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Taxonomic revision of the genus *Thereianthus* (Iridaceae: Crocoideae)

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ABSTRACT

Thereianthus G.J.Lewis is revised, with full descriptions and synonomy, distribution maps, and notes on ecology and taxonomic history. All species are illustrated, and capsule and seed morphology are described for many of the species for the first time. Novel characteristics of the bract, seed, and pollen operculum are used to separate the species into two sections: sect. **Brevibracteae** *Goldblatt & J.C.Manning* is distinguished by relatively small bracts, 3–8 mm long and uniformly leathery or soft-textured without thickened veins, seeds with filiform chalazal extension, and pollen grains with 1-banded operculum; and sect. *Thereianthus* by relatively larger bracts, (7–)8–15 mm long with prominently sclerified veins, seeds without any extension to the chalazal crest, and pollen grains with ± 2-banded operculum. Species in sect. *Thereianthus* are further segregated into ser. *Thereianthus*, with heavily ribbed leaves and suberect flowers with arcuate or erect stamens, and ser. *Bracteolatus*, with plane, inconspicuously veined leaves and ± spreading flowers with declinate stamens. Eleven species are recognized in the genus, all restricted to the southwestern portion of Western Cape. Two new species are described in sect. *Thereianthus*: *T.* **bulbiferus** *Goldblatt & J.C.Manning*, known from three populations along the West Coast, is distinguished by the unique development of cormels in the lower leaf axil, and by its actinomorphic perianth with white marks at the base of each tepal and ± declinate stamens; and *T.* **elandsmontanus** *Goldblatt & J.C.Manning*, known from a single population in Elandsberg Nature Reserve near Wellington, has distinctive cream-coloured, moderately long-tubed flowers with unusually narrow, linear tepals heavily marked with purple near the base. In adddition, *T. lapeyrousioides* [now *T. minutus*] var. *elatior* G.J.Lewis in sect. **Brevibracteae** is raised to species status as *T.* **intermedius** *Goldblatt & J.C.Manning*, differing from typical *T. minutus* by the shorter perianth tube (10–13 vs 20–30 mm), shorter bracts (3–5 vs 6–8 mm), and smaller, ovoid capsules, 4–5 mm long, containing ovoid seeds vs flask-shaped capsules 6–8 mm long and fusiform seeds.

INTRODUCTION

Thereianthus G.J.Lewis is a small genus of deciduous geophytes endemic to the southwestern, winter rainfall region of Western Cape, where it is essentially restricted to mainly montane soils derived from quartzitic sandstone (Manning *et al.* 2002). Eight species are currently recognized, all of them flowering during the hot summer months, mostly November to January. Most are ± pyrophytes, flowering most profusely in the season after the veld has been cleared by burning.

Cladistic analysis of plastid DNA sequence data locates *Thereianthus* as sister to *Micranthus* (Pers.) Eckl., with these two genera together placed as sister to *Watsonia* Mill. plus *Pillansia* L.Bolus (Reeves *et al.* 2002; Goldblatt *et al.* 2008). These four genera, with *Cyanixia* Goldblatt & J.C.Manning, *Lapeirousia* Pourr. and *Savannosiphon* Goldblatt & Marais, are now treated as the tribe Watsonieae of subfamily Crocoideae (Goldblatt *et al.* 2008; Goldblatt & Manning 2008), characterized by axillary corm development in which the current season's corm develops from an axillary bud at the base of the stem rather than by expansion of the lower stem internodes as in other crocoid genera. Morphological synapomorphies for *Micranthus* plus *Thereianthus* are the superposed leaves, small, blue flowers, and ± dry bracts with membranous margins (Goldblatt *et al.* 2006). The leaves in both *Micranthus* and *Thereianthus* are all strictly cauline (Lewis 1954), with the lowermost sub-basal, and the corm tunics are thus formed solely from the cataphylls, without any contribution from the bases of the lower leaves. Chromosome number, $2n = 20$, and a karyotype of one long and nine short chromosome pairs in *Micranthus* and *Thereianthus* is likely plesiomorphic for the tribe. *Watsonia*, in contrast, has a derived base chromosome number of $x = 9$.

