahari bis Gibeon, (–BA, –BB), May 1912, *Range 1455* (SAM).

SOUTH AFRICA. LIMPOPO.—**2428** (Nylstroom): Waterberg, Zandrivierspoort near Alma, Farm Witpoort, (–AC), 5 Mar. 1979, *Van Wyk 2680* (M, PRE).

NORTHERN CAPE.—**2420** (Unions End): Kalahari Park, Khaapan, (–BD), Jan. 1978, *Van der Walt* (PRE). **2520** (Mata-Mata): Kalahari Gemsbok Park, 2 km north of Kameelsleep, (–DC), 26 Feb. 1962, *Leistner & Werger 3498* (PRE). **2622** (Tsabong): Kuruman District, Vanzylsrust, Farm Floradale, red sand, dune woodland, (–CD), 30 Mar. 1988, *Venter 12858* (PRE). **2723** (Kuruman): Farm Uitkoms, (–CA), *Gubb 146/38* (PRE). **2821** (Upington): ± 40 km north of Upington at southern edge of Kalahari, (–AB), 1 Apr. 1980, *Snijman 235* (NBG). **2822** (Glen Lyon): sandveld west of Padkloof, on dune running parallel to Langebergen, (–DA), 15 Mar. 1937, *Acocks 2057* (PRE); 90 km west of Griquatown, (–CD), 6 Mar. 2010, *Goldblatt & Porter 13489* (MO, NBG).

17. **Lapeirousia macrospatha** *Baker*, Flora capensis 6: 94 (1896); Goldblatt & Manning: 345 (1994). Type: South Africa, [Northern Cape], between Port Nolloth and Eleven Mile Station, 22 Aug. 1883, *H. Bolus 697* (K, holo.!; B!, BOL!, G!, SAM!, iso.).

[*macrospatha* – Latin, large spathes but alluding to the prominent floral bracts]

Plants 60–100 mm high including flowers, usually branched, then from base, stem compressed and lightly 2-angled, angles smooth or lightly serrated. *Corm* ± 7–8 mm diam., ± bell-shaped, usually 40–60 mm below ground; tunics dark brown, fairly smooth, basal margin lightly serrated with teeth directed downward. *Leaves* 3–6 (or more), lowermost usually conspicuously longer than others, ± twice as long as stem, linear, ascending to falcate, 2.0–3.5 mm wide, strongly ribbed, upper cauline leaves shorter, sometimes resembling bracts and not ribbed, usually subtending branches. *Inflorescences* 2–4-flowered spikes; outer bracts green, firm, 20–35 mm long, lanceolate, acute, slightly keeled, margins hyaline, those of lower flowers unifacial and ribbed distally; inner bracts forked at tips, transparent in centre, ± $^1/_2$ to $^2/_3$ as long as outer. *Flowers* zygomorphic, cream to ivory, fading to dull pink, pink on outside of tepals and tube, lower tepals each marked with a small yellowish basal mark surrounded by a dark purple zone, usually with a small claw-like cusp at base of lowermost or all 3 lower tepals; perianth tube 30–35 mm long, widening and lightly curving outward near apex; tepals unequal, lanceolate and acute, dorsal largest, ± 20 × 7 mm, initially erect or arching forward over stamens later reflexed, upper lateral tepals slightly reflexed, lower 3 tepals united for ± 2 mm, ± 13 × 5 mm, held at right angles to tube, tilted at ± 30° below horizontal. *Stamens* unilateral, arcuate; filaments ± 9 mm long, reaching mouth of tube or exserted up to 2 mm; anthers contiguous, 3–5 mm long, mauve, pollen pale violet. *Style* dividing opposite middle of anthers, style branches ± 3 mm long, divided for ± $^2/_3$ their length. *Capsules* oblong, 12–15 × ± 7 mm, apices of locules forming auriculate lobes decurrent on weakly developed locular ridges. *Seeds* globose, ± flattened or lobed at chalazal end, ± 1.6 mm diam., red-brown. *Chromosome number* unknown. *Flowering time*: August to late September. Figure 16

Distribution and biology: restricted to northern Namaqualand, Northern Cape, *Lapeirousia macrospatha* has a fairly localised distribution in the southern Richtersveld. It has been collected repeatedly on the Anenous plains between Port Nolloth and Anenous Pass, but occurs to the north near Eksteenfontein, near Steinkopf, and in the sandy country east and north of Port Nolloth. It also extends southward at least as far as Grootmis (Figure 17). *L. macrospatha* appears to occur mainly in deep, fine-grained red sand. Sometimes, possibly due to heavy overgrazing, it may be extremely common locally and even dominant, but more often it grows in association with sandveld annuals such as *Cotula* (Asteraceae), *Manulea*, *Sutera* and *Zaluzianskya* (Scrophulariaceae), *Heliophila* (Brassicaceae) and low succulent shrubs (Aizoaceae).

Diagnosis and relationships: *Lapeirousia macrospatha* can be recognised by its large flower with a long, slender perianth tube 30–35 mm long, widening noticeably towards the apex and white to beige tepals red on the outside and with red markings on the lower tepals. The red-brown, bell-shaped corms bear fine marginal, downward directed teeth and are virtually identical with those of *L. arenicola*, which has similarly coloured flowers, much smaller in size and with a ± cylindric perianth tube 20–33 mm long. The larger flower of *L. macrospatha* is reflected in a dorsal tepal ± 20 × 7 mm whereas the smaller flowers of *L. arenicola* have a dorsal tepal 8–11 × 3–4 mm. The longer anthers of *L. macrospatha*, 3–5 mm long, also reflect the larger flowers than those of *L. arenicola*, in which the anthers are 1.5–2.5 mm long. The two species appear to grow in an identical habitat, deep red sand, *L. arenicola* extending along the Atlantic coast from near Klawer in Western Cape through the sand plains and coastal dunes of western Namaqualand to the southern Richtersveld on the Anenous flats in Northern Cape, slightly overlapping but largely complementing the more northern distribution of *L. macrospatha*. The DNA sequence-based phylogeny supports the hypothesis that *L. arenicola* and *L. macrospatha* are closely allied, and are in current analyses, sister species (Forest et al. 2014).

History: described by J.G. Baker in 1896, *Lapeirousia macrospatha* was based on a collection made by Harry Bolus in 1883 on his only expedition to Namaqualand. It was until recently represented in herbaria by limited material, much of it poorly preserved, and this led Goldblatt (1972) to regard the species as merely a longer-tubed variant of then equally poorly understood *L. barklyi*. Examination of living plants in the southern Richtersveld of Namaqualand has now made it clear that the two are separate species (Goldblatt & Manning 1994). Their flowers, seen alive, are quite different, those of *L. barklyi* mauve-pink rather than ivory with pink reverse and have a relatively wide floral cup formed by the upper part of the perianth tube and the tepal bases. We no longer believe that they are even immediately related. The corms also differ, those of *L. macrospatha* resembling those of *L. arenicola* in their bell-shape with fine, marginal teeth, whereas those of *L. barklyi* are triangular in profile with laterally extended spines like those of *L. fabricii* and its allies.

Selected specimens

SOUTH AFRICA. NORTHERN CAPE.—**2816** (Oranjemund): north of Port Nolloth at Holgat River, (–DD), 6 Sept. 1987, *Germishuizen 4795* (PRE); 12 Sept. 1961, *Hardy 603* (PRE). **2817** (Vioolsdrif): 1 km west of Eksteenfontein, (–CD), 1 Sept. 1986, *Williamson 3608* (NBG); Eksteenfontein, in sand, 29 Aug. 1980, *Venter 8062* (PRE). **2916** (Port Nolloth): 8 km east of Port Nolloth, (–BD), 13 Sept. 1974, *Rösch & Le Roux 670* (PRE). **2917** (Springbok): near Abbevlakte, Aug. 1883, *H. Bolus 6576* (BOL); road to Eksteenfontein, 2–4 km north of Port Nolloth road, (–AB), 8 Sept. 1980,

FIGURE 16.—*Lapeirousia macrospatha*, *Goldblatt & Manning 9138*. Scale bar: 10 mm. Artist: John Manning.

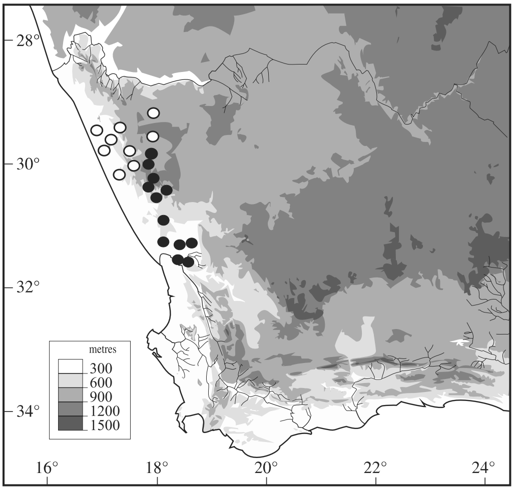


FIGURE 17.—Distribution of *Lapeirousia arenicola*, ●; *L. macrospatha*, ○.

Goldblatt 5716 (M, MO, NBG); Farm Grasvlakte, sandy flats, (–AB), 19 Sept. 1989, *Viviers 2042* (NBG), 28 Aug. 1991, *Goldblatt & Manning 9138* (K, MO, NBG, PRE, M); Grootmis [Grootmist] to Springbok, 28 Aug. 1937, (CA/CB), *Verdoorn & Dyer 1880* (K, PRE); sandveld just east of Grootmis at turnoff to Port Nolloth, (–CA), 25 Aug. 1993, *Goldblatt & Manning 9655* (MO, NBG); ± 48 km west of Springbok, (–CB), *Thompson 1056* (NBG); sandveld ± 55 km west-northwest of Komaggas, Nuttrabooi 199, 0.5 km south of Buffelsrivier, (–CB), 27 Aug. 1999, *Desmet 294* (NBG).

18. **Lapeirousia arenicola** *Schltr*. in Botanische Jahrbucher für Systematik 27: 105 (1900); Goldblatt: 54 (1972). Type: South Africa, [Western Cape], Atties [near Vredendal], 30 July 1896, *Schlechter 8329* (B, holo.!; BM!, BOL!, COI!, E!, G!, GRA!, K!, MO!, P!, PH!, PRE!, S!, UPS!, iso.).

[*arenicola* – growing in sand, referring to the habitat, deep sandy ground.]

Plants 100–120(–150) mm high, often ± tufted, usually branched mainly at base, stem compressed and 2-angled, angles often weakly winged, slightly serrated, normally without cormlets at below ground nodes. *Corm* bell-shaped, 35–50 mm below ground, ± 6 mm diam.; tunics red-brown, smooth, basal rim lightly serrated, teeth directed downward. *Leaves* 3–6(–many), lowermost usually conspicuously longer than others, linear and ascending to falcate, 2–3 mm wide, strongly ribbed, upper cauline leaves shorter, usually resembling bracts and not or barely ribbed, usually subtending branches. *Inflorescences* 2–6-flowered spikes, lax or crowded; outer bracts green, leaf-like, 15–25 mm long, lanceolate, acute, keeled throughout or at least distally, unifacial apically for 3–5 mm, keels often red, minutely serrated, margins hyaline, inner bract transparent with 2 green keels, $^{1}/_{2}$ to $^{2}/_{3}$ as long as outer, forked at tip. *Flower* zygomorphic, cream to biscuit-pink, lower tepals each with red mark near base; perianth tube 15–25(–33) mm long, cylindric, curving slightly outward at apex; tepals subequal or dorsal slightly larger, lanceolate and acute or obtuse, 8–11 × 3–4 mm, usually spreading ± horizontally when fully open, all in same plane. *Stamens* unilateral, erect; filaments ± 7 mm long, exserted ± 3.5 mm from tube; anthers contiguous, 1.5–2.5 mm long, violet, pollen mauve. *Style* dividing opposite upper half of anthers, style branches ± 1.5 mm long, divided for ± half their length. *Capsules* oblong, (8–)10–12 × ± 6 mm, apices of locules forming auriculate lobes decurrent on wing-like locular ridges in upper half. *Seeds* globose, flattened at chalazal end, ± 1.4 mm diam., dark shiny brown. *Chromosome number* 2*n* = 16. *Flowering time*: August to September, occasionally in early October. Figure 18.

Distribution and biology: restricted to the South African west coast and near interior, *Lapeirousia arenicola* extends from near Vanrhynsdorp and Vredendal in Western Cape northward through the sandveld and low coastal hills of Namaqualand as far north as the Anenous flats at the southern edge of the Richtersveld (Figure 17). It favours deep sandy soils, especially the rather fine-grained, red-tinged sands of lowland and coastal Namaqualand. It is commonly found in association with the spiny perennial grass *Eragrostis spinescens*, succulent-leaved *Trachyandra falcata* and *T. bulbinifolia* (Asphodelaceae) and strandveld annuals such as *Heliophila* (Brassicaceae), *Manulea* and *Lyperia tristis* (Scrophulariaceae), and *Cotula* (Asteraceae). It is a self-compatible species, but probably facultatively outcrossing early in the flowering season when plants produce fairly large, long-tubed flowers with stronger colouring than later in the season. Towards the end of the flowering season the flowers of some populations have weakly contrasting markings, are smaller, and have a perianth tube 15–18 mm long (compared with ± 25 mm on the same plants earlier in the season). We assume these late-blooming flowers are primarily autogamous. *L. arenicola* co-occurs at several localities with the florally almost identical *L. simulans*.

Diagnosis and relationships: low-growing and typically a small plant, *Lapeirousia arenicola* can readily be distinguished from most other species of *Lapeirousia* by its small size, pale pinkish-beige, slender-tubed flowers and narrow tepals. Perhaps most easily confused with *L. macrospatha*, which has similarly coloured flowers, *L. arenicola* has a uniformly narrow, cylindric perianth tube 17–33 mm long and tepals 10–11 × 3–4 mm, whereas *L. macrospatha* has a wider tube, 25–35 mm long, expanded toward the apex and considerably larger tepals, the uppermost largest and ± 20 × 7 mm. Although the two species appear similar on casual examination, they are quite distinct and do not intergrade although their ranges overlap slightly. Both have been found growing together just north of the Port Nolloth road below Anenous Pass and here they maintain their differences. Perianth tube length may coincide but the tepals of *L. arenicola* are always smaller and the tube more often than not is substantially shorter than in *L. macrospatha*. As discussed above under *L. macrospatha*, we regard *L. arenicola* as immediately related to this longer-tubed species, an association supported by the DNA-based phylogeny (Figure 1).

FIGURE 18.—*Lapeirousia arenicola*, *Goldblatt & Manning 9453*. A, flower and corm; B, flower; C, capsules. Scale bar: 10 mm. Artist: John Manning.

Although *Lapeirousia arenicola* bears a superficial resemblance to the Western Cape *L. anceps* in flower colour and in the narrowly cylindric perianth tube, these similarities are evidently due to convergence as the molecular phylogeny (Figure 1) shows them to be distantly related. More puzzling is the striking resemblance between *L. arenicola* and *L. simulans*, which co-occur at several sites along the west coast, where their nearly identical flowers make a strong impression. Vegetatively, *L. arenicola* is always more compact in habit and often has a somewhat shorter perianth tube, so that they can be distinguished when seen growing side-by-side. More significant differences are underground: the corms of *L. arenicola* lie 35–50 mm below the surface and the underground part of the stem rarely produces cormlets whereas corms of *L. simulans* are usually 60–80 mm below ground and always have a fairly large cormlet at each of two underground nodes. Apart from an apparently close relationship to the northern Namaqualand *L. macrospatha*, and possibly with *L. simulans*, the affinities of *L. arenicola* are uncertain. Molecular data place *L. arenicola* closest to *L. macrospatha* in the sect. *Lapeirousia* clade. The relationship with *L. jacquinii* suggested by Goldblatt (1972), largely on the basis of their similar corms and additionally by similar capsules with auriculate apical lobes, is no longer tenable.

Representative specimens

SOUTH AFRICA. NORTHERN CAPE.—**2917** (Springbok): Eksteenfontein road, 3 km north of Port Nolloth road, (–AB), 8 Sept. 1980, *Goldblatt 5715* (MO, NBG); Spektakel, sand dunes, (–DA), 20 July 1967, *Van der Schijff 6970* (PRE); c. 6 km south of Wildepaardehoek Pass, (–DC), *Thompson 1077* (BOL, STE); sandy flats below Wildepaardehoek Pass, (–DC), 9 Sept. 1980, *Goldblatt 5760* (MO). **3017** (Hondeklipbaai): between Hondeklipbaai and Wallekraal, (–AD), 4 Sept. 1932, *Leighton s.n.* (*BOL30718*), 28 Sept. 1976, *Goldblatt 4242* (MO); road to Soebatsfontein from Buffels River, (–BB), 6 Sept. 1945, *Leighton 1209* (BOL); near Soebatsfontein, (–BB), Sept. 1945, *Lewis 1384* (SAM); Grootvlei, (–BB), 7 Sept. 1941, *Barker 3710* (NBG); ± 25 km east of Wallekraal toward Garies, (–DA), 17 Sept. 1991, *Goldblatt 9228* (MO); Farm Hardekoppie northwest of Kotzesrus on road to Groen River Mouth, 180 m, (–DC), 9 Sept 1987, *Reid 1296* (PRE). **3018** (Kamiesberg): Eenkokerboom, (–CC), Sept. 1897, *Schlechter 11071* (GRA).

WESTERN CAPE.—**3118** (Vanrhynsdorp): ± 26 km north of Vanrhynsdorp, (–BC), 24 July 1948, *Compton 20705* (NBG); Koekenaap to Graafwater, Farm Kommandokraal, (–CA), 10 Sept. 2008, *Goldblatt & Porter 13102* (MO); 3 km northeast of Vredendal, (–DA), 7 Aug. 1970, *Hall 3714* (NBG), *3784* (NBG); north of Klawer, (–DA), 2 Sept. 1951, *Barker 7401* (NBG); Sept. 1945, *Lewis 1406* (SAM); red sand flats 10 km north of Vanrhynsdorp, (–DA), 14 Sept. 1992, *Goldblatt & Manning 9453* (MO, NBG).

19. **Lapeirousia simulans** *Goldblatt & J.C.Manning* in Novon 4: 341 (1994). Type: South Africa, [Western Cape], sandveld ± 11 km north of Vanrhynsdorp, 14 Sept. 1992, *Goldblatt & Manning 9454* (NBG, holo.!; K!, MO!, PRE!, WAG!, iso.).

[*simulans* – 'imitating', for the close resemblance to *L. arenicola*, with which it was confused until 1994.]

Plants 100–180 mm high, 2–3(–5)-branched (rarely simple), branching ± divaricate, bearing a cormlet at each of 2 subterranean nodes, stem compressed and 2-angled, angles minutely serrated. *Corm* bell-shaped, 7–8 mm diam., 55–85 mm below ground; tunics dark brown, glossy, margins lightly serrated, teeth directed downward. *Leaves* 3 or more, lowermost longest, usually ± twice as long as stem, linear, 2.0–4.5 mm wide, corrugately ribbed, remaining leaves progressively shorter, becoming ± bract-like and usually subtending branch. *Inflorescence* lax spikes of (2)3–5 flowers; outer bracts green, transparent on veins, with slightly serrate keels decurrent on stem angles, 10–18 mm long; inner bracts ± $^{1}/_{2}$ as long as outer. *Flowers* zygomorphic, ± white, reddish-brown on reverse, lower 3 tepals each with small, claw-like tooth near base and with small basal and larger median dark red spot, unscented; perianth tube cylindric, 27–35 mm long, slightly wider and curved near apex; tepals unequal, upper 3 slightly larger than lower 3, when fully open all held ± horizontally at right angles to tube, ± 11 × 4 mm, lower 3 held closely together, 10 × 3.0–3.3 mm. *Stamens* unilateral, erect; filaments 5–6 mm long, exserted ± 3 mm from tube; anthers 2.0–2.5 mm long, purple; pollen light purple. *Style* erect, adaxial to stamens, dividing between mouth of tube and anther bases, style branches ± 2 mm long, divided for slightly > $^{1}/_{2}$ their length. *Capsules* oblong, 8–12 mm long, slightly warty in upper 1/2, without auriculate apices or locular ridges. *Seeds* globose, light brown, 1.2–1.4 mm diam. *Chromosome number* unknown. *Flowering time*: early to late September. Figure 19.

FIGURE 19.—*Lapeirousia simulans*, *Goldblatt & Manning 9454*. A, plant; B, capsules; C, seed. Scale bar: A, B, 10 mm; C, 0.5 mm. Artist: John Manning.

Distribution and biology: restricted to southern Namaqualand, *Lapeirousia simulans* extends from the Groen River west of Garies to Vanrhynsdorp in the south (Figure 20). Originally thought to be restricted to deep red sands at the southern margins of the Knersvlakte, it has now been recorded more widely in Namaqualand. Plants often co-occur with *L. arenicola*, which it closely resembles, and sometimes with *L. anceps* and *L. fabricii*, which have larger but similarly coloured flowers with nearly identical markings. We infer a shared pollination system using long-proboscid flies for *L. simulans*, but there are no records of pollinator visits to the species, which blooms somewhat earlier than its presumed pollinators are on the wing. Self-compatibility and autogamy, which we determined by pollinator exclusion, assure reproduction by seed in the absence of insect-mediated pollen transfer. Vegetative reproduction is ensured by production of cormlets at the underground nodes of the deeply buried stem.

Diagnosis and relationships: the small corms with glossy dark brown tunics and a basal rim of minute, downward directed teeth closely resemble those of *L. arenicola* and several other members of sect. *Lapeirousia*. Although remarkably similar in general appearance to *L. arenicola*, the immediate affinities of *L. simulans* probably do not lie with that species, which is not surprising given that they are sometimes sympatric. Their flowers are so similar in tube length and general size and markings that they can be distinguished only with difficulty. Their flowering times overlap, but that of *L. simulans* is generally somewhat later in the season, usually mid- to late September, by which time the last flowers of *L. arenicola* are often depauperate and have shorter tubes and duller colouring than earlier in the season. The two are most readily distinguished by the underground part of the stem. While the corms of *L. arenicola* lie 35–55 mm below the surface on a straight stem that lacks axillary cormlets, the underground stem of *L. simulans* is 55–85 mm long so that the corm lies at a greater depth than in *L. arenicola*. Each of the two underground nodes consistently bears a large cormlet in *L. simulans*, a feature fairly rare in the genus, although also known in some other species including *L. anceps* and *L. divaricata*. Molecular studies show *L. simulans* to be a member of the sect. *Lapeirousia* clade, but not immediately allied to *L. arenicola* and *L. macrospatha*.

Representative specimens

SOUTH AFRICA. NORTHERN CAPE.—**3017** (Hondeklipbaai): Farm Steenkampskraal, 9 km north of foot of Killians Pass, (–BA), 12 Aug. 1997, *Goldblatt & Manning 10653* (MO); slopes between Soebatsfontein and Skilpad, (–BB), 15 Aug. 2005, *Steyn 718* (PRE).

WESTERN CAPE.—**3117** (Lepelfontein): Katdoringvlei, sandy slopes, (–BB), 10 Sept. 2009, *Goldblatt & Porter 13316* (MO); Brand-se-Baai, strandveld, (–BD), 14 Sept. 1991, *Van Rooyen 2030* (PRE). **3118** (Vanrhynsdorp): between Koekenaap and the coast, deep red sands, (–CA), *Goldblatt, Manning & Porter 12867* (MO, NBG); 1.5 km northwest of Vredendal (Cohen's farm), (–DA), 8 Sept. 1970, *Van der Merwe 151* (BOL, NBG); ± 10 km north of Vanrhynsdorp, (–DA), 20 Aug. 1993, *Goldblatt & Manning 9609* (MO, NBG), 10 Sept. 1993 (fr.), *Goldblatt & Manning 9701* (MO, NBG); Vanrhynsdorp, (–DA), 2 Sept. 1951, *Martin 825* (MO, NBG).

20. **Lapeirousia spinosa** *(Goldblatt) Goldblatt & Manning* in Novon 4: 343 (1994). *L. divaricata* var. *spinosa* Goldblatt: 66 (1972). Type: South Africa, [Northern Cape], ± 68 km west of Steinkopf to Port Nolloth, 24 Sept. 1970, *Goldblatt 567* (BOL, holo.!).

[*spinosa* – 'spiny', referring to long, spine-like, rigid teeth that extend outwards from the corm base.]

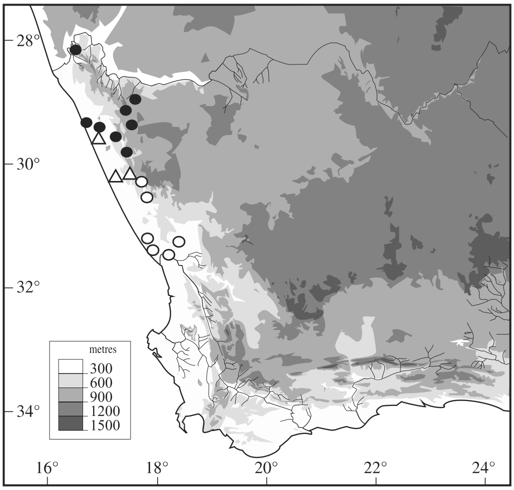


FIGURE 20.—Distribution of *Lapeirousia simulans*, ○; *L. spinosa*, ●; *L. tenuis*, Δ.

Plants 50–90(–140) mm high; stem erect, sometimes branched at base, somewhat compressed but not often angled; without cormlets at nodes below ground. *Corm* ± bell-shaped (to ± obconic), 9–15 mm diam., 20–40 mm below ground; tunics blackish, often glossy, basal rim with prominent horizontal spines. *Leaves* 3–4 (or more if plants branched), lowermost usually much the longest and usually shortly exceeding stem, linear to narrowly lanceolate, ascending or falcate, 2–4 mm wide, strongly corrugately ribbed; remaining leaves shorter and progressively more bract-like above, ribs weakly or not developed. *Inflorescences* spikes of (3–)5–9 flowers, usually moderately crowded; outer bract green or flushed reddish below, firm, 12–20(–35) mm long, enclosing slender part of tube, veins transparent, margins narrowly hyaline; channelled below, lightly keeled in upper $^1/_2$, keels minutely serrated or crisped; inner bract up to $^1/_2$ as long as outer, 2-keeled, with broad transparent margins. *Flowers* zygomorphic, white or flushed pink to lilac (more so with age and when dry), lower tepals yellow below and each with one or two purple median marks near limb base, bearing basal tooth-like ridge ± 2 mm long, lightly sweet scented; perianth tube 9–12 mm long (shorter in dried material), narrow below, curved and widening above; tepals unequal, lanceolate, acute, dorsal largest, 18–23 × 7–8 mm, erect, held apart from others, lower margins undulate or lightly crisped, upper lateral tepals united with lower 3 for ± 5 mm, directed forward below, reflexed distally, lower 3 tepals horizontal below, limbs 12–14 × 7–8 mm, flexed sharply downward at ± 45°, margins undulate. *Stamens* unilateral and arcuate; filaments 9–12 mm long, exserted 7–9 mm from tube; anthers parallel, 4–6 mm long, white; pollen white. *Style* arching over stamens, dividing between base and middle of anthers; branches 4–5 mm long, forked for slightly more than $^1/_2$ their length, recurved. *Capsules* ovoid, 6–7 mm long, with auricular lobes above locules. *Seeds* globose, ± 1.2 mm diam., flattened at chalazal end, smooth, brown. *Chromosome number* $2n = 16$. *Flowering time*: mid-August to mid-September.

Distribution and biology: restricted to west-central and northern Namaqualand, *Lapeirousia spinosa* extends from the Orange River at Arris Drift southward to Wallekraal, east of Hondeklipbaai (Figure 20). Although not yet recorded in Namibia, *L. spinosa* almost certainly occurs there, as it grows close to the south bank of the Orange River, the border of that country. Plants are usually found in compacted sandy soil in places where the ground is covered by small quartz pebbles, but on the plains west of Anenous Pass, *L. spinosa* occurs in its thousands in light clay devoid of stones. The species is most common in the north of its range, from the Anenous plains to the Orange River, but populations occur below the main Namaqualand escarpment as far south as Wallekraal. The lightly scented flowers appear to be pollinated by anthophorid bees, but pollinator activity, observed only in the Anenous Pass area, is low and more observations are needed. It seems likely that noctuid moths also visit and pollinate the species, as they do in *L. divaricata*, which has nearly identical flowers.

Diagnosis and relationships: early collections of *Lapeirousia spinosa* were first included in the broadly similar *L. divaricata* and Goldblatt (1972) treated it as var. *spinosa* of that species. The flowers of the two are alike in their white (or palest pink) perianth, short perianth tube, lower three tepals united with the upper laterals for several mm, and tooth-like median ridges on the lower tepals. Goldblatt & Manning (1994) raised var. *spinosa* to species rank due to their quite separate geographic ranges, different habitats and differences in flower size and corm shape. Flowers of *L. spinosa* are larger, have a perianth tube 9–12 mm long and a dorsal tepal 18–23 mm long compared with a tube 7–10 mm long and dorsal tepal 14–16 mm long in *L. divaricata*. The latter, restricted to moist, sandy habitats in the Bokkeveld, Cederberg and Olifants River Mtns, usually seasonally waterlogged, is also taller, has relatively lax spikes, bell-shaped corms and corm tunics with margins minutely serrated. *L. spinosa* occurs on dry, well-drained sandy flats, is a fairly compact plant, and has obconic corms and tunics with prominent, laterally directed spines.

History: an early collection of *Lapeirousia spinosa* at the Kew Herbarium, without date, locality or collector but annotated 'Herb Forsyth' indicates its source – William Forsyth's private herbarium, auctioned by Sotheby's in 1835 and purchased for the Kew Herbarium. The collector may have been William Paterson who collected in Namaqualand in the late 1700s. Forsyth supported Paterson for a time, which explains how he acquired some of

Paterson's collections. The species was recollected in August 1883 by Harry Bolus east of Port Nolloth on his only expedition to Namaqualand, which he had reached by ship from Cape Town. The species remained confused with the superficially similar *L. divaricata* until treated as var. *spinosa* of that species by Goldblatt (1972). Later collections made it clear that the taxon merits separate species rank (Goldblatt & Manning 1992). Although floral morphology suggests the two species are related, they have different corms, those of *L. divaricata* lacking the prominent lateral spines found in of *L. spinosa*. Molecular studies retrieve the species in separate clades and we now place *L. spinosa* in sect. *Lapeirousia*, whereas *L. divaricata* is nested in sect. *Chasmatocallis*.

Specimens examined

SOUTH AFRICA. NORTHERN CAPE.—**2816** (Oranjemund): stony gravel flats near Arrisdrif, 31 Aug. 1925, (–DA), *Marloth 12389B* (PRE). **2817** (Vioolsdrif): 5 km east of Eksteenfontein, quartzite plain, (–CD), 1 Sept. 1986, *Williamson 3610* (MO, NBG). **2916** (Port Nolloth): between Port Nolloth and Holgat, Sept. 1929, (–BB), *M. Schlechter s.n.* (PRE, NBG); between Port Nolloth and Eleven Mile Station, 22 Aug. 1883, (–BD), *H. Bolus 6577* (BOL). **2917** (Springbok): Richtersveld, Anenous Flats, Farm Grasvlakte, (–AB), 15 Sept. 1992, *Goldblatt & Manning 9456* (MO); road to Eksteenfontein, 4 km north of Port Nolloth highway, deep sand, (–AB), 8 Sept. 1980, *Goldblatt 5730* (K, MO, NBG, PRE, S, WAG); 8 km west-northwest of Vaalheuvel, Stryd River valley, 24 Aug. 1957 (–AD), *Acocks 19428* (PRE); stony river valley near Harras House, (–AD), 24 Aug. 1980, *Van Berkel 237* (MO, NBG); 5.7 km from N7 on road to Kommagas, from Wildepaardehoek–Koingnaas intersection, common on quartzite pebble areas, (–CD), 21 Aug. 2002, *Goldblatt & Porter 12088* (MO, NBG, PRE); Komaggas, (–CD), 9 Sept. 1950, *Barker 6675* (NBG). **3017** (Hondeklipbaai): 4 km from Wallekraal to Kamieskroon, stony ground, (–BC), 28 Sept. 1976, *Goldblatt 4246* (MO, NBG, PRE); Wallekraal, (–BC), 30 Aug. 1935, *Compton 5420* (BOL, NBG).

21. **Lapeirousia tenuis** *(Goldblatt) Goldblatt & Manning* in Novon 4: 344 (1994). *L. divaricata* var. *tenuis* Goldblatt: 66 (1972). Type: South Africa, [Northern Cape], between Eleven Mile Station and Oograbies Poort (Port Nolloth and the mountains of the interior), 23 Aug. 1883, *H. Bolus 6575* '*Lapeirousia divaricata* Baker' (BOL, holo.!; G, K!, SAM!, iso.).

[*tenuis* – slender or thin, referring to the flowers with narrow, almost linear tepals.]

Plants 60–160(–220) mm high, mostly 2–3-branched or unbranched; branches produced well above ground level; stem lightly compressed, oval in section, occasionally lightly or obscurely angled, angles smooth. *Corm* broadly obconic (triangular in outline), 10–15 mm diam., up to 40 mm below ground; tunics dark brown to blackish, basal margins with fine laterally extended teeth 1–3(–4) mm long, often massively accumulating. *Leaves* 3–4, only lowermost well-developed, straight and linear or falcate, usually ± as long as to twice as long as stem, rarely slightly shorter, 2–3(–4) mm wide, corrugately ribbed; remaining leaves < $^1/_2$ as long as lowermost and progressively more bract-like above. *Inflorescences* spikes of 9–16 flowers, lateral spikes with fewer flowers, 2-ranked in bud, becoming spiral after anthesis; outer bract grey-green, transparent on veins, acute, 7–11 mm long, folded on midline but not keeled, apices acute and curving upward, inner bract $^1/_2$ to $^1/_3$ as long as outer, transparent with two green keels, forked at tip. *Flowers* zygomorphic, pale lilac-pink, lower tepals each with darker blotch or streak in midline and claw-like cusp near base, cusp ± white surrounded basally by red-purple zone, occasionally upper lateral tepals also lightly marked in lower $^1/_2$, lightly sweet scented; perianth tube 10–15 mm long, slender below, curving outward and wider in upper $^1/_3$; tepals narrowly lanceolate to ± linear, dorsal 9–11 × 2–3 mm, ± erect, upper laterals recurving from base, lower 3 united for ± 2 mm, extending horizontally below, flexed downward distally. *Stamens* unilateral, ± erect; filaments ± 6 mm long, exserted ± 3 mm from tube; anthers ± 3 mm long, parallel, light purple; pollen ± white. *Style* straight, adaxial to stamens, dividing between middle and apex of anthers; branches ± 2.5 mm long, deeply divided and recurved. *Capsules* globose-trigonous, ± 4–5 mm long. *Seeds* globose, 1.6–2.0 mm diam., smooth, brown, glossy. *Chromosome number* unknown. *Flowering time*: mainly in July, occasionally mid- to late August, and once recorded in bloom in early September.

Distribution and biology: poorly known and evidently rare, *Lapeirousia tenuis* appears to be restricted to coastal central Namaqualand (Figure 20). All but two of the few known collections are from the coastal plain north and east of Kleinzee suggesting a very local distribution. The remaining two collections lack precise locality data, but at least one is from some distance to the north, inland from Port Nolloth. The Namaqualand coast between Port Nolloth and Hondeklipbaai is not well collected and the distribution of *L. tenuis* may be wider than the present record suggests. The species favours stony gravel slopes and is most often found in fine sandy clay mixed with granite and quartzite pebbles. At one site we have seen it growing close to *L. spinosa* and *L. macrospatha*, and a clear distinction was evident in the habitat preferences of the three. *L. tenuis* grew on sloping ground in pebbly places, *L. spinosa* grew on flat, less stony ground, and *L. macrospatha* was restricted to deep sands on flat ground.

Diagnosis and relationships: although when first accorded formal taxonomic rank, *Lapeirousia tenuis* was regarded as a variety of *L. divaricata* (Goldblatt 1972), additional collections of the latter, and of the related *L. spinosa*, also regarded by Goldblatt as a variety of *L. divaricata*, make it clear that three species are involved. They share spiny corm tunic rims and comparatively small bracts but the flowers differ markedly. In both *L. divaricata* and *L. spinosa* the lower tepals are united with the upper laterals for some distance and the lower tepals have large, tooth-like median ridges. This is not the case in *L. tenuis*, the narrow tepals of which spread ± uniformly from the apex of the perianth tube. The lower tepals appear to be united for a short distance but are not fused to the upper tepals at all, and they have claw-like basal cusps rather than tooth-like median ridges.

History: discovered by Harry Bolus in August 1883 east of Port Nolloth, and recollected much later by Rudolf Marloth in 1925, *Lapeirousia tenuis* was at first identified as *L. setifolia* (the name then used for *L. divaricata*). The narrow tepals and distinctively obconic corm with spiny basal margins prompted Goldblatt (1972) to treat the four collections then known as a separate varieties of *L. divaricata*. As the latter has become better known, it was evident that *L. divaricata* is restricted to the northwestern Cape, and that the two Namaqualand variants deserve species rank. The spiny corm tunics of *L. tenuis* appear to most closely resemble those of *L. dolomitica* and *L. lewisiana* rather than *L. divaricata* and molecular studies retrieve them as only distantly related. *L. tenuis* and *L. spinosa* are retrieved as a terminal species pair in our molecular phylogeny.