The moderately short spikes of spirally inserted flowers, bracts with narrow membranous margins, and monosulcate pollen distinguish *Thereianthus* from *Micranthus*, which has elongate, distichous spikes, bracts with broad membranous margins, and zonasulcate pollen (Goldblatt & Manning 2008). Our investigation of leaf anatomy in the genus (see Results and discussion of characters) indicates that a simple leaf margin is an additional anatomical apomorphy for *Thereianthus*.

Thereianthus was published by Lewis (1941), who recognized seven species in the genus. One new species has been described since then (Manning & Goldblatt 2004), at which time we also reduced *T. lapeyrousioides* var. *elatior* G.J.Lewis to synonymy in *T. minutus* (= *T. lapeyrousioides* var. *lapeyrousioides*). We have now had the opportunity of examining fresh material of var. *elatior*, which makes it clear that this taxon is in fact a distinct species. We also describe another two new species that appeared after a burn near Tulbagh, bringing the total number of species in the genus to eleven.

Taxonomic history: the taxonomic history of *Thereianthus* is closely linked to that of *Micranthus*, reflecting the marked similarities between the two genera and the uncertainty that existed around their circumscription. The first species of both genera known to science were referred to either *Ixia* or to *Gladiolus*, following the rather vague generic circumscriptions prevailing at

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the time but Ker Gawler (1804) subsequently included all known species in *Watsonia* based on their divided style branches. This treatment was not followed by Ecklon (1827), who concluded that the two genera were distinct from *Watsonia* and who also appreciated the differences between them. His new genus *Micranthus* (Ecklon 1827), which was established for the small-flowered species with strongly distichous spikes, was recognized by most later authors but acceptance of a second new genus for the larger-flowered species with longer perianth tubes was less than universal. Ecklon (1827) placed the two species of *Thereianthus* then known, *Gladiolus spicatus* L. (now *T. spicatus*) and *G. triticeus* Thunb. (now *T. bracteolatus*), in his new genus *Beilia* but failed to provide a validating description, and *Beilia* was thus not validly published. Heynhold (1847) remained unconvinced that generic rank was appropriate for Ecklon's species of *Beilia*, preferring to include them with the species of *Micranthus*, and he accordingly made the new combinations *M. spicatus* (L.) Heyn. and *M. triticeus* (Thunb.) Heyn. English bulb specialist, J.G. Baker (1877), in his account of the family, was of yet another opinion, reverting to Ecklon's circumscription of *Micranthus* but following Ker Gawler (1804) in retaining *Thereianthus* in *Watsonia*, as the unranked taxon *Beilia*. Here he recognized just one species, *W. punctata* (Andrews) Ker Gawl., with the earlier name, *Gladiolus spicatus* L., in synonymy. At the same time he described the third known species of *Thereianthus*, *T. juncifolius*, in the genus *Morphixia* (now a synonym of *Ixia*). *Beilia* was subsequently accorded the rank of subgenus within *Watsonia* by Baker (1892, 1896), who admitted four taxa at species rank, among them his erstwhile *Morphixia juncifolia* and also *W. lapeyrousioides*. At this stage, therefore, although Baker (1896) accepted both *Micranthus* and *Thereianthus* as currently circumscribed, only the former was accorded generic rank.

Klatt (1882), a contemporary of Baker's, utterly confused the situation in his account of the Iridaceae. Here, he included only two species in *Micranthus*, *M. spicatus* (L.) Klatt and *M. triticeus* (Burm.f. [sic]) Klatt, both of them actually species of *Thereianthus*, evidently unaware that Heynhold (1847) had already made the combinations for these species in *Micranthus*. We also assume that the attribution of the basionym to Burman fil. was an error for Thunberg, as *Ixia triticea* Burm.f. (1768) is a very different species [*Tritoniopsis triticea* (Burm.f.) Goldblatt]. Like Baker (1877) before him, Klatt (1882) did not associate *T. juncifolius* with the other two species, treating it instead in the genus *Anomatheca* as *A. calamifolia*. He then spread his options still wider by describing a fourth species of *Thereianthus* in *Watsonia* as *W. racemosa* Klatt. Inexplicably, Klatt overlooked any species of *Micranthus* (as now understood) in his account, an omission that he later partly corrected (Klatt 1894) when he included *M. plantagineus* [= *M. alopecuroides* (L.) Eckl.] in *Micranthus* with one variety, var. *junceus* Baker [now *M. junceus* (Baker) N.E.Br.]. In this work, *T. spicatus* remained in *Micranthus* and *T. racemosus* in *Watsonia*, where it was joined by *T. bracteolatus* (as *W. subulatus*) but *T. juncifolius* was transferred to *Freesia* as *F. juncifolia* (Klatt 1894). This confusing species was later removed to yet another genus by Brown (1931) as *Lapeirousia juncifolia*, by which time it had been shuffled among no less than five different genera. Lewis (1941) had no doubt that it correctly belonged in *Thereianthus*.

The nomenclatural tangle between *Micranthus* and *Thereianthus* took a further turn when Kuntze (1891) erected a new genus, *Paulomagnusia*, in which he included both what are now *Micranthus alopecuroides* and *Thereianthus spicatus*. The lectotype of *Paulomagnusia* is *P. alopecuroides* (now *M. alopecuroides*), designated by Goldblatt & Manning (2008) and the genus is now a nomenclatural synonym of *Micranthus*. Ecklon's *Beilia* was raised to generic rank by Kuntze (1898), who included only *B. spicata* (L.) Eckl. ex Kuntze in the genus. Unfortunately *Beilia* Kuntze is nomenclaturally superfluous since Kuntze listed the validly published *Paulomagnusia* in synonymy without any further explanation. Kuntze also recognized var. *brevifolia* in his *B. spicata*, and although this taxon has never been identified, its provenance from the Cape Town suburb of Mowbray, and its broad leaves (10–20 mm) make it certain this is not a species of *Thereianthus*. It remained for G.J.Lewis (1941), over a century after Ecklon proposed *Beilia*, to publish the genus *Thereianthus* for the two species of Ecklon's *Beilia* plus an additional four more species that were until then included in *Watsonia*.

Chromosome cytology: chromosome numbers are known for just two species of *Thereianthus*, *T. minutus* (sect. *Brevibracteae*) and *T. bracteolatus* (sect. *Thereianthus*). Both have a diploid number of $2n = 20$ and an identical karyotype of one long and nine short chromosome pairs (Goldblatt 1971). A report of $2n = 20$ by Goldblatt & Takei (1997) for *T. spicatus* is an error for *T. bracteolatus*, thus representing a second count for that species. The base number and karyotype match exactly those of *Micranthus* but both are likely plesiomorphic and thus uninformative about relationships. The two species of *Thereianthus* counted, one from each section of the genus, and the matching counts for *Micranthus*, suggest that the basic karyotype is unlikely to differ among the other species of *Thereianthus*.

Pollination systems: there are few published observations on the pollination of *Thereianthus*, and neither Scott Elliot (1891) nor Vogel (1954) mentioned the genus in their early studies of pollination in the South African flora. Flowers of the genus are, however, diverse and obviously adapted to a variety of mainly long-tongued insect pollinators. At least *T. ixioides* has been reported to be visited by the hopliine beetles, *Heterochelus* sp. and *Peritrichia* sp. (Scarabaeidae: Hopliini). Individuals of *Peritrichia* were observed moving indiscriminately between the flowers of this species and the remarkably similar blooms of *Ixia metelerkampiae*, the pale mauve flowers of which also have a dark centre (Goldblatt *et al.* 2000). These authors suggested this was a possible example of Batesian mimicry. Although both species have a filiform perianth tube in which the style is tightly enclosed by the walls of the tube, *T. ixioides* offers small amounts of nectar, visible at the mouth of the tube, suggesting that the species offers a secondary reward and may have a more generalist pollination system than *I. metelerkampiae*, which does not offer nectar. Goldblatt *et al*. (1998) also reported apparent pollination of *T. racemosus* by the hopliine, *Khoina bilateralis*, in

the Grootwinterhoek Wilderness area. This species, too, produces traces of nectar and has a strong floral scent and is likely to have alternative pollinators, probably various bees.