Representative specimens

SOUTH AFRICA. NORTHERN CAPE.—**2917** (Springbok): 15 km north of Kleinzee, (–CA), 24 July 1983, *Van Wyk s.n.* (BOL); 8 km north of Grootmis [Grootmist], (–CA), 20 Aug. 1952, *Hall 579* (NBG); (K, MO, NBG, PRE); sandveld between Grootmis and Springbok, (–CA/CB), 28 July 1937, *Verdoorn & Dyer 1882* (PRE); Spektakel–Kleinzee road, 1 mile [1.5 km] east of Langhoogte Mine, (–CB), 25 Aug. 1993, *Goldblatt & Manning 9651* (K, MO, NBG, PRE), 17 Aug. 1980, *Van Berkel 196* (MO, NBG); 62 km west of Springbok, road to Grootmis, (–CB), 21 Aug. 1994, *Goldblatt & Manning 9935* (MO, NBG); ± 6 km north of Uguabis [not Uhabis, northeast of Vioolsdrif in Namibia], 6 Sept. 1925, (–DA), *Marloth 12665* (PRE).

22. **Lapeirousia violacea** *Goldblatt* in Contributions from the Bolus Herbarium 4: 59 (1972). Type: South Africa, [Western Cape], Biedouw Valley, 26 Aug. 1970, *Goldblatt 569* (BOL, holo.!; K!, MO!, iso.).

[*violacea* – 'violet', the flower colour.]

Plants 60–100 mm high, simple or 1–4-branched from near base, stem lightly compressed, generally 1-angled, angles decurrent on leaves or bract keels. *Corm* broadly obconic, 8–10 mm diam.; tunics dark brown, with light vertical ridging, basal rim with spreading spines 2–5 mm long. *Leaves* 4–6 (or more when stem branched), lowermost longest, generally shorter than stem and ascending, narrowly lanceolate or falcate, 5–7 mm wide, corrugately ribbed other leaves $^1/_2$ as long or less, only lightly ribbed, upper of these often bract-like. *Inflorescences* (2)3 or 4-flowered spikes; outer bracts pale green, firm, 15–22(–30) mm long, folded and keeled in midline, keels minutely crisped, often 2–3 mm wide near apex; inner bracts mostly green with broad transparent margins, $^2/_3$ to ± as long. *Flowers* zygomorphic, dark violet, lower tepals each with dark purple to red spear-shaped basal mark and white lines along lower margins; when fully open tepals held ± in one plane, lowermost or all three lower tepals bearing a small basal claw-like cusp; perianth tube 35–40 mm long, slender, widening and curving toward apex; tepals unequal, narrowly lanceolate, dorsal largest, ± 10 × 5 mm wide, sepa-

FIGURE 21.—*Lapeirousia violacea*, *Goldblatt & Manning 10290*. Scale bar: 10 mm. Artist: John Manning.

rated from others, upper lateral tepals reflexed, lower 3 tepals joined basally for 3–4 mm, free parts held closely together, 7–8 × ± 4 mm. *Stamens* unilateral, ± erect; filaments ± 9 mm long, exserted ± 5 mm from tube; anthers ± 2.5 mm long, purple; pollen purple. *Style* dividing opposite base or middle of anthers, style branches ± 2 mm long, deeply forked and recurved. *Capsules* oblong-trigonous, remaining enclosed in bracts, 9–11 mm long, without locular ridges. *Seeds* globose, slightly domed outward at chalazal end, 1.1–1.3 mm diam., light brown. *Chromosome number* $2n = 16$. *Flowering time*: August to mid-September. Figure 21.

Distribution and biology: *Lapeirousia violacea* is restricted to the mountains and intermontane valleys of northwestern Western Cape and adjacent Northern Cape, where it extends from the valleys of the Biedouw and Doorn rivers in the south through Botterkloof as far north as Papkuilsfontein south of Nieuwoudtville (Figure 22). Plants grow in sandy soil, mostly in stony ground, and tend to be scattered and seldom common. Surprisingly, they seem to occur with the same frequency in valley bottoms as on exposed hilly sites. Plants are often found growing sympatrically with *L. jacquinii*, which has flowers nearly identical in colour, shape and size. They share the same pollinators, *Prosoeca* sp. and *P. peringueyi* (Nemestrinidae), long-proboscid flies that pollinate several species of *Lapeirousia* and *Babiana* that have dark blue to purple, violet or red, long-tubed flowers (Goldblatt et al. 1995). Despite their sympatry and sharing the same pollinators, no hybrids between the two are known. Both *L. violacea* and *L. jacquinii* are self-compatible and facultatively autogamous, but are, we assume, frequently outcrossing, for both species are regularly visited by *Prosoeca* species in the wild. As in most *Lapeirousia* species, the flowers close at night and in cool weather.

Diagnosis and relationships: the dark violet flowers with reddish to purple and white markings on the lower tepals of *Lapeirousia violacea* are so like those of *L. jacquinii* that plants must be examined closely to tell them apart, especially as they sometimes grow together. The two differ in their floral bracts and corms and examination of these organs makes them easy to distinguish. The corms of *L. jacquinii* are bell-shaped and lack the long spiny, laterally projecting teeth typical of the obconic corms of *L. violacea*, which has inflated outer bracts folded or slightly keeled, thus very different from the shorter, typically 2-keeled bracts of *L. jacquinii*. Despite the similarity of their flowers, *L. violacea* and *L. jacquinii* are not immediately related and are here assigned to separate sections of the genus, an action supported by our molecular phylogeny. The bracts and especially the obconic, basally toothed corms of *L. violacea* suggest a close relationship with *L. dolomitica* and its allies of Namaqualand and southern Namibia as well as *L. purpurea* from the Swartruggens Mtns of Western Cape.

History: evidently recorded in 1897 by Rudolf Schlechter, who gave his collection the manuscript name *L. affinis*, *Lapeirousia violacea* remained undescribed until 1972 when it was formally named (Goldblatt 1972). Schlechter's epithet was most likely intended to refer to the similarity of the flowers to those of the common and sometimes sympatric and co-blooming *L. jacquinii*.

Representative specimens

SOUTH AFRICA. NORTHERN CAPE—**3119** (Calvinia): Nieuwoudtville Escarpment, Farm Papkuilsfontein, (–AC), 5 Sept. 1995, *Goldblatt & Manning 10290* (MO,

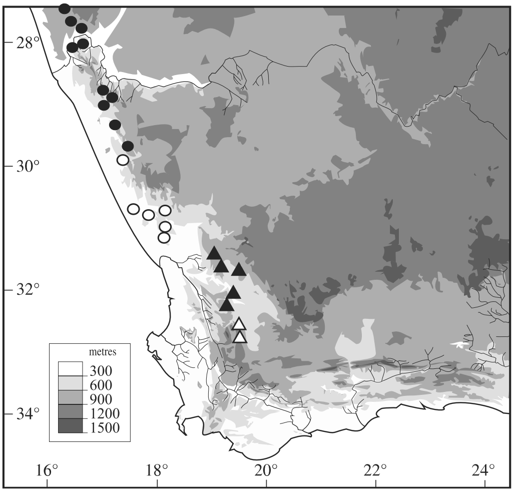


FIGURE 22.—Distribution of *Lapeirousia dolomitica*, ●; *L. lewisiana*, ○; *L. purpurea*, Δ; *L. violacea*, ▲.

NBG); Lokenburg, (–CA), *Barker 1308* (NBG), *Leistner 324* (PRE); Karoskloof, Ceres Karoo, (–DC), 27 Aug. 1983, *Bayer 3507* (NBG).

WESTERN CAPE—**3119** (Calvinia): top of Botterkloof Pass, among sandstone rocks and pavement, (–CC), 31 Aug. 2006, *Goldblatt & Porter 12730* (MO); 1 mile [1.5 km] south of Doorn River bridge, (–CC), *Lewis 2345* (SAM). **3219** (Wuppertal): Biedouw Valley, Welbedacht (growing with *L. jacquinii*), (–AA), 5 Sept. 1991, *Goldblatt 9197* (MO); Lammkraal, (–?AA), 14 Aug. 1897, *Schlechter 10841* (BOL, GRA, K, MO).

23. **Lapeirousia purpurea** *Goldblatt & J.C.Manning*, sp. nov.

TYPE.—South Africa, Western Cape, 3219 (Wuppertal): Swartruggens, Gansfontein, rocky sandstone slopes, (–DA), Sept. 2008, *Manning & Roux 3179* (NBG, holo.; K, MO, PRE, S, iso.).

Plants 100–150 mm high, simple or few- to many-branched, mostly from base, stem compressed and 1- or 2-angled. *Corm* triangular in outline, basal rim prominently serrated, 24–28 mm diam. at base. *Leaves* several, the basal ribbed, $^1/_3$ to ± as long as stem, to 5 mm wide, upper leaves progressively smaller above, smooth, the uppermost resembling floral bracts. *Spike* 6–10-flowered; bracts green, outer 10–18 mm long, with shallow, slightly serrated keel, inner ± $^1/_3$ to $^1/_2$ as long as outer, membranous with two darker keels, notched at apex. *Flowers* blue-purple, lower tepals with V-shaped white mark above base surrounded by darker violet to ± black zone, lower median tepal with a small claw-like tooth above base, unscented; perianth tube slender below, widening and curving outward in upper $^1/_3$, 35–38 mm long; tepals unequal, dorsal erect, ovate, ± 15 × 6 mm, upper laterals slightly smaller, recurved, lower tepals united basally for ± 3 mm, curving downward, ± 8 × 4 mm. *Stamens* unilateral, arcuate; filaments ± 7 mm long, exserted ± 3 mm from mouth of tube; anthers suberect, prominently tailed, ± 4 mm long; pollen yellow. *Style* arching above stamens, dividing opposite lower $^1/_3$ to middle of anthers, style branches ± 3.5 mm long, divided for slightly > $^1/_2$ their length. *Capsules* ovoid, ± 12 mm long, showing outline of seeds, with moderately well-developed locular ridges. *Seeds* unknown. *Chromosome number* unknown. *Flowering time*: September. Figure 23.

Distribution and biology: *Lapeirousia purpurea* is known from just two collections from interior valleys of the Swartruggens that drain into the Tanqua Basin (Figure 22). Plants grow in sandy soil among sandstone rocks. The intensely blue-purple flowers with white markings on the lower tepals and long perianth tube exhibit the typical adaptations for the *Prosoeca peringueyi* long-proboscid fly pollination system (Goldblatt & Manning 2000). Floral biology of the species remains to be investigated.

Diagnosis and relationships: first collected in September 2008, *Lapeirousia purpurea* is a surprising discovery, and emphasises the pattern of local endemism of so many members of the Cape flora. The corms, triangular in profile, have fine teeth projecting from the base, and resemble closely corms of *L. dolomitica*, *L. lewisiana* and *L. violacea*, also long-tubed species. *L. violacea* can be distinguished by the rich violet colour of the perianth with the upper lateral tepals strongly reflexed and the lower three tepals with a V-shaped white mark above the base surrounded by a dark violet to black zone. The lower median tepal bears a small claw-like cusp near the base. In *L. violacea* all three lower tepals usually bear a small tooth near the base, but such teeth are lacking in *L. dolomitica* and *L. lewisiana*.

Additional specimens

SOUTH AFRICA. WESTERN CAPE.—**3219** (Worcester): Swartruggens, De Mond to Farm Elandsdrif, Kaggakamma Nature Reserve (–DA), Sept. 2007, *Harrower 3590* (NBG).

24. **Lapeirousia dolomitica** *Dinter* in Repertorium specierum novarum regni vegetabilis 29: 255 (1931); Goldblatt: 61 (1972). Type: Namibia, Alicetal, pump station near Pomona, June 1929, *Dinter 6432* (B, holo.!; BM!, BOL!, G!, GH!, K!, iso.).

Plants (50–)100–150 mm high, simple or 1–2-branched from base, stem terete or compressed and 2-ridged to 2-winged below first flower. *Corm* 10–15 mm diam., broadly conic (triangular in outline); tunics dark brown, rugose, basal rim with well-developed, laterally projecting spines. *Leaves* 1–3, lowermost basal

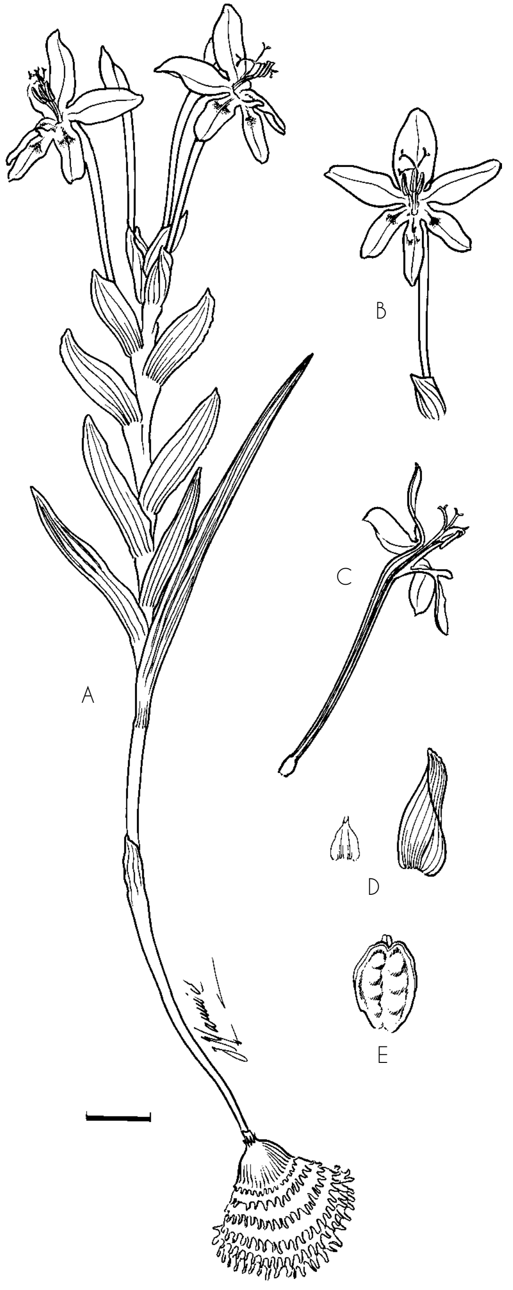


FIGURE 23.—*Lapeirousia purpurea*, *Manning & Roux 3179*. A, plant; B, flower; C, half flower; D, outer (right) and inner (left) bracts; E, capsule. Scale bar: 10 mm. Artist: John Manning.

and longest, straight to falcate, 100–150 mm long, usually ± as long as stem, 3.5–5.0 mm wide, strongly ribbed, smooth or minutely papillate along rib margins, remaining leaves much smaller, resembling floral bracts. *Inflorescences* spikes of (5–)8–15 flowers, initially 2-ranked, becoming spiral; outer bract 12–20 mm long, pale to dark green, margins hyaline or red, semi-transparent over veins, inflated, ± round in section, abaxial surface weakly keeled, keels usually restricted to distal half, inner bract $^1/_2$ to $^1/_3$ as long as outer, with two broad green keels. *Flowers* zygomorphic, pale blue to violet or lilac, lower 3 tepals partly or entirely yellow near base and darker blue or purple in median upper half, sometimes with short median ridges near base usually curving downward, sometimes sweetly scented; perianth tube slender, ascending, arching outward near apex, 25–35(–40) mm long (in severely stressed plants occasionally less than 25 mm); tepals unequal, lanceolate and acute, dorsal longest and erect, (12–)15–17 × 5–7 mm, narrowed below, upper laterals lightly shorter, spreading or reflexed, lower 3 tepals united for 2–3 mm, slightly narrowed toward base, held closely together, (10–)12–14 mm long. *Stamens* unilateral, ± erect; filaments ± 10 mm long, exserted 2–4 mm, arching outward; anthers 4.0–4.8 mm long, parallel, purple or cream, pollen lilac or cream. *Style* arching adaxial to stamens, usually dividing opposite middle $^1/_3$ of anthers (rarely below anther bases in northern populations), dark violet; style branches 3–4 mm long, recurved, divided for $^1/_2$ their length. *Capsules* ovoid-oblong, weakly trigonous, 12–14 mm long, without locular ridges, usually warty or papillose. *Seeds* globose, chalazal end somewhat flattened, ± 1.8 mm diam., glossy dark brown. *Chromosome number* $2n = 16$. *Flowering time*: June to late July, sometimes in August.

Distribution and biology: restricted to the most arid parts of the southern African winter rainfall zone, *Lapeirousia dolomitica* is most common in northern Namaqualand but extends north into southwestern Namibia as far as Pomona (Figure 22). It is probably fairly common in southern Namibia although the number of collections from there is scant owing to the rough terrain and few passable roads. Despite the epithet *dolomitica* the species does not normally grow in dolomite or any other type of limestone but it seems to favour rocky situations where the parent rock is at least partly quartzite and does not often grow in the granite-derived soils that predominate in Namaqualand.

Although variable in flower colour, perianth tube length and even for presence of fragrance, *Lapeirousia dolomitica* is most probably consistently pollinated by the long-proboscid nemestrinid fly, *Prosoeca peringueyi*. We wonder whether floral fragrance, notable only in populations with pale blue flowers, is merely an added attraction, or signifies an alternative pollinator here, then most likely moths.

Diagnosis and relationships: *Lapeirousia dolomitica* is recognised by its distinctive, obconic corms with blackish, rough-surfaced tunics bearing prominent spines extending outward from the base and the rather inflated bracts with only weakly developed keels. When seen alive the bracts are unusual in having alternating longitudinal bands of pale translucent and dark opaque colouring. The flowers are pale blue, lilac, or said in some collections to be violet, always with pale yellow markings at the bases of the lower tepals and sometimes short, tooth-like basal ridges. Among the long-tubed species of *Lapeirousia*, it has a shorter than usual perianth tube, mostly 25–35 mm long. In overall appearance flowers of *L. dolomitica* are particularly reminiscent of the central Namaqualand species, *L. tenuis* but this species has a perianth tube 10–15 mm long and very well-developed, tooth-like ridges on the lower tepals. The two also have similar corms.

In an earlier treatment of *Lapeirousia dolomitica*, Goldblatt (1972) recognised two subspecies, the northern subsp. *dolomitica* and the central and southern Namaqualand subsp. *lewisiana*. Additional collections of both, then poorly collected, have shown that their differences are consistent and of greater degree than usual for subspecies and we now recognise the latter as a separate species, *L. lewisiana*. The two share similar corms with spiny basal margins but that character has been documented in *L. spinosa*, *L. kamiesmontana* and *L. violacea* as well. Another shared feature, not until now recognised, are particularly long style branches, up to 4 mm long. However, smooth leaves in *L. dolomitica* versus sparsely hairy leaves in *L. lewisiana* plus differences in capsule surface texture, perianth tube length, perianth colour and markings, and shape of the lower tepals emphasise their differences (Table 5). *L. dolomitica* always has paler coloured flowers with a somewhat shorter tube, mostly 25–35 mm long, whereas *L. lewisiana* has larger, deep magenta red flowers with a tube mostly 40–48 mm long. The bracts of *L. dolomitica* are only lightly inflated and generally have weakly developed keels but *L. lewisiana* has strongly inflated bracts lacking keels. Lastly, the capsules of *L. dolomitica* are often papillose to warty but the character is not consistent in the species. Capsules of *L. lewisiana* are always smooth as are those of other species of the genus.

Representative specimens

NAMIBIA.—**2715** (Bogenfels): Sperrgebiet, east of Pomona, (–AB), 3 Aug. 2001, *Smook 11128* (MO, PRE, WIND); Klinghardt Mtns, west-facing slopes, (–BC), 26 July 1977, *Müller 660* (M, WIND). **2716** (Witputz): Sperrgebiet, Auros Mtns, eastern side of highest peak, 905 m, quartzite slope, (–CB), 10 Aug. 2001, *Smook 11307* (PRE); Auros Mtns, (–CB), 11 Aug. 2001, *Smook 11335* (MO, PRE); Zebrafontein 87, rocky ground, ± 1 100 m, (–DA), 11 Sept. 1973), *Giess 12887* (M, NBG, PRE, WIND); 22 Aug. 1983, *Venter 8918* (PRE); Witputs, (–DA), July 1939, *Herre s.n.* (BOL 30721); 12 km west of Lorelei Mine, riviergeröll, (–DD), 30 Aug. 1963, *Merxmuller & Giess 3318* (M, WIND). **2718** (Grünau): Karas District, Aurus Mtns, saddle overlooking Roter Kamm, rock cracks, (–CB), 27 Sept. 1996, *Mannheimer & Mannheimer 334* (PRE, WIND). **2816** (Oranjemund): Rooilepel summit, July 1989, (–BA), *Williamson 4262* (NBG); quartz ridges north of Obib, (–DA), 1 Sept. 1963, *Merxmuller & Giess 3420* (BR, M, WIND).

SOUTH AFRICA. NORTHERN CAPE.—**2816** (Oranjemund): Daveras Diamond Area 1, (–BB), June 1977, *Williamson 2551* (BOL); Richtersveld, Numees, (–BD), Aug. 1983, *Jurgens 20* (PRE); gravel flats at Arrisdrif, 70 m, (–DA), 31 Aug. 1925, *Marloth 12389a* (PRE). **2817** (Vioolsdrif): between Eksteenfontein and Little Helskloof, rocky outcrop among quartz pebbles, (–CA), 9 Aug. 1979, *Snijman 163* (NBG); Stinkfontein Mtns, near foot of Cornelsberg, (–CA), 22 Aug. 1994, *Goldblatt & Manning 9949* (MO, NBG, PRE); 10 km west of Eksteenfontein, (–CC), 9 Aug. 1986, *Williamson 3539* (BOL, NBG); 20 km west of Eksteenfontein, (–CD), 1 Sept. 1986, *Williamson 3606* (MO, NBG); east of Eksteenfontein in open quartz pebble sites, (–CD), July 1989, *Williamson 4276* (NBG). **2917** (Springbok): Lekkersing, (–AA), 230 m, 24 Aug. 1925, *Marloth 12278* (PRE); Karuchab Poort south of Lekkersing, (–AA), 18 Aug. 1970, *Tölken s.n.* (BOL 30720); mountains north of Grasvlakte on Eksteenfontein road, (–AB), Aug. 1992, *Goldblatt & Manning 9308* (MO, NBG, PRE).

25. **Lapeirousia lewisiana** *B.Nord.* in Botaniska Notiser 123: 434 (1970). *L. dolomitica* subsp. *lewisiana* (B.Nord.) Goldblatt: 64 (1972). Type: South Africa, [Western Cape], Komkans, 11 Aug. 1962, *Nordenstam 965* (NBG, holo.!; S!, iso.).

Plants (50–)100–200 mm high, simple or 2-branched from base, stem terete or compressed and 2-ridged to 2-winged below first flower. *Corms* 10–15 mm diam., broadly obconic; tunics dark brown, rugose, basal rim with well-developed, slender, laterally projecting spines. *Leaves* 1–3, lowermost basal and longest, straight to somewhat falcate, 100–150 mm long and usually ± as long as stem, 3.5–5.0 mm wide, strongly ribbed, sparsely and irregularly white-hairy on rib edges at least in lower half, remaining leaves small, resembling floral bracts. *Inflorescences* spikes of up to 14 flowers; outer bract ± 20 mm long, inflated, usually rounded and without keels except occasionally near tips. *Flowers* reddish purple to magenta, lower tepals with broad ± white median streak in lower, narrow half and darker red-purple blotch in upper centre; perianth tube (35–)40–48 mm long; tepals unequal, lanceolate to ± spathulate or obovate, apex acute or rounded, dorsal ± 12 × 6–7 mm, lower 3 united for ± 3 mm, narrow at base for 2–3 mm, held at ± 45° to horizontal, ± 10 × 5.5 mm. *Stamens* unilateral, ± erect; filaments exserted ± 3.5 mm; anthers 3–4 mm long, dark violet. *Style* arching over stamens, between middle and apex of anthers, style branches 3–4 mm long, recurved, divided for $^{1}/_{2}$ their length. *Capsules* ovoid-oblong, weakly trigonous, 12–14 mm long, without locular ridges, smooth. *Seeds* globose, ± flattened at chalazal end, 1.9–2.2 mm diam., glossy dark brown. *Flowering time*: mid-July to mid-August. Figure 24.

Distribution and biology: never common, *Lapeirousia lewisiana* is recorded from several collections from central and southern Namaqualand. It is best known from the area between Garies and Bitterfontein, but also occurs locally to the west toward the coast (Figure 22). The type locality is in the extreme southern end of its range near Komkans, west of Nuwerus. An isolated population from near Komaggas is the most northern record.

Diagnosis and relationships: described in 1970 and shortly thereafter reduced to subspecies rank in *Lapeirousia dolomitica* (Nordenstam 1970; Goldblatt 1972), the status and affinities of *L. lewisiana* have proven difficult to assess. With several additional records of both taxa now available, we consider it most useful to treat them as separate species. Although they share virtually identical obconic corms with prominent, spreading marginal spines, and long tubed flowers, several differences between them have been confirmed in all new collections. These include different flower colour and markings, perianth tube length and leaf vestiture. *L. lewisiana* has magenta red (also sometimes described as purple) flowers, the lower three tepals with prominent white, median streaks in the proximal $^{1}/_{3}$, and the perianth tube is typically 40–45 mm long (Table 5). Unusual for *Lapeirousia*, the basal foliage leaf is finely, but sparsely, hairy in all specimens we have examined. In contrast *L. dolomitica* has smooth leaves, a pale blue to violet perianth with paired white streaks on the lower tepals, a perianth tube 25–35 mm long, rarely slightly longer. Capsules are poorly known in *L. dolomitica*, but are slightly warty or papillose where recorded, whereas *L. lewisiana* has smooth capsules. There are also slight differences in the bracts of the two species, although somewhat inflated in both:

TABLE 5.—Comparison of critical taxonomic features of *Lapeirousia dolomitica*, *L. kamiesmontana* and *L. lewisiana*

Species	Leaf surface	Perianth colour	Lower tepal markings	Perianth tube, mm	Capsule surface
L. dolomitica	smooth	pale blue to pale lilac	white-edged blue to violet	25–35(–40)	often warty or papillose
L. kamiesmontana	± hairy	white	red	45–56	smooth
L. lewisiana	± hairy	dark magenta-red	white-edged dark magenta	(35–)40–48	smooth

FIGURE 24.—*Lapeirousia lewisiana*, *Goldblatt & Manning 9198*. Scale bar: 10 mm. Artist: John Manning.

bracts of *L. dolomitica* have a weakly developed keel in the distal half, whereas those of *L. lewisiana* are rounded or become slightly folded only along the midline near the tips.

Despite its close relationship to *Lapeirousia dolomitica*, *L. lewisiana* is most easily confused with the common Namaqualand species, *L. silenoides*, which it resembles in its long-tubed, darkly pigmented magenta-red flowers. The latter has the bell-shaped corms without spiny projections of any sort that place it in sect. *Chasmatocallis*, and the superficial resemblance to *L. lewisiana* is evidently due to convergence for the same pollinator, the long-proboscid fly, *Prosoeca peringueyi*.

Also closely related to *Lapeirousia lewisiana* but readily distinguished from it, *L. kamiesmontana* has similar vegetative features, including the corm tunics with spiny margins and slightly hairy foliage leaf. Flowering later in the season, usually two to three weeks after *L. lewisiana*, even at the same elevation, *L. kamiesmontana* has white flowers, the lower tepals marked with red, the tube and the reverse of the tepals flushed dark red, and a perianth tube mostly 45–56 mm long. We have considered that the two species are closely related but adapted for pollination by different species of long-proboscid flies. An immediate relationship is not, however, supported by the molecular phylogeny (Figure 1).

Representative specimens

SOUTH AFRICA. NORTHERN CAPE.—**2917** (Springbok): Wolfberg-Komaggas, 800 m, (–CB), 23 Aug. 1981, *Van Berkel 364* (MO). **3017** (Hondeklipbaai): Kotzesrus, granitic soil, (–DD), Aug. 1980, *Van Berkel 172* (NBG); 10 km south of Garies on road to Bitterfontein, (–CA), 27 Aug. 1970, *Goldblatt 538* (BOL), 29 Aug. 1991, *Goldblatt & Manning 9198* (K, M, MO, NBG, PRE); 8.5 km north of Garies on the road to Leliefontein, (–CA), 19 Sept., 1991 (fr.), *Goldblatt 9269* (MO, NBG, PRE); 30 km south of Garies, stony east-facing slope, (–CC), 2 Aug. 1994, *Goldblatt & Manning 9893* (MO, NBG).

WESTERN CAPE.—**3118** (Vanrhynsdorp): 4 km north of Farm Komkans, Geelkop, stony quartzite, (–AA), 7 Sept. 1974 (fl. & fr.), *Nordenstam & Lundgren 1715* (MO, NBG, S).

26. **Lapeirousia kamiesmontana** *Goldblatt & J.C.Manning*, sp. nov.

TYPE.—South Africa, Northern Cape, 3018 (Kamiesberg): between De Kom and Garies, (–AC), 27 Aug. 1976, *Goldblatt 3980* (NBG, holo.; K, MO, PRE, S, iso.).

Plants 100–180 mm high, simple or 2-branched from base; stem round to slightly compressed. *Corm* 10–14 mm diam., broadly obconic; tunics dark brown, rugose, basal rim with long, slender, spreading spines. *Leaves* 1–3, lowermost basal and longest, straight to somewhat falcate, 80–160 mm long, sometimes exceeding flowers, 3.5–5.0 mm wide, strongly ribbed, sparsely woolly (rarely ± smooth), remaining leaves much smaller, resembling floral bracts. *Inflorescence spikes* of (5–)8–10 flowers, initially 2-ranked, becoming spiral; outer bract 10–15 mm long, acute, ± inflated, rounded, without keels, inner bract ± half as long, transparent with 2 green keels. *Flowers* white (pale yellow when dry), flushed red on reverse of tepals and tube, lower tepals with red blotch in lower 1/3 and paired, red lines near base running into throat (purple when dry); perianth tube mostly 45–56 mm long, ± uniformly wide throughout; tepals unequal, obovate and markedly narrowed in basal 2 mm, dorsal 16–18 × (7–)9–10 mm, lower tepals held ± horizontally, united basally for ± 1.5 mm, ± 15 × 5.5–6.5 mm. *Stamens* ± 10 mm long, exserted 2–3 mm; anthers 4.5–5 mm, violet, pollen purple. *Style* dividing opposite anther tips, style branches ± 3.5 mm long, divided for half their length, recurved, white. *Capsules* and *seeds* unknown. *Flowering time*: late August to early October. Figure 25.

Distribution and biology: *Lapeirousia kamiesmontana* is restricted to the southern Kamiesberg where it has been recorded from the flats around the Farm Doornkraal at ± 600 m and in the Langkloof at elevations of up to at least 950 m (Figure 26). The rugged area is poorly explored except alongside the road from Doornkraal to Welkom and we suspect the species has a wider range than is documented. Plants grow in decomposed granitic soil and occasionally in granite outcrops. The form and colour of the long-tubed flowers suggest pollination by long-proboscid flies, but no insect visitors have been recorded for the species.

Diagnosis and relationships: the broadly obconic corm with dark brown, rugose tunics spiny along the rim of *Lapeirousia kamiesmontana* are shared with *L. dolomitica* and *L. lewisiana*. Observations in the field show that the

FIGURE 25.—*Lapeirousia kamiesmontana*, *Goldblatt & Manning 10010*. A, plant and corm; B, half flower; C, outer (left) and inner (right) bracts. Scale bar: 10 mm. Artist: John Manning.

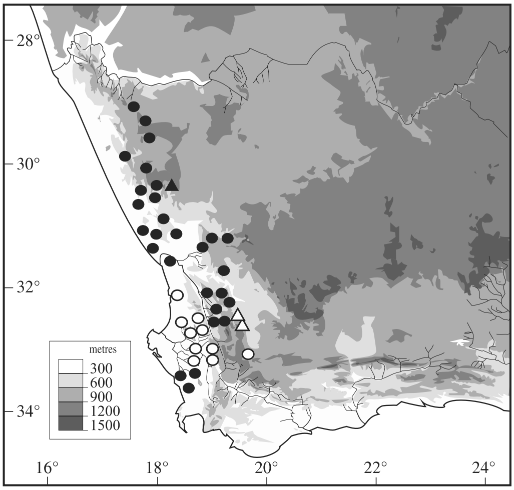


FIGURE 26.—Distribution of *Lapeirousia fabricii* subsp. *compressa*, ○; subsp. *fabricii*, ●; subsp. *purpurascens*, Δ; *L. kamiesmontana*, ▲.

three do not intergrade: relatively late-blooming *L. kamiesmontana* consistently has white flowers with distinctive red markings and a perianth tube mostly 45–60 mm long (Table 5). In contrast, early-blooming *L. lewisiana* has dark red-purple to magenta flowers with white markings and a perianth tube (35–)40–48 mm long. The ranges of the two do not overlap and flowering times, even at the same elevation, are separated by at least two to three weeks, if not longer, in any particular year. We consider *L. kamiesmontana* to be most closely related to *L. lewisiana* despite its position as sister to *L. fabricii* in the molecular phylogenetic study.

Representative specimens

SOUTH AFRICA. NORTHERN CAPE.—**3018** (Kamiesberg): Kamiesberg, Langkloof south of Welkom, (–AC), 20 Sept. 1994, *Goldblatt & Manning 10010* (MO, NBG); Kamiesberg, near Farm Naartjiesdam, south of Karas, (–CA), 1 Sept. 2002, *Goldblatt & Porter 12135* (MO, NBG); Kamiesberg, Rondefontein, slopes south of Nartjiesdam, 780 m, (–CA), 1 Sept. 1975, *Oliver 5969* (NBG, PRE).

27. **Lapeirousia fabricii** *(D.Delaroche) Ker Gawl.* in Curtis's Botanical Magazine 31: sub t. 1246 (1810); Goldblatt: 69 (1972). *Ixia fabricii* D.Delaroche: 18, no. 5 (1766). *Gladiolus fabricii* (D.Delaroche) Thunb.: 186 (1800). *Ovieda fabricii* (D.Delaroche) Spreng.: 147 (1824). *Peyrousia fabricii* (D.Delaroche) Sweet: 499 (1830a). *Meristostigma fabricii* (D.Delaroche) A.Dietr.: 597 (1833). Type: South Africa, Olifants River valley, *Leipoldt s.n.* [*BOL17111*, neo.!, designated by Goldblatt & Barnard: 305 (1970)].

Plants mostly 100–250 mm high, usually 4–6-branched; stem compressed, angled and 2-winged, wings irregularly serrated. *Corm* 10–15 mm diam., broadly obconic; tunics brown, lightly ridged vertically, basal rim with short, spreading spines 1–2 mm long. *Leaves* several, lowermost longest, linear to falcate, ribbed, shorter or longer than stem; remaining leaves cauline, progressively shorter, not or barely ribbed, often subtending branches, upper becoming bract-like. *Inflorescences* (2–)4–8-flowered spikes; outer bract green or flushed red, (10–)14–20(–25) mm long, keeled, acute, margins often reddish, keel crisped or minutely serrate; inner bract transparent with 2 green keels, $^{1}/_{2}$ to $^{2}/_{3}$ as long as outer, forked at apex. *Flowers* zygomorphic, white to pale yellow or beige, purple or rarely pink, usually red or pink on reverse of tepals and tube, lower tepals each with red spot in midline, throat marked with fine red lines inside and out, decurrent on lower part of tube; perianth tube obliquely funnel-shaped, 30–65 mm long, narrow and cylindric below, abruptly expanded into wide upper part up to 10 mm long; tepals usually unequal (rarely subequal), all straight below and continuing upper part of tube as a tepal cup, then spreading horizontally, upper 3 largest, 20–24 × 7–12 mm (subsp. *fabricii*), 15–18 × 7–10 mm (subspp. *compressa* and *purpurascens*), lower 3 with claws ± 4 mm long, limbs 10–20 × 3.0–7.5 mm, each often with short, claw-like cusp arching over limb base. *Stamens* unilateral, arched; filaments 6–10 mm long (subspp. *compressa* and *purpurascens*) or 10–17 mm long (subsp. *fabricii*), exserted 3–7 mm from upper part of tube and 1–3 mm from tepal cup; anthers 3–5 mm long, dark purple; pollen purple. *Style* arching over stamens; branches 3–5 mm long, usually dividing near middle of anthers, forked for $^{1}/_{2}$ their length, recurved. *Capsules* oblong, 10–12 mm long, apices of locules forming ear-like lobes decurrent on low locular ridges. *Seeds* globose, flattened at chalazal end, 1.2–1.3 mm diam. *Chromosome number* 2*n* = 16. *Flowering time*: August to October depending on subspecies, usually fairly late in spring. Figures 27 & 28.

Distribution and biology: widespread in the drier, western half of Western Cape and common in Namaqualand in Northern Cape, *Lapeirousia fabricii* extends from near Steinkopf in the north to Malmesbury in the south and inland to the western edges of the Tanqua Basin along the eastern foothills of the Swartruggens and Cederberg (Figure 26). Plants most often grow in rocky sandstone- or granite-derived soils in mountainous areas, but occasionally in deep, hard sand, or in crevices in rocks. The long-tubed flowers of the typical subspecies are known to be pollinated by long-proboscid flies (Goldblatt et al. 1995; Manning & Goldblatt 1996) and we infer the same pollination for subsp. *compressa* and subsp. *purpurascens*, probably using a different fly species in the latter.

Diagnosis and relationships: the flowers of *Lapeirousia fabricii* are among the largest in the genus, with its long perianth tube and often wide throat. The perianth tube ranges from 30–65 mm long and is usually expanded in the upper 5–10 mm in a short to long cup or gullet. The tepals are shortly clawed, particularly the lower three, which are united basally for ± 2 mm and the erect claws form the upper part of the floral cup. When fully open the lower and sometimes the upper tepal limbs spread at right angles to the tube, or the dorsal is suberect. The lower tepal claws often bear claw-like cusps that arch forward over the limb bases; these cusps are sometimes absent and represented by thickened median ridges. Vegetatively, *L. fabricii* has distinctive flattened, narrowly winged stems, the wings usually minutely crisped or serrated. The well-developed outer floral bracts are ribbed and have crisped to serrated keels.

Variation across the range of *Lapeirousia fabricii* has prompted us to recognise three subspecies, the most common and widespread of which, subsp. *fabricii*, is centred in the northern half of its range. It has predominantly pale yellow to beige flowers with red markings, lower tepals about half as wide as the dorsal, and a perianth tube mostly 50–65 mm long with a wide, deep throat up to 10 mm long. South and west of the Olifants River Mtns, plants that we treat as subsp. *compressa* have white or pale pink flowers with pink markings, lower tepals not or only slightly narrower than the dorsal, a perianth tube 30–45 mm long, and a short, relatively narrow throat usually only ± 5 mm long. The third subspecies, subsp. *purpurascens*, is restricted to the dry interior valleys of the Cederberg and northern Swartruggens and has blue-purple flowers, lower tepals ± $^1/_2$ as wide as the upper and a perianth tube 30–45 mm long. Its flowers also differ from the typical in having a relatively shallow gullet ± 5 mm deep and correspondingly shorter filaments 7–9 mm long.

History: few southern African species have been subjected to as much confusion as *Lapeirousia fabricii*. It was described by D. Delaroche (also de la Roche) in 1766, without illustration and perhaps without a preserved specimen, but, nevertheless, in considerable detail. Thunberg (1784), and later Jacquin (1794: t. 269) and other contemporary botanists, confused the species with *L. anceps*, which has similarly coloured but smaller flowers, and this name was applied to *L. fabricii* even by Baker (1896). The two were not distinguished from one another by most botanists, although Lamarck (1789) and Sweet (1830b) did recognise both *L. fabricii* and *L. anceps*, naming the larger-flowered species *Gladiolus denticulatus* and *Peyrousia aculeata* respectively. Few at the time seem to have associated Pourret's (1788) *L. compressa*, type of the genus, with either *L. anceps* or *L. fabricii*, even when *Lapeirousia* (or the variant *Peyrousia*) was recognised. Because *L. anceps* and *L. fabricii* were regarded as the same species by Baker (1892; 1896), *Schlechter* (1897) described *L. serrulata* for the large-flowered northern form of *L. fabricii*. Unravelling this web of confusion, Goldblatt (1972) recognised *L. fabricii* as distinct from *L. anceps*, but did not recognise infraspecific taxa, although he pointed out the differences between the northern populations, now subsp. *fabricii*, from those in the south of the range, now subsp. *compressa*. The populations we assign to subsp. *purpurascens* were not known at the time.

FIGURE 27.—*Lapeirousia fabricii* subsp. *compressa*, *Goldblatt & Manning 9695*. A, plant; B, half flower; C, capsule. *L. fabricii* subsp. *purpurascens*, *Goldblatt & Manning 13252*. D, flower; E, half flower. Scale bar: 10 mm. Artist: John Manning.

FIGURE 28.—*Lapeirousia fabricii* subsp. *fabricii*, *Goldblatt & Manning 9711*. Scale bar: 10 mm. Artist: John Manning.

Key to subspecies

1a Flowers with deep gullet 9–13 mm long including limbs of lower tepals; perianth usually beige to pale yellow, or ± white, flushed red on reverse, with prominent red stripes in lower throat; filaments 13–20 mm long . . . . 27a. subsp. *fabricii*

1b Flowers with shallow gullet ± 5 mm long; filaments 7–9 mm long:

  2a Perianth white to pale or deep pink; anthers 3–4 mm long; lower tepals only slightly narrower than upper tepals and with or without tooth-like cusps . . . . 27b. subsp. *compressa*

  2b Perianth blue-purple (rarely pink-purple) with red markings; anthers 4–5 mm long; lower tepals ± half as wide as upper tepals and always with short tooth-like cusp near limb base . . . . 27c. subsp. *purpurascens*

27a. subsp. **fabricii**

Gladiolus denticulatus Lam.: 728 (1786), nom. illegit. superfl. pro *Gladiolus anceps* L.f. (1782). *Lapeirousia denticulata* G.H.M.Lawr.: 134 (1955), as nom. nov. pro *G. denticulatus* nom. illegit. Type: South Africa, without precise locality or collector, Herb. Lamarck (P, holo.!).

Peyrousia aculeata Sweet: t 39 (1830b) [*Lapeirousia aculeata* Sweet: 396 (1827), name without description]. *Meristostigma aculeatum* (Sweet) Steud.: 130 (1841). *Ovieda aculeata* (Sweet) Klatt: 777 (1864). *Lapeirousia anceps* var. *aculeata* (Sweet) Baker: 156 (1877). Type: South Africa, without precise locality or collector, illustration in British Flower Garden ser. 2: t. 39 (1830).

Lapeirousia serrulata Schltr.: 432 (1897). Type: South Africa, [Western Cape], Clanwilliam, *Leipoldt 383* (B, holo.!; BOL!, SAM!, iso.).

Flowers pale yellow or beige to ± white, often red or pink on reverse of tepals and tube, lower tepals each with red spot in midline and claw-like projection at top of claw, throat marked with fine red lines inside and out decurrent on lower part of tube; perianth tube mostly 50–65 mm long, slender and cylindric below, expanded upper part 9–13 mm long; tepals unequal, straight below and continuing upper part of tube as a cup for ± 4 mm, then spreading, upper 3 tepals largest, 20–24 × 7–12 mm, lower 3 tepals much narrower, 10–12 × 3–4 mm. *Stamens* with filaments 14–17 mm long, exserted ± 7 mm from tube and ± 3 mm from tepal cup; anthers 5–6 mm long. *Style* dividing between base and apex of anthers, style branches ± 5 mm long. Figure 28.

Distribution: subsp. *fabricii* ranges from near Steinkopf in northern Namaqualand along the Bokkeveld Mtns to Clanwilliam and the Biedouw Valley, and along the Atlantic coast as far south as Darling (Figure 26). The flowers are adapted for pollination by long-proboscid flies. Recorded pollinators include the horse fly, *Philoliche gulosa* and the nemestrinid, *Moegistorhynchus longirostris* (Goldblatt et al. 1995; Manning & Goldblatt 1997).

Representative specimens

SOUTH AFRICA. NORTHERN CAPE.—**2917** (Springbok): Klipfontein, (–CA), *Hutchinson 923* (K); hills at Concordia '*L. maximiliani* Schltr. n. sp.', (–CB), 20 Sept. 1897, *Schlechter 11342* (B, COI, E, G, K, MO); between Brakwater and Kommagas, (–CD), *Barker 22091* (NBG); near top of Spektakel Pass, (–DA), 11 Sept. 1993, *Goldblatt & Manning 9711* (MO). **3017** (Hondeklipbaai): 45 km south of Springbok, (–BB), 15 Oct. 1976, *Goldblatt 3068* (MO); 52 km from Garies to Wallekraal, (–BC), 28 Sept. 1976, *Goldblatt 4215* (MO); Garies, (–DB), *Thorne s.n.* (*NBG61563*); Farm Roodeheuwel, 9 km west of Nariep, (–DC), 28 Sept. 1987, *Reid 1275* (PRE). **3018** (Kamiesberg): border of Western Cape, slopes facing Swartdoorn River, (–CC), 24 Sept. 2008, *Goldblatt & Porter* (MO). **3119** (Calvinia): Grasberg road, northwest of Nieuwoudtville, (–AC), 13 Nov. 1974, *Snijman 30* (NBG); Botterkloof Pass, (–CC), *Hall 3877* (NBG); Soutpan, Calvinia, (–CD), 20 Nov. 1961, *Lewis 5755* (NBG), 13 Oct. 1983, *Goldblatt 7081* (MO).

WESTERN CAPE.—**3117** (Lepelfontein): 40 km from Lutzville to Brand-se-Baai, (–BB), 15 Sept. 2008, *Goldblatt & Porter 13121* (MO, NBG). **3118** (Vanrhynsdorp): Bitterfontein, (–AB), *Salter 1584* (BM); Vredendal Commonage, (–DA), 25 Sept. 1970, *Hall 3845* (HUS, NBG). **3119** (Calvinia): foot of Vanrhyns Pass, (–AC), *Lewis 2903* (SAM). **3218** (Clanwilliam): Clanwilliam, (–BB), *Leipoldt 383* (BOL, P, SAM); between Clanwilliam and Citrusdal, near Patrysberg, (–BD), 8 Nov. 1974, *Boucher 2616* (MO, NBG). **3219** (Wuppertal): Brandewyn River, (–AA), 20 Sept. 1937, *Barker 253* (NBG); 13 Sept. 1947, *Compton 19982* (NBG); Pakhuis Pass, (–AA), 30 Sept. 1940, *Barker 1223* (NBG); Welbedacht, Biedouw, (–AA), 22 Sept. 1952, *Johnson 538* (MO, NBG), 21 Sept. 1952, *Lewis 2511* (SAM); Algeria Forest Station, (–AC), 6 Oct. 1976, *Botha & Coetzee 1723* (PRE); Cederberg, Matjiesrivier Nature Reserve, (–AD), 5 Oct. 1997, *Lechmere-Oertel 871* (NBG); Farm Rockwood (Appalto), 1 km south of homestead, (–CA), 19 Oct. 2001, *Hanekom 3341* (MO, NBG). **3318** (Cape Town): Malmesbury District, near Modder River, north of Bok River, (–AD), 22 Nov. 1970, *Acocks 24489* (PRE); Waylands, Darling, (–AD), *Thompson 82* (NBG); ± 10 km north of Malmesbury between farms Klipfontein and Saamstaan, (–BC), 6 Nov. 1982, *Goldblatt 6714* (K, MO, PRE).

27b. subsp. **compressa** (*Pourr.*) *Goldblatt & J.C.Manning*, stat. nov. *Lapeirousia compressa* Pourr.: 79 (1788). *Ixia lapeirousia* J.F.Gmel.: 108 (1791), nom. illegit. superfl. pro *L. compressa* Pourr. Type: South Africa, without locality, said to have been collected by Philibert Commerson in Isle de France [Mauritius], but probably by Pierre Sonnerat, his colleague, who spent a short time at the Cape en route to Mauritius (P: Herb. Lamarck, holo.!).

Like subsp. *fabricii* in vegetative features. *Flowers* white to ivory or pale (rarely dark) pink, flushed pink to red on reverse, lower tepals with red markings at limb bases; perianth tube 35–55 mm long, expanded in upper ± 5 mm into wide throat; tepals extending upward for ± 3 mm as a cup, spreading distally, dorsal 16–18 × 6–8 mm, lower tepals 15–20 × 5.5–7.5 mm. *Stamens* with filaments 6–10 mm long; anthers 3–4 mm long. *Style* dividing opposite lower to middle $^1/_3$ of anthers, branches ± 3 mm long. *Flowering time*: September to mid-October, occasionally in early November. Figure 27A–C.

Distribution: subsp. *compressa* occurs locally in the upper Olifants River valley, but is more common south and west of the Olifants River Mtns, extending as far south as Moorreesburg. Isolated populations occur to the east along the margins of the Tanqua Basin from the interior Cederberg south to Karoo Poort (Figure 26).

Diagnosis: usually recognised by the nearly subequal tepals and almost radially symmetric flower, subsp. *compressa* has a white to ivory or pink (rarely almost red) perianth, the lower tepals marked with pink to red near the base of the limbs. Vegetatively plants are identical to subsp. *fabricii*. The two subspecies intergrade in the mid- to upper Olifants River Valley at Piekeniers Kloof and south of Citrusdal where it can be difficult to assign plants to subspecies. Further north and to the west and south, plants can readily be recognised as subsp. *fabricii* and have a beige to almost yellow perianth and lower tepals ± half as wide as the upper.

Hybrids between *Lapeirousia fabricii* subsp. *compressa* and *L. jacquinii* have been recorded south of Piketberg near the old bridge over the Berg River where flowering times of the two taxa overlap (*Goldblatt & Manning 9955* MO). We have also seen hybrids between subsp. *compressa* and *L. anceps* at sites where both were in flower and growing together. These are among the few interspecific hybrids known in the genus.

Selected specimens

SOUTH AFRICA. WESTERN CAPE.—**3218** (Clanwilliam): south of Lamberts Bay, (–AB), 20 Sept. 1953, *Taylor 4009* (NBG); Zwartboskraal, northeast of Boekenberg, (–BC), 7 Sept. 1972, *Oliver 3885* (MO, NBG, PRE); Swartrug, Piketberg, east of Engelsman-se-Baken, flats, (–DA), 10 Oct. 1977, *Thompson 3550* (NBG); Piketberg, Moutonsvlei, (–DA), 21 Aug. 1984, *Goldblatt 7201* (MO); road junction south of Het Kruis, (–DB), 20 Sept. 1975, *Wisura 3502* (NBG); top of Piekenierskloof Pass, (–DB), 10 Sept. 1993, *Goldblatt & Manning 9695* (MO, NBG); Berg River near Piketberg, (–DB), 10 Sept. 1894, *Schlechter 5265* (BM, BOL, COI, G, GRA, K, MO); 11 Sept. 1981, *Goldblatt 6213* (MO, PRE, S, US); Middelpos, west of Piketberg, 250 m, (–DC), 10 Oct. 1984, *Morley 241* (PRE); Piketberg to Sauer, (–DC), 20 Sept. 1974, *Goldblatt 2728* (MO); south bank of Berg River, west of old bridge, (–DC), 1 Sept. 1992, *Goldblatt & Manning 9337* (MO, NBG, PRE). **3219** (Wuppertal): Olifants River Mtns, Dasklip Pass, rocky shale slope, (–CC), 30 Sept. 1972, *Oliver 3998* (NBG); slopes of Dasklip Pass, (–CC), 8 Nov. 1976, *Goldblatt 4436* (MO). **3318** (Cape Town): Oshoekkop, north of Moorreesburg, shale hillside, (–BA), 17 Sept. 1982, *Van Zyl 3287* (NBG). **3319** (Worcester): De Hoek, (–AA), 28 Sept. 1952, *Lewis s.n.* or *2656* (MO, SAM); *Barker 2571* (NBG); 2 miles [3 km] north of Karoo Poort, (–BC), 11 Nov. 1974, *Snijman 12* (NBG).

27c. subsp. **purpurascens** *Goldblatt & Manning*, subsp. nov.

TYPE.—South Africa, Western Cape, 3219 (Wuppertal): rocky sandstone slope 2 km south of Wuppertal, (–AC), 25 Aug. 2009, *Goldblatt & Manning 13252* (NBG, holo.; K, MO, PRE, iso.).

Plants mostly 100–200 mm high. *Flowers* pale to deep purple, darker on reverse of tepals and tube, lower tepals each with dark red ± triangular mark in lower midline and with short yellow, claw-like cusp near base, throat dark turquoise to violet, often with pale narrow lines; perianth tube ± straight, slender, 30–45 mm long, expanded in upper ± 5 mm; tepals unequal (rarely subequal), upper three 15–18 × 7–10 mm, spreading distally; lower 3 erect below continuing upper part of tube as tepal cup for ± 4 mm, spreading distally, 10–12 × 4–5 mm. *Stamens* with filaments ± 7–8 mm long, dark turquoise, exserted 2–3 mm from tube; anthers 4–5 mm long. *Style* suberect, usually dividing between middle and apex of anthers; branches ± 3.5 mm long. *Flowering time*: mid-August to mid-September, thus early to mid-spring. Figure 27D, E.

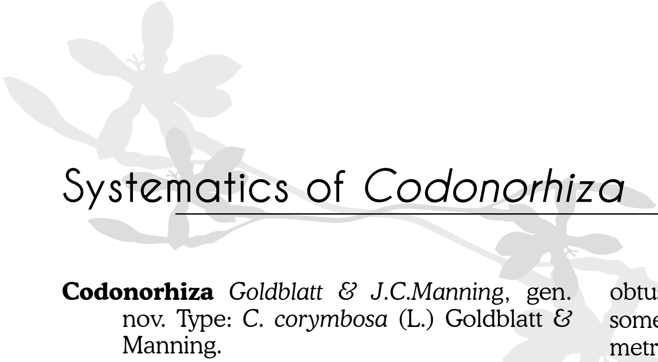
Distribution: subsp. *purpurascens* has a narrow range in the interior valleys of the Western Cape, extending from Wuppertal in the north through the drier valleys of the interior northern Cederberg and adjacent Swartruggens (Figure 26). The flowers, with their dark blue- or rarely red-purple colour and long perianth tube, combined with August to mid-September blooming, suggest pollination by the long-proboscid fly *Prosoeca peringueyi* (Goldblatt et al. 1995), but to date there are no observations on pollination of the subspecies.

Diagnosis: subsp. *purpurascens* is distinguished by its predominantly purple flowers with darker purple markings on the lower tepals, each of which bears a short, yellow, claw-like cusp near the base, and the short, dark violet to turquoise throat ± 5 mm long. Flowers of subsp. *fabricii*, which occurs within the range of subsp. *purpurascens* but blooms two to three weeks later, are creamy yellow with bright red markings on the lower tepals. The throat in subsp. *fabricii* is up to 10 mm deep and the perianth tube is usually longer, 40–60 mm vs. 35–45 mm in subsp. *purpurascens*. Flowering in subsp. *fabricii* usually begins in mid-September, continuing into October, sometimes even as late as November, so that the two subspecies are isolated by flowering time as well as pollinator preference. The habitat is essentially the same for both – rocky sandstone slopes – although in Namaqualand, subsp. *fabricii* grows on granite-derived soils and granite outcrops.

We hypothesise that subsp. *purpurascens* is a local segregate of the widespread subsp. *fabricii* that has shifted pollination from the *Philoliche–Moegistorhynchus* system to the *Prosoeca peringueyi* system (Goldblatt & Manning 2000). Species belonging to the latter guild have red to purple flowers with pale nectar guides, and frequently a somewhat shorter perianth tube than those pollinated by *Philoliche* and *Moegistorhynchus*, exactly the floral features of subsp. *purpurascens*. We know of no intermediates between subsp. *fabricii* and subsp. *purpurascens*, but have chosen subspecies rank for the two taxa because of the weak morphological differences between them, primarily perianth colour and gullet length.

Representative specimens

SOUTH AFRICA. WESTERN CAPE.—**3219** (Wuppertal): near Wuppertal, Stormvlei, stony ground, (–AA), 11 Sept. 1897, *Leipoldt 542* (NBG); Wuppertal, (–AA), 20 Aug. 1959, *Jackson s.n.* (NBG); Ceres Karoo, Karretjies, west of Elandsvlei, (–AB), 12 Sept. 2006, *Bruyns 10526* (NBG); Swartruggens, Farm Doornfontein, rocky sandstone slopes, (–DA), 12 Aug. 2009, *Manning 3228* (NBG).



Systematics of *Codonorhiza*

Codonorhiza *Goldblatt & J.C.Manning*, gen. nov. Type: *C. corymbosa* (L.) Goldblatt & Manning.

Lapeirousia sect. *Fastigiatae* [as *Fastigiata*] Goldblatt in Contributions from the Bolus Herbarium 4: 15 (1972). [*L.* subg. *Paniculatae* Goldblatt & J.C.Manning sect. *Fastigiatae* (Goldblatt) Goldblatt & J.C.Manning 77: 373 (1990).] Type: *L. corymbosa* (L.) Ker Gawl. (= *Codonorhiza corymbosa* (L.) Goldblatt & J.C.Manning).

Deciduous geophytes. *Corm* flat-based, broadly obconic (± triangular in profile), rooting from base and axillary in origin; tunics of dark brown to blackish, densely compacted fibres. *Foliage leaves* 2 or 3, lowermost inserted at ground level, longest plane with ± prominent main vein, upper leaves progressively smaller. *Stem* aerial, compressed and angled to winged, simple or repeatedly branched. *Inflorescence* either a spike or a ± flat-topped, false panicle with sessile flowers; bracts 2, opposed, green, firm textured, usually obtuse to ± truncate, inner ± as long as outer, sometimes notched apically. *Flowers* radially symmetric or zygomorphic, long-lived, salver- or bowl-shaped, blue, purple, red, pink or white, usually with contrasting darker or lighter markings, sometimes sweetly scented; perianth tube ± cylindric or funnel-shaped, short or elongate; tepals subequal or unequal with outer whorl larger. *Stamens* symmetrically disposed or unilateral and arcuate; filaments slender, free; anthers oblong-linear, dehiscence longitudinal. *Ovary* globose; style filiform, branches usually forked for ± $^{1}/_{2}$ their length, occasionally barely forked at tips. *Capsules* cartilaginous, globose to ± top-shaped and 3-lobed. *Seeds* ovoid(–orbicular), flattened at chalazal end, with reticulate to rugulose sculpturing; funicular collar prominent, surface cells ± flat (obscurely domed). *Basic chromosome number x* = 10.

Species: 7; restricted to Western Cape, South Africa.

Key to species

1a Inflorescence a spike; flowers white to pink, lower tepals with purple or red marks in basal half; perianth tube cylindric .... 1. *C. falcata*
1b Inflorescence a flat-topped, false panicle with ultimate branches bearing 1–5 sessile flowers; flowers predominantly blue, yellow or maroon to light brown; perianth tube cylindric or funnel-shaped:
  2a Perianth tube (14–)18–20 mm long; tepals 7–8 mm long .... 3. *C. pillansii*
  2b Perianth tube 3–12 mm long; tepals other:
    3a Flowers dull yellow, creamy brown or maroon; perianth tube cylindric 8–10 mm long, ± twice as long as tepals .... 2. *C. micrantha*
    3b Flowers blue to violet or pale yellow; perianth tube funnel-shaped, shorter than tepals:
      4a Flowers zygomorphic with unilateral stamens; perianth blue to violet, with white or dark, blue-black, contrasting markings:
        5a Flowers medium to dark blue(–violet) with white, bracket-shaped band in basal $^{1}/_{3}$ of lower tepals; anthers 3–4 mm long; pollen blue or grey; tepals 12–15 mm long .... 5. *C. elandsmontana*
        5b Flowers deep blue(–violet) with dark blue, red-purple or blackish mark (sometimes outlined in white) at base of lower tepals; anthers 3–5 mm long; pollen usually dark red-brown, blue or pale grey; tepals 14–20 mm long .... 4. *C. azurea*

4b Flowers actinomorphic with stamens ascending; perianth blue (rarely white) or pale yellow:
  6a Perianth light to dark blue with white, star-shaped mark in centre outlined in darker colour; tepals 6–10 mm long; filaments 5–6 mm long . . . . 6. *C. corymbosa*
  6b Perianth pale yellow, each tepal with small dark mark in lower midline; tepals 14–15 mm long; filaments ± 10 mm long . . . . 7. *C. fastigiata*

Spp. 1–7

1. **Codonorhiza falcata** *(L.f.) Goldblatt & J.C.Manning*, comb. nov. *Gladiolus falcatus* L.f., Supplementum plantarum: 96 (1782). *Lapeirousia falcata* (L.f.) Ker Gawl.: 238 (1804); Goldblatt: 28 (1972). *Ovieda falcata* (L.f.) Spreng.: 147 (1824). *Peyrousia falcata* (L.f.) Sweet: 499 (1830a). *Meristostigma falcatum* (L.f.) A.Dietr.: 594 (1833). Type: South Africa, without precise locality, *Thunberg s.n. UPS-THUNB1025* (UPS-THUNB, holo.!).

Lapeirousia pappei Baker: 170 (1892). Type: South Africa, [Western Cape], Winterhoeksberg, Tulbagh, *Pappe s.n.* (K, holo!; BOL!, iso.).

Plants short and compact to fairly slender, seldom exceeding 100 mm, simple or with up to 3 branches from near base, stem terete. *Corm* ± 8 mm diam., broadly obconic; tunics dark brown to black, rugose, split longitudinally at base and apex. *Leaves* usually 2, lowermost basal, longest, falcate, ± plane with main vein slightly raised, ± leathery, mostly 5–8 mm wide; upper leaf much shorter. *Inflorescence* a spike, with up to 12 flowers in 2 ranks; bracts green with red margins, outer ± 6 mm long, inner 4–5 mm long. *Flowers* zygomorphic, pale pink to nearly white, lower 3 tepals each with dark pink to mauve or red spot in lower midline, unscented; perianth tube ± cylindric, 12–17 mm long, slightly wider in upper 3–4 mm; tepals ovate-oblong 7–8 × ± 3 mm. *Stamens* unilateral, ± erect; filaments ± 6 mm long, exserted ± 3 mm; anthers ± 1.2 mm long, white, pollen white. *Style* erect, dividing shortly below apex of filaments, branches ± 2.3 mm long, deeply divided, spreading between anthers. *Capsules* top-shaped and 3-angled, 4–5 mm long. *Seeds* ovoid-orbicular, flattened at chalazal end, brown, ± 0.6–0.9 × 0.5 mm, reticulate, funicular collar up to 0.3 mm long. *Chromosome number* $2n = 20$. *Flowering time*: mainly September and October at lower elevations but as late as mid-December at high elevations.

Distribution and biology: like most other members of the genus, *Codonorhiza falcata* has a relatively narrow range, extending from Matroosberg and Lakenvlei, east of Ceres, through the Agterwitsenberg Vlakte and Cold Bokkeveld to Elandskloof, south of Citrusdal (Figure 29). A collection, *Templemann sub MacOwan in Herb. Norm. Austr. Afr. 1656*, said to be from the Swartberg at Caledon, is almost certainly not from there. Plants occur exclusively on sandstone substrate and often in crevices in rock outcrops or in seeps on sandstone pavement. Most records are from middle elevations between 800 and 1 200 m, but there are collections from Matroosberg at 2 200 m, also the most easterly station. Additional collecting in the Hex River Mtns will likely yield additional records. Flowering is stimulated by fire but plants may be found in bloom in open sites several years after a fire. Pollination in the species has not been studied.

Diagnosis and relationships: both morphology, especially the corms, and molecular data

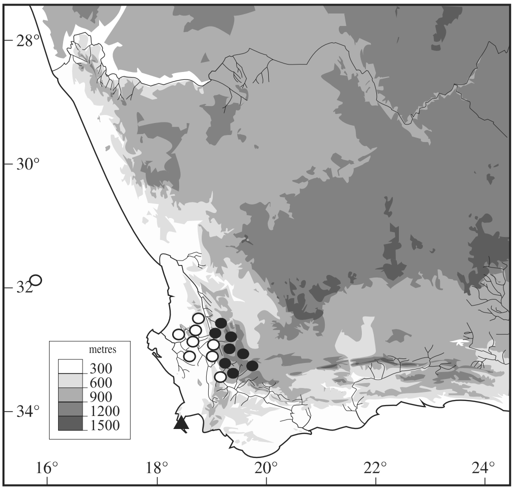


FIGURE 29.—Distribution of *Codonorhiza falcata*, ●; *C. fastigiata*, ○; *C. pillansii*, ▲.

confirm the relationship of *Codonorhiza falcata* to the *C. corymbosa* complex. In the DNA-based phylogeny (Figure 1), *C. falcata* is consistently retrieved as sister to the remaining species of the genus. Unlike all other *Codonorhiza* species, the inflorescence is a spike rather than a flat-topped false panicle, and we infer that a spike is the ancestral condition for the genus on the basis of outgroup comparison since all genera except *Pillansia* of the sister clade have spicate inflorescences. The blackish, rough-textured corm tunics, plane, falcate leaf and green floral bracts with red margins accord exactly with the *C. corymbosa* complex, as do the small, ± ovoid seeds with reticulate sculpturing and prominent funicular collar. The flowers are pale pink to ± white with dark pink to mauve or red markings on the lower tepals, colours that are unique in the genus. *C. falcata* is one of only three species with a cylindrical perianth tube, but the other two, *L. micrantha* and *L. pillansii*, are immediately distinguished by their flat-topped inflorescences and flowers of different colour.

Described by the younger Linnaeus in 1782, as *Gladiolus falcatus*, the species was based largely, if not entirely, on a Thunberg collection and probably in part on Thunberg's manuscript notes. Early confusion with *Freesia verrucosa* and its illegitimate synonym, *Anomatheca juncea*, which is superficially similar to *Codonorhiza falcata*, was the result of their flowers of similar size and proportions, but they differ in almost all vegetative features. Linnaeus fil. confused them and a specimen of *F. verrucosa* in the Linnean Herbarium annotated by him has a question mark against the name *Gladiolus falcatus*. Thunberg's (1784) more detailed account in the *Dissertatio de Gladiolo* clearly applies only to his collection (Goldblatt 1972). *G. falcatus* was transferred to *Lapeirousia* by Ker Gawler (1804). Later in the 19th century the name *L. falcata* was abandoned in favour of the later synonym, *L. pappei* (Baker 1892).

Representative specimens:

SOUTH AFRICA. WESTERN CAPE—**3219** (Wuppertal): Elandskloof, (–CA), *Lewis s.n. 3128* (BOL 30699); 29 Sept. 1944, *Barker 3081* (NBG); northern Cold Bokkeveld, flats at west base of Geelberg, 2400 ft [731 m], (–CA), 2 Oct. 1972, *Thompson 1547* (PRE); sandy plateau, Twenty Four Rivers Mtns, (–CC), 22 Oct. 1947, *Esterhuysen 16163* (BOL, NBG); Cold Bokkeveld, near De Keur, (–CD), 1 Oct. 1944, *Barker 3128* (NBG); Cold Bokkeveld, sandstone rocks between Rosendal and Liberty, (–CD), 12 Oct. 2000, *Goldblatt 11620* (MO); Groenfontein, Zeekoegat, west of Riet River, (–DC), 2 Oct. 2002, *Stobie 2* (NBG). **3319** (Worcester): Agterwitsenberg Vlakte, (–AA), *Mauve 4078* (PRE); Gydo Pass, (–AB), 1 Oct. 1944, *Barker 3128* (NBG); 20 Sept. 1993, *Goldblatt & Manning 9742* (MO); Ceres Nature Reserve, top of Michell's Pass, (–AD), 29 Sept. 2009, *Goldblatt & Porter 13464* (MO, NBG); Lakenvlei, (–BC), Nov. 1917, *Phillips 2069* (SAM); Matroosberg, near beacon, 2 200 m, (–BC), 10 Dec. 1981, *Kotze 101* (NBG); *Esterhuysen s.n.* (MO).

2. **Codonorhiza micrantha** *(E.Mey. ex Klatt) Goldblatt & J.C.Manning*, comb. nov. *Ovieda micrantha* E.Mey. ex Klatt in Linnaea 32: 781 (1864). *Lapeirousia micrantha* (E.Mey. ex Klatt) Baker: 156 (1877); Goldblatt: 27 (1972). Types: South Africa, [Western Cape], Worcester, waterfall, *Ecklon & Zeyher Irid 253* (K, lecto.!, designated here; MO!, isolecto.). [South Africa, [Western Cape], Gifberg, *Drège s.n.* (SAM, syn.)].

Lapeirousia manuleiflora Eckl.: 31 (1827), nom. nud. *Meristostigma manuleiflorum* (Eckl.) Steud.: 130 (1841).

Plants mostly 120–250 mm high, repeatedly branched, branches subtended by bracts (1–)2–5 mm long, these sometimes leaf-like below, stem flexuose, compressed and 2–4-winged. *Corm* 10–12 mm diam., broadly obconic; tunics dark brown to blackish, basal rim ± crenate, splitting vertically from base. *Leaves* 2 or 3, lowermost basal, ± falcate, 80–300 × 8–16 mm, margins usually undulate or slightly crisped, main vein prominent, upper leaves inserted near middle of stem, smaller than basal, not or hardly sheathing at base. *Inflorescence* a congested, ± flat-topped false panicle, flowers crowded at branch tips, ultimate branchlets 1–3-flowered; bracts green, ± leathery, 2–3 mm long, margins red, inner ± as long as outer, obtuse or inner slightly emarginate. *Flowers* weakly zygomorphic with perianth radially symmetric and stamens and style unilateral, dull yellow to buff or brown to dull maroon, acrid-sweet or clove scented; perianth tube ± cylindric, 8–10 mm long; tepals subequal, ± elliptic, obtuse, 3–5 × ± 1.5–2.0 mm. *Stamens* unilateral, ± erect; filaments ± 3.5 mm long, exserted ± 1.5 mm; anthers 1.5–2.0 mm long, pollen dull yellow to buff. *Style* dividing between base and upper $^{1}/_{3}$ of anthers, style branches ± 1 mm long,

FIGURE 30.—*Codonorhiza micrantha*, *Goldblatt 10795C*. Scale bar: 10 mm. Artist: John Manning.

usually divided for up to $^1/_2$ their length or undivided. *Capsules* top-shaped, triangular, 5–6 mm long, with up to 6 seeds per locule. *Seeds* ± ovoid, dark brown, 1.3–1.6 mm long, funicular appendage up to 0.5 mm long, surface reticulate. *Chromosome number* 2*n* = 20. *Flowering time*: late September to December. Figure 30.

Distribution and biology: the most widespread species of *Codonorhiza*, *C. micrantha*, extends from the Gifberg–Matsikamma mountain complex in the northwest to the Langeberg at Garcia's Pass in the southeast, thus embracing the major part of the sandstone mountains of the Cape Floristic Region (Figure 31). Despite the wide range, this inconspicuous species is seldom seen, for it rarely flowers except in the first and second season after fire. We infer settling moth pollination for the species because of the dull flower colour and heavy, often clove-like floral odour that are matched in some moth-pollinated species of *Gladiolus* (Goldblatt & Manning 2002).

Diagnosis and relationships: *Codonorhiza micrantha* stands out among the species with crowded, flat-topped inflorescences in its cylindrical perianth tube, 8–10 mm long, and small, yellow to brown or maroon, strongly scented flowers. In the molecular phylogeny (Figure 1) *C. micrantha* is retrieved as sister to *C. corymbosa*.

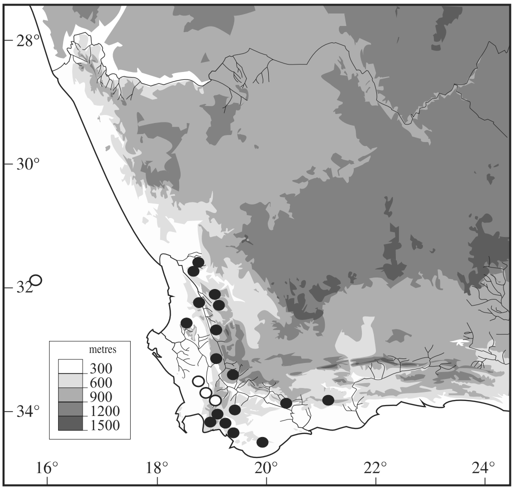


FIGURE 31.—Distribution of *Codonorhiza azurea*, ○; *C. micrantha*, ●.

History: although first recorded by William Burchell in late 1814 near Riversdale, *Codonorhiza micrantha* was based on the later collections of J.-F. Drège (circa 1830) and Ecklon & Zeyher (before 1827). The Drège collection was distributed under the manuscript name *Ovieda micrantha* and was so listed by Meyer (1843) in the publication that dealt with the distribution ranges of plants collected by Drège. Klatt (1864) formally named the species based on both the Drège and Ecklon & Zeyher collections, assigning it to the illegitimate genus *Ovieda* (= *Lapeirousia*). The very apt epithet *manuleiflora* (the flowers do indeed closely resemble those of several, small-flowered *Manulea* species) was used by *Ecklon* (1827), who assigned the species to *Lapeirousia*, but without any description, the name is thus invalid.