Goldblatt & Manning (2006) inferred long-proboscid fly pollination for *Thereianthus longicollis,* which has a perianth tube 25–40 mm long. That prediction has recently been validated: the long proboscid fly, *Philoliche rostrata* (proboscis ± 40 mm long), was captured visiting flowers of this species in the mountains above Tulbagh Waterfall in December 2010 (unpublished obs.). Other representatives of this pollination guild at the site included *T. minutus*, *Geissorhiza confusa* (Iridaceae) and a long-tubed and large-flowered race of *Lobelia coronopifolia* (Lobeliaceae) with a pink corolla. Visits by *P. rostrata* to *T. minutus* (perianth tube 20–30 mm long) were also recorded at this site. Another species, *T. elandsmontanus,* also has flowers with the hallmarks of long-proboscid fly pollination, notably a slender perianth tube mostly 20–23 mm long and a white or pale pinkish perianth with red markings. We predict that it is also pollinated by the long-proboscid flies *Prosoeca gulosa* and/or *P. rostrata*.

We have noted the butterfly, *Cynthia cardui* (Nymphalidae), visiting the moderately long-tubed flowers of *Thereianthus spicatus* at Jonkershoek, and moving from flower to flower in a constant pattern. This insect may be one of the legitimate pollinators of this widespread species. We infer bee or generalist pollination for the shorter-tubed species *T. bracteolatus, T. bulbiferus* and *T. intermedius*. The long-tubed, violet flowers of *T. montanus* appear to be adapted for pollination by long-proboscid flies or butterflies.

MATERIALS AND METHODS

All relevant types were examined, as well as all herbarium material from BOL, NBG and SAM (acronyms after Holmgren *et al.* 1990), the primary collections of species from the southwestern Cape. Most species were also studied in the field.

For SEM work, fresh pollen grains were fixed in FAA, critical point dried following standard procedures, and examined at the SEM Unit, University of Cape Town by Miranda Waldron. For operculum and sculpturing study, dry pollen from herbarium specimens was rehydrated and stained in Calberla's fluid (Goldblatt *et al.* 1991). Pollen was sampled from at least two flowers per voucher. Seed shape and size was determined by examining seeds from one or more capsules from two or more different plants of each species.

For anatomical investigation, fresh material was fixed in FAA and then embedded in wax before sectioning and double-staining with alcian blue and safranin following Rudall (1995). Mature leaf anatomy of the following species was examined: *Thereianthus racemosus*, *T. minutus, T. bulbiferus* and *T. spicatus*. Anatomical descriptions and terminology follow Rudall (1995). Bract and bracteole anatomy was examined in *T. minutus* and *T. spicatus*.

RESULTS AND DISCUSSION OF CHARACTERS

Leaf blade anatomy (Figures 1A–F; 2)

Outline: surfaces smooth and ± parallel in *Thereianthus bulbiferus, T. minutus* and *T. racemosus* (Figures 1A–C; 2A–D), terete in *T. juncifolius* (Figure 1F), elliptical and fistulose in *T. bracteolatus* (Figures 1D; 2E), and abruptly raised over larger vascular bundles in *T. spicatus* and surface thus ribbed or corrugated (Figures 1E; 2F); pseudomidrib not evident except in *T. minutus* but never raised in fresh leaves.

Margin: simple, i.e. without prominent marginal vein or subepidermal sclerenchyma, rarely with small marginal bundle along one edge in *T. bulbiferus*; epidermal cells unspecialized.