Representative specimens:

SOUTH AFRICA. WESTERN CAPE.—**3118** (Vanrhynsdorp): Matsikamma Mtns, north of Farm Die Vlei, (–DB), 11 Nov. 1985, *Snijman 959* (NBG); Gifberg slopes at Farm Colinshoek, (–DD), 11 Sept. 2009, *Goldblatt & Porter 13320* (MO). **3218** (Clanwilliam): Kransvlei, Clanwilliam, (–BB), *Leipoldt 4427* (BOL); Piketberg, Moutonsvlei, (–DC), Nov. 2008, *Ebrahim s.n.* (NBG); Piketberg, Sandleegte, (–DC), 5 Nov. 1973, *Linder 93* (BOL). **3219** (Wuppertal): Biedouw Mtns, (–AA), Nov. 1929, *Thode A2140* (NBG); 3 km west of Algeria, Clanwilliam road, (–AC), 16 Nov. 1979 (fl. & fr.), *Goldblatt 5150* (MO, S); Cederberg State Forest, research site 12, six months after fire (–AC), 10 Nov. 1981, *Le Maitre 295* (PRE); Cold Bokkeveld Mtns, Keerom, (–CC), 4 Dec. 1950, *Esterhuysen 17937* (BOL, MO, NBG). **3319** (Worcester): Roodezand Pass, Tulbagh, stony clay slope, (–AA), 22 Oct. 1994, *Oliver 10589* (NBG); Matroosberg near Lakenvlei, (–BC), *Phillips 2068* (SAM); Goudini, Farm Groenvlei, (–CB), 6 Nov. 1981, *Walters 2552* (NBG); Franschhoek Pass, eastern end on south-facing slopes burned last summer, (–CC), *Goldblatt 8580* (MO). **3321** (Ladismith): Langeberg slopes, near Swellendam, (–CD), 5 Nov. 1962, *Taylor 4224* (NBG, PRE). **3418** (Simonstown): Kogelberg, northern slopes of main peak, after fire, 490 m, (–BB), 21 Nov. 1990, *Oliver 9790* (NBG, PRE). **3419** (Caledon): Nuweberg, in two year old fynbos, (–AA), 11 Nov. 1982, *Viviers 759* (NBG, PRE). Houw Hoek, (–AA), 24 Nov. 1896, *Schlechter 9397* (BM, BOL, GRA, K, MO); top of Houw Hoek Pass, (–AA), 20 Nov. 1958, *Lewis 5313* (NBG); slopes southeast of Villiersdorp, burned last [previous] summer, (–AB), 25 Oct. 1997, *Goldblatt 10795C* (MO); Vogelgat, Psoralea Gully, (–AD), 10 Nov. 1982, *Williams 3355* (NBG); Hermanus, Vogelgat Nature Reserve, after fire, 3 Dec. 1975, *Rourke 1508* (MO, NBG); Bredasdorp Mtns, recently burnt north slope, (–BD), 21 Nov. 1970, *Barker 10804* (MO, NBG). **3421** (Riversdale): between Little Vet River and Kampscheberg, Riversdale, (–AB), *Burchell 6883* (K).

3. **Codonorhiza pillansii** *Goldblatt & J.C.Manning*, sp. nov.

TYPE.—South Africa, Western Cape, 3418 (Simonstown): Cape Peninsula, western edge of plateau west of Buffels Bay, (–AD), 22 Nov. 1921, *Pillans 8928* (BOL, holo.!; MO!, iso.).

Plants 100–150 mm high, repeatedly branched, upper branches subtended by bracts up to 10 mm long, stem ± flexuose, compressed and 2-winged. *Corm* ± 10 mm diam., broadly obconic; tunics blackish, splitting vertically at base and apex. *Leaves* 2 or 3, lowermost basal and longest, usually falcate, 40–100 × 3–4 mm, acute, with prominent main vein, margins plane, slightly thickened, not or hardly sheathing at base; upper leaves similar, inserted in middle of stem, 25–30 mm long. *Inflorescence* a congested, flat-topped false panicle, flowers crowded at branch tips, ultimate branchlets mostly 2- or 3-flowered; bracts 5–7 mm long, green, leathery, inner ± as long as outer or slightly longer, obtuse or inner ± emarginate. *Flowers* zygomorphic, dark blue, evidently uniformly coloured, scent unknown; perianth tube ± cylindric, (14–)18–20 mm long, ± 1 mm diam. at base, ± 2 mm diam. at mouth; tepals 7–8 × ± 3 mm. *Stamens* unilateral; filaments inserted ± 4 mm below mouth of tube, 7–8 mm long, exserted 3–4 mm; anthers ± 3 mm long, pollen colour unknown. *Style* dividing opposite middle and apex of anthers, ± 2.5 mm long, divided for ± $^1/_2$ their length. *Capsules* top-shaped, 3-lobed, ± 5 mm long (mature capsules and seeds unknown). *Chromosome number* unknown. *Flowering time*: October and November.

Distribution and biology: poorly understood, *Codonorhiza pillansii* is known from several plants collected in 1921 by N.S. Pillans in Cape Point Nature Reserve. The area where the plants were said to have been collected is low fynbos on sandy, stony ground. We suspect plants flower only after fire (Figure 29). The long perianth tube, up to 20 mm, suggests that the flowers are adapted for pollination by an insect with a relatively long proboscis.

Diagnosis and relationships: it is with some hesitation that we recognise here a particularly unusual population of *Codonorhiza* said to be from the west end of the plateau west of Buffels Bay on the southern Cape Peninsula as a separate species, *C. pillansii*. Plants collected there by N.S. Pillans in November 1921, but incorporated into the Bolus Herbarium only after publication of a revision of *Lapeirousia* (Goldblatt 1972), resemble *C. corymbosa* in general appearance, but the flowers have a slender tube (14–)18–20 mm long. We have determined by dissection that the filaments are unilateral and that the tepals are subequal in size and evidently also in disposition. The tepals appear uniformly coloured, which accords with Pillans's comment 'flowers blue'. These plants clearly represent a distinct variant, which we describe as *C. pillansii*, honouring N.S. Pillans who discovered the species. Pillans's locality was burned in the summer of 1991, providing ideal conditions for spring flowering of *Codonorhiza*, but we could locate only typical *C. corymbosa* on a visit there. Until more material can be found we remain ignorant of the biology and several details of the morphology of *C. pillansii*.

4. **Codonorhiza azurea** *(Eckl. ex Baker) Goldblatt & J.C.Manning*, comb. nov. *Meristostigma azureum* Eckl. ex Steud.: 131 (1841), nom. nud. *Lapeirousia corymbosa* var. *azurea* Eckl. ex Baker: 90 (1896) [*L. azurea* Eckl.: 31 (1827), nom. nud.]. *Lapeirousia azurea* (Eckl. ex Baker) Goldblatt in Goldblatt & Manning: 333 (1992). Type: South Africa, [Western Cape], between Paarl and Pont, *Drège 8509a* (K, lecto.!, designated by Goldblatt & Manning: 334 (1992); BM!, G!, MO!, P!, isolecto.).

Plants 70–180(–260) mm high, 5–7-branched, branches subtended by bracts (1–)2–5 mm long, those below appearing leaf-like, stem compressed and winged. *Corms* 12–16 mm in diam.; tunics blackish, basal rim split vertically. *Leaves* 2, lowermost inserted at ground level, largest, falcate, 50–120(–240) × (6–)10–15 mm, margins undulate and crisped, obtuse to subapiculate, with prominent main vein and a pair of secondary veins (rarely one) on either side almost as prominent, second leaf inserted near middle of stem, 20–70 mm long, oblong-lanceolate, margins ± straight, not or hardly sheathing at base. *Inflorescence* a congested, flat-topped false panicle, flowers crowded at branch tips, ultimate branchlets 1- or 2-flowered; bracts green, firm-textured, 9–11 mm long, outer folded in midline, margins often red, inner obtuse or slightly emarginate. *Flowers* zygomorphic, tilted backward, dark blue to violet, with triangular, dark blue-black or red-purple blotch at base of lower 3 and sometimes adjacent upper lateral tepals; perianth tube funnel-shaped, 10–12 mm long; tepals elliptic-ovate, obtuse, mostly 17–20 × 7–8 mm. *Stamens* unilateral, ascending or extended horizontally due to adaxial tilting of flower, 11–15 mm long, exserted for 8–10 mm; anthers 3–5 mm long, pollen dark blue or red-brown. *Style* unilateral, dividing opposite upper $^{1}/_{3}$ of anthers; branches 2.5–3.0 mm long, divided for ± $^{1}/_{2}$ their length. *Capsules* ± top-shaped and 3-lobed, ± 6 mm long, with up to 8 seeds per locule. *Seeds* red-brown, ovoid, truncate at chalazal end, rugulo-reticulate, ± 1.0 × 1.0–1.3 mm, with funicular appendage 0.2–0.4 mm long. *Chromosome number* $2n = 20 + 0$–2B. *Flowering time*: late September to late October. Figure 32.

Distribution and biology: *Lapeirousia azurea* is restricted to lowland sites in the southwestern Cape between Paarl, Mamre and Riebeeck Kasteel north of Malmesbury (Figure 31). It favours granite-derived gravel soils rather than the shale-derived clay soils, also common in the area. Because of the relatively high fertility of these soils this habitat is now extensively cultivated, and *L. azurea* has become increasingly rare. In 1992 we wrote that it was probably not in immediate danger of extinction as it was known in sites away from cultivation. Some of these are now lost to urban expansion and some of its remaining sites are being developed for housing.

We suspect that the dark-coloured flowers with even darker, blue-black or red-purple markings are adapted for pollination by hopliine beetles. At a site in Malmesbury large, buff-brown hopliines were the only insects we have seen on the flowers, using the flowers as sites of assembly and mating. Goldblatt et al. (1995) also reported visits to flowers of *C. azurea* (as *Lapeirousia*) by the anthophorine bee, *Anthophora diversipes*, suggesting a possible bimodal pollination system, using both large-bodied bees and hopliine beetles.

Diagnosis and relationships: although initially treated taxonomically as a variety of *Codonorhiza corymbosa*, *C. azurea* is distinguished by its larger, zygomorphic, intensely dark blue flower bearing large black or dark red blotches on the adaxial tepals. The perianth tube is 8–12 mm long and the tepals (12–)16–20 mm long. The flower is tilted back toward the axis, especially in crowded inflorescences, when the posterior (adaxial) tepals, usually erect, are tilted out of position and come to lie horizontally, thus below the abaxial (lower) tepals. This type of floral presentation is not unique in *Codonorhiza*, but also occurs in *C. elandsmontana*. Although united with *C. fastigiata* (as *Lapeirousia corymbosa* subsp. *fastigiata*) by Goldblatt (1972), molecular data (Figure 1) suggest that *C. azurea* is not directly related to *C. fastigiata* despite their comparably large perianth. In the molecular phylogeny (Figure 1) *C. azurea* is sister to *C. corymbosa* + *C. micrantha*.

History: *Codonorhiza azurea* was figured as early as 1791 by Jacquin in his *Icones plantarum rariorum* under the name *Ixia corymbosa* in a composite painting that included true *C. corymbosa* as well. The earliest extant herbarium records appear to be the collections of Ecklon & Zeyher, made in the late 1820s, and those made by J.-F. Drège at about the same time or shortly thereafter. It is not entirely clear whether Ecklon considered *L. azurea* distinct from *L. corymbosa*, for although he mentioned both names in his *Topographisches Verzeichniss* (1827), *L. azurea* without description, his collections of both species bear the latter manuscript name. *C. azurea* was regarded as a variety of *C. corymbosa* (as *Lapeirousia*) by Baker (1896) and as conspecific with *C. corymbosa* subsp. *fastigiata* by Goldblatt (1972). Only recently have sufficient specimens become available to help establish the status and rank of this plant. Reasons for treating *C. azurea* and *C. fastigiata* as separate species are discussed in detail under the latter.

Representative specimens

SOUTH AFRICA. WESTERN CAPE.—**3318** (Cape Town): Darling, (–AD), 27 Sept. 1890, *Guthrie 2069* (NBG); Groene Kloof [Mamre], (–CB), *MacOwan 2280* (SAM); commonage at Malmesbury, (–BC), 14 Sept. 1953, *Lewis 3644* (SAM); *Barker 8047* (NBG); 13 Sept. 1981, *Goldblatt 6279* (MO); 28 Oct. 1986 (fr.), *Goldblatt 8016* (MO); hills around Malmesbury, (–BC), 1 Oct. 1892, *Schlechter 1616* (B, G, GRA, P); Riebeeck Kasteel, (–BD), Oct. 1951, *Pillans 10710* (G, MO); 18 Oct. 1941, *Barker 1311* (NBG); top of Bothmaskloof, Riebeeck Kasteel, (–BD), *Esterhuysen 6033* (BOL); clay flats near Paarl, (–DB), 24 Sept. 1974, *Goldblatt 2740* (MO, NBG); north slopes of Paardeberg, (–DB),

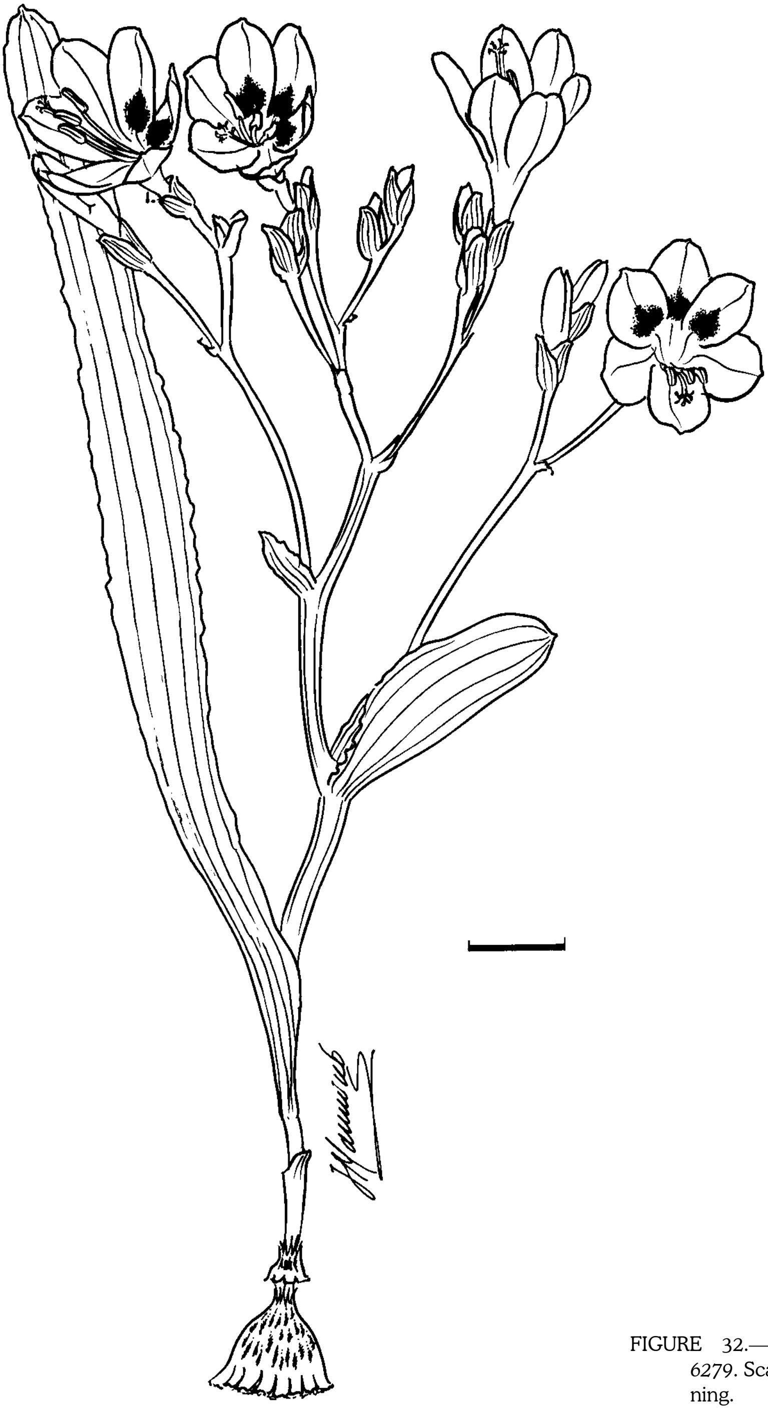


FIGURE 32.—*Codonorhiza azurea*, *Goldblatt 6279*. Scale bar: 10 mm. Artist: John Manning.

Goldblatt 647 (BOL); east slopes of Paardeberg, (–DB), *Pillans 7785* (BOL); Slent Farm, southeast end of Paardeberg, (–DB), 28 Sept. 1999, *Goldblatt 11176* (MO); hillside near Joostenberg, (–DD), *Esterhuysen 17339* (BOL).

5. **Codonorhiza elandsmontana** *Goldblatt & J.C.Manning*, sp. nov.

Type: South Africa, Western Cape, 3319 (Worcester): foot of Elandskloof Mtns, Elandsberg Nature Reserve, stony ground, (–AC), 11 Sept. 2010, *Goldblatt & Manning 13518* (NBG, holo.; MO, PRE, iso.).

Plants 150–210 mm high, several-branched, branches subtended by bracts (1–)2–5 mm long, or sometimes leaf-like below and longer; stem ± flexuose, compressed and 2-winged. *Corm* obconic, 10–15 mm diam.; tunics blackish, splitting vertically from base and apex. *Leaves* 2(3), lower 1(2) basal, usually falcate (lanceolate), 100–250(–400) × 10–14 mm, subacute to acute, with prominent main vein and 1 or pair of secondary veins on either side also raised; margins usually ± straight to slightly undulate, rarely slightly crisped; uppermost leaf inserted near middle of stem, 25–80 mm long, narrowly oblong, not or hardly sheathing at base. *Inflorescence* a congested, flat-topped false panicle, ultimate branchlets 1- or 2-flowered; bracts green, leathery, 4–7 mm long, usually red distally and slightly warty, outer obtuse to truncate, keeled, inner ± obtuse to slightly emarginate. *Flowers* zygomorphic, tilted backward with adaxial (dorsal and upper lateral) tepals often nearly horizontal, light to dark blue with white throat and basal $^1/_2$ of abaxial tepals with white, bracket-shaped band, not scented; perianth tube funnel-shaped, 8–10 mm long; tepals elliptic, obtuse, 10–15 × 4–5 mm. *Stamens* ± unilateral, ± horizontal and facing upward; filaments 9–10 mm long, exserted 7–8 mm; anthers 3.0–3.5 mm long, pollen blue to blue-grey, or purple. *Style* unilateral, dividing opposite or shortly beyond anther apices, held below stamens, style branches 1.5–2.0 mm long, divided for ± $^1/_2$ their length. *Capsules* top-shaped, 3-lobed, ± 5 mm long, with up to 6 seeds per locule. *Seeds* ovoid, reticulately sculptured, ± flattened to concave at chalazal end, dark brown, ± 0.8–1.0 × 1.0–1.2 mm; funicular collar up to 0.3 mm long. *Chromosome number* unknown. *Flowering time*: late September and October. Figure 33.

Distribution and biology: locally common in the Tulbagh Valley, *Codonorhiza elandsmontana* extends from Tulbagh eastward through the upper Breede River Valley to Botha and westward to Gouda and the lower slopes of the Elandskloof Mtns as far south as Bain's Kloof (Figure 34). Plants favour rocky ground, often in clay or clay loam. Plants at Elandsberg were actively visited by the tabanid fly, *Philoliche angulata*, which has a body ± 17 mm long and a proboscis ± half as long. These flies carried visible loads of the pale blue-grey pollen of *C. elandsmontana* and must be regarded as legitimate pollinators.

Diagnosis and relationships: long confused with *Codonorhiza corymbosa* or sometimes with *C. azurea*, both of which it broadly resembles, especially in dry herbariums specimens, *C. elandsmontana* differs from *C. corymbosa* in the zygomorphic flowers with unilateral stamens and white, bracket-shaped markings only on the three abaxial tepals. Other floral details include the slightly longer perianth tube, 8–10 mm long vs. 4–7(8) mm long and the larger tepals, 10–15 mm long vs. 6–10 mm long in *C. corymbosa*. Flowers of *C. corymbosa* are strictly actinomorphic, with all six tepals bearing white, bracket-shaped markings. *C. elandsmontana* may also be confused with *C. azurea* and *C. fastigiata*, which are similar in stature and have a broad basal leaf with undulate to crisped margins. The larger flowers of *C. azurea* are zygomorphic like those of *C. elandsmontana*, but have a perianth tube 10–12 mm long and tepals mostly 17–20 × 7–8 mm and the three abaxial tepals have a dark blue-black or red markings in the lower half.

Possible hybrids between *Codonorhiza azurea* and *C. fastigiata* have been recorded at Piketberg Road (Gouda) [*Bolus 13650* (BM, BOL, PH), *Guthrie 2697* (NBG)].

Representative specimens

SOUTH AFRICA. WESTERN CAPE.—**3319** (Worcester): Saron, renosterveld east of town, (–AA), 23 Sept. 2012, *Goldblatt & Porter 13784A* (MO); Tulbagh, (–AC), *Grant 2427* (MO); Tulbagh, near cemetery, pebbly clay ground, (–AC), 24 Nov. 1979 (fr.), *Goldblatt 5226* (MO); 1 mile [± 1.5 km] south of Tulbagh Road Station, (–AC), *Goldblatt 203* (BOL); rocky road verge south of Tulbagh, (–AC), *Goldblatt & Porter 13455* (MO, NBG, PRE); Tulbaghskloof (77.9), (–AC), *Ecklon & Zeyher Irid. 245* (G, MO); foot of the Elandskloof Mtns, Farm Elandsberg, (–AC), 23

FIGURE 33.—*Codonorhiza elandsmontana*, *Goldblatt & Manning 13518*. Scale bar: 10 mm. Artist: John Manning.

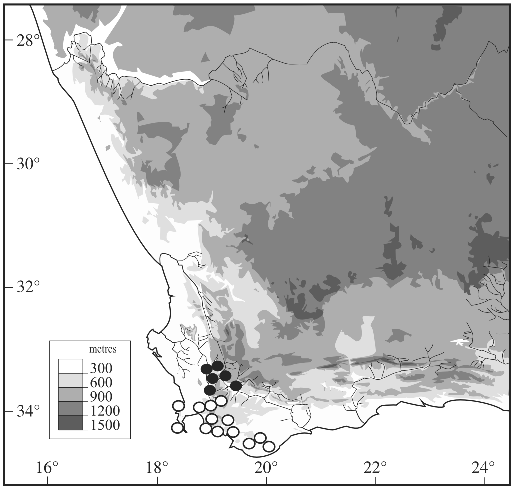


FIGURE 34.—Distribution of *Codonorhiza corymbosa*, ○; *C. elandsmontana*, ●.

Sept. 1980, *Goldblatt 5852* (MO); Gouda [Piquetberg Road Station], (–AC), Oct. 1892, *Guthrie 2697* (NBG); *H. Bolus 13650* (BM, BOL, PH) (mixed with hybrids with *L. fastigiata*); Bain's Kloof, lower west slopes (–CA), *Goldblatt 590* (BOL); bottom of Bain's Kloof, Wellington, (–CA), 16 Oct. 1970, *Strauss 50* (NBG); Botha, Farm Schoonuitzig, (–CB), 16 Oct. 1974, *Walters 1230* (NBG).

6. **Codonorhiza corymbosa** *(L.) Goldblatt & J.C.Manning*, comb. nov. *Ixia corymbosa* L., Centuria plantarum: 4 (1756). *Ovieda corymbosa* (L.) Spreng.: 147 (1825). *Lapeirousia corymbosa* (L.) Ker Gawl.: t. 595 (1802); Baker: 90 (1896) [incl. *C. azurea*]; Marloth: pl. 43 (1915); Goldblatt: 20 (1972), excl. subsp. *fastigiata* and subsp. *alta*. *Peyrousia corymbosa* (L.) Poir.: 365 (1826). *Meristostigma corymbosum* (L.) A.Dietr.: 594 (1833). Type: South Africa, [Western Cape], near Camps Bay, sandy rocky ground, *MacOwan s.n.* in *Herb. Norm. Austr. Afr. 268* (SAM, neo.!, designated by Goldblatt & Manning: 332 (1992); BM!, BOL!, G!, iso.).

Ixia crispifolia Andrews: t. 35 (1798). Type: South Africa, without precise locality or collector, figure in Andrews: t. 35 (1798).

Lapeirousia corymbosa var. *grandiflora* Klatt: 204 (1885). Type: South Africa, [Western Cape], mountains near 'Houw Hoek' (Noord Hoek probably intended), Sept. 1883, *MacOwan 2284a* (K!, SAM 20988!, syn.).

Lapeirousia corymbosa var. *purpurea* Klatt: 204 (1885). Type: South Africa, [Western Cape], sandy depressions, Fish Hoek, Sept. 1883, *MacOwan 2284b* (SAM, as Noord Hoek, syn.!).

Plants 60–150 mm high, 4–10-branched, branches subtended by bracts (1–)2–5 mm long, these sometimes leaf-like below and longer, stem ± flexuose, compressed and 2-winged. *Corm* obconic, 10–15 mm diam.; tunics blackish, splitting vertically from base and apex. *Leaves* 2 or 3, lower 1(2) basal, usually falcate (or ± lanceolate), 100–130 × 4–8(–10) mm, subacute to acute, with prominent main vein and 1 or a pair of secondary veins on either side slightly less prominent, margins ± straight, slightly undulate, rarely slightly crisped, uppermost leaf inserted in middle $^{1}/_{3}$ of stem, 25–80 mm long, narrowly oblong, not or hardly sheathing at base. *Inflorescence* a congested, flat-tipped false panicle, ultimate branchlets 1- or 2-flowered; bracts green, leathery, 3.5–7.0 mm long, margins usually red, obtuse or inner slightly emarginate. *Flowers* actinomorphic, light to dark blue with white throat and lower half of tepals with white, bracket-shaped band (rarely ± white with pale blue markings), not scented; perianth tube funnel-shaped, 4–7(–8) mm long; tepals elliptic, obtuse, 6–10 × 2.3–3.5 mm. *Stamens* symmetrically arranged around style; filaments 5–6 mm long, exserted 3–4 mm; anthers 1.8–3.0 mm long, usually blue; pollen blue to grey, or ± white. *Style* dividing between base and upper $^{1}/_{3}$ of anthers, often deflexed in older flowers, style branches 1.5–2.0 mm long, divided for ± $^{1}/_{2}$ their length. *Capsules* top-shaped, 3-lobed, 4.5–6.5 mm long, with up to 6 seeds per locule. *Seeds* ovoid, reticulately sculptured, flattened to concave at chalazal end, dark brown, 0.7–1.0 mm long; funicular collar up to 0.5 mm long. *Flowering time*: late September and October, occasionally until mid-November. Figure 35.

Distribution and biology: *Codonorhiza corymbosa* extends from the coastal plain of Western Cape near Darling through the Cape Peninsula and Cape Flats to Bredasdorp and Elim (Figure 34). Flowering relatively late in spring, plants are usually found on sandy, well-drained soils derived from Cape Sandstone or weathered granite, but occasionally also on clay loam. Once

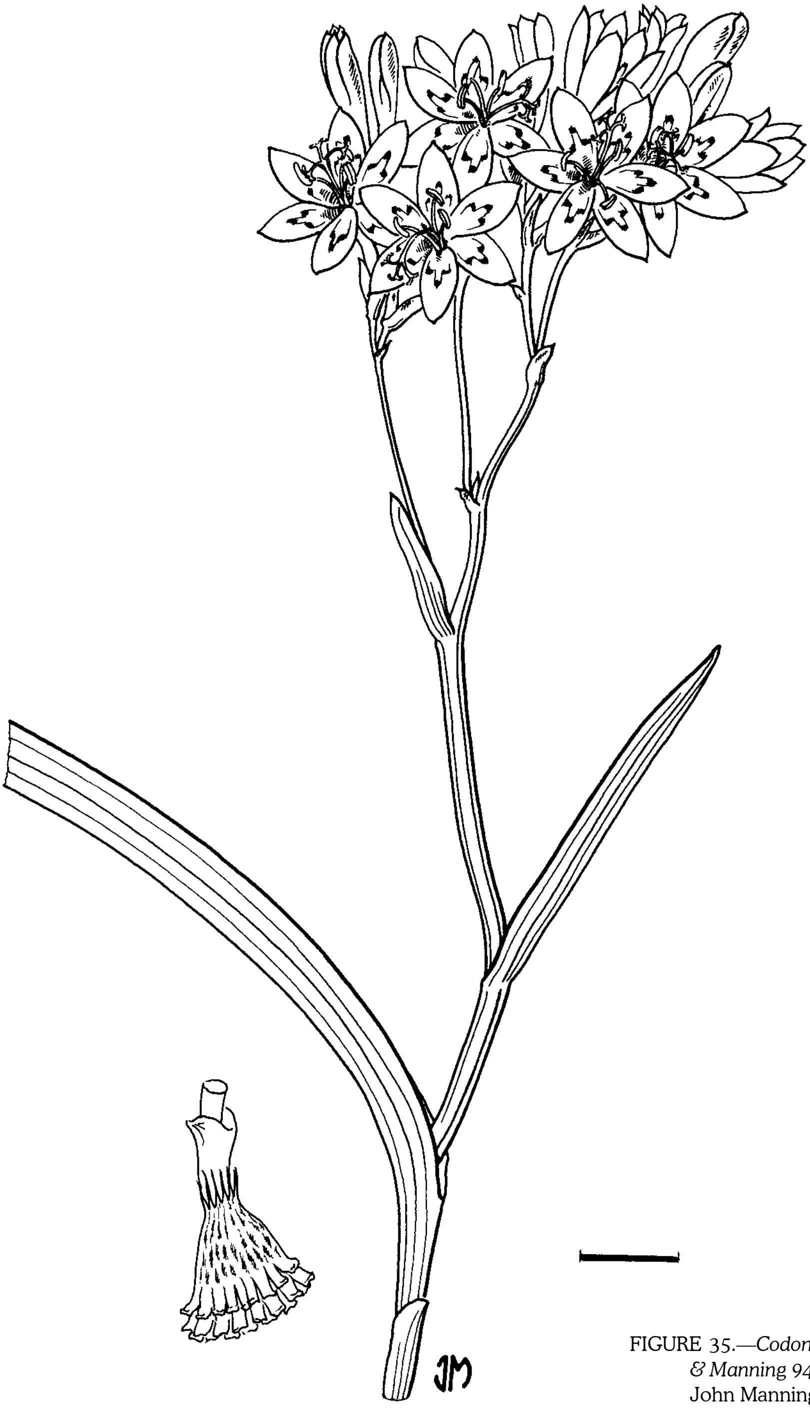


FIGURE 35.—*Codonorhiza corymbosa*, *Goldblatt & Manning 9499*. Scale bar: 10 mm. Artist: John Manning.

fairly common, it is becoming rare, especially on lowland sites, now mostly given over to farmland or urban development. It can still be found on lower mountain slopes and, especially after fires, may be common. Pollination of *C. corymbosa* has not been investigated (Goldblatt et al. 1995) but we infer that it has a generalist pollination strategy.

Diagnosis and relationships: the crowded, ± flat-topped inflorescence of radially symmetric flowers with a pale to fairly dark blue perianth and white bracket-shaped marks in the lower middle of the tepals, distinguish *Codonorhiza corymbosa* from other *Codonorhiza* species. Although small, the upright flowers are particularly attractive with their white, star-shaped central marking. *C. corymbosa* is most easily confused with *C. elandsmontana* from the Worcester and Tulbagh districts, but that species has unilateral stamens, and although the perianth shape and colouration is similar, the flowers are larger and only the lower (abaxial) tepals have white markings. The perianth tube of *C. elandsmontana* is 8–10 mm long and the tepals 10–15 mm long vs. a tube 4–7(8) mm long and tepals 6–10 mm in *C. corymbosa*. Confusion is also possible with the deep blue-flowered *L. azurea,* especially when specimens are poorly preserved, but the flowers and bracts of *L. corymbosa* are always smaller than those of *L. azurea*, the tepals of which are 17–20 mm long. When alive the larger, dark blue, zygomorphic, abaxially tilted flowers of *L. azurea* with unilateral, horizontally extended stamens are unmistakable.

White-flowered plants occur occasionally in populations across the range of *Codonorhiza corymbosa*, but at Riverlands near Malmesbury the entire population has white flowers. In other respects the plants from Riverlands appear to conform closely to typical *C. corymbosa*. Plants tentatively included in *C. corymbosa* by Goldblatt & Manning (1992) from Cape Point Nature Reserve (*Pillans 8928*, Nov. 1921, BOL), with slender perianth tube 18–20 mm and tepals 7–8 × ± 3 mm, are now regarded as a separate species, *C. pillansii*. The perianth tube length and shape are inconsistent with *L. corymbosa*, the funnel-shaped perianth tube of which is 4–7 mm long.

History: known to science at least since the last decade of the 17th century when it was figured by Plukenet (1696) as *Caryophyllus monomatapensis*, *Codonorhiza corymbosa* was assigned to the genus *Ixia* by Linnaeus in 1756. John Ker Gawler transferred the species to *Lapeirousia* (then spelled *Lapeyrousia*), where it has remained until now. Because the original specimen on which the species was based is lost, Goldblatt (1972) chose a neotype for the species. The specimen in the Linnaean Hebarium was collected by Anders Sparrman, circa 1771, some years after the publication of the protologue of *Ixia corymbosa*.

Baker's account of *Lapeirousia corymbosa* in *Flora capensis* (1896) included as a variety the plant we here recognise as *Codonorhiza azurea*. Baker also regarded what we consider a second species, *C. fastigiata*, as a synonym of typical *L. corymbosa*, although he did recognise *L. purpureo-lutea*, the type of which is conspecific with *C. fastigiata*. *Codonorhiza azurea* and *C. fastigiata* were regarded by Goldblatt (1972) as a single subspecies of *L. corymbosa*, but were later recognised by Goldblatt & Manning (1992) as separate species, a treatment that is most consistent with their morphological and ecological differences.

Representative specimens

SOUTH AFRICA. WESTERN CAPE.—**3318** (Cape Town): Riverlands between Mamre Road and Malmesbury, 23 Oct. 1980, (–BC), *Esterhuysen s.n.* (MO); Lions Head, (–CD), *H. Bolus 2819* (BOL, K); Table Mtn, (–CD), *Ecklon s.n.* or *545* '*L. azurea*' (C, G, K); Claremont flats, (–CD), *Wolley Dod 389* (BOL, K); Paarl Mtn, southern end near Taal Monument, (–DB), 17 Oct. 1986, *Goldblatt 7922* (MO); Jonkershoek, (–DD), 1 Oct. 1958, *Werdermann & Oberdieck 353* (B, MO); 28 Oct. 1976, *Kruger 211* (NBG, PRE). **3319** (Worcester): Franschhoek, between Pniel and Robertsvlei (–CC), *Phillips 1314* (SAM); between Groot Drakenstein and the foot of Paarl Mtn, (–CC), *Drège 8510* (E, G, MO). **3418** (Simonstown): Bergvliet Farm, (–AB), *Purcell s.n.* (SAM 90197, 90200); burnt lower slopes of Klaasjagersberg, opposite Cape Point Reserve, (–AD), 26 Nov. 1979, *Goldblatt 5259* (MO); Smitswinkel, (–AD), *Compton 8024* (NBG); Buffels Bay, (–AD), *Compton 6381* (NBG); Cape Point Nature Reserve, west of Diaz Cross, (–AD), 3 Jan. 1993 (fr.), *Goldblatt & Manning 9499* (MO); near Sir Lowry's Pass, 250 m, (–BB), *Schlechter 5362* (G, GRA, K); Lourensford Estate, Somerset West, (–BB), *Parker 4208* (BOL, NBG); Steenbras River mouth, (–BB), *Compton 18831* (NBG); Betty's Bay, Porter Reserve, (–BD), *Ebersohn 162* (NBG). **3419** (Caledon): Caledon, 300 m, (–AB), 17 Oct. 1894, *Schlechter 5569* (B, GRA, MO, Z); Hermanus, Vogelklip, (–AD), 16 Oct. 1980, *Williams 511* (MO); Vogelgat near Hermanus, (–AD), 15 Oct. 1986, *Goldblatt 7914*

(MO); 8 miles [± 12 km] from Stanford on road to Elim, (–AD), 9 Oct. 1938, *Gillett 4503* (BOL, MO); Fairfield, (–BD), 5 Oct. 1993, *Nänni* 3 (NBG); between Baardscheerdersbos and Elim, (–DA), 15 Oct. 1983, *Goldblatt 7106* (MO); 4 km west of Elim, (–DA), 9 Nov. 2011 (fl. & fr.), *Goldblatt & Porter 13741* (MO). **3420** (Bredasdorp): Strandkloof, 8 Oct. 1950, (–CA), *Martin 601* (NBG).

7. **Codonorhiza fastigiata** *(Lam.) Goldblatt & J.C.Manning*, comb. nov. *Lapeirousia fastigiata* (Lam.) Ker Gawl. in König & Sims Annals of Botany 1: 238 (1804). *Ixia fastigiata* Lam.: 337 (1789). *L. corymbosa* subsp. *fastigiata* (Lam.) Goldblatt: 25 (1972). Type: South Africa, without precise locality or collector (P: Herb. Lamarck, holo!).

Ovieda purpureolutea Klatt, Linnaea 32: 781 (1864). *Lapeirousia purpureolutea* (Klatt) Baker: 515 (1877); 91 (1896). Type: South Africa, [Western Cape], Tulbagh, collector unknown, *Herb. Bergius s.n.* [SBT, lecto.! designated by Goldblatt: 25 (1972)].

Lapeirorosea corymbosa var. *rosea* Suess.: 88 (19%). Type: South Africa, [Western Cape], Saron, 29 Sept. 1946, *Rehm s.n.* (M, holo.).

Plants 100–200 mm high, several-branched, branches subtended by bracts (1–)2–3 mm long, lower sometimes ± leaf-like and longer, stem ± flexuose, compressed and narrowly winged, sheathed below by 2 membranous, pale or light brown cataphylls. *Corm* obconic, 10–16 mm diam.; tunics blackish, splitting vertically from base and apex. *Leaves* 2, lowermost inserted at ground level, largest, falcate, 80–150(–250) × 11–18 mm, obtuse to subacute, with prominent main vein and pair of secondary veins on either side almost as prominent, margins usually undulate and crisped, rarely ± straight; upper leaf inserted near middle of stem, (12–)25–45 mm long, oblong-lanceolate, margins straight, not or hardly sheathing at base. *Inflorescence* a congested, ± flat-topped false panicle, ultimate branchlets (1)2–5-flowered; bracts green, often red on margins, 6–10 mm long, obtuse or inner emarginate. *Flowers* actinomorphic, pale yellow to nearly white with purple or brown median triangular mark in basal $^1/_3$ of each tepal, sometimes flushed dull purple or brown outside, not scented; perianth tube funnel-shaped, 6.5–8.0 mm long; tepals elliptic, obtuse, 14–15 × 5–6 mm. *Stamens* symmetrically disposed, diverging; filaments ± 10 mm long; anthers 3–4 mm long, yellow, pollen white to pale yellow. *Style* dividing between base and middle of anthers, style branches 2.5–3.5 mm long, divided for ± $^1/_2$ their length. *Capsules* top-shaped and 3-lobed, 5–6 mm long, with up to 6 seeds per locule. *Seeds* ovoid, reticulately sculptured, red-brown, darker on ridges, 0.8–0.9 mm long with funicular appendage up to 0.4 mm long. *Chromosome number* $2n = 20$. *Flowering time*: late September to mid-October. Figure 36.

Distribution and biology: once fairly common locally in Western Cape from Saron and Moorreesburg in the south to Piekeniers Kloof Pass in the north, *Codonorhiza fastigiata* is most often seen on shale soils on hills and lower mountain slopes in renosterveld shrubland, but plants are sometimes found on rocky, sandstone slopes (Figure 29). Flowering is enhanced by clearing or burning, but it also blooms in undisturbed vegetation, when plants are smaller and bear fewer flowers. A collection from Gydouw (in the Ceres valley), *Leipoldt 3867*, some distance from other records for *C. fastigiata*, requires verification [Gydouw may be a transcription error for Gouda, where the species does grow]. Pollination of *C. fastigiata* has been little studied, but Goldblatt et al. (1995) reported visits to the species by the large-bodied bees, *Anthophora diversipes* (Apidae) and *Hoplitis similis* (Megachilidae) (sex not recorded). We suspect *C. fastigiata* flowers offer only pollen as a reward as we were unable to detect even a trace of nectar at the base of the perianth tube in unbagged flowers.

Diagnosis and relationships: pale yellow flowers and relatively large perianth with a tube 6–8 mm long and tepals 14–15 mm long are sufficient to distinguish *Codonorhiza fastigiata* in the genus. Other species of the genus with flat-topped inflorescences have light to dark blue or violet flowers except *L. micrantha*, which has a buff to brown or maroon perianth, but smaller flowers with a cylindric perianth tube. Both perianth and stamens of *L. fastigiata* are symmetrically arranged so that *L. azurea*, which has flowers of similar size and shape, can immediately be distinguished by its asymmetrically disposed stamens and perianth with markings only on the lower three tepals, as well as by its dark blue perianth.

Collections from Piketberg (*Guthrie 2696*) and Gouda (as Piketberg Road Station) (*H. Bolus*

FIGURE 36.—*Codonorhiza fastigiata*, *Goldblatt & Manning 13005*. Scale bar: 10 mm. Artist: John Manning.

13650) that comprise plants with either yellow or blue flowers were thought by Goldblatt (1972) to represent populations of plants intermediate between *Codonorhiza fastigiata* and *C. azurea*, and based largely on these collections, Goldblatt concluded that the two were conspecific. Additional field study has failed to reveal any other intermediates while several more populations corresponding exactly to one or other of the two species have been found. We are now convinced that *L. fastigiata* and *L. azurea* are separate species and the two gatherings of intermediate plants now seem more likely to represent hybrid individuals. That the flowers of the yellow-flowered plants of these collections differ in the intensity of purple colouration on the reverse of the tepals seems to support this argument. Such variation within a population is rare except among hybrids.

History: available records indicate that *Codonorhiza fastigiata* was first collected sometime before 1789, when the species was described by the French scientist J.P. Lamarck, then referred to *Ixia*. The source of several Cape species now in the Lamarck and Jussieu collections at the Paris Herbarium is uncertain, although sometimes attributed to Philibert Commerson, who did not visit the Cape (Gunn & Codd 1981). His colleague, Pierre Sonnerat, did, however, briefly collect there en route to Mauritius where he worked with Commerson. Specimens in the Bergius Herbarium in Stockholm, Sweden, assembled between 1760 and 1790, are contemporary, and their source is also unknown. Later collections made by Ecklon and Zeyher, probably in 1829, as well as the material in the Bergius Herbarium, formed the basis for Klatt's *Ovieda purpureo-lutea*, described in 1864. Baker transferred the species to *Lapeirousia* in 1877. *Lapeirousia purpureo-lutea*, *L. fastigiata* and *L. azurea* were united at subspecific rank under *L. corymbosa* by Goldblatt (1972), a decision based primarily on two collections of plants that appeared to be intermediate between the two species.

Representative specimens

SOUTH AFRICA. WESTERN CAPE.—**3218** (Clanwilliam): Piketberg, east of Farm Weltevrede, (–DA), 19 Sept. 2007, *Goldblatt & Manning 13005* (MO, NBG); top of Grey's Pass [Piekeniers Kloof], (–DB), *Taylor 967* (BOL); Piketberg, (–DC), *Fremantle s.n.* (BOL 30698); *Guthrie 2696* (BOL) (partly hybrid); between Piketberg and Berg River bridge, (–DC), *Barnes s.n.* (NBG); 5 miles [7.5 km] north of Piketberg, (–DC), *Salter 2720* (BOL); slopes of Versfeld Pass, Piketberg, (–DC), *Goldblatt 671* (BOL); north slopes of Heuningberg, (–DD), *Goldblatt 650* (BOL). **3219** (Wuppertal): lower slopes of the Olifants River Mtns at Cardouw Pass, (–CC), 27 Sept. 1976, *Goldblatt 4211* (MO). **3318** (Cape Town): Moorreesburg, (–BA), *Bachmann 775* (B); near Moorreesburg, clay soil, (–AC), *H. Bolus 9983* (BOL); Porterville, (–BB), *Loubser 498* (NBG). **3319** (Worcester): near Saron, (–AA), Oct. 1896, *Schlechter 10622* (BM, E, G, GRA, K, MO, P, PH); Gydouw, (–AB), *Leipoldt 3867* (BOL); Tulbaghskloof, (–AC), *Ecklon & Zeyher Irid. 246* (G, MO).

Systematics of *Schizorhiza*

Schizorhiza *Goldblatt & J.C.Manning*, gen. nov. Type: *S. neglecta* (Goldblatt) Goldblatt & J.C.Manning.

Deciduous geophytes. *Corm* ellipsoid with small flat base, rooting from base, axillary in origin, producing several new corms in place of parent corm at end of growing season; tunics of ± corky layers. *Foliage leaves* several, linear to sword-shaped, evidently plane but slightly pleated, with visible main vein; lowermost often longest and inserted on stem near ground level, upper leaves progressively smaller. *Stem* aerial, compressed and angled, branching repeatedly, producing cormlets in leaf axils above and below ground. *Inflorescence* much branched, forming a ± round-topped false panicle, with sessile flowers; bracts green, firm, inner ± as long as outer, acute or emarginate. *Flowers* zygomorphic, long-lived, often salver-shaped, lower (abaxial) tepals with contrasting darker markings; perianth tube ± cylindric; tepals subequal, but dorsal slightly larger. *Stamens* unilateral; filaments slender, free; anthers oblong-linear, dehiscence longitudinal. *Ovary* globose, sessile; style filiform, branches forked for ± $^1/_2$ their length. *Capsules* cartilaginous, ± top-shaped, 3-lobed above. *Seeds* ± globose, flattened at chalazal end, slightly wrinkled; surface cells ± flat. *Basic chromosome number* $x = 6$; $2n = 12$ and 24.

Species: 1, mountains of the southwestern Cape, South Africa.

1. **Schizorhiza neglecta** *(Goldblatt) Goldblatt & J.C.Manning*, comb. nov. *Lapeirousia neglecta* Goldblatt in Goldblatt & Manning, South African Journal of Botany 58: 335 (1992). Type: South Africa, [Western Cape], Jonkershoek, slopes near Berg River Nek, Nov. 1989, *Esterhuysen 36923* (BOL, holo.!; B, BR!, E, G, K!, M, MO!, NBG!, P, PRE!, S!, SRGH!, US, WAG, iso.).

L. corymbosa subsp. *alta* Goldblatt: 24 (1972). Type: South Africa, [Western Cape], near Steenbras Dam, Dec. 1945, *Lewis 1595* (SAM, holo.!; BOL!, SAM!, iso.).

Plants 280–450(–550) mm high, laxly 5–7-branched, branches subtended by bracts 3–5(–12) mm long, those subtending lower branches becoming ± leaf-like, stem ± straight, compressed, 2-winged below, often ± square above and 4-angled to narrowly 4-winged; bearing 2 or more cormlets in axils of lower leaves. *Corm* 12–14 mm diam., with several cormlets at base; tunics corky to somewhat papery, brown, not accumulating. *Leaves* 3–6, lower 2–4 inserted below ground level and largest, narrowly lanceolate, lowermost reaching to middle to shortly exceeding inflorescence, 7–15 mm wide, with prominent main and a pair of secondary veins (rarely 2 pairs) on either side ± as prominent; upper 1–3 leaves inserted in lower half of stem, progressively shorter above, not or hardly sheathing at base. *Inflorescence* a lax, rounded to ± flat-topped false panicle, flowers crowded distally, ultimate branchlets 1- or 2(–4)-flowered; bracts green, margins often red, 4–7 mm long, inner usually slightly longer than outer, ± membranous above at anthesis, acute or inner slightly emarginate. *Flowers* zygomorphic, either white, then lower tepals usually with one or a pair of purple median spots (Jonkershoek), or blue with darker blue to violet spear-shaped markings in lower midline and often white-dotted in centre of dark colour (Bain's Kloof), with slight sweet scent; perianth tube ± cylindric, 7–10 (Jonkershoek), 12–14 (Bain's Kloof and Steenbras) mm long, flared from 1 mm diam. at base to 2 mm at mouth; tepals elliptic, obtuse, unequal, dorsal 10–13 × ± 4.5 mm, lower held closely together, 10–12 × ± 4 mm wide. *Stamens* unilateral and arcuate; filaments 5–6 (Jonkershoek), ± 9 (Bain's Kloof) mm long, exserted 3–5 mm; anthers 3.3–4.5 mm long, pollen ± white. *Style* arching adaxial to filaments, dividing opposite lower to middle $^1/_3$ of anthers, style branches ± 2 mm long, divided for ± $^1/_3$ their length. *Capsules* top-shaped and 3-lobed, 4–5 mm long, sometimes flushed red before drying; with 1 or 2(3) per locule. *Seeds* globose to ovoid, sometimes flattened by pressure, slightly wrinkled, ± 2.0–2.5 × 1.7–2.5 mm, with small funicular collar. *Chromosome numbers* $2n = 12, 24$. *Flowering time*: mid-November to late January. Figure 37.

Distribution and biology: restricted to a 65 km portion of the north–south trending mountains in the extreme southwest of Western Cape, South Africa, *Schizorhiza neglecta* is known from just three extended populations in Bain's Kloof, Jonkershoek and in the Steenbras Mtns to the south (Figure 38). Before 1989, when it flowered profusely at Jonkershoek near Stellenbosch, *S. neglecta* had been recorded only a handful of times since its discovery by R.H. Compton in November 1943 in the Jonkershoek Mtns. Its presence in Baviaans Kloof, a tributary valley of Bain's Kloof, was established shortly thereafter by Compton and G.J. Lewis in January 1945. It grows in rocky sandstone-derived soil at elevations of 400–1 000 m, generally in sheltered, wetter sites such as slopes below cliffs and near streams where additional moisture is available. Its habit of flowering in the early summer following a fire the previous summer or autumn partly explains why it is so seldom collected. It is fairly common locally at Jonkershoek, where it occurs in several isolated sites, and can form extensive and dense populations, notably at Berg River Nek, where it carpets the slopes with white when in full bloom. Pollination of *S. neglecta* has not been critically studied, but Goldblatt et al. (1995) recorded visits by *Xylocopa hottentotta* (Apidae: Xylocopidae), a large-bodied but short-tongued bee. More study is needed before this observation can be placed in context.

Diagnosis and relationships: when first described, *Schizorhiza neglecta* was associated with the Cape species of *Lapeirousia* (now *Codonorhiza*), but its basic chromosome number of $x = 6$ is discordant with those species, which have $x = 10$ (excluding B chromosomes). Corm morphology is likewise unlike that of *Codonorhiza* and is unique for Crocoideae in the ellipsoid shape with the flat base of narrower diameter than the middle of the corm. The corky to papery tunics, rather than woody (*Lapeirousia*) or of compacted fibres (*Codonorhiza, Psilosiphon*), are likewise distinctive. The large, smooth to slightly wrinkled, ± globose seeds nearly match those of *Lapeirousia* and *Psilosiphon*, but are quite unlike the smaller, ovoid, reticulate seeds of *Codonorhiza*. Leaf anatomy, including the absence of marginal veins or subepidermal sclerenchyma strands and closed vascular bundle sheaths conform to the condition in *Codonorhiza*, but the alternate main vascular bundles and slightly plicate leaf blades are unique. Pollen grains with a single banded operculum recall *Codonorhiza*, whereas all *Lapeirousia* and *Psilosiphon* species examined for the character have a 2-banded operculum. Morphologically, the flowers of *S. neglecta* appear most like those of the short-tubed *P. erythranthus* alliance, particularly the southern African *P. sandersonii*, especially in having the upper tepal reflexed to lie in the same plane as the lower tepals. The production of multiple cormlets in the lower nodes of the stem and in place of the parent corm at the end of the growing season is also unique for the *Lapeirousia* clade.

In the DNA-based phylogeny (Figure 1) *Schizorhiza neglecta* is retrieved as sister to the *Lapeirousia* plus *Psilosiphon* clades (using plastid DNA sequences alone it is retrieved in a polytomy with these two clades). This result at first seemed puzzling as *S. neglecta* seemed to accord with *L.* sect. *Paniculatae,* now *Psilosiphon*, in floral and seed morphology and cytology, although discordant geographically. Careful re-examination of the species has shown that its leaf anatomy and corm morphology is unique, thus not conforming to *Psilosiphon,* and the pollen grains with a 1-banded operculum also differ from that genus, resembling instead those of *Codonorhiza* among the *Lapeirousia* group of genera.

Variation: the type population of *Schizorhiza neglecta* from Jonkershoek, with white flowers and a shorter perianth tube, 8–10 mm long is diploid, $2n = 12$ (Goldblatt & Manning 1992), but counts from blue-flowered plants from Bain's Kloof with a longer perianth tube, 12–14 mm, are tetraploid, $2n = 24$ (Table 4). These differences led us to consider whether they might be better regarded as separate taxa and in the description above, we separate the significant differences between these populations. The longer-tubed Bain's Kloof and Steenbras popula-

FIGURE 37.—*Schizorhiza neglecta*. A, flowering stems; B, corm and cormlets [see text]; C, fruiting stem; D, flowers. A–C, *Goldblatt & Manning 9022*; D, *Goldblatt & Manning 9489*. Scale bar: 10 mm. Artist: John Manning.

tions also have longer floral bracts 6–7 mm long (vs. 4–6 mm) and anthers 4.0–4.5 mm long (vs. 3.3–3.8 mm) than the Jonkershoek plants. The size differences may be explained by the ploidy difference, although chromosome number for the Steenbras population is unknown and flower colour is uncertain (residual pigmentation on herbarium specimens suggests that they were blue). We defer recognition of infraspecific taxa for this rare Cape plant, known from just three extended populations, pending additional study.

History: although thought by G.J. Lewis, a specialist on the systematics of southern African Iridaceae, to be a new species of *Lapeirousia* when first collected in the 1940s, *Schizorhiza neglecta* remained unnamed until Goldblatt (1972) treated it as *L. corymbosa* subsp. *alta*. Our examination of living plants in 1989 at Jonkershoek made it clear that these populations represented a separate species, which was then described as *L. neglecta* (Goldblatt & Manning 1992). At the time we considered it to be not even particularly closely related to the *L. corymbosa* complex, and placed the species in the otherwise tropical and eastern southern Africa sect. *Paniculatae*, now *Psilosiphon*.

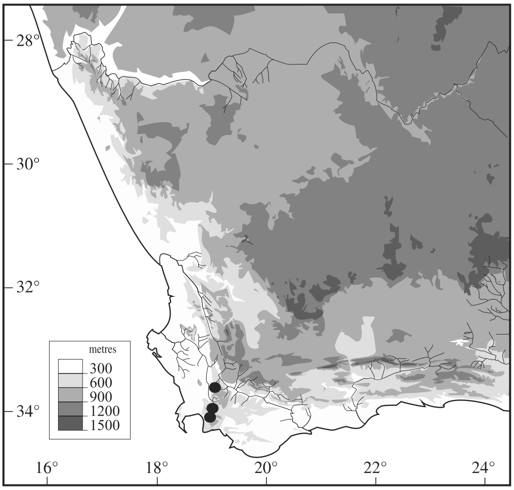
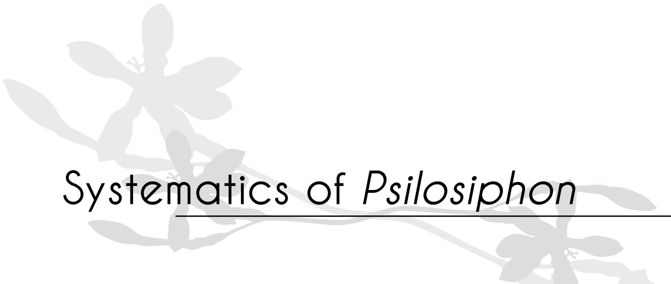


FIGURE 38.—Distribution of *Schizorhiza neglecta*, ●.

Representative specimens

SOUTH AFRICA. WESTERN CAPE—**3318** (Cape Town): Jonkershoek, near waterfall, (–DD), 6 Nov. 1943, *Compton 15299* (PRE); Jonkershoek Valley, wet gully along trail to Berg River Nek, (–DD), 29 Dec. 1989, *Goldblatt & Manning 9022* (B, K, MO, NBG, PRE, WAG); Jonkershoek, Dwarsberg, upper contour path, among rocks in recently burnt firebreak, (–DD), 19 Jan. 1975, *Kerfoot & Haynes 14* (MO, PRE); trail at foot of cliffs above Berg River Nek, (–DD), 29 Dec. 1989, *Goldblatt & Manning 9031* (K, MO, NBG, PRE, WAG). **3319** (Worcester): Bain's Kloof, (–CA), 17 Jan. 1945, *Compton 16918* (NBG); *Lewis 979* (SAM); Baviaanskloof, (–CA), 31 Dec. 1992, *Goldblatt & Manning 9489* (MO, NBG). **3418** (Simonstown) Jonkershoek, Swartboskloof, upper west-facing slope at base of cliffs, 1 000 m (–BB), 2 Dec. 1989, *Oliver 9338* (K, NBG); near Steenbras Dam, (–BB), Dec. 1945, *Lewis 1595* (BOL, SAM).



Systematics of *Psilosiphon*

Psilosiphon *Welw. ex Goldblatt & J.C.Manning*, gen. nov. Type: *P. sandersonii* (Baker) Goldblatt & J.C.Manning.

> *Lapeirousia* subg. *Paniculatae* [*Paniculata*] Goldblatt & J.C.Manning [sect. *Paniculatae* only] in Annals of the Missouri Botanical Garden 77: 373 (1990). Type: *L. erythrantha* (Klotzsch ex Klatt) Baker (= *P. erythranthus* (Klotzsch ex Klatt) Goldblatt & J.C.Manning).

Deciduous geophytes. *Corm* flat-based, bell-shaped, rooting from base, axillary in origin; tunics of compacted fibres, outer layers decaying into loose fibrous network or vertical strips. *Foliage leaves* few to several, linear to sword-shaped, falcate or ± terete, plane with visible main vein; lowermost often longest and inserted on stem near ground level, upper leaves progressively smaller. *Stem* aerial, compressed and angled to winged, usually branched, often repeatedly. *Inflorescence* either much branched, forming a ± a round or flat-topped false panicle, with sessile flowers, or a simple or branched spike; bracts green and ± soft-textured, often becoming dry distally, inner ± as long as outer, often forked near apex. *Flowers* usually zygomorphic, or radially symmetric, long-lived, often salver-shaped or rotate, when zygomorphic, lower tepals usually with contrasting darker or lighter markings, sometimes sweetly scented; perianth tube cylindric or funnel-shaped, short to extremely long; tepals subequal or unequal with dorsal largest. *Stamens* symmetrically disposed or unilateral and arcuate; filaments slender, free; anthers oblong-linear, dehiscence longitudinal. *Ovary* globose, sessile; style filiform, branches forked for $^{1}/_{3}$ to $^{1}/_{2}$ their length, undivided or notched apically. *Capsules* cartilaginous, ± globose. *Seeds* ± globose, flattened at chalazal end, smooth or slightly wrinkled; surface cells usually domed or ± flat. *Basic chromosome number* uncertain, diploid numbers, $2n = 16, 12, 10, 8$ (diploids); $2n = 14, 12, 10, 8, 6$ (tetraploids).

Species: 15; sub-Saharan Africa, from Ethiopia to Zimbabwe, Mozambique and Angola, one species also in Nigeria, several in Botswana and Namibia, two in eastern South Africa.

Key to species in southern Africa

1a Perianth tube 1–2 mm long; flowers actinomorphic; all tepals with contrasting markings:
  2a Tepals 11.0–15.5 × (4–)5–7 mm (appearing shorter in poorly preserved specimens); flowers 1(2) on ultimate branches of inflorescence; corm tunics dark brown to blackish and decaying irregularly into vertical strips .... 2. *P. avasmontanus*
  2b Tepals 7.0–9.5 × 3–5 mm; flowers (2)3–5 on ultimate branches of the inflorescence; corm tunics light brown, outer layers of fine reticulate fibres .... 6. *P. coeruleus*
1a Perianth tube 3–150 mm long; flowers zygomorphic with arcuate to ± erect unilateral stamens; contrasting markings when present confined to 3 lower (abaxial) tepals:
  3a Perianth tube 100–150 mm long; flowers white, sometimes flushed pale blue to purple outside .... 11. *L schimperi*
  3b Perianth tube 3–50 mm long; flower variously coloured:
    4a Inflorescence a divaricately branched false panicle with main branches 1- or 2(3)-flowered:
      5a Perianth white to pale pink; corm tunics straw-coloured and outer layers ± fibrous and reticulate; floral bracts dry before anthesis, becoming membranous, dry and light brown with tips often darker brown .... 10. *P. bainesii*

5b Perianth blue to violet, lower tepals with white markings edged dark blue to violet; corm tunics dark brown and outer layers breaking into vertical strips, not fibrous; floral bracts acute-attenuate and dark brown in distal half . . . . 1. *P. sandersonii*
4b Inflorescence a ± false panicle or spike with at least some main branches 3–8-flowered:
  6a Perianth tube 25–50 mm long:
    7a Flowers creamy white, lower tepals with purple median spear-shaped markings; perianth tube 40–45 mm long; tepals 15–19 × 4–5 mm . . . . 9. *P. otaviensis*
    7b Flowers blue to violet, rarely pale blue to almost white, lower tepals with blue to violet markings; perianth tube 25–38 mm long; tepals 10–14 × 3–6 mm:
      8a Flowers violet, lower tepals with white median mark edged in darker violet; tepals ± 14 mm long; floral bracts 8–10 mm long; perianth tube 35–37 mm long . . . . 4. *P. erongoensis*
      8b Flowers pale blue to white with bluish markings on lower tepals; tepals 10–12 mm long; floral bracts 3–6(–7) mm long; perianth tube 25–38 mm long. . . . . 3. *P. gracilis*
  6b Perianth tube 3–25 mm long:
    9a Perianth tube (15–)18–25 mm long:
      10a Perianth greenish or blue-violet with red to purple and white markings on lower tepals; floral bracts 5–7 mm long; plants of Malawi, Mozambique, South Africa (Limpopo Province) and Zimbabwe . . . . 8. *P. masukuensis*
      10b Perianth pale blue or white; floral bracts 3–6(–7) mm long; plants of Namibia . . . . 3. *P. gracilis*
    9b Perianth tube (5–)7–15 mm long:
      17a Dorsal tepal suberect or arched over stamens; lower tepals often (?always) with tooth-like median ridge up to 1 mm long; style branches undivided or notched at tips . . . . 5. *P. rivularis*
      17b Dorsal tepal reflexed, lying in same plane as lower tepals; lower tepals without tooth-like median ridges; style branches divided for $^{1}/_{3}$–$^{1}/_{2}$ their length. . . . . . . 7. *P. erythranthus*

Spp. 1–11

1. **Psilosiphon sandersonii** *(Baker) Goldblatt & J.C.Manning*, comb. nov. *Lapeirousia sandersonii* Baker, Handbook of the Irideae: 169 (1892), 95 (1896), 7: 352 (1898, excl. specimens cited); Goldblatt: 463 (1990a). Type: South Africa, 'Transvaal', *Sanderson s.n.* [K, lecto.! designated by Goldblatt: 463 (1990a)].

[*Lapeirousia bainesii* var. *breviflora* Baker: 156 (1877), nom. nud.] [no specimen cited, but *Nelson 402*, K, from Rhenosterpoort is so annotated by Baker].

Plants 200–350(–450) mm high, divaricately and often intricately branched, stem compressed, 2-angled below, 3-angled above branches, slightly winged, sheathed below by dark brown cataphylls, inner reaching shortly above ground. *Corms* 25–30 mm in diam.; tunics dark brown, hard-leathery internally, decaying irregularly into vertical sections, seldom becoming fibrous and never netted. *Leaves* 2–4, ± linear to falcate, 2–3 mm wide, firm to rigid, main and secondary vein pairs ± prominent, closely set; lowermost leaf longest, sometimes exceeding inflorescence, upper leaves progressively shorter. *Inflorescence* a rounded to ± flat-topped false panicle but with main axis sometimes evident, ultimate branches 1-or 2(3)-flowered; bracts 5–12 mm long, green with brown tips in bud, often flushed purple, becoming dry and dark brown with age, acute-attenuate, inner sometimes longer than outer, usually notched at apex. *Flowers* zygomorphic, blue to violet, lower 3 tepals each with deep red to purple and white spear-shaped mark guide in lower midline; perianth tube 8–12 mm (subsp. *limpopoensis*), or mostly 15–30 mm (subsp. *sandersonii*), slender, widening slightly in upper 2–3 mm; tepals subequal, lanceolate, 10–11 × 2–4 mm, dorsal held apart from others, reflexed, lower 3 joined for ± 1 mm and held close together, when fully open all ± spreading. *Filaments* unilateral, ± erect, ± 5 mm long, exserted 2.5–3.5 mm from tube; anthers 3–5 mm long, purple; pollen pale yellow or white. *Style* dividing near apex of anthers or shortly (rarely much) exceeding anther tips; branches 1–2 mm long, divided for up to $^1/_3$ their length, notched apically or undivided. *Capsules* depressed globose, 4–5 × 4–5 mm. *Seeds* nearly globose, ± 1.5–2.0 mm diam. *Chromosome number* 2*n* = 10. *Flowering time*: mainly February and March, occasionally from late December or in April. Figures 39, 40.

Distribution: *Psilosiphon sandersonii* is native to the interior of eastern Botswana and the adjacent northern South Africa where it occurs in relatively dry habitats in North West and Limpopo provinces, as well as in Northern Cape and western Mpumalanga (Figure 41). It appears to be especially common in the Magaliesberg from Pretoria west to Rustenburg, and according to the collection record, is relatively rare in Limpopo and Botswana. The easternmost records from the cool, high, well-watered Dullstroom, Belfast and Middelburg areas of Mpumalanga are surprising in view of the rest of the range in semi-arid country, but the eastern populations differ only in their slightly longer perianth tube, 20–25 mm long, from those occurring further to the west. The habitat is always rocky, and usually well drained, including hill slopes, ridges and summits. The distinctive corms are seldom collected, which probably reflects the difficulty in their extraction from rocky ground. We recognise two subspecies, subsp. *sandersonii* extending from eastern Botswana and adjacent South Africa as far east as Dullstroom in Mpumalanga and as far south as the Kuruman hills in Northern Cape, where some populations have a perianth tube up to 30 mm long; and subsp. *limpopoensis*, with a short perianth tube 8–12 mm long and most common in the Waterberg of Limpopo Province, but extending north into the Soutpansberg, where subsp. *sandersonii* also occurs.

Diagnosis and relationships: allied to the *Psilosiphon erythranthus* complex of short-tubed species, *P. sandersonii* has the repeatedly branched, panicle-like inflorescence and blue-violet flowers that characterise most tropical African species of the genus. It can be distinguished from the related *P. erythranthus* by its typically longer perianth tube, mostly 15–30 mm long, and ± divaricately and often intricately branched inflorescence with 1 or 2 (rarely 3) flowers on the major terminal branches. The floral bracts are often relatively long, 8–12 mm, acute-attenuate and flushed purple or brown and aging dark brown. The corm tunics too, are distinctive, being dark brown and fragmenting into vertical strips rather than becoming a fibrous network. *P. erythranthus* typically has fewer-branched inflorescences with 3–6 flowers per main terminal branch and a perianth tube usually 6–11 mm long, rarely up to 15 mm. The floral bracts are 4–6 mm long, shorter than those in most populations of *P. sandersonii*. A good illustration of *P. sandersonii* is in *Flowering Plants of Africa* 31: t. 1226 (1956).

The strongly asymmetric karyotype of *Psilosiphon sandersonii*, with 2*n* = 10 (Goldblatt, 1990b: one population counted), consists of a pair of very long chromosomes and 9 pairs of much shorter chromosomes. This contrasts sharply with populations of *P. erythranthus*, which have 2*n* = 8, 14 or 12 and a relatively symmetric karyotype.

The variation in perianth tube length, not evident to Goldblatt (1990a), correlates with geographical distribution. Plants from Limpopo, mainly in the Waterberg and nearby, have particularly short tubes, 8–12 mm long, whereas populations in the southwest of the range, in the Kuruman hills and adjacent country in Northern Cape, stand out in having a much longer perianth tube, 25–30 mm long. The regional variation is not always consistent and plants from Mpumalanga sometimes have perianth tubes almost as long as those from further west. In other respects, especially the branching pattern and rust-brown, acute-attenuate floral bracts, the long- and short-tubed plants accord with typical *P. sandersonii*. We recognise just two geographic subspecies to reflect the variation in tube length, referring populations from the Waterberg and nearby to subsp. *limpopoensis* and the remaining, longer-tubed populations to subsp. *sandersonii*. Subsp. *limpopoensis*, in particular, broadly resembles *P. erythranthus* in its short perianth tube, 8–12 mm long, and relatively short floral bracts, 5–6 mm long (see under subsp. *limpopoensis*). The plants, however, have the divaricately branched stem and brown floral bracts typical of *P. sandersonii* except in their shorter length. They may represent recent or ancient hybridisation between *P. sandersonii* and *P. erythranthus*, the ranges of which do not overlap today but lie less than 100 km apart in Botswana. The southernmost stations of *P. erythranthus* in Zimbabwe and the northernmost stations of *P. sandersonii* subsp. *limpopoensis* in South Africa lie substantially further apart.

FIGURE 39.—*Psilosiphon sandersonii* subsp. *sandersonii*, *Goldblatt & Manning 9806*. Scale bar: 10 mm. Artist: John Manning.

FIGURE 40.—*Psilosiphon sandersonii* subsp. *sandersonii*, *Goldblatt & Manning 9806*. Scale bar: 10 mm. Artist: John Manning.

Psilosiphon masukuensis is sometimes confused with *P. sandersonii*, but the inflorescence of that species is comparatively sparsely branched with the main branches 5–9-flowered, and the flowers are smaller, although perianth tube length, 20–25 mm long, overlaps that of *L. sandersonii*. The corms of the two species also differ, those of *P. masukuensis* being smaller and having paler, fibrous tunics. *P. masukuensis* appears to favour wetter, lowland sites in contrast to the montane, rocky, well-drained habitats of *P. sandersonii*.

History: collected first by John Sanderson, probably in 1852 when he travelled to Rustenburg and the Magaliesberg on his only journey to then Transvaal Republic (Gunn & Codd 1981), *Psilosiphon sandersonii* first appeared in the literature as the nomen nudum *Lapeirousia bainesii* var. *breviflora* (Baker 1877). Baker subsequently described *L. sandersonii* in 1892 and the species was so treated in *Flora capensis* (Baker 1896). In *Flora of tropical Africa* (Baker 1898), specimens cited as *L. sandersonii* are not this species, but the superficially similar, blue- or red-flowered *P. erythranthus*, then poorly understood.

Key to subspecies

1a Perianth tube mostly 15–30 mm long; floral bracts 8–12 mm long; style branches 1.5–2.0 mm long .... 1a. subsp. *sandersonii*

1b Perianth tube mostly 8–12 mm long; floral bracts 5–6 mm long; style branches 1.0–1.3 mm long .... 1b. subsp. *limpopoensis*

1a. subsp. **sandersonii**

Plants 200–350(–450) mm high. *Corms* 25–30 mm diam. *Inflorescence* with bracts 8–12 mm long. *Flowers* with *perianth tube* 15–30 mm long; *tepals* 10–12 × 3–4 mm. *Stamens* with filaments 5–7 mm long, exserted 3.0–4.5 mm. *Style* dividing near apex of anthers, branches 1.5–2.0 mm long, divided for up to $^1/_4$ their length or barely notched at tips (or apparently undivided). Figures 39, 40 & 41.

Representative specimens

BOTSWANA.—**2424** (Dikgomo di Kae): Jwaneng TV hill, 37 km southeast of Jwaneng to Kanye, (–DD), 24 Feb. 1997, *Cole 1214* (MO, PRE). **2425** (Gaborone): near Molepolole, shale, (–BC), 15 Mar. 1930, *Van Son s.n.* (PRE 28664); west of Gaborone Dam, (–DB), 1976, *Mott 928* (SRGH, UCBG); Gaborone, near Notwane sewage ponds, (–DB), 22 Mar. 1981, *Barnes 185* (PRE). **2525** (Mafeking): 6 miles [9 km] west of Kanye, (–AB), 12 Feb. 1971, *Van Rensburg B4226* (PRE).

SOUTH AFRICA. LIMPOPO.—**2229** (Waterpoort): Zoutpansberg, 1 mile [1.5 km] from Dandy Farm, road to Sand River, south slopes in rocky outcrop, (–DC), 3 Apr. 1957, *Meeuse 10212* (K, M, PRE, SRGH); Farm Thornhill 743, red sand in riverine woodland, (–DD), 18 Mar. 1985,

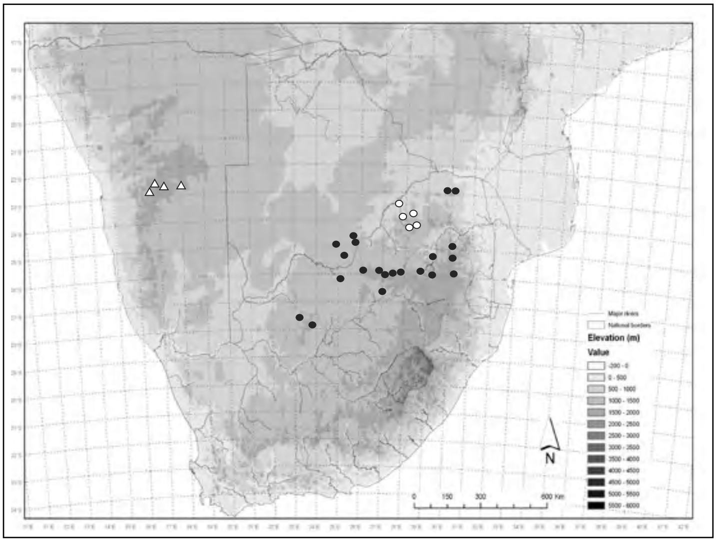


FIGURE 41.—Distribution of *Psilosiphon avasmontanus*, Δ; *P. sandersonii* subsp. *limpopoensis*, ○; subsp. *sandersonii*, ●.

Raal 434 (PRE). **2230** (Messina): Louis Trichardt, Farm Rietbok 226, among rocks in montane scrub forest, 1476 m, (–CC/CD), 25 Mar. 1982, *Venter 7812* (PRE).