Mesophyll: cells ± isodiametric with no tissue differentiation except at midrib area in *T. minutus* or with evident differentiation between parenchyma and chlorenchyma (*T. bulbiferus* and *T. juncifolius*) or ± radially elongated with clear differentiation between peripheral chlorenchyma and central mesophyll (*T. bracteolatus*, *T. racemosus* and *T. spicatus*).

Vascular bundles: arranged in two rows, with larger (primary and secondary bundles) in opposite pairs and smaller (tertiary) bundles opposite or subopposite, xylem poles usually separated, rarely fused in lateral secondary bundles in *T. minutus*; primary bundles in *T. bulbiferus* with tertiary bundle on each side contiguous with sclerenchyma sheath; a single pair of primary bundles can be identified in all species but this is most evident in *T. minutus* with differentiation between the primary bundle and secondary bundles less marked in other species, particularly *T. spicatus*.

Bundle sheaths: bundle sheath sclerenchyma extending to epidermis as girder in primary bundles in all species and also in secondary bundles in *T. bracteolatus, T. bulbiferus* and *T. spicatus*, cells of outer bundle sheath each containing solitary styloid crystal at phloem poles in larger bundles; larger (primary) bundles with complete sclerenchyma sheaths in *T. bulbiferus, T. bracteolatus, T. juncifolius, T. minutus* and *T. spicatus* but sclerification restricted to phloem caps in *T. racemosus*.

The most obvious distinction in leaf outline among the species is between the ribbed/corrugated blade of *Thereianthus spicatus* and the smooth blades of the other species examined. The leaves of *T. minutus* and *T. racemosus* are least sclerified, with only the primary bundle significantly sclerified, compared with *T. bulbiferus, T. bracteolatus, T. juncifolius* and *T. spicatus*, in which some or all of the secondary vascular bundles have completely sclerified sheaths. This is most marked in *T. spicatus*.

Leaf blade anatomy in *Thereianthus* accords with the general description for the genus (Rudall 1995) with the significant exception that the leaf margin in all species examined is essentially simple (i.e. lacking a prominent marginal vascular bundle and with unspecialized epidermis) (Figure 2A, C–F). Rudall (1995), who examined only *T. spicatus*, describes this species as possessing a marginal vascular bundle. The outermost vascular bundle is treated as marginal if it is prominent and solitary (not paired) and oriented at right angles to the margin with the phloem pole facing the margin. In *T. minutus* and *T. spicatus* the outermost bundles at the leaf edges