NORTH WEST.—**2526** (Zeerust): Zeerust, (–CA), Jan. 1928, *Thode A1503* (GH, K), Feb. 1912, *Jenkins TM11660* (K, PRE); 15 m [22 km], east of Swartruggens, bushveld on ridges, 14 Feb. 1956, (–DB), *Acocks 18747* (K, PRE). **2527** (Rustenburg) Rustenburg, 4000 ft [1 240 m], stony hillside near town, (–CA), 1904 (fl. & fr.), *Pegler 1108* (GRA, K, PRE, SAM); 22 m west of Rustenburg, (–CA), 14 Feb. 1956, *Leistner 539* (K, PRE); Rustenburg, Tierkloof, moeras by wildreservaathek, (–CA), 13 Mar. 1976, *Venter 654* (K, MO, PRE, SRGH, WAG); Brits, Silikaatsnek, top of poort in shallow sand over quartzite, (–DB), *Codd 736* (PRE). **2624** (Vryburg): Vryburg, (–DC), 5 Feb. 1948, *Rodin 3501* (K, MO, P, PRE, S). **2625** (Delareyville): Vryburg District, Gold Ridge Farm, koppie peak in banded ironstone rocks, (–AB), 15 Feb. 1980, *Gubb 80-45* (PRE). **2627** (Potchefstroom): Dassiesrand, Potchefstroom, (–CA), 23 Mar. 1940, *Van der Westhuizen 1114* (PRE).

GAUTENG.—**2527** (Rustenburg): Krugersdorp, Jack Scott Nature Reserve, (–DC), 2 Feb. 1961, *Wells 2305* (K). **2528** (Pretoria): Magaliesberg, Hornsnek, 12 km west of Pretoria, (–CA), 12 Jan. 1956, *Schlieben 7751* (B, BR, G, HBG, K, M); 31 Jan. 1983, *Perry 2017* (MO, NBG); The Willows, Pretoria, (–CA), 9 Mar. 1906, *Burtt Davy 5333* (GRA, K); Cullinan, Farm Vaalwaterkrans, 25.2 km from Pretoria on Roodeplaat Dam road, (–CB), 28 Jan. 1980, *Retief & Herman 159* (MO, PRE); Tierpoort Vakansieoord, east of Pretoria, sandstone rock crevices and slopes, (–CD), 8 Mar. 1977, *Van Jaarsveld 1870* (NBG); Donkerhoek, 20 miles [± 30 km], east of Pretoria, (–CD), 19 Mar. 1959, *Codd 9908* (K, PRE); Premier Mine, (–DA), Jan. 1919, *Rogers 22415* (K, MO, P, SAM), June 1921, *Rogers 24146* (B, BR, G, GRA, K, LISC, MO, P, S, SAM); Renosterkop, Bronkhorstspruit Distr., (–DB), 7 Mar. 1932, *Young 2116* (K, PRE); north of Bronkhorstspruit to Groblersdal, (–DB), 1 Feb. 1994, *Goldblatt & Manning 9806* (MO).

MPUMALANGA.—**2430** (Pilgrims Rest): 5.3 miles (± 8 km] from Burgersfort on Steelpoort road, 2500 ft [762 m], (–CB), 14 Mar. 1953, *Story 4067* (GRA, K, PRE, SRGH). **2529** (Witbank): Loskop Dam, Nooitgedacht, shallow ground on summit, (–AD), 9 Feb. 1967, *Theron 1214* (PRE); 5 miles west of Middelburg, (–CD), 30 Jan. 1929, *Hutchinson 2716* (K, PRE); Botsabelo, Renosterpoort, mountain summit, (–CD), Mar. 1878, *Nelson 402* (K, PRE). **2530** (Lydenburg): hills above Dullstroom, (–AC), 23 Feb. 1937, *Van der Merwe 1255* (B, K, PRE); Dullstroom, among dolerite rocks on Farm Valleispruit, 6500' [1 920 m], (–AC), 30 Jan. 1933, *Galpin 13369* (K, P, PRE); Belfast, Feb. 1909, (–CA), *Doidge 4800* (K).

NORTHERN CAPE.—**2723** (Kuruman): Mansfield Farm, among ironstone rocks, top of beacon hill, (–CB), 13 Mar. 1981, *Gubb 181-73* (PRE); Kuruman Hills, Brancote Farm, red sandy loam, 1 700 m, (–CB), 31 Mar. 1988, *Venter 12894* (PRE); Klipfontein Farm, sandy ground with ironstone pebbles, (–DC), *Gubb 158-29* (PRE); 7 miles [10.5 km] southwest of Kuruman, (–DC), 16 Mar. 1971, *Wisura 2003* (NBG).

1b. subsp. **limpopoensis** *Goldblatt & J.C.Manning*, subsp. nov.

TYPE.—SOUTH AFRICA, Limpopo, **2327** (Ellisras): Waterberg, between Groothoek and Vaalwater, 1 000 m, (–BD), 6 Jan. 1959, *Werdermann & Oberdieck 1640* (PRE, holo.!; B!, BR!, GH, K!, MO!, WAG!).

Like subsp. *sandersonii* but *corms* 15–25 mm diam.; tunics sometimes becoming fibrous and netted with age. *Spike* with floral bracts 5–6 mm long. *Flowers* with *perianth tube* 8–12 mm long; *tepals* 10–11 × 3.0–3.5 mm. *Stamens* with filaments ± 5 mm long, exserted 2.5–3.0 mm. *Style* dividing near or beyond apex of anthers, branches ± 1.0–1.3 mm long, divided for up to 1/3 their length.

Distribution: subsp. *limpopoensis* is restricted to the western Limpopo Province of South Africa in the Waterberg Mtns and surrounding country (Figure 41). As outlined above it bears a superficial similarity to the mainly tropical African *Psilosiphon erythranthus* because of its relatively short perianth tube. The dark, tough, non-reticulate corm tunics, intricate branching pattern and rather dark floral bracts all accord better with the more widespread *P. sandersonii* subsp. *sandersonii*.

Representative specimens

SOUTH AFRICA. LIMPOPO.—**2327** (Ellisras): Waterberg 67 miles [± 101 km] north of Vaalwater on Beauty road, (–DB), 3 Feb. 1983, *Reid 656* (PRE); Waterberg, 30 km west of Vaalwater, (–BD), 12 Mar. 1990, *Balkwill* et al. *5518* (J, MO). **2328** (Baltimore): Doornleegte Farm, 6.5 km from main gate of Lapalala Wilderness, 29 Mar. 2004, *Bredenkamp 3009* (PRE). **2428** (Nylstroom): Vlakfontein, 3 miles north of P.O. Palala, (–BC), 29 Jan. 1960, *Codd 9975* (PRE); 16 km from Palala on road to Bamboeskloof, (–BC), 9 Mar. 1978, *Germishuizen 735* (PRE); Sterkrivier Nature Reserve, rocky slope in mixed woodland, below slabs of bedrock, (–BD), 13 Mar. 1973, *Jacobsen 2794* (PRE); Nylstroom, Heuningfontein, Farm Donkerkloof, woodland on sand, (–AD), 13 Feb. 1987, *Westfall 2231* (PRE).

2. **Psilosiphon avasmontanus** *(Dinter) Goldblatt & J.C.Manning*, comb. nov. *Lapeirousia avasmontana* Dinter in Repertorium specierum novarum regni vegetabilis 29: 256 (1931); Goldblatt: 447 (1990a). Type: Namibia, Lichtenstein, Auas Mtns., 20 Feb. 1923, *Dinter 4454* (B, holo.!; GH!, S!, Z [3 sheets]!, iso., K!, [photo of specimen at B]).

Plants 200–300 mm high, ± divaricately branched in upper half, stem rounded to slightly triangular in section, sometimes obscurely winged or ridged at one or more angles. *Corm* bell-shaped, 15–20 mm diam.; tunics dark brown to blackish, inner layers ± woody, outer decaying irregularly, often into vertical strands. *Leaves* 3 or 4, linear, 2–3 mm wide, main vein prominent, lowermost inserted near ground level and longest, usually slightly exceeding inflorescence, others inserted above ground and progressively smaller above, those subtending branches ± bract-like. *Inflorescence* a rounded, ± flat-topped false panicle, ultimate branches with 1(2) flowers; bracts 5–6 mm long, green below, membranous in upper half and bent outwards by tepals, becoming completely dry in fruit, inner ± as long as or slightly longer than outer. *Flower* actinomorphic, blue to light purple with median white heart-shaped mark feathered purple on edges in basal half of each tepal; perianth tube ± 1 mm long, cylindric below, widening in upper $^1/_2$; tepals spreading but curving upwards near tips, subequal, lanceolate to elliptic, 11.0–15.5 × (4–) 5–7 mm. *Stamens* symmetrically arranged; filaments 4–5 mm long, diverging distally; anthers diverging, 4–5 mm long, apices curving inward after dehiscence; pollen light blue-purple to ± white. *Style* straight, 6–7 mm long, dividing near anther apices, branches ± 1.2 mm long, barely notched apically. *Capsules* ± globose, weakly 3-lobed, showing outline of seeds, 6–8 × ± 7 mm. *Seeds* globose, dark brown, 1.5–2.0 mm diam., rounded to weakly angled by pressure, tapering toward attached funicle, surface smooth. *Chromosome number* 2*n* = 16. *Flowering time*: February to April. Figure 42.

Distribution and biology: endemic to central interior Namibia, *Psilosiphon avasmontanus* is locally common on the hills and mountains around Windhoek, extending north toward Okahandja and east to Wit Vlei (Figure 41). Apparently preferring well-drained sites, it grows in open, stony, sloping ground or sometimes in light scrub. Depending on rainfall, flowering may last between 3 and 8 weeks. New branches continue to be produced from the cauline leaf axils as long as the ground remains moist, and late rainfall can stimulate production of a second flush of flowering from new branches. The pale blue flowers are visited by a variety of insects including bees, wasps and butterflies. We were unable to detect nectar in excised flowers and we assume that the only reward to the bees and wasps is pollen and that butterfly visits are exploratory.

Diagnosis and relationships: the relatively large, pale blue flowers with a white centre, radially symmetric perianth and stamens, and large, ± flat-topped inflorescence distinguish *Psilosiphon avasmontanus* from other tropical and subtropical African species of the genus. It is most easily confused with the more widespread *P. coeruleus*, which has similar, but smaller, actinomorphic flowers. *P. avasmontanus* has dark brown ± woody corm tunics that break into vertical strips as they decay and a divaricately branched inflorescence, the terminal branches of which bear a single (rarely 2) flowers. Corm tunics in *P. coeruleus* are light brown, becoming finely fibrous and netted as they decay, and the inflorescence is less strongly branched with ascending branches, some of which terminate in spikes of 3–5 flowers. The flowers of *P. avasmontanus* have relatively larger, pale blue tepals, 11.0–15.5 mm long, with heart-shaped white markings, whereas *P. coeruleus* has smaller tepals, 8–9 mm long, with spear-shaped white markings.

Although they are the only two species of *Psilosiphon* in Namibia with radially symmetric flowers, chromosome cytology confirms that *P. avasmontanus* and *P. coeruleus* are not immediately related. *P. avasmontanus* is diploid with 2*n* = 16 and the strongly bimodal karyotype consists of 1 long and 7 short chromosome pairs (Goldblatt 1990b), a pattern quite different from *P. coeruleus*, which has 2*n* = 8 and a karyotype of 2 long and 2 shorter chromosome pairs. Despite the apparent numerical polyploid relationship, their very different karyotypes have about the same total chromosome length (a proxy for total DNA per cell), making it clear that a polyploid relationship is not involved here. The similar corm tunics and dichotomously branched inflorescences of *P. avasmontanus* and the eastern southern African *P. sandersonii* suggest to us that the two are closely related. *P. sandersonii* also has a bimodal karyotype, in this case consisting of 1 long and 5 much smaller chromosome pairs.

History: *Psilosiphon avasmontanus* was discovered in 1923 by Kurt Dinter and described by him in 1931 as *Lapeirousia avasmontana*. In

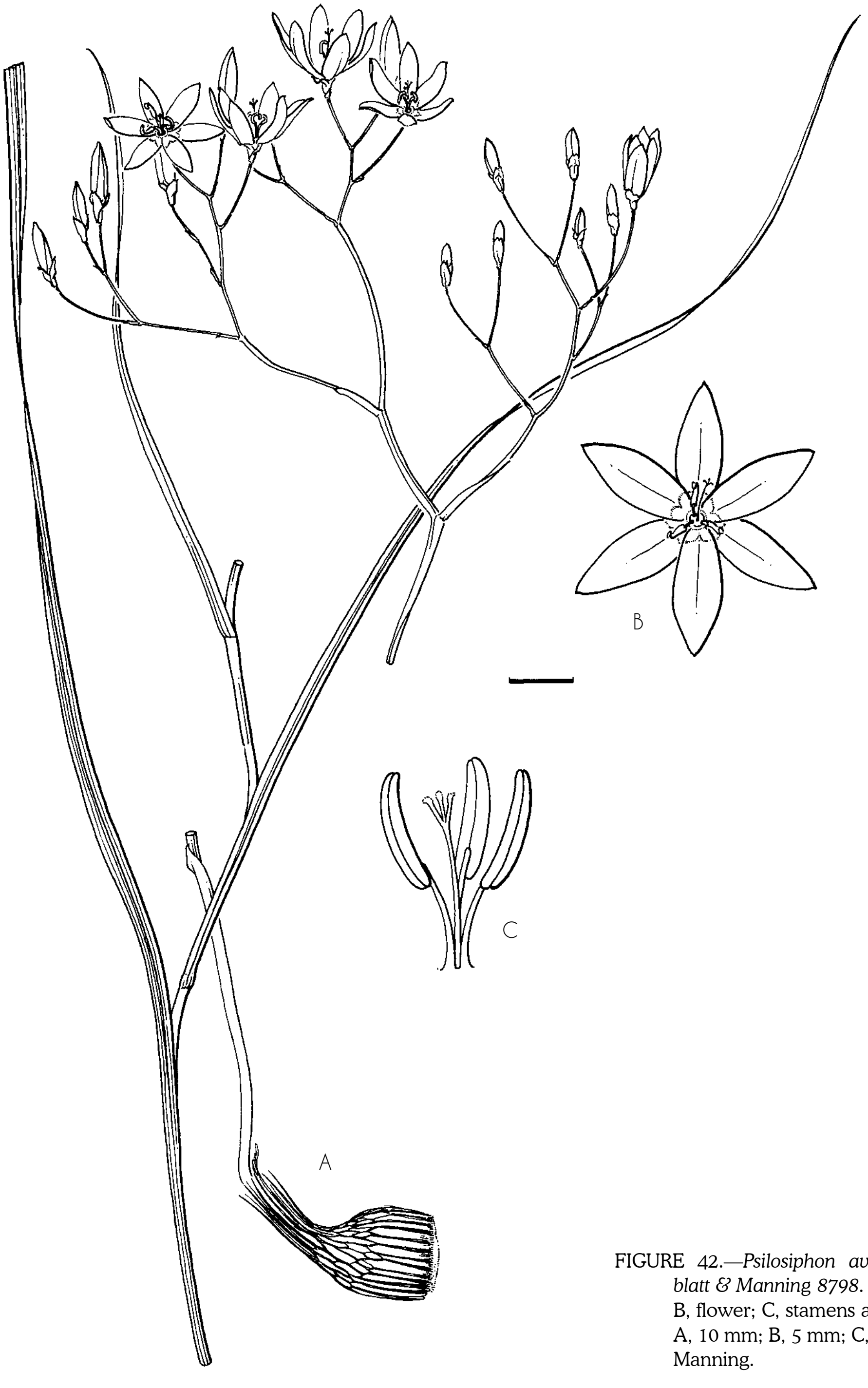


FIGURE 42.—*Psilosiphon avasmontanus*, *Goldblatt & Manning 8798*. A, plant and corm; B, flower; C, stamens and style. Scale bar: A, 10 mm; B, 5 mm; C, 2 mm. Artist: John Manning.

the protologue he compared the species to the superficially similar *P. coeruleus*, which, as Dinter pointed out, grows in a different habitat and differs in several vegetative and floral features. Although *P. avasmontanus* was included in *P. coeruleus* (as *Lapeirousia*) in the *Prodromus einer Flora von Südwestafrika* by Sölch (1969). Goldblatt (1990a) treated them as separate species.

Representative specimens

NAMIBIA.—**2216** (Otjimbingwe): Farm Onduno, Hochflaeche, (–BD), 27 Feb. 1966, *Meyer 115* (MO, WIND); Farm Terra Rossa, rocky slope, (–CD), 13 May 1973, *Giess 13498* (K, M, NBG, PRE, WAG, WIND); Farm Friedenau, (–DB), 25 Mar. 1982, *Müller & Kolberg 2039* (PRE, WIND). **2217** (Windhoek): Elisenheim, Erosberge, below Wächter, smooth shale slopes, (–AC), 28 Feb. 1974, *Merxmüller & Giess 30017* (K, M, S, PRE, SRGH, WAG, WIND); near Brakwater on the Windhoek-Okahandja road, (–AC), 14 Mar. 1959, *De Winter & Giess 7136* (M, PRE, WIND); 5 km west of Windhoek on Daan Viljoen road, stony quartz hill slopes, (–AC), 14 Mar. 1988, *Goldblatt & Manning 8798* (E, K, M, MO, NBG, PRE, S, WAG, WIND). **2218** (Gobabis): sandy grassland at Wit Nossob River between Seeis and Witvley, (–AC), 7 Mar. 1997, *Germishuizen 9504* (MO, PRE).

3. **Psilosiphon gracilis** *(Vaupel) Goldblatt & J.C.Manning*, comb. nov. *Lapeirousia gracilis* Vaupel in Botanische Jarhbucher für Systematik 48: 548 (1912); Sölch 155: 9 (1969); Goldblatt: 465 (1990a). Type: Namibia, 'Great Namaqualand, Doorns', dolomite, 1 450 m, Mar. 1907, *Range 292* (B, holo.! [(K, photo!]; M! [fragment], iso.).

Plants 120–300 mm high, often slender, stem 2–several branched, main axis dominant, branches ascending, flexed at base of main spike, 2-angled and winged below first branch, 3-angled or ± winged above. *Corm* bell-shaped, 12–18 mm diam.; tunics light brown, of layers of compacted fibres, becoming loosely fibrous with age, fibres extending upwards as short, soft spines. *Leaves* 2 or 3(4), lowermost inserted just below ground, linear to narrowly lanceolate, 3–5(–8) mm wide, ± as long as or somewhat longer than inflorescence, thickened around main vein, second leaf usually largest, upper leaves decreasing in size, becoming bract-like. *Inflorescence* a spike or somewhat panicle-like, main terminal branches 2–6-flowered; bracts 3–6(–7) mm long, soft, green below, becoming ± membranous above, sometimes flushed purple, or membranous and dry before anthesis, then usually transparent with fine brown veins, subequal or outer slightly larger. *Flowers* zygomorphic, pale blue to mauve or white, then often with blue tube, lower three tepals white or pale yellow in lower third, edged distally with darker blue to violet, occasionally one or more lower tepals with a small, median tooth-like ridge, lightly fragrant [also said to be unpleasantly scented]; perianth tube cylindric, slightly curved outwards at apex, (18–)25–38 mm long; tepals lanceolate, dorsal largest and held apart, suberect to reflexed, 10–12 × 4–6 mm, margins slightly undulate, lower three slightly smaller, held close together. *Stamens* unilateral; filaments exserted ± 2 mm; anthers 4–5 mm long, pale lilac, blue or ± white; pollen cream. *Style* arching over to filaments, dividing between middle and tips of anthers, branches 1.5–2.0 mm long, divided for ± $^1/_4$ their length. *Capsules* ± globose, obtusely trigonous, 4–5 × 5–6 mm. *Seeds* globose to weakly angular, ± 2 mm diam., dark brown, smooth. *Chromosome number* 2*n* = 12. *Flowering time*: mainly late January to April (May), also recorded in October.

Distribution and biology: restricted to western Namibia, *Psilosiphon gracilis* extends in a relatively broad band along the western part of the country from the Fish River Canyon in the south to the Hoanib River in the Kaokoveld in the northwest (Figure 43). It favours rocky sites, often on limestone, dolomite or other calcareous rock types, but is also said to grow on sandy flats and, especially in more arid places, is often associated with springs and places where additional water is available to supplement the sparse rainfall. Flowering normally occurs at the end of summer, mostly in February and March, but sometimes as late as May. One collection, *Craven 1341*, from the Brandberg and blooming in October, is difficult to explain, and perhaps indicates an unusual pattern of rainfall that particular year. The spring-blooming plants do not differ in any way from those flowering in late summer. The relatively long perianth tube, up to 38 mm long, pale perianth and floral scent suggests that the flowers are adapted for pollination by moths or butterflies with relatively long probosces.

Diagnosis and relationships: the slender perianth tube, typically 22–35 mm long (occasionally slightly longer or shorter), either pale

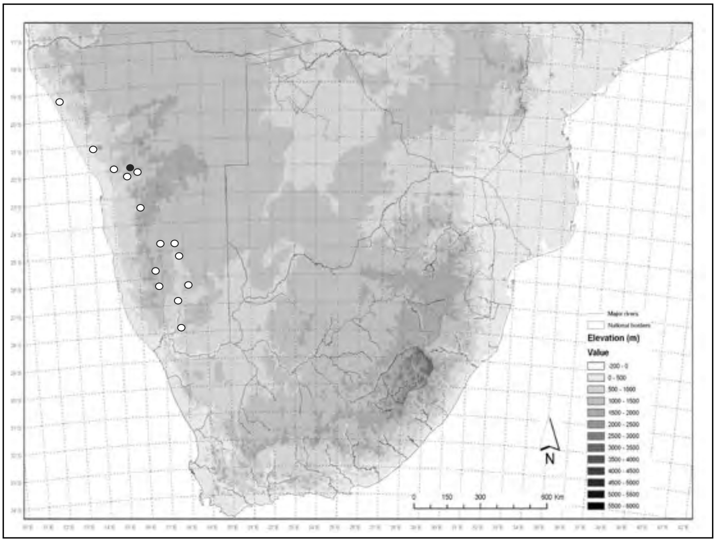


FIGURE 43.—Distribution of *Psilosiphon erongoensis*, ●; *P. gracilis*, ○.

blue or white perianth, usually short floral bracts, 3–6(–7) mm long and comparatively slender habit with up to 6 flowers per terminal branch make *Psilosiphon gracilis* relatively easy to recognise. It most closely resembles *P. bainesii* and *P. otaviensis*, both of which also have long-tubed flowers, but *P. bainesii* has white to pale pink flowers with dark red to brown markings, a tube 40–47 mm long, and a more robust habit, longer floral bracts, 7–12 mm long, and the highly ramified inflorescence has only 1(2) flowers per ultimate branch. Confusion with *P. otaviensis* is more likely as, like *P. gracilis*, it has an inflorescence with the main terminal branches bearing 2–5 flowers. The flowers of *P. otaviensis* are unscented, larger and have a perianth tube somewhat longer, 40–45 mm, and longer floral bracts, (7–)8–11 mm long. The flowers of *P. gracilis* are usually pale blue but fade after drying and appear white, but in a few collections the flower colour is noted as being white.

Phylogenetic relationships are difficult to assess with confidence in *Psilosiphon* but Goldblatt (1990a) postulated that *P. gracilis*, *P. bainesii* and *P. otaviensis* were probably closely allied, sharing derived pale-coloured flowers with an extended perianth tube and light brown, fibrous corm tunics. Countering this is the chromosome cytology (Table 4). *P. gracilis* has $2n = 12$ and a bimodal karyotype (Goldblatt 1990b), quite different from *L. otaviensis* and *L. bainesii*, which have $2n = 10$ (or 6 in some populations of the latter), non-bimodal karyotypes and are cryptic polyploids with a DNA amount per cell ± twice that in *P. gracilis*. A closer relationship with the long-tubed *L. erongoensis* of central Namibia and *L. masukuensis* of eastern southern Africa now seems more likely. Chromosome number of both these species is unknown.

History: evidently first collected by the German geologist, Paul Range, in 1907 near Doorns in southern Namibia, this collection formed the basis for *Lapeirousia gracilis*, described in 1912 by Vaupel. It remained poorly known for many years, but botanical exploration in Namibia since the 1960s has filled in its range so that its distribution now forms a coherent pattern.

Representative specimens

NAMIBIA.—**1912** (Hoanib Mouth): Hoanib river valley ± 20 km inland, rocky hills among boulders, (–BD), 20 Apr. 1985, *Moss & Jacobsen K311* (PRE, WIND). **2114** (Uis): Brandberg, (–AB), 17 Oct. 1981, *Craven 1341* (WIND); Brandberg, Orabeswand, 2 000 m, (–AB), 6 Apr. 1964, *Nordenstam 3666* (M, S). **2115** (Karibib): Farm Klein Spitzkoppe, coarse granitic sand, western slopes and below the summit, (–CC), 23 Feb. 1965, *Geiss 8496* (B, K, M, MO, PRE, S, WAG, WIND). **2215** (Trekkopje): Farm Tsabichab, cracks in marble rock around spring, (–BA), 19 June 1973, *Giess 12744* (K, M, MO, S, WIND). **2216** (Otjimbingwe):

Namibrand, Karibib, Otjosandu, (–AA), 1 Mar. 1963, *Seydel 3419* (B, C, G, GH, K, MO, S, SRGH, WAG, WIND). **2316** (Nauchas): Farm Weisenfels, (–AD), 11 Mar. 1953, *Walter & Walter 1675* (B, WIND). **2417** (Mariental): Farm Haribes, dry sterile vlei, (–DA), 1 Mar. 1963, *Giess* et al. *5571* (M, PRE, WIND). **2416** (Maltahohe): north-northwest of Maltahohe on district road D850 to Bullspoort, (–DB), 11 Mar. 1995, *Smook 9337* (MO, PRE, WIND). **2516** (Helmeringhausen): Farm Chamchawib, (–DB), 23 Jan. 1974, *Giess & Robinson 13255* (K, M, MO, PRE, WAG, WIND). **2517** (Gibeon): Asab, hard clay along the rail tracks, (–BD), May 1913, *Dinter 3061* (SAM), 13 Mar. 1988, *Goldblatt & Manning 8770* (K, MO, NBG, PRE, S, WIND). **2616** (Aus): west-southwest of Bethanien loop road D437, (–BC), 15 Mar. 1995, *Smook 9468* (PRE, WIND). **2618** (Keetmanshoop): Spitzkoppe, (–AD), 7 Apr. 1984, *Craven 1666* (WIND). **2717** (Chamaites): Fish River Canyon, river camp, (–DA), 30 Mar. 1953, *Walter & Walter 2263* (B, WIND).

4. **Psilosiphon erongoensis** *Goldblatt & J.C.Manning*, sp. nov.

TYPE: Namibia, 2115 (Karibib): Erongo Mtns, western edge of the Erongo Mtns above Farm Ameib, (–DA), 27 Mar. 1976, *Craven & Craven 115* (WIND, holo.; PRE, iso.).

Plants 300–550 mm high, repeatedly branched, main axis ± straight, dominant, lateral branches diverging at ± 30°; stem weakly compressed below, triangular in middle part and rectangular above, angles slightly winged. *Corm* 15–20 mm diam.; tunics light brown, coarsely fibrous. *Leaves* 4–7, ± linear, grey-green, main vein prominent, lowermost 2 basal and longest, mostly 4–5 mm wide, reaching to ± apex of inflorescence, upper leaves cauline and decreasing in size above, those subtending branches becoming ± bract-like. *Inflorescence* ± a rounded to flat-topped false panicle, main terminal branches with (2–)4 or 5 flowers in short spikes; bracts 8–10 mm long, soft-textured, ± green with translucent, membranous margins, lanceolate, acute, becoming dry apically, inner slightly shorter than outer. *Flowers* zygomorphic, violet-blue, lower three tepals with white mark near base edged dark violet distally, ?unscented; perianth tube 36–38 mm long, cylindric, expanded and curved in upper 3 mm; tepals subequal or dorsal slightly larger, lanceolate, ± acute, margins evidently straight, ± 14 × 3–4 mm, lower 3 united for 1.5 mm. *Stamens* unilateral, ± erect; filaments ± 8 mm long, exserted ± 5 mm; anthers 5–6 mm long, evidently yellow; pollen yellow. *Style* nearly straight, dividing opposite anther tips; branches ± 3 mm long, forked for ± $^1/_3$ their length, violet. *Capsules* and *seeds* unknown. *Chromosome number* unknown. *Flowering time*: March and April.

Distribution and biology: *Psilosiphon erongoensis* is evidently restricted to the Erongo Mtns of west central Namibia (Figure 43). We suspect that it grows in pockets of soil around the granite domes that characterise the area, where additional water is available to plants in this arid terrain. Other details of its biology remain to be studied.

Diagnosis and relationships: included in *Psilosiphon otaviensis* by Goldblatt (1990a), the violet flowers and slightly shorter perianth tube, ± 37 mm long, and shorter, narrower tepals, ± 14 × 3–4 mm, serve to distinguish *P. erongoensis* from that species, which has creamy white flowers with violet longitudinal markings on the lower tepals, a somewhat longer perianth tube, 40–45 mm long, tapering gradually from base to apex, and tepals 15–19 × 4–5 mm. The branching of the inflorescence and general aspect of the two species differ hardy at all. However, we now think *P. erongoensis* may be more closely related to *P. gracilis*, which has pale blue or less often white flowers, a perianth tube (18–)25–38 mm long and, significantly, short, pale floral bracts 4–6(–7) mm long (vs. 8–10 mm in *P. erongoensis*). Chromosome number, useful in determining relationships in *Psilosiphon*, is unknown and so far we have been unable to obtain material for DNA extraction and molecular study.

Additional specimen

NAMIBIA.—**2115** (Karibib): Erongo Plateau, among granite boulders, (–DC), 1985, *Lavranos 22693* (E, K, M, MO, P, PRE, S).

5. **Psilosiphon rivularis** *(Wanntorp) Goldblatt & J.C.Manning*, comb. nov. *Lapeirousia rivularis* Wanntorp in Svensk Botanisk Tidskrift 65: 53 (1971); Roessler: 394 (1979); Goldblatt: 448 (1990a). Type: Namibia, Karibib, Ameib Ranch, ± 25 km northeast of Usakos, granite kopje [koppie] south of track, ± 5 km east of farmhouse, 15 Apr. 1968, *Wanntorp & Wanntorp 907* (S, holo.!; M!, iso.).

Plants 100–300 mm high, laxly few-branched, stem weakly compressed and 3–4-angled. *Corm* bell-shaped, 8–12 mm diam.; tunics dark brown, fibres medium-textured, reticulate. *Leaves* mostly 2(3), lower 1 or 2 ± basal, linear, 2–3 mm wide, reaching to ± middle of inflorescence, firm, main vein lightly raised, lowermost longest, upper leaves subtending branches, progressively shorter. *Inflorescence* a laxly branched spike, main axis mostly laxly 2–5(6)-flowered; bracts 4–5 mm long, green below, membranous in upper half, apices dry becoming light brown, inner bract ± as long as outer, entire or shallowly forked at tip. *Flowers* zygomorphic, pale blue with white nectar guides on lower three tepals outlined in blue-violet, with tooth-like median ridge up to 1 mm long, distal half of throat lined dark blue on abaxial side; perianth tube ascending, widening gradually from base, ± 1.3 mm wide at base, 3 mm at mouth, (5–)7–9 mm long, ± straight; tepals narrowly lanceolate, margins usually straight, subequal, (7–)10–13 × 2.0–2.5 mm wide, dorsal tepal suberect to arching forward, held apart from others, lower tepals directed forward, nearly horizontal, united basally for ± 1.5 mm. *Stamens* unilateral and arcuate; filaments ± 7.5 mm long, exserted ± 4 mm; anthers parallel, contiguous, ± 4 mm long, pale blue-mauve; pollen pale blue-mauve. *Style* suberect, adaxial to stamens, ± 15 mm long, dividing opposite upper $^1/_3$ of anthers; branches ± 1 mm long, undivided or notched at apex, spreading. *Capsules* 3.5–4.5 mm long, top-shaped in profile, 3-lobed in distal half, with 2 or 3 seeds per locule. *Seeds* ± globose, dark brown, ± 2 mm diam. *Chromosome number* unknown in Namibian populations, 2*n* = 12 (in one Zambian population). *Flowering time*: mostly late February to early April. (Description based only on plants from Namibia).

Distribution and biology: primarily a plant of seasonally wet depressions on rock outcrops and seasonally waterlogged grassland on shallow soils, *Psilosiphon rivularis* occurs across the northern half of Namibia into adjacent Angola (Figure 44). In Namibia it is particularly common in the Erongo Mtns, a range characterised by massive granite outcroppings, and also occurs on the Brandberg, the Paresis Mtns near Otjiwarongo and north of Etosha Pan. Taller, more robust plants, sometimes with larger flowers from Zambia and eastern Angola were included here by Goldblatt (1990a), but may represent a separate species.

Diagnosis and relationships: an often diminutive plant, *Psilosiphon rivularis* is recognised by the pale blue flowers with a relatively narrow perianth tube mostly 7–9 mm long, tepals usually 10–13 mm long (occasionally smaller), the lower

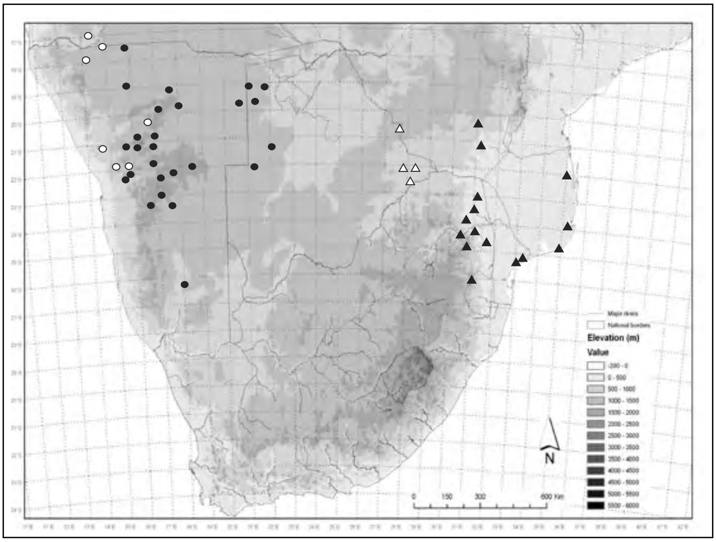


FIGURE 44.—Distribution of *Psilosiphon coeruleus*, ●; *P. erythranthus*, Δ; *P. masukuensis*, ▲; *P. rivularis*, ●, in southern Africa.

three bearing a white marking edged in darker blue and often a prominent tooth-like ridge in the lower midline. The style, ± 15 mm long, divides into short, undivided branches ± 1 mm long. Plants at the type area, the Erongo Mtns, rarely exceed 200 mm in height, but elsewhere in Namibia may reach up to 270 mm. Goldblatt (1990a) included populations from Zambia and central Angola in *L. rivularis*. These plants, sometimes up to 450 mm tall, have larger flowers, which lack ridges on the lower tepals, and among other differences have a longer style, 16–20 mm long and style branches 2–3 mm long, divided for ± one third to half their length in contrast to the undivided style branches of *P. rivularis*. More field work is needed to establish the status of the Zambian populations, which may represent another taxon. Zambian plants have a diploid chromosome number of $2n = 12$, suggesting a relationship with the widespread *P. erythranthus*, which has the same number in south-tropical African populations. Chromosome number is not known for *P. rivularis* in Namibia.

History: *Psilosiphon rivularis* was described by the Swedish botanist Hans-Erik Wanntorp in 1971, although he was not the first to record the species. It appears to have been collected in Namibia by the South African biologist, K.H. Barnard, on the northern border of Namibia along the Cunene River in 1921. The type locality of *L. rivularis*, the Farm Ameib at the southern end of the Erongo Mtns, is its southernmost known station.

Representative specimens

NAMIBIA.—**1715** (Ondangua): Engela Mission, shallow vlei in black sticky clay, (–BD), 16 Feb. 1959, *De Winter & Giess 7061* (B, K, M, PRE, SRGH, WIND); Uutapi District, Uutapi–Ogongo road, in standing water, (–CA), 27 Mar. 2006, *Kangombe & Kruger 269* (WIND). **2016** (Otjiwarongo): Otjiwarongo, not on summit but high up, 16 Mar. 1980 (BC), *Craven 1129* (WIND). **2114** (Uis): Brandberg, Sonuseb, common on top of Sonuseb saddle at water hole, (–BA), 12 Apr. 1985, *Craven 2277* (WIND). **2115** (Karibib): granite koppies south of Gross Spitzkoppe 71, wet granite rocks, (–CC), *Sullivan 418* (WIND); Farm Ameib, below Jatow cave, somewhat marshy, granite soil, (–DC) 19 Mar. 1963, *Giess 13132* (B, M, PRE, WIND); 22 Mar. 1965, *Giess 8452* (K, M, MO, WAG, WIND); 17 Mar. 1963, *Giess* et al. *5795* (B, M, PRE, WIND); Farm Ameib, coarse sandy, marshy ground below granite outcrops at the Devils Pulpit, (–DC), 18 Mar. 1968, *Giess 10248* (M, WIND); 5 Apr. 1974, *Merxmüller & Giess 30699* (B, M, K, PRE, SRGH, WAG, WIND).

[Exsiccatae assigned to *Psilosiphon rivularis* from Angola and Zambia are cited in Goldblatt (1990a).]

6. **Psilosiphon coeruleus** *(Schinz) Goldblatt & Manning*, comb. nov. *Lapeirousia coerulea* Schinz in Verhandlungen des botanische Vereins der Provinz Brandenburg 31: 212–213 (1890); Goldblatt: 445 (1990a). Type: Namibia, (Upingtonia), Ombale, südost Ondonga, Mar. 1886, *Schinz 13* (K, lecto.!, designated by Goldblatt: 445 (1990a); COI!, isolecto.).