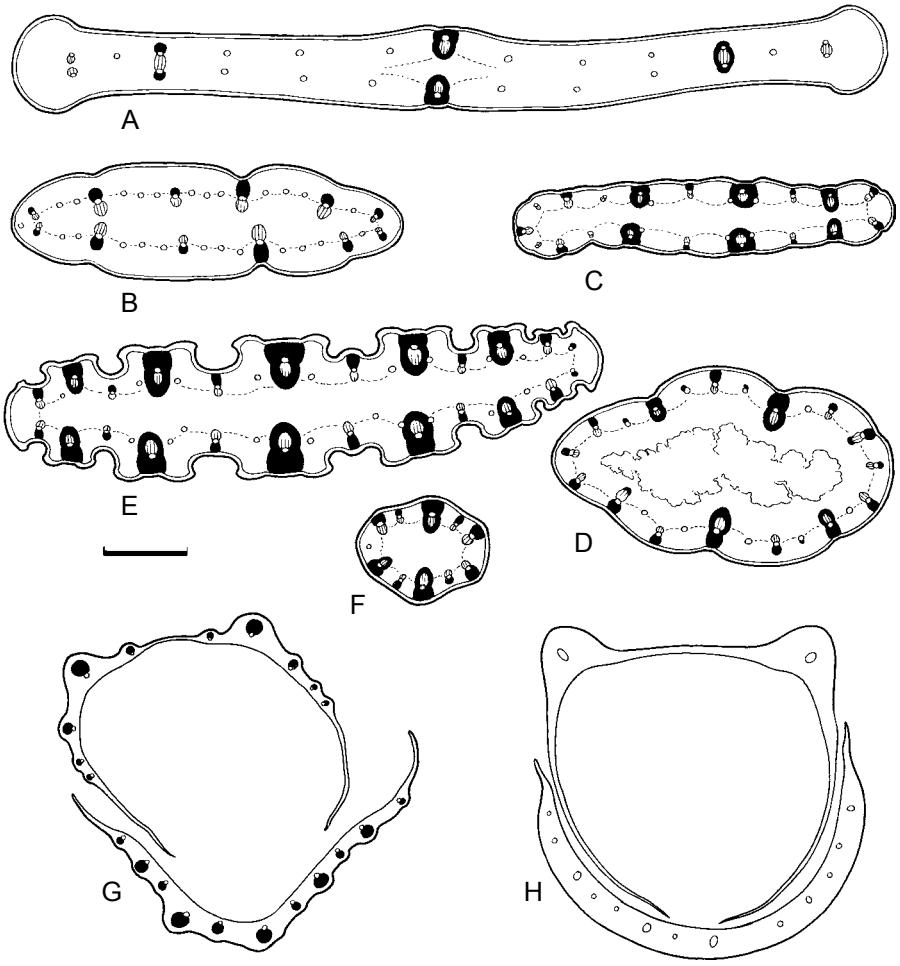

FIGURE 1.—A–F, leaf tissue plans of *Thereianthus* species: A, *T. minutus*; B, *T. racemosus*; C, *T. bulbiferus*; D, *T. bracteolatus*; E, *T. spicatus;* F, *T. juncifolius*. G, H, bract tissue plans: G, *T. spicatus*; H. *T. minutus*. Scale bar: A–F, 500 µm; G, H, 2 mm. Sclerenchyma solid shading; xylem hatched. Artist: John Manning.