Ixia dinteri Schinz: 14 (1900). Type: Namibia, Karibib, Spitzkop, marshy ground, in 1898, *Dinter 22* (32 on the type) (Z, holo.!).

Plants (120–)150–300 mm high, repeatedly branched, stem compressed, 2- or 3-angled. *Corm* bell-shaped, 12–16 mm diam., light brown; tunics of pale compacted fibres decaying to become coarsely to finely fibrous and netted. *Leaves* 2–4, only lowermost inserted at base, this longest and reaching to at least middle, and sometimes shortly exceeding inflorescence, ± linear, 2–4(–5) mm wide, remaining leaves decreasing in size above. *Inflorescence* a laxly branched, round-topped false panicle, larger ultimate branches (2)3–5-flowered; bracts 3–4 mm long, subequal, green below, membranous distally, becoming completely dry in fruit, inner ± as long as outer. *Flower* actinomorphic, ± rotate, blue to light purple with white, spear-shaped mark outlined in dark blue to purple on basal $^1/_2$ of each tepal; perianth tube 1.5–2.0 mm long, narrowly funnel-shaped; tepals spreading below, curving upward distally, subequal, lanceolate, 7.0–9.5 × 3–5 mm. *Stamens* symmetrically arranged; filaments united basally for < 0.5 mm by an obscure corona-like ring, erect, ± 4 mm long, nearly contiguous around style; anthers diverging, 3.0–3.5 mm long, curving inwards after anthesis; pollen pale blue-purple (white to yellow when dry). *Style* erect, 6–7 mm long, dividing near anther tips, style branches ± 1.2 mm long, shallowly notched apically. *Capsules* obovoid–globose, weakly 3-lobed, ± 4 mm long; *seeds* dark brown, globose to weakly angled by pressure, 1.3–2.0 mm diam., tapering near attached funicle. *Chromosome number* $2n = 8$. *Flowering time*: (January)February to April, occasionally in December. Figure 45.

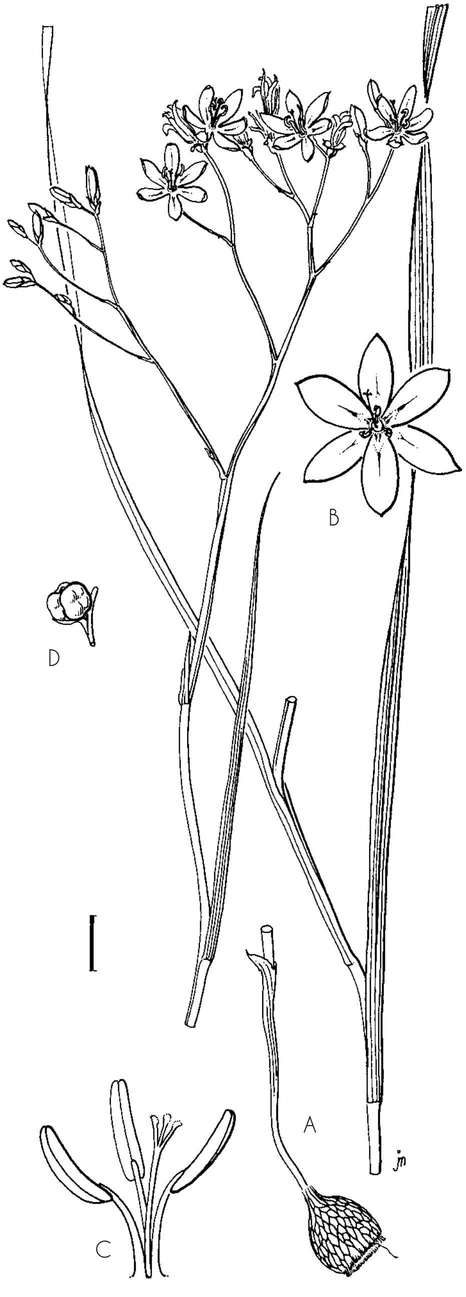


FIGURE 45.—*Psilosiphon coeruleus*, *Goldblatt & Manning 8811A*. A, plant and corm; B, flower; C, stamens and style; D, capsule. Scale bar: A, D, 10 mm; B, C, 5 mm. Artist: John Manning.

Distribution and biology: typically a species of seasonally wet habitats, *Psilosiphon coeruleus* is widespread throughout the summer rainfall part of Namibia, extending locally into northwestern Botswana, where it has only occasionally been reported (Figure 44). Plants grow in seeps, seasonal marshes, poorly drained grassland and shallow soil in rock outcrops where water accumulates in the wet season. The pollination biology is unknown. The flowers produce no detectable nectar and the only potential pollinators we have seen are small bees (family unknown) nestling in the open flowers.

Several collections are accompanied by notes indicating that corms of *Psilosiphon coeruleus* were in the past eaten by the indigenous population, particularly the !Kung, for whom the corms may have been a staple, eaten after roasting in hot ash (*Story 6121*), or sometimes raw (Rodin 1985).

Diagnosis and relationships: *Psilosiphon coeruleus*, with its radially symmetric flower and short perianth tube 1.5–2.0 mm long, and undivided style branches appears to be taxonomically isolated in the genus. The chromosome number, $2n = 8$, recorded in seven populations, and small corm with dark brown, fibrous tunics match other blue-flowered species including *P. erythranthus* (some populations $2n = 12$) and *P. rivularis* ($2n = 12$) suggesting a relationship with this group of species, which have zygomorphic, bilaterally symmetric flowers, often of the same colour, although sometimes red in *P. erythranthus*. One other species of *Psilosiphon* has radially symmetric flowers, *P. avasmontanus*, but this more robust species has a different inflorescence with the ultimate branches bearing 1 or 2 larger flowers, and dark brown corm tunics that fragment into vertical strips, like those of *P. sandersonii*. Its chromosome number, $2n = 16$, with a karyotype consisting of one long and seven short chromosome pairs make *P. avasmontanus* an unlikely close relative of *P. coeruleus*. The differences between *Psilosiphon coeruleus*, a species of wet low-lying places, and *P. avasmontanus*, which grows in well-drained, stony banks and hills, are discussed in detail under *P. avasmontanus*. The morphological differences, combined with their disparate habitat preferences and chromosome cytology, compel their separation despite the alternative treatment by Sölch (1969) uniting them.

The simple flower structure is deceptive – radially symmetric flowers are specialised and derived in the genus. Chromosome number in *P. rivularis* from Namibia, retrieved as sister to *P. coeruleus* in the plastid and combined plastid and nuclear DNA-based phylogeny (Figure 1), is unknown.

History: *Psilosiphon coeruleus* was first collected in 1879 by the Swedish traveller-explorer, Ture Een, on his second expedition to Namibia (Gunn & Codd 1981). This early record received no attention, and later collections made independently after 1885 by Hans Schinz, August Lüderitz and Waldemar Belck formed the basis for the protologue of *Lapeirousia coeruleus* published by Schinz in 1890. Schinz (1900) also described *Ixia dinteri*, a species undoubtedly conspecific with *P. coeruleus*, based on specimens collected by Kurt Dinter in 1898.

Representative specimens

BOTSWANA.—**1921** (Aha Hills): Xangwe, (–CB), Mar. 1961, *Gibson 186* (MO, WIND); Dobe region, north of Aha Hills near Namibian border, dry pan, (–CB), 25 Apr. 1980, *Smith 3496* (MO, PRE, SRGH); hard clay in dry pan, Quangwa River catchment, (–CB), 23 Apr. 1981, *Smith 3674* (BR, PRE). **2122** (Kobe): pan on Farm 102, Kuki, (–AC), 21 Feb. 1970, *Brown & Brown 8723* (C, PRE, SRGH). **2221** (Okwa): 53 km northeast of Ghanzi on road to Maun, seasonally flooded limestone outcrops, (–AB), 29 Dec. 1977, *Skarpe S-213* (K, MO, PRE, UCBG).

NAMIBIA.—**1715** (Ondangua): 3 km south of Oshikango, (–BD), 3 Apr. 1973, *Rodin 9203* (K, M, MO, PRE, WIND). **1815** (Okahakana): Etosha Pan, large vlei 5 miles [± 7.5 km] west of Okondeka, (–DD), 27 Mar. 1963, *Giess* et al. *6056* (M, WIND). **1917** (Tsumeb): 25 km from Tsumeb towards Ondangua, (–BA), 14 Feb. 1983, *Lavranos & Pehlemann 21101* (WIND); Farm Toevlug, lime marl, (–BA), 5 Feb. 1971, *Giess 11292* (K, MO, PRE, SRGH, WAG, WIND); Farm Goab, spring meadows, (–CA), 29 Jan. 1978, *Giess 14955* (M, MO, PRE, WAG, WIND). **1918** (Grootfontein): Grootfontein, red loamy flats, (–CA), Jan. 1935, *Schoenfelder 35* (K, PRE). **1920** (Tsumkwe): pans at Tsumkwe, (–DA), 14 Jan. 1971, *Giess* et al. *11076* (M, S, PRE, WIND); Tsumkwe, (–DA), 14 Jan. 1958, *Story 6121* (M, PRE, SRGH). **2016** (Otjiwarongo): 30 km south of Otjiwarongo, (–CB), 1985, *Lavranos 22698* (MO). **2017** (Waterberg): *omuramba* [Herero: ancient river bed] at Omam, (–CA), 11 Mar. 1940, *Volk 2845* (WIND). **2115** (Karibib): Ohere-Oos, granite flats, (–BA), 14 Feb. 1958, *Merxmüller & Giess 1583* (M, PRE, WIND); Ameib Ranch, granite rock flushes at Bull Parties, (–DC), 15 Mar. 1988, *Goldblatt & Manning 8811A* (M, MO, PRE, WAG, WIND). **2118** (Steinhausen): Farm Wilhelmsruhe, (–DC), 10 Feb. 1982, *Rauh 57762* (WIND). **2215** (Trekkopje): Okongawa, Granitbankberg, (–BB), 4 Feb. 1934, *Dinter 6957* (B, BOL, G, K, HBG, M, PRE, S, WIND, Z). **2116** (Okahandja): Farm Omatako View, (–BA), 15 Feb. 1974, *Woortman 116* (M, PRE, WIND); Farm Omongongua, shallow depressions in *omuramba*, (–DB), 27 Mar. 1960, *Seydel 2203* (B, K, HUH, MO, WIND); Farm Okambahe, ± 16 miles [24 km] west of Okahandja, road to Karibib, (–DC), 21 Dec. 1963, *Giess* et al. *5058* (M, MO, PRE, WIND). **2215**: (Otjihorongo): Farm Goreis, red loam sand, 17 Feb. 1971 (–BB), *Giess 11248A* (K, M, PRE, WIND). **2217** (Windhoek): Neudam Experimental Farm, (–AD), 22 Mar. 1960, *Van Vuuren 1027* (K, M, PRE, SRGH, WIND); Farm Otjikundua 67 miles [± 100 km] west-southwest of Steinhausen, open vlei, (–BA), 19 Feb. 1955, *De Winter 2409* (K, M, NBG, PRE, WIND); Farm Aris, south of Windhoek, *omuramba*, (–CA), 1 Mar. 1953, *Walter & Walter 1550* (B, BR, WIND). **2316** (Nauchas): Farm Göllschau, (–BC), 27 Jan. 1972, *Giess & Hübsch 11600* (M, PRE, WIND). **2317** (Rehoboth): Farm Gravenstein, (–BC), 20 Nov. 1956, *Volk 11503* (M, MO, WIND); Farm Tsumis, sandy soil, (–CA), *Müller 1396* (M, PRE, WIND). **2618** (Keetmanshoop): Spitzkoppe, (–AD), 7 Apr. 1984, *Craven 1533* (WIND). Without precise locality: Damaraland, 1879, *Een s.n.* (BM).

7. **Psilosiphon erythranthus** *(Klotzsch ex Klatt) Goldblatt & J.C.Manning*, comb. nov. *Ovieda erythrantha* Klotzsch ex Klatt in Peters, Naturwissenschaftliche reise nach Mossambique. Botanik 6(2): 516, t. 58 (1864). *Lapeirousia erythrantha* (Klotzsch ex Klatt) Baker: 155 (1877); Geerinck et al.: 335–344 (1972), excluding var. *teretifolia* and var. *welwitschii*; Goldblatt: 451 (1990a). Type: Mozambique, Boror, Caboceira, *Peters s.n.* (B, holo.!).

[See full synonymy in Goldblatt (1990a)].

Plants (150–)200–450 mm high, branched repeatedly; stem compressed, 2-angled below, 3-angled above. *Corm* ± bell-shaped, 8–16 mm diam.; tunics light to dark brown, of densely compacted fibres, outer layers becoming coarsely fibrous, ultimately forming a matted mass. *Leaves* 3 or 4, lower 2 or 3 longest and $^{1}/_{3}$ to $^{2}/_{3}$ as long as stem, ± linear to lanceolate or ± falcate, (2–)4–8(–11) mm wide, main vein prominent when alive; upper leaves becoming progressively bract-like. *Inflorescence* a several to many branched false panicle, often ± flat-topped, ultimate branches mostly (2)3–6-flowered, flowers crowded terminally; bracts 3–6 mm long, green below, dry and membranous above, becoming entirely dry and transparent, brownish in upper $^1/_3$, outer obtuse, inner acute or apically forked, usually slightly shorter than outer. *Flowers* zygomorphic, either blue-violet with spear-shaped white mark outlined in dark blue to purple on lower tepals or crimson red, then without markings or lower tepals each with white or dark red median streak; perianth tube (6–)7–11(–15) mm long, slender below, expanded and slightly curved near throat; tepals subequal, lanceolate-spathulate, acute to obtuse, (6–)7–11 × 2–3(–4) mm, dorsal held apart, reflexed to lie ± same plane as lower tepals; lower 3 tepals narrowed at base thus ± clawed, set closely together and joined for ± 1 mm. *Stamens* unilateral, ± erect; filaments 4–6 mm long, exserted 3.5–5.5 mm from tube; anthers 2.5–4.0 mm long, pale bluish to white, purple or red; pollen ± white. *Style* arched to erect, adaxial to stamens, dividing opposite middle to apex of anthers, ± 15 mm long; branches 1.0–1.5 mm long, forked for $^1/_3$–$^1/_2$ their length, recurved. *Capsules* ± globose in profile, 3-lobed, 3–4 mm long, showing outline of seeds. *Seeds* 2–5 per locule, ± globose, 1.6–1.9 mm diam., dark brown, ± smooth to rugulose. *Chromosome number* 2*n* = 14, 12 + 0–3B (polyploids), 8 (diploids). *Flowering time*: late January to March, occasionally from mid-December. Figure 46.

Distribution and biology: although restricted in southern Africa to eastern Botswana (Figure 44), *Psilosiphon erythranthus* has a wide distribution across tropical Africa (Goldblatt 1990a), extending from eastern Angola and southern Democratic Republic of the Congo, through Zambia to Zimbabwe, Malawi, western and southern Tanzania, and central Mozambique. A disjunct series of populations also occur in northeastern Nigeria. The most common species of *Psilosiphon* in central Africa, *P. erythranthus*, can frequently be found in rocky outcrops throughout its range, or less often in open grassland or woodland. Its frequency in thin soils in rocky sites suggests that the corms are protected in such habitats while in deeper ground they are accessible to rodents, porcupines and other herbivores. Cultivated plants grow well in almost any type and depth of soil. The small flowers, conspicuous in the many-flowered inflorescences, are visited and presumably pollinated by a variety of bees, wasps and even butterflies, which forage in large numbers in warm weather for nectar and/or pollen.

Annotations on two specimens indicate that *Psilosiphon erythranthus* is edible (*Simpathu 90*, Victoria Falls; *Buchanan 426*, Shire Highlands 'eaten in time of great famine'). However, there appears to be no record of the species being significant in the regular diet of any human populations.

Diagnosis and relationships: one of the several species of *Psilosiphon* with a strongly ramified, ± round- or flat-topped inflorescence, *P. erythranthus* can be distinguished by its relatively small flowers, typically (but not always) soft-textured leaves with a conspicuous main vein, and flowers with a short perianth tube seldom exceeding 12 mm. The flowers are somewhat crowded at the branch tips, which are in effect spikes of up to 6 sessile flowers. The orientation of the tepals is also distinctive – the tepals lie in ± the same plane, with the three lower tepals joined together for ± 1 mm and held closely together, while the upper tepal is reflexed and held apart from the others. Similar flowers also characterise *P. sandersonii* and *P. masukuensis*, both of which have a longer perianth tube, mostly at least 15 mm long and in some populations of *P. sandersonii* up to 30 mm long, and which also has different corms tunics and an inflorescence in which the ultimate branches have only one or two flowers. Notably *P. sandersonii* subsp. *limpopoensis* has a perianth tube 8–12 mm long, thus comparable with that of *P. erythranthus*, but the subspecies can immediately be distinguished by the branching pattern and different corm tunics.

Less closely related, *Psilosiphon rivularis* is almost indistinguishable from *P. erythranthus* when pressed, but they have different flowers. In *P. rivularis* the upper tepal is arched forwards over the stamens and style branches. This important difference between the two species is generally obscured in herbarium specimens. *P. rivularis* grows in seasonally wet sites from central Zambia, across southern Angola to northern Namibia, and its range thus partly overlaps that of *P. erythranthus*.

Other species of the *Psilosiphon erythranthus* complex outside southern Africa, including *P. abyssinicus*, *P. setifolius* and *P. teretifolius*, were discussed in depth by Goldblatt (1990a).

History: *Psilosiphon erythranthus* was first collected by the German physician and explorer

FIGURE 46.—*Psilosiphon erythranthus*, no voucher. Scale bar: 10 mm. Artist: John Manning.

Wilhelm Peters in the years 1842–1848 when he travelled in Mozambique under the Prussian King Friedrich Wilhelm IV's patronage. Later, the Scottish explorer, Sir John Kirk, who accompanied David Livingstone on his Zambezi expedition in 1858, also recorded the species in the lower Shire valley in Mozambique. The species was described by F.W. Klatt (in Peters 1864), who saw only the Peters collection, in the illegitimate genus *Ovieda*. Baker (1877) transferred *O. erythrantha* to *Lapeirousia* and in *Flora of Tropical Africa* he reserved *L. erythrantha* for red-flowered plants and referred those with blue flowers to *L. sandersonii* (Baker 1898). Later, plants from Zimbabwe currently included here, were assigned to *L. rhodesiana* by N.E. Brown (1906), while those from Mozambique were treated by Vaupel (1912) as *L. graminea* and *L. plagiostoma*. Other species, now regarded as synonyms of *P. erythranthus* include *L. spicigera* Vaupel from Angola and *L. nigeriensis* R.C.Foster (= *L. montana* Hutch.) from Nigeria (Goldblatt 1990a). The species deserves additional study, especially the larger-flowered populations from Zimbabwe that were treated as *L. rhodesiana*.

Representative specimens

BOTSWANA.—**2026** (Nata): Bakalaka area, between Francistown–Maun road and Marapong, (–AC), 26 Jan. 1967, *McClintock K73* (K); between Francistown and Nata River, on Maun road, (–AC), 21 Jan. 1959, *West 3898* (BR, K, LISC, PRE). **2027** (Plumtree): Ramakqwebane area near Tsessebe Station, (–DC), 6 Jan. 1974, *Ngoni 243* (MO, SRGH); border near Plumtree, sandy flat roadside, (–DC), 7 Mar. 1961, *Richards 14552* (K, SRGH). **2227** (Palapye): Selebi, (–BB), Jan. 1978, *Kerfoot 8007* (PRE).

[Exsiccatae from tropical Africa are cited by Goldblatt (1990a).]

8. **Psilosiphon masukuensis** *(Vaupel & Schltr.) Goldblatt & J.C.Manning*, comb. nov. *Lapeirousia masukuensis* Vaupel & Schltr. in Vaupel, Botanische Jahrbucher für Systematik 48: 545 (1912); Goldblatt: 461 (1990a). Type: Mozambique. Inhambane: Masuku forest [Insilva Maseku], 10 Feb. 1898, *Schlechter 12109* (B, holo.!; BR!, COI!, G!, K!, P!, PRE!, SAM!, iso.).

Plants 400–600 mm high, stem usually several-branched, compressed and 2-angled to winged below, 3-angled and slightly winged above branches. *Corm* bell-shaped, ± 15 mm diam.; tunics light brown, of ± leathery layers with reticulate surface, becoming loosely fibrous and netted with age. *Leaves* 4–6, lowermost inserted close to ground and longest, usually shortly exceeding inflorescence, linear-lanceolate, central vein prominent, 3–5 mm wide, remaining leaves progressively shorter above. *Inflorescence* a branched spike or round-topped false panicle, main axis ± straight, dominant, major ultimate branches 5–9-flowered, often crowded distally with bracts overlapping and (1.0–)1.5–2.0 internodes long; bracts 5–7 mm long, green at anthesis, later dry and membranous, then either pale below or throughout or brownish above, streaked brown on veins, inner ± as long as outer or slightly shorter. *Flowers* zygomorphic, either dark blue to violet or greenish cream, lower tepals each with purple to red and white spear-shaped median streak in basal half; perianth tube cylindric, (15–)20–25 mm long, slightly expanded in upper 4 mm; tepals subequal with dorsal slightly larger, lanceolate, 8–10 × ± 3 mm, spreading at right angles to tube and lying in ± same plane with dorsal reflexed and held apart. *Stamens* unilateral, ± erect; filaments ± 5 mm long, exserted 2.5–3.0 mm; anthers 3.5 mm long, probably pale yellow when alive. *Style* unilateral, arching over stamens, dividing opposite middle to upper $^{1}/_{3}$ of anthers; branches ± 2.2 mm long, divided for ± $^{1}/_{2}$ their length. *Capsules* ± globose, slightly 3-lobed, 3.5–5.0 mm diam., showing outline of seeds. *Seeds* globose, ± 2 mm diam. *Chromosome number* unknown. *Flowering time*: February to April.

Distribution and biology: restricted to southeastern Africa, *Psilosiphon masukuensis* extends from central and southern Mozambique in the provinces of Inhambane and Maputo [Sul do Save] and adjacent Malawi south and west into southeastern Zimbabwe and lowland Limpopo and Mpumalanga of South Africa (Figure 44). The presence of *P. masukuensis* in Malawi was uncertain when Goldblatt's (1990a) account was published but we have now seen collections from there that match the species well. Collection data make it clear that *P. masukuensis* prefers relatively wet habitats during its growing season. Most specimens are recorded as growing in vleis, the edge of marshes, or in seasonally waterlogged flats. Pollination biology is unknown.

The Mozambique populations are all coastal and probably from sandy habitats.

Diagnosis and relationships: the comparatively tall stature, usually over 450 mm high, alternate branching pattern with the main axis dominant, ultimate inflorescence branches bearing 5–9 apically crowded flowers and the long straight perianth tube, usually 20–25 mm long, are the main diagnostic characters of *Psilosiphon masukuensis*. Plants from the Mozambican coast have greenish flowers with red markings (Bandeira et al. 2007), unusual in the genus. In eastern South Africa, Zimbabwe and Malawi the flowers are shades of blue-mauve or violet with the white and dark blue markings typical of the *P. erythranthus* group, which we believe includes *P. masukuensis*. The long perianth tube and general appearance of the flowers, including their colour, suggest a relationship with *P. sandersonii* of eastern South African and Botswana, but this is typically a shorter plant, rarely exceeding 350 mm, with a divaricate, often intricately branched habit, and the ultimate branches of the inflorescence bearing 1 or 2, rarely 3 flowers. The corms of the two species also differ, those of *P. masukuensis* being relatively small and having the outer tunic layers fibrous and reticulate whereas the larger corms of *P. sandersonii* have dark brown tunics that decay irregularly into vertical strips. The corm tunics of *P. masukuensis* resemble closely the brown, fibrous and reticulate tunics of *P. erythranthus* to which it is probably most closely allied.

Plants from South Africa and Zimbabwe are more variable than those from Mozambique, particularly in the length of the perianth tube and the number of flowers on the terminal branches of the inflorescence. Generally plants from Malawi, South Africa and Zimbabwe have 5–6 flowers per main branch compared with 6–9 in Mozambique. A notable example is *Mauve 4326*, 10 miles north of Abel Erasmus Pass, which has some flowers with a perianth tube just 15 mm long, while others have a tube up to 22 mm. Such apparently gross variation in perianth tube length may be due to ecological stress during the growing season or possibly some flowers could have opened while in a press without developing further. This degree of variability in tube length is sometimes encountered in collections of other tropical African *Psilosiphon*, particularly in *P. bainesii*. When more collections are available from Mozambique, the possibility that these represent a separate taxon from populations in South Africa and Zimbabwe should be reconsidered. The interior populations occur at higher elevation and in different habitats.

History: discovered in 1898 by the widely travelled German botanist and prolific collector Rudolf Schlechter, at a site Schlechter called Insilva Maseku, near Massinga and north of Inhambane in central Mozambique, the collection formed the basis of *Lapeirousia masukuensis*, described by Vaupel & Schlechter in 1912. *Psilosiphon masukuensis* appears to be comparatively rare, particularly in Malawi, Mozambique and Zimbabwe where it has been gathered only a few times. An early collection made by French missionary, Henri Junod at Shilouvane in Limpopo Province, South Africa, bears the manuscript name *L. junodii* N.E.Br. Evidently Brown at one time considered the species distinct from what was then *L. sandersonii*, to which early collections were often referred.

Representative specimens

SOUTH AFRICA. LIMPOPO.—**2231** (Pafuri): Kruger National Park, Klopperfontein, (–CA), 21 Jan. 1953, *Van der Schijff 1858* (PRE). **2330** (Tzaneen): Hans Merensky Nature Reserve, mopane veld in damp earth along sloot, (–DA), 11 Feb. 1971, *Oates 371* (PRE); Hans Merensky Nature Reserve, waterlogged clay loam in vlei, 2000 ft [620 m], (–DA), 15 Mar. 1977, *Zambatis 737* (PRE). **2331** (Phalaborwa): Mahlangeni, 4 km from Nsihana windpomp, (–AC), *Wentzel 163* (PRE). **2430** (Pilgrims Rest): Shilouvane, (–AB), Jan. 1919, *Junod 4139* (G, M, PRE); Shilouvane plain, '*L. junodii* N.E.Br.', (–AB), *Junod 736* (G, K); 10 m [15 km], north of Abel Erasmus Pass, grass in bushveld, (–DA), 16 Dec. 1964, *Mauve 4326* (K, PRE). **2431** (Acornhoek): Farm Grootdraai, stony flats, 1500 ft [457 m], (–AA), 15 Nov. 1973, *Zambatis 543* (MO); Klaserie Private Nature Reserve, Farm Sark, seasonal seep in sandy clay, (–AC), 28 Jan. 1982, *Zambatis 1345* (PRE); Kruger National Park, Pumbe, Satara, sandy ground, (–BB), Mar. 1967, *Van Wyk 4783* (PRE).

MPUMALANGA.—**2630** (Carolina): Eerstehoek, Songimvelo Nature Reserve, Doornhoek, south of Komati River, (–BB), 31 Jan. 1992, *Stalmans 2618* (J, MO).

[Exsiccatae from Malawi, Mozambique, and Zimbabwe are cited in Goldblatt (1990a).]

9. **Psilosiphon otaviensis** *(R.C.Foster) Goldblatt & J.C.Manning*, comb. nov. *Lapeirousia otaviensis* R.C.Foster in Contributions from the Gray Herbarium 127: 45–46 (1939); Goldblatt: 467 (1990a). Type: Namibia, Farm Auros near Otavi, 11 Feb. 1925, *Dinter 5577* (GH, holo.!; B!, G!, PRE!, SAM!, Z (3 sheets)!, iso.).

Plants 300–550 mm high, repeatedly branched, stem with main axis ± straight and dominant, lateral braches diverging at 45–80°, stem weakly compressed below, triangular in middle, ± rectangular above, angles lightly winged. *Corm* bell-shaped, 20–25 mm diam.; tunics light brown, firm-leathery at first, becoming coarsely fibrous with age, sometimes ultimately finely fibrous. *Leaves* 4–7, ± linear(–narrowly lanceolate), glaucous, main vein prominent, lower 2–4 basal and longest, 5–9 mm wide, exceeding inflorescence by 50–100 mm, upper leaves decreasing in size above, becoming ± bract-like. *Inflorescence* a rounded to ± flat-topped false panicle, main terminal branches 3–5-flowered; bracts soft-textured, green, lanceolate, acute, often flushed red above, becoming dry from tips toward end of flowering, (7–)8–11 mm long, inner often slightly longer than outer. *Flowers* zygomorphic, white to cream, sometimes flushed pale lilac, lower three tepals with broad violet or purple median streak, with darker, paired purple to red lines near base, rarely upper 3 tepals with pale purple median line, unscented; perianth tube 40–45 mm long, straight, gradually flared from base, ± 1.2 mm diam. below, ± 2.2 mm diam. at mouth; tepals unequal, dorsal slightly larger than others, lanceolate, ± acute, margins straight, 15–19 × 4–5 mm, reflexed ± at right angles to tube. *Stamens* unilateral, ± erect; filaments 5–6 mm long, exserted for 2–4 mm, white; anthers 5–6 mm long, grey-purple; pollen light yellow-brown. *Style* nearly straight, adaxial to filaments, style usually dividing between apex of anthers to 3 mm beyond apex; branches ± 2 mm long, forked for $^1/_3$ to $^1/_2$ their length, diverging, but barely or not at all recurved. *Capsules* ± globose, 3-lobed, ± 7 mm long. *Seeds* not known. *Chromosome number* $2n = 10$. *Flowering time*: February to April. Figure 47.

Distribution and biology: with a relatively restricted geographic range, *Psilosiphon otaviensis* extends in a wide arc from the hills west and south of Etosha Pan in western Namibia to the Otavi Hills in the northeast and locally also in adjacent southern Angola (Figure 48). It is apparently confined to rocky sites, usually growing in granite but in the Otavi Hills, the type area, it occurs on shale outcrops and not, as far as we know, in dolomite, the most common rock type in the area. Nothing is known of its pollination biology, but the long-tubed, unscented flowers that open in mid-morning have stereotypical characteristics of those adapted for pollination by long-proboscid flies.

Diagnosis and relationships: the relatively large flower with a perianth tube 40–45 mm long, white to lilac perianth with lanceolate tepals and ultimate branches of the inflorescence with up to 5 flowers (rarely less than 2) distinguish *Psilosiphon otaviensis*. It has often been confused in herbaria with similarly long-tubed *P. bainesii*, which can be separated by a series of characters including flowers with a slightly shorter perianth tube, 30–40 mm long, often flushed pink to red-purple outside, and white to pale pink tepals narrowed below into claws and with undulate margins. The inflorescence is divaricately branched and the ultimate branches have 1, rarely 2 flowers. The habitats of the two species also differ: *P. otaviensis* is evidently restricted to rocky sites, mostly granite or shale, whereas *P. bainesii* occurs in deep, hard sand in savanna or bushveld. Goldblatt (1990a) included blue-violet flowered plants from the Erongo Mtns in *P. otaviensis*, but we now consider these a separate species, *P. erongoensis*, distinguished in addition to perianth colour by a shorter perianth tube ± 37 mm long, and shorter, narrower tepals, ± 12 × 3 mm (vs. 15–19 × 4–5 mm).

History: although first collected in 1879 in 'Damaraland' by Ture Een, the traveller and botanical explorer, *Psilosiphon otaviensis* was only described in 1939 by the American, R.C. Foster, from a gathering made in 1925 by Dinter at the Farm Auros near Otavi. Dinter's collection of *P. otaviensis* was the first to be distributed widely to herbaria, and appears to have been recognised as a distinct species by accident, as Foster compared it to the very different, short-tubed *P. avasmontanus* (as *Lapeirousia*) in the protologue. The reason for this is obscure and may have been because he had misidentified material of the latter. Foster was unaware at the time of the

FIGURE 47.—*Psilosiphon otaviensis*, *Goldblatt & Manning 8837*. A, plant and corm; B, flower from front. Scale bar: 10 mm. Artist: John Manning.

similarity between *L. otaviensis* and *L. bainesii*, with which it was later confused. In the *Prodromus Einer Flora von Südwestafrika*, Sölch (1969) treated *L. otaviensis* and *L. bainesii* as conspecific and distinguished the two in the key by the several flowered ultimate inflorescence branches (a feature only of *P. otaviensis*). Sölch reserved the name *L. vaupeliana* for what is now *P. bainesii* (Goldblatt 1990a).

Representative specimens

NAMIBIA.—**1712** (Posto Velho): granite slope at Ombepera, rock crevices, corms edible, (–BD), 10 Apr. 1957, *De Winter & Leistner 5481* (B, K, M, PRE, WIND). **1914** (Kamanjab): 8 km north of Kamanjab Nord, granite domes, (–DB), 18 Mar. 1974, *Merxmüller & Geiss 30392* (K, M, PRE, WAG, WIND); Kamanjab, granite hills in rock crevices, (–DB), 2 Mar. 1957, *De Winter & Leistner 5132* (B, K, M, PRE, WIND). **1917** (Tsumeb): Farm Auros, shale hills near farmhouse, (–DA), 21 Mar. 1988, *Goldblatt & Manning 8837* (E, K, M, MO, NBG, PRE, S, WAG, WIND). **2015** (Otjihorongo): 90 km from Omaruru to Fransfontein, Table Mtn, by Ozondati, (–BB), 11 Apr. 1968, *Wanntorp & Wanntorp 840* (K, S). **2016** (Otjiwarongo): Paresis Mtns, (–AD), *Barnard 201* (SAM).). **2215** (Trekkopje): Okongava, Kalkberg, granite slope, (–BB), 4 Feb. 1934, *Dinter 6962* (B, BM, G, HBG, K, M, PRE, S, WIND, Z). Without precise locality: Damaraland, 1879, *Een s.n.* (BM).

[Exsiccatae from Angola are cited by Goldblatt (1990a).]

10. **Psilosiphon bainesii** *(Baker) Goldblatt & J.C.Manning*, comb. nov. *Lapeirousia bainesii* Baker in Journal of Botany 14: 338 (1876); 352 (1898); Sölch: 8 (1969) [name misapplied to *L. otaviensis*]; Goldblatt: 469 (1990a). Type: Botswana, Kobe Pan [as 'inter Koobie et N Shaw valley'], *Baines s.n.* (K, lecto.!, effectively designated by N.E.Brown on specimen).

Lapeirousia vaupeliana Dinter: 436 (1922). Sölch: 8 (1969). Type: Namibia, Gameros (cultivated at Okahandja), *Dinter 3087* [B, lecto.!, designated by Sölch: 8 (1959)].

Plants 300–600 mm high, usually repeatedly branched, stem compressed and 2-winged below, 3–4-angled and winged above, wings sometimes slightly crisped or finely serrated. *Corm* bell-shaped, 13–20 mm diam.; tunics mid- to dark brown, ± leathery internally with veins sharply outlined, becoming ± fibrous, fibres coarse and wiry. *Foliage leaves* narrowly lanceolate to linear, main vein prominent and a pair of lateral veins on either side evident, 5–7 mm wide, usually slightly exceeding inflorescence. *Inflorescence* a rounded, divaricately branched false panicle, ultimate branches 1(2)-flowered, axes sharply 3-angled; bracts green below, becoming dry and membranous at anthesis, later dry and light brown, apices often darker brown,

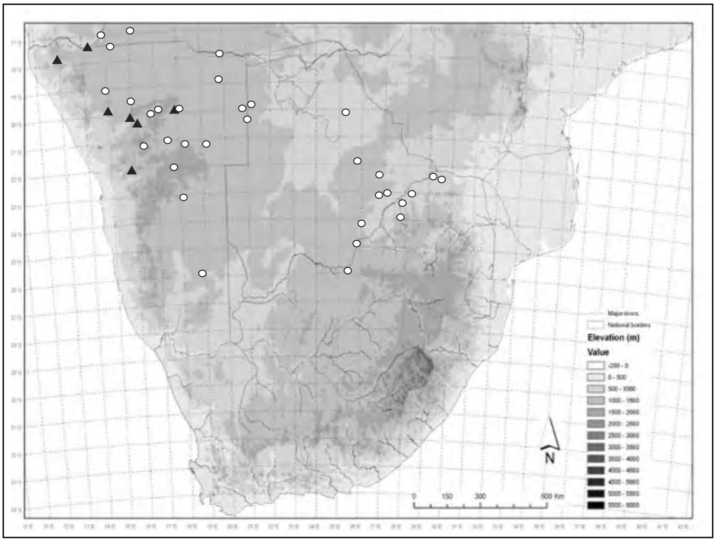


FIGURE 48.—Distribution of *Psilosiphon bainesii*, ○; *P. otaviensis*, ▲, in southern Africa.

7–10(–12) mm long, inner slightly larger than outer. *Flowers* zygomorphic, ± white, often flushed or fading pale pink, tube pale pink to purple outside, lower 3 tepals each usually marked with red to brown streak in basal $^1/_2$ and with dark mark at base, top of throat red on abaxial side, sweetly scented; perianth tube cylindric, slightly expanded in upper 5 mm, (25–)32–40 mm long, usually inclined; tepals subequal or dorsal slightly larger, ± spathulate, ± clawed (rarely with a tooth-like ridge in lower midline of lower tepals, margins undulate, dorsal ± upright to reflexed at right angles to tube, 9–12(–15) × 3–4 mm, lower 3 tepals held close together, forming lip. *Stamens* unilateral, straight; filaments exserted 3.5–5.0 mm, white; anthers 4.5–6.2 mm long, pale purple; pollen ± white. *Style* arching over stamens, dividing between middle and apex of anthers or sometimes exceeding them, branches spreading, ± 2 mm long, ± undivided or notched apically. *Capsules* obovoid to globose, 5–6 mm long. *Seeds* globose, ± 2 mm diam. *Chromosome number* $2n = 10$, 6. *Flowering time*: January to April, rarely late November or December. Figure 49.

Distribution and biology: a species of the dry plains of central interior southern Africa, *Psilosiphon bainesii* extends from near Windhoek in central Namibia north into southern Angola and across the Kalahari to eastern Botswana and northwestern Limpopo in South Africa (Figure 48). It favours hard flat sandy ground where the corms may be lodged up to 300 mm below the surface. We have never seen it in rocky terrain, the habitat preferred by the related and morphologically similar *P. otaviensis*. The flowers open in the late afternoon and last through the night and into the following day, but rapidly become wilted in the dry and hot daylight conditions. The freshly opened flowers have a strong sweet and pleasant odour and produce a fair quantity of nectar and this combined with the pale perianth colour suggest adaptation to pollination by hawk moths.

Like several other species of *Psilosiphon* in Namibia and elsewhere (see Ethnobotany pp. 20), the corms of *P. bainesii* are eaten raw or roasted by the indigenous population (Rodin 1985).

Diagnosis and relationships: the divaricately branched inflorescence with branches bearing 1 or rarely 2 flowers, long perianth tube, and ± white perianth with pink to red markings near the base of the lower tepals distinguish *Psilosiphon bainesii*. The perianth tube is usually 25–35 mm long, rarely up to 40 mm or less than 20 mm. The corm tunics are composed of light brown, densely compacted fibres, the outer layers of which become increasingly netted with age. These corm tunics, combined with the pale, long-tubed flower and the basic chromosome number of $x = 5$, suggest a close relationship with *P. otaviensis* and *P. schimperi*, which have similar karyotypes (Goldblatt 1990b). The similarity in the size and general shape of the flowers of *P. bainesii* and *P. otaviensis* led to their confusion in the past, but our field studies in Namibia have shown convincingly that these are separate species with different ranges and habitat preferences as well as different floral and inflorescence morphology. Populations of *P. bainesii* from west-central Namibia have a derived chromosome number, $2n = 6$, most likely the result of Robertsonian fusion of chromosomes to yield large metacentric pairs (Goldblatt & Takei 1995). This number is, incidentally, the lowest recorded in the Iridaceae, coincidentally shared with some species of *Crocus* L.

Specimens from eastern Botswana near Macheng, *Hansen 3357*, represent an unusual form of *Psilosiphon bainesii*: the flowers have a short tube, 14–20 mm vs. 25–40 mm in most other collections of the species. In other respects the plants accord with *P. bainesii*, including the fairly distinctive translucent, pearly perianth colouring. The collection may represent a hybrid population, and then most likely with *P. sandersonii*, which also occurs in eastern Botswana. One of the few collections that we have seen from Angola, *Barbosa & Moreno 10181* from Chibia, is unusual in having a wine red perianth tube. The reverse of the outer tepals is a similar dark colour, although the condition in the living plants may have been somewhat different. We cannot properly assess the significance of this variant until more material from Angola becomes available.

History: apparently first collected in 1863 by the nineteenth century English landscape artist Thomas Baines and named in his honour, *Psilosiphon bainesii* was described by J.G. Baker in 1876, as *Lapeirousia*. The species was based on Baines's collection, but also on a second gathering from the Transvaal made by a certain Mr. Todd, about whom nothing seems to be

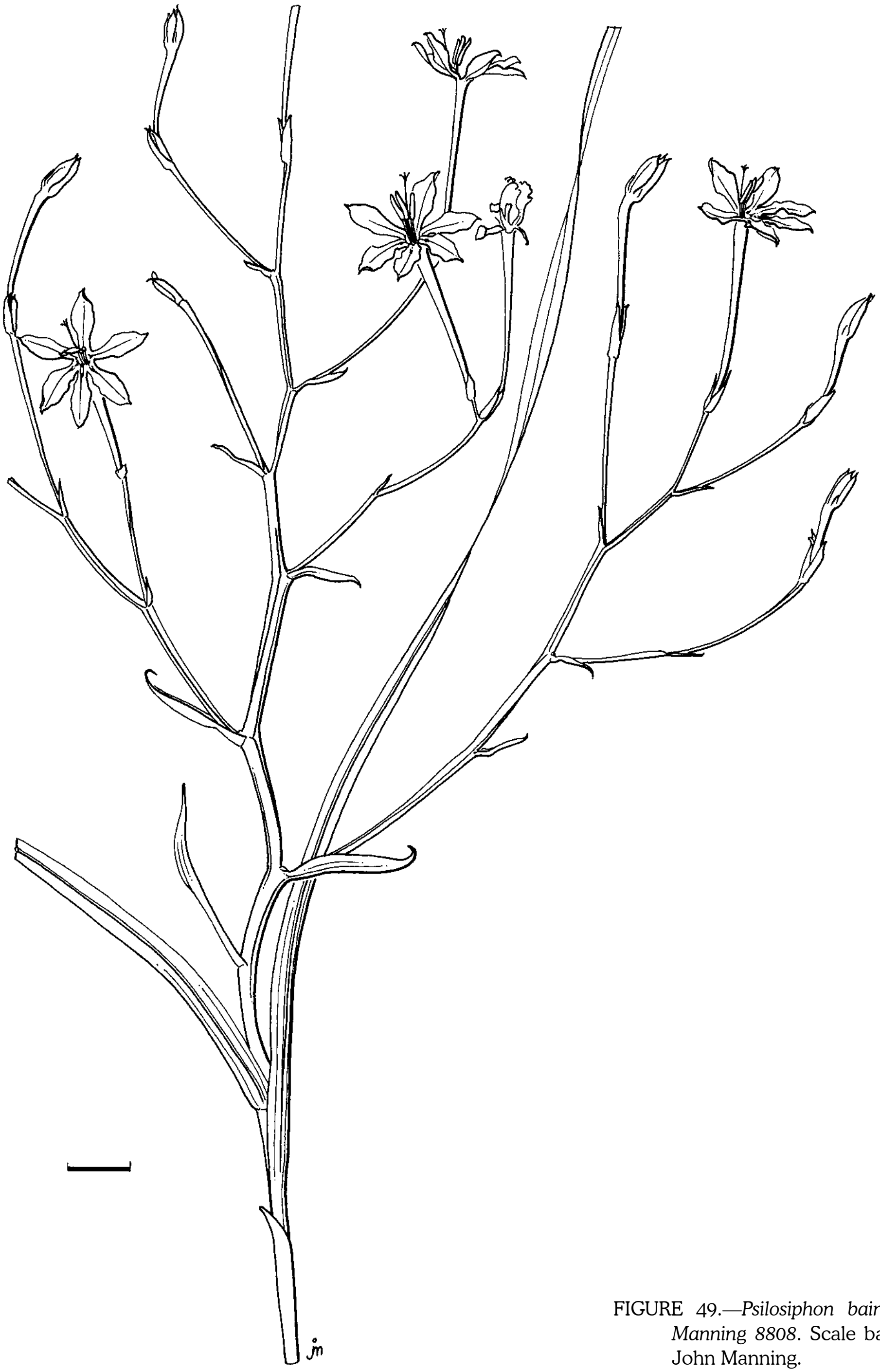


FIGURE 49.—*Psilosiphon bainesii*, *Goldblatt & Manning 8808*. Scale bar: 10 mm. Artist: John Manning.

known. Baines's plants were collected in western Botswana near Kobe Pan, an area still not well-known botanically. Plants from west central Namibia were described in 1922 as *L. vaupeliana* by Dinter, based on three of his own collections. The distinction that Dinter made between this and the avowedly related *L. bainesii* was the red-violet flower with darker veins in his species compared to the white flowers of *L. bainesii* with dark brown markings. These differences did not seem significant to Goldblatt (1990a) and we endorse his decision to include *L. vaupeliana* in *P. bainesii*.

Psilosiphon otaviensis was regarded as a synonym of *Lapeirousia bainesii* by Sölch (1969) in his account of Iridaceae for *Prodromus Einer Flora von Südwestafrika*. However, he upheld *L. vaupeliana*, distinguishing it in the diagnostic key by the ultimate branches of the inflorescences each bearing a single flower in contrast to *P. bainesii* in which the ultimate branches were said to have two or more sessile flowers. The type specimen of *P. bainesii* has, however, single-flowered ultimate inflorescence branches and we have no doubt it is conspecific with the later *L. vaupeliana* whereas *P. otaviensis* has 3–5 flowers on the ultimate branches of the inflorescence and also has fairly different flowers.

Representative specimens

BOTSWANA.—**1921** (Aha Hills): Aha hills, 110 km west of Nokaneng, (–CB), *Wild & Drummond 6919* (BM); Dobe, 26 km north of Aha Hills, SWA [Namibia] border, (–CA), *Wild & Drummond 7202* (K, PRE). **2021** (Koanaka Hills): near SWA [Namibia] border fence, sandy grassland, (?), *Smith 3330* (MO). **2023** (Kwebe Hills): Ngamiland, Kwebe, *Lugard & Lugard 179* (GRA, K, SAM). **2025** (Mompse): Odiakwe, savanna, west of Francistown just north of Mkarikari Pan, (–AB), *Wild & Drummond 6826* (K). **2125** (Lothlekane): Ngamiland, near Bachakuru, white and chocolate, (–DD), *Lugard 242* (K). **2226** (Serowe): Kweneng, Serowe, roadside, sandy grass veld, (–BC), 2 Mar. 1991, *Barnard 639* (PRE). **2326** (Mahalapye): Mahalapye Exp. Morale, shallow gritty sandy loam, (–BB), *Yalala 356* (K, LISC, PRE). **2327** (Ellisras): 10 miles west of Macheng towards Mahalapye, woodland, (–AB), *Hansen 3357* (C, K, PRE, WAG). **2425** (Gaborone): 12 km south of Gaborone, Mmokolodi, (–DD), 24 Mar. 1994, *Cole 546* (PRE). **2426** (Mochudi): Mochudi, (–AC), Jan. 1915, *Harbor* sub *Rogers 6569* or *Harbor s.n.* (G, K, PRE, SAM).

NAMIBIA.—**1715** (Ondangua): 100 km east Oshikango, corm eaten raw or roasted, (–BD), *Rodin 9295* (K, M, MO, PRE, WIND). **1719** (Rundu): 14.6 m [22 km] east of Runtu on Sambiu road, (–DD), *De Winter & Marais 4558* (K, M, WIND). **1819** (Karakuwise): Cigarette, northeast of Karakuwise, (–DC), *Maguire 2381* (NBG, PRE). **1916** (Gobaub): north of Outjo, between Farms Grensplaas and Tsabis, stony sandy hill slope, (–AD), 12 Mar. 1997, *Germishuizen 9692* (PRE); Farm Norabis 387, west of Otavi, thornveld on red sand, (–DD), *Goldblatt & Manning 8826* (MO, PRE, WIND). **1917** (Tsumeb): Otavi, (–CB), *Dinter 5755* (B, G, PRE, Z); Grootfontein, Otjirukaku, (–DB), *Seydel 2068* (B, BR, C, GH, K, M, MO, S, WAG, WIND). **1918** (Grootfontein): Farm Oliewenhof, sehr häufig auf der Palmflache, (–CB), *Merxmuller & Giess 30153* (K, M, WIND, PRE, S, SRGH, WAG). **1920** (Tsumkwe): 6 km east of Tsumkwe on the road to Botswana, white sand, (–DA), *Giess* et al. *11033A* (WIND); 2 km west of Kremetartkop, open grassland, (–DD), 26 Feb. 1986, *Hines 587* (PRE). **2116** (Okahandja): Farm Omatako View, (–BA), *Woortman 152* (M, WIND). **2017** (Waterberg): Quickborn, sand, (–AA), *Bradfield 196* (K, PRE). **2117** (Otjosondu): 48 km along Kapps Farm road from Steinhausen, compact sand, (–DC), *Goldblatt & Manning 8808* (E, K, M, MO, NBG, PRE, S, WAG, WIND). **2118** (Steinhausen): Farm Mex, 45 km north of Witvlei, red sand, (–AB), *Germishuizen 2662* (PRE, WIND). **2518** (Tses): Kalaharirand, Tutara, Farm Okamatangara, (–DB), *Seydel 2549* (BR, K, M, MO, SRGH, WAG).

SOUTH AFRICA. LIMPOPO.—**2229** (Waterpoort): 10 miles [15 km] southeast of Dongola Reserve, Farm Coila, (–AD), *Codd & Dyer 3780* (E, K, PRE); Dongola, Soutpansberg, (–BC), *Pole Evans 4305* (K, MO, PRE, SRGH). **2327** (Ellisras): Potgietersrus, 2 miles northeast of Tomburke, red gritty flats, (–BB), *Codd 6614* (K, PRE, SRGH). **2328** (Baltimore): Farm Dansfontein, red, sandy loam, (–AB), 31 Jan. 1996, *Du Toit 4965* (PRE).

NORTH WEST.—**2525** (Mafikeng): Mafikeng, Farm Panvlakte 3, thornveld, sandy soil, (–DC), 22 Jan. 1985, *Knollys 3* (GRA).

[Also in southern Angola (Goldblatt 1990a).]

11. **Psilosiphon schimperi** *(Aschers. & Klatt) Goldblatt & J.C.Manning*, comb. nov. *Tritonia schimperi* Aschers. & Klatt in Klatt in Linnaea 34: 697 (1866b). *Acidanthera unicolor* Hochst. ex Baker: 160 (1877), 359 (1898), nom. superfl. pro *Tritonia schimperi* Aschers. & Klatt. *Lapeirousia schimperi* (Aschers. & Klatt) Milne-Redh.: 307 (1934); Goldblatt: 472 (1990a). *Acidanthera schimperi* (Aschers. & Klatt) R.C.Foster: 42 (1936). Type: Ethiopia. Tigray: woods and thickets near Goelleb on the river Tacazze, 4000 ft [1 220 m], *Schimper 2304* (B lecto.! designated by Goldblatt: 472 (1990a); B!, G!, K!, P!, isolecto.).

Anomatheca angolensis Baker: 337 (1876). *Lapeirousia monteiroi* Baker: 355 (1898), illegitimate superfluous name for *A. angolensis* Baker (1876). *Freesia angolensis* (Baker) Klatt: 187 (1894). *Lapeirousia angolensis* (Baker) R.C.Foster: 48 (1936). Type: Angola, without precise locality, cult. Hort. Kew, *Monteiro s.n.* (K, holo.!).

Lapeirousia fragrans Welw. ex Baker: 272 (1878). Type: Angola. Huila: ad Morro de Lopollo, 5200′ [1 585 m], stony and rocky places, Dec. 1859, *Welwitsch 1552* (K, holo.!; BM!, C!, COI!, G!, P!, iso.).

Lapeirousia cyanescens Welw. ex Baker: 272 (1878). Type: Angola. Huila: hills near Humpata, Apr. 1860, *Welwitsch 1553* (K, lecto.! designated by Goldblatt: 472 (1990a); B!, BM!, COI!, G!, iso.).

Lapeirousia edulis Schinz, Bull. Herb. Boissier 4, Appendix 3: 49 (1896). Type: Namibia, Amboland, west of Olukonda, 5 Apr. 1893, *Rautanen 106* (Z, lecto.!, designated by Goldblatt: 472 (1990a); K!, P (2 sheets)!, Z (3 sheets)!, isolecto.).

Lapeirousia porphyrosiphon Baker: 353 (1898). Type: Botswana, Ngamiland, Kalahari Desert near Mamunwe, 26 Feb. 1897, *Lugard 338* (K, holo.!).

Lapeirousia erythreae Chiovenda: 139 (1911). Type: Eritrea, Accheli Guzai (Ocule Cusai) near Loggo Sarda, Deggahen, 2 600 m, 15 Sept. 1902, *Pappi 1414* (G, lecto.!, designated by Goldblatt: 472 (1990a); GH!, MO!, isolecto.).

Lapeirousia montaboniana Chiovenda: 9 140 (1911). Type: Eritrea, Bogos near Cheren, 24 Aug. 1906, *Pappi 7087* (? FI, not seen).

Lapeirousia dinteri Vaupel: 544–545 (1912). Type: Namibia, Damaraland, Aukos-Kreyfontein, 28 Dec. 1908, *Dinter 810* (B, holo.!; B!, SAM (2 sheets)!, iso.).

Lapeirousia uliginosa Dinter: 13, 14 (1912). Type: unknown, none cited.

Plants (200–)300–800 mm high, usually laxly few(several)-branched, stem rounded below to nearly square and 4-angled to 4-winged above. *Corm* bell-shaped, 18–22 mm diam.; tunics of compacted fibres, light to dark brown, outer layers becoming loosely fibrous and netted. *Foliage leaves* 3 or more, lower 2 largest, usually slightly exceeding inflorescence, decreasing in size above, narrowly lanceolate to ± linear, 5–10(–15) mm wide, main vein slightly raised. *Inflorescence* a lax false panicle or branched spike, ultimate branches 1–3-flowered; bracts (10–)20–35(–45) mm long, green, becoming membranous to ± dry and papery above, then light to dark brown, tips dark brown. *Flowers* zygomorphic, white to cream, rarely pale violet, when whitish sometimes fading lilac on drying especially on tube; opening at sunset and then sometimes scented; perianth tube cylindric, slender, 100–140(–150) mm long; tepals lanceolate, extended ± at right angles to tube, 18–22(–25) × 6–8(–11) mm. *Stamens* unilateral, ± erect; filaments exserted 5–7 mm from tube; anthers 6–7 mm long, cream or purple; pollen cream or blue. *Style* filiform, arching over filaments, dividing opposite anther apices or to up to 3 mm beyond anthers; branches ± 2 mm long, forked for ± $^1/_3$ their length. *Capsules* obovoid-oblong, 8–12 mm long, partly enclosed in bracts. *Seeds* globose to slightly angular, 2.0–2.5 mm in diam. *Chromosome number* 2*n* = 10. *Flowering time*: mid- to late summer, December to March, in central and south tropical Africa [north of the equator mostly in September and October but in Kenya and Ethiopia also April to June]. Figure 50.

Distribution and biology: with a remarkably wide distribution across Africa, *Psilosiphon schimperi* extends from southwestern Angola and north-central Namibia across northern Botswana, southern Zambia and Zimbabwe in an almost continuous belt (Figure 51). Further north its distribution is scattered, and it occurs in northern Tanzania, eastern Kenya, southern Ethiopia and then again in northern Ethiopia, Eritrea, Somalia and the Jebel Marra and Jebel Gurgeil highlands of northwest Sudan. It is almost certainly absent from the Democratic Republic of the Congo, Uganda, central and western Kenya, and southern Tanzania. A plant from Yemen in the southern Arabian Peninsula is cited in the protologue, but we have not been able to confirm its presence there. *P. schimperi* grows in locally moist sites in otherwise largely arid country, typically in washes, the *omurambas* [ancient river beds] of Namibia, dambo margins, stream banks and seasonal marshes as well as in damp grassland. The flowers open in late afternoon and last through the night, but gradually wilt the next day. Some collections note a sweet odour when the flowers are open but live plants from Namibia that we have examined were scentless during the day and early evening hours, indicating variation for scent.

The corms are edible, and eaten either raw or roasted by the Ovambo of northern Namibia (Rodin 1985).

FIGURE 50.—*Psilosiphon schimperi*, *Goldblatt & Manning 8831*. Scale bar: 10 mm. Artist: John Manning.

Diagnosis and relationships: the large white flower with a perianth tube 100–150 mm long and the laxly branched inflorescence readily distinguish *Psilosiphon schimperi* from other species in the genus. Its immediate relationships probably lie with the Namibian and Angolan long-tubed species, *P. bainesii* and *P. otaviensis*, with which it shares a similar karyotype and diploid chromosome number of $2n = 10$ (Goldblatt 1990b). These two species, centred in northern Namibia, also have pale flowers with relatively long perianth tubes, up to 45 mm long, but more compact inflorescences and they are not likely to be confused with *P. schimperi*.

Unusually long-tubed white flowers characterise another tropical African species, *Lapeirousia odoratissima*, but this species has the corrugate leaves and woody corm tunics that place it firmly in *Lapeirousia* rather than *Psilosiphon*. The floral similarity is evidently due to convergence, presumably for pollination by hawk moths. *P. schimperi* exhibits relatively little variation for a species with such a wide distribution. Some specimens from Angola and Namibia in the southwest of its range have unusually short bracts, 15–20 mm long (e.g., *Giess & Loutit 14123*), but at least some plants from Namibia have bracts up to 35 mm long, thus comparable with those in plants from tropical and northeast Africa in which the bracts range from 35–45 mm. Although lanceolate-elliptic tepals 18–20 × 6–8 mm are the norm, plants collected in southern Angola (*Harrower* et al. *s.n.* NBG) have unusually large, ovate tepals up to 25 × 11 mm. Other features are consistent with *P. schimperi*. As noted by Goldblatt (1990a), some collections of *P. schimperi* from Ethiopia and Sudan (e.g., *Schimper 2304*, *431*) also have particularly short bracts, 10–15 mm long, and either pale or fairly dark brown. These plants have a perianth tube only 70–80 mm long and may be depauperate owing to a poor growing season or they may represent an ecotype or race constant for these features.

History: although not particularly variable, *Psilosiphon schimperi* has a long and confused history, largely due to its wide distribution rather than to a conviction that any of the later synonyms represented separate species. The type locality is in northern Ethiopia where collections were made in the 1840s by the French botanists Quartin Dillon and Petit and later by Georg Schimper in 1852–1864. It was named in Schimper's honour by Ascherson & Klatt (in Klatt 1866b), who referred it to the southern African genus *Tritonia*. Three separate collections from southwestern Angola made at this period by Joachim Monteiro and Friedrich Welwitsch were described by J.G. Baker as *Anomatheca angolensis* (1876), *Lapeirousia cyanescens*

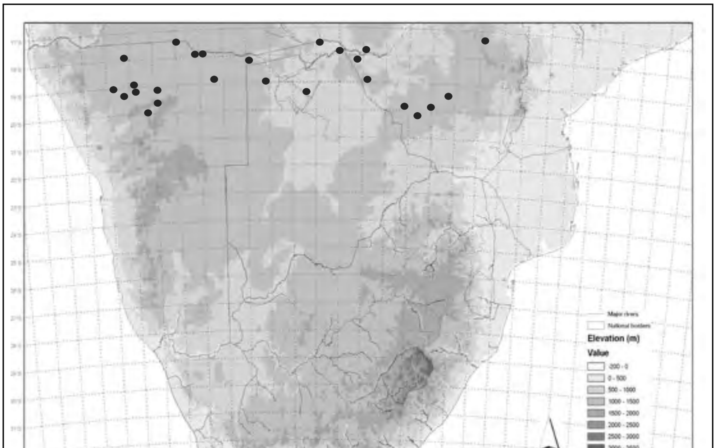


FIGURE 51.—Distribution of *Psilosiphon schimperi* in southern Africa, ●.

(1877), and *L. fragrans* (1878) respectively, without reference to the Ethiopian species. Later collections from Namibia were named independently by Hans Schinz as *L. edulis* in 1896 and Friedrich Vaupel as *L. dinteri* in 1912. Plants from Botswana, collected by E.J. Lugard were assigned to *L. porphyrosiphon* (Baker 1898) while in 1911 A. Chiovenda described *L. erythreae* and *L. montaboniana* based on contemporary collections from Eritrea. *Tritonia schimperi* was transferred to *Lapeirousia* in 1934, replacing the name *L. porphyrosiphon*, until then used for the species in south tropical Africa.

Representative specimens

BOTSWANA.—**1725** (Livingstone): south side of Chobe River, above Kasane, (–?), May 1972, *Sheppe 167* (SRGH); Chobe National Park, Savuti, Gogha Hills, (–CC), 13 Mar. 1994, *Roodt 110* (PRE). **1821** (Andara): southwest end of Tsodilo Hills, open savanna, (–DD), 11 Mar. 1985, *Long 12330* (E). **1923** (Maun): Khwai/Maxwe road, Moremi Wildlife Reserve, (–BC), 16 Mar. 1977, *Smith 1936* (BR, K, SRGH). **2124** (Rakops): Rakops, Makuba Dukuwe Fence, marsh, (–AB), 2 March 1991, *Barnard 661* (PRE).

NAMIBIA.—**1715** (Ondangua): 100 km east of Oshikango, (–BD), 19 Apr. 1973, *Rodin 9295A* (M, MO, PRE, WIND). **1718** (Kuring Kuru): Katui-Tui, maize land in sandy loam, (–AD), 15 May 1965 (fr.), *Barnard 191* (WIND); Kuring-Kuru, Okavango River bank in forest, 28 Mar. 1966, (–DA), *Soni s.n.* (WIND 3938). **1719** (Runtu): swampy marshes below Runtu, 31 Jan. 1956, (–AD), *De Winter & Marais 4469* (K, M, PRE, WIND, Z). **1724** (Katima Mulilo): Katima Mulilo, vlei, (–AD), 30 Jan 1975, *Vahrmeijer & Du Preez 2496* (MO, PRE). **1816** (Namutoni): Etosha National Park, Bigales Huh, (–C), 15 Feb. 1974, *Le Roux 644* (PRE, WIND). **1819** (Karakuwisa): grass flats, Karakuwisa, 4 Mar. 1958, (–DC), *Merxmüller & Giess 1795* (BM, K, M, PRE, WIND). **1821** (Andara): Kaprivi side of the river at Andara Mission, crevices on rocky outcrops, 23 Feb. 1956, (–AB), *De Winter & Marais 4820* (K, PRE, WIND); Okavango River, 19 km north of Shakawe on Botswana border, (–BA), 16 Mar. 1965, *Wild & Drummond 7093* (K, LISC, M, PRE, SRGH). **1915** (Okakuejo): Etosha Pan, black peat soil on the road to Ombika, (–BB), 4 Apr. 1980, *Giess 15472* (M, MO, PRE, WIND); Etosha National Park, 2.5 km east of Okakuejo–Ombika road, (–BD), 5 Mar. 1976, *Giess & Loutit 14123* (K, M, MO, PRE, WIND); grey-black peat flats north of Ombika, (–BD), *Le Roux 321* (PRE, WIND). **1916** (Gobaub): Etosha Game Park, near Homob water hole, (–AA), 11 Feb. 1966, *Tinley 1285* (M, PRE, WIND); Farm Neidaus North 78, heavy black clay with limestone, seasonally waterlogged, (–DC), 19 Mar. 1988, *Goldblatt & Manning 8831* (MO, WIND). **1917** (Tsumeb): Farm Malta, (–AB), 5 Feb. 1971, *Giess 11226* (M, PRE, WIND); Farm Kumkauas, large colonies among tough grasses, (–CA), 30 Jan. 1971, *Giess 11212* (M, WAG, WIND), 9 Mar. 1974, *Merxmüller & Giess 30175* (K, M, S, PRE, SRGH, WAG, WIND).

New combinations for *Psilosiphon* species not represented in southern Africa

Psilosiphon abyssinicus *(R.Br. ex A.Rich.) Goldblatt & J.C.Manning,* comb. nov. *Lapeirousia abyssinica* (R.Br. ex A.Rich.) Baker in Journal of the Linnean Society, Botany 16: 155 (1877). *Geissorhiza abyssinica* R.Br. ex A.Rich.: 308 (1850) [*Geissorhiza abyssinica* R.Br. in Salt: App. 1 (1814), nom. nud.]. Type. Ethiopia, 'Maigoigoi ad Dobre Sina', *Quartin Dillon & Petit s.n.* (P, lecto.! designated by Goldblatt: 459 (1990a); P!; BR!, isolecto.).

Montbretia abyssinica Hochst. ex A. Rich.: 308 (1850) [*Montbretia abyssinica* Hochst., Flora 24(1 Intell.): 21 (1841), nom. nud.]. *Tritonia abyssinica* (Hochst.) Walp.: 613 (1852). Type: Ethiopia, hills near Adoa, October (fl. & fr.), *Schimper 329* (P, lecto.!, designated by Goldblatt: 459 (1990a); BM!, BR!, G!, K!, M!, P!, isolecto.).

Psilosiphon setifolius *(Harms) Goldblatt & J.C.Manning,* comb. nov. *Lapeirousia setifolia* Harms in Botanische Jahrbucher für Systematik 30: 278 (1901). *Lapeirousia erythrantha* var. *setifolia* (Harms) Geerinck et al.: 337 (1972). Type: Tanzania, Eastern Livingstone Mtns, Ubena, Tsausingewe district, 2 100 m, March 1899, *Goetze 812* (B, holo.!; BR!, E!, iso.).

Psilosiphon teretifolius *(Geerinck* et al.*) Goldblatt & J.C.Manning*, comb. nov. *Lapeirousia teretifolia* (Geerinck et al.) Goldblatt in Annals of the Missouri Botanical Garden 77: 457 (1990a). *Lapeirousia erythrantha* var. *teretifolia* Geerinck, Lisowski, Malaisse & Symoens: 342 (1972). Type: Zaire [Democratic Republic of the Congo], Shaba, Plateau de la Manika, env. 2 km west de Katema, 20 Jan. 1969, *Lisowski, Malaisse & Symoens 182* (LSHI, holo., BR!, BRVU, K, POZG, iso. [the lectotypification by Goldblatt: 457 (1990a) was made in error].

Psilosiphon zambeziacus *(Goldblatt) Goldblatt & J.C.Manning,* comb. nov. *Lapei-*

rousia zambeziaca Goldblatt in South African Journal of Botany 57: 226 (1991), nom. nov. pro *L. angolensis* Goldblatt: 458 (1990a), illegitimate homonym. Type: Angola, Moxico, a few miles west of River Kaperu (Kapelu), boggy grassland, 10 Jan. 1938, *Milne-Redhead 4037* (K, holo.!; BM!, BR!, LISC!, P!, PRE!, iso.).

Excluded species

Lapeirousia welwitschii Baker, Handbook of the Irideae 168 (1892). Type: Angola: Malange, Pungo Andongo, Jan. 1857, *Welwitsch 1531* (BM, annotated as lectotype in unknown hand; C, COI, G, K, P, isolecto.). *L. erythrantha* var. *welwitschii* (Baker) Marais ex Geerinck, Lisowski, Malaisse & Symoens: 340 (1972), applied to *L. erythrantha* as *L. briartii*. [The type specimens are poorly preserved, especially the flowers, and are most likely either *Psilosiphon erythranthus* or *P. rivularis*. The type locality must be visited to resolve this question. Neither species has otherwise been recorded at Pungo Andongo in north-central Angola and *P. rivularis* is only known from Angola only in the south of the country.]

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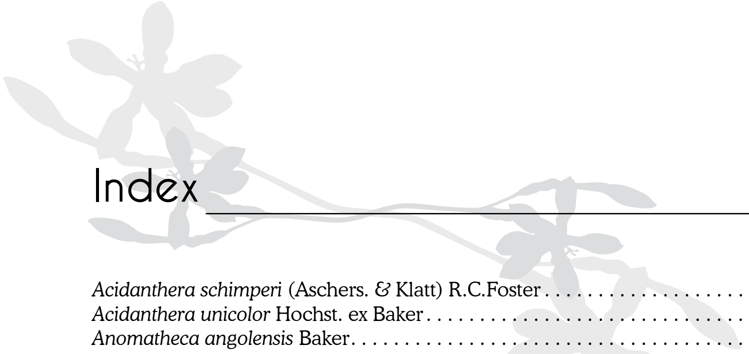

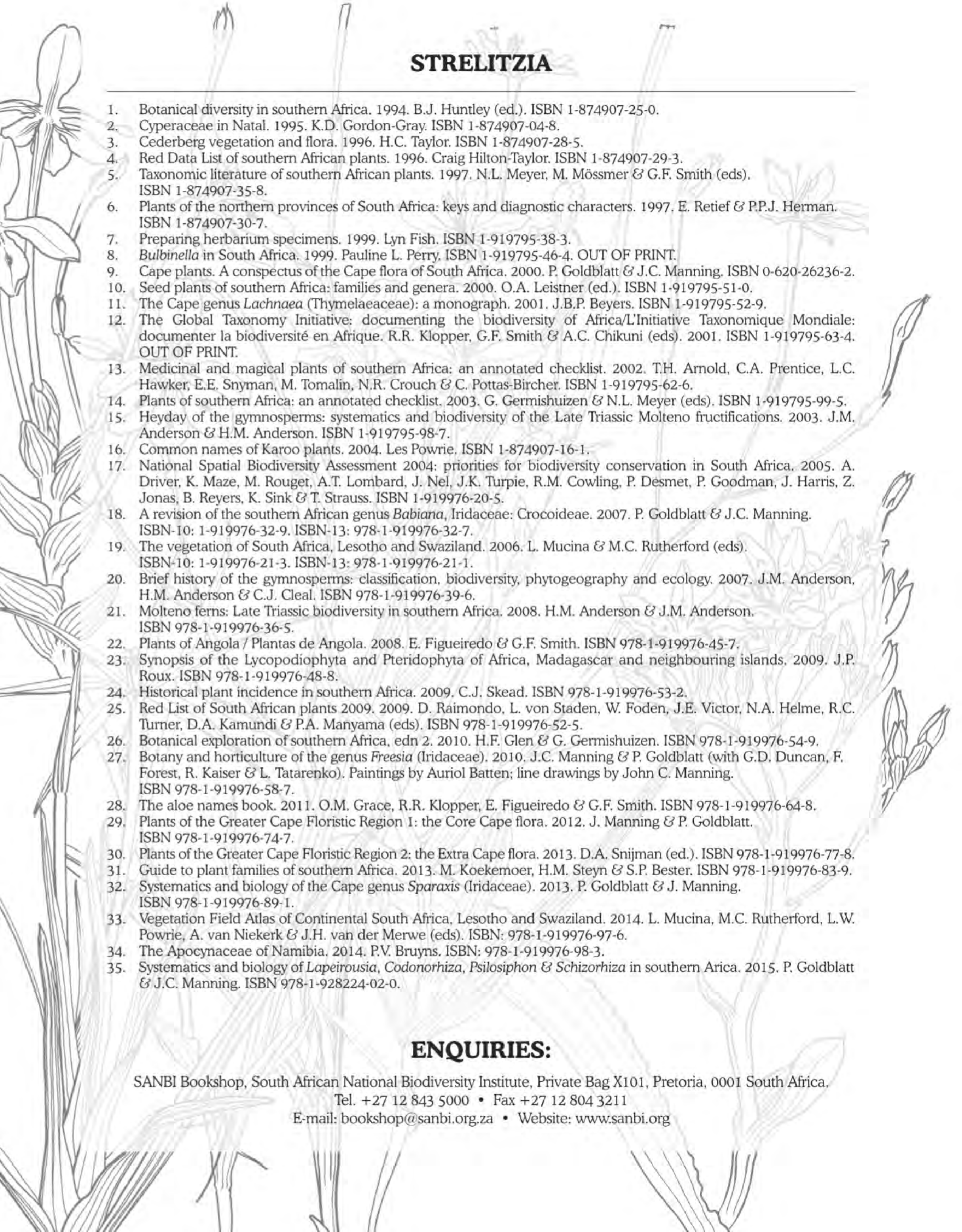

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Plastid and nuclear DNA sequence analyses show that the sub-Saharan African genus *Lapeirousia* Pourr. is paraphyletic as presently circumscribed. Species of *Lapeirousia* are retrieved as a clade in which are nested the tropical African genera *Cyanixia* Goldblatt & J.C.Manning and *Savannosiphon* Goldblatt & Marais as sister to *Lapeirousia* sect. *Paniculatae* Goldblatt plus the taxonomically isolated *L. neglecta* Goldblatt. To preserve taxonomic monophyly we dismember *Lapeirousia*, recognising the new genera **Codonorhiza** Goldblatt & J.C.Manning for *L.* sect. *Fastigiatae* Goldblatt (7 spp.) and **Schizorhiza** Goldblatt & J.C.Manning (1 sp.) for *L. neglecta*, both from the Cape Floristic Region, as well as **Psilosiphon** Welw. ex Goldblatt & J.C.Manning (15 spp.) for *L.* sect. *Paniculatae*, all from tropical and eastern southern Africa. This leaves *Lapeirousia* (27 species) centred in western southern Africa, but also represented in south tropical Africa. We revise the infrageneric taxonomy of *Lapeirousia* in light of the molecular phylogeny, recognising sect. **Chasmatocallis** (R.C.Foster) Goldblatt & J.C.Manning, sect. *Lapeirousia* and sect. **Sophronia** (Licht. ex Roem. & Schult.) Goldblatt & J.C.Manning. We provide dichotomous keys to the four genera in southern Africa and full revisions of all four genera. Six new species, two of *Codonorhiza*, three of *Lapeirousia* and one *Psilosiphon* are recognised; two subspecies are raised to species rank, and *L.* **angustifolia** Schltr., currently included in *L. pyramidalis* (Lam.) Goldblatt, is also recognised at species rank. Four new subspecies are described.

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