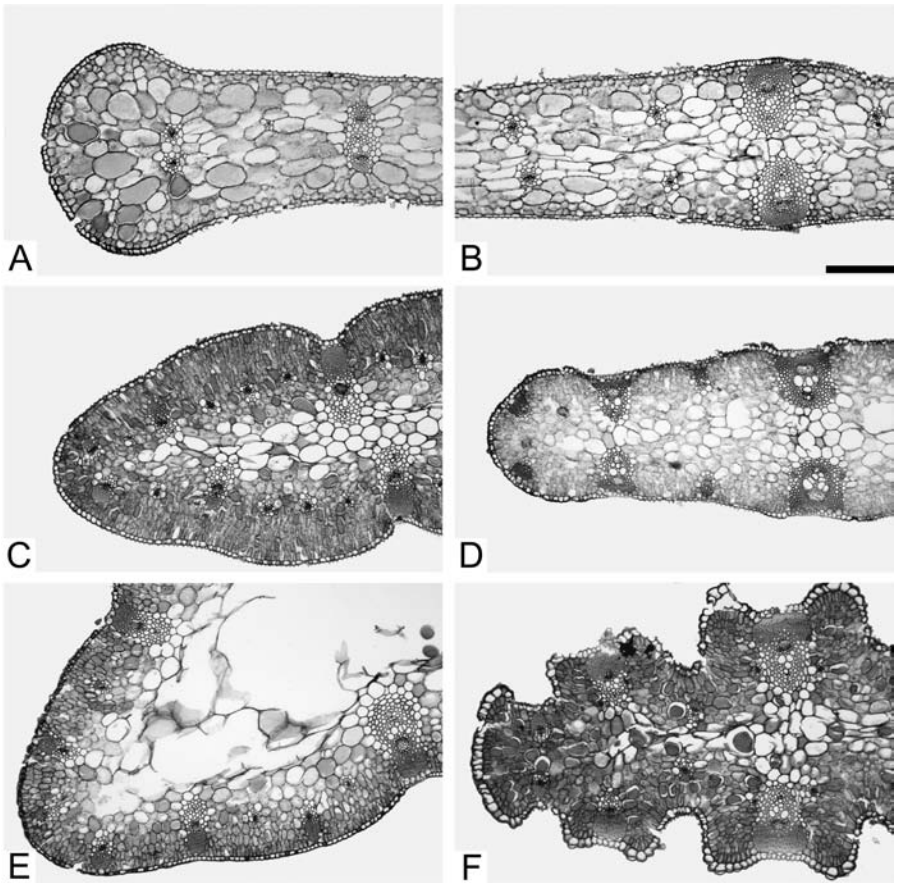

FIGURE 2.—Leaf anatomy of *Thereianthus* species: A, *T. minutus* leaf margin; B, *T. minutus* pseudomidrib; C, *T. racemosus* margin; D, *T. bulbiferus* margin; E, *T. bracteolatus* margin; F, *T. spicatus* margin. Scale bar: 200 µm.

are clearly paired with the phloem poles facing the leaf surface, and the leaves thus clearly lack marginal veins. This is evidently also the condition in centric-leaved *T. bracteolatus* and *T. juncifolius* but is less clear in *T. bulbiferus*, in which a smaller bundle is located marginally along only one edge of the leaf. In *T. racemosus* a very small tertiary bundle occurs in a similar position along one margin but is embedded within the chlorenchyma and not located at the parenchyma/chlorenchyma boundary as usual and is thus probably a minor branch. A simple leaf margin is also characteristic of *Pillansia* but not of *Micranthus* and *Watsonia*, both of which have a well-developed marginal bundle with sclerenchyma girder (Rudall 1995).

The presence of a marginal bundle is likely the plesiomorpic condition in Watsonieae (Rudall 1995). Optimizing leaf margin condition on the molecular phylogeny of the family in Goldblatt *et al.* (2006, 2008) indicates that it is most parsimonious to treat the simple leaf margin as independently derived in *Thereianthus* and *Pillansia*. Reversals to the simple leaf margins have occurred several times elsewhere in the Crocoideae (e.g. some species of *Geissorhiza* Ker Gawl., *Hesperantha* Ker Gawl. and *Lapeirousia*). The character is most parsimoniously treated as a homoplasious autapomorphy in each instance.

Bract anatomy (Figure 1G, H)

The floral bracts of *Thereianthus minutus* are inconspicuously veined, with the vascular bundles lacking sclerified phloem caps (Figure 1G), in contrast to the prominently veined bracts in *T. spicatus*, in which the vascular bundles have well-developed sclerenchyma phloem caps (Figure 1H). As the bracts dry and the mesophyll tissue collapses, the vascular bundles in *T. spicatus* become raised and very conspicuous whereas those in *T. minutus* remain inconspicuous.

Pollen aperture and sculpturing (Figure 3)

Pollen aperture condition and exine sculpturing of most species of *Thereianthus* was examined by Goldblatt *et al.* (1991). Their findings and those of the present study covering the remaining species, are presented here (Table 1). Pollen in all species is monosulcate and operculate, with a tectate-columellate, sparsely scabrate tectum. Operculum condition and exine sculpturing vary in the genus. Exine sculpturing in most species is perforate (diameter of the lumina 0.25–1.0 × the width of the intervening walls) (Figure 3A, B) but is reticulate (diameter of the lumina 2–3 × the width of the intervening walls) in *T. intermedius* (Figure 3C, D), *T. montanus* and *T. racemosus*, except on the operculum, where it is perforate. The reticulate exine in these species recalls the pollen of the sister genus *Micranthus*, the only other genus of Crocoideae with reticulate exine but this genus differs from *Thereianthus* and other Crocoideae in its zonasulcate aperture (Goldblatt *et al.* 1991).

The operculum in most species is 1-banded (Figure 3A, B) but is completely or incompletely 2-banded in *Thereianthus intermedius* (Figure 3C), *T. juncifolius*, *T. minutus*, *T. montanus* and *T. racemosus* (Table 1). A completely 2-banded (rarely 1-banded) operculum (the bands well separated by the apertural membrane) is characteristic of *T. intermedius*, *T. juncifolius* and *T.*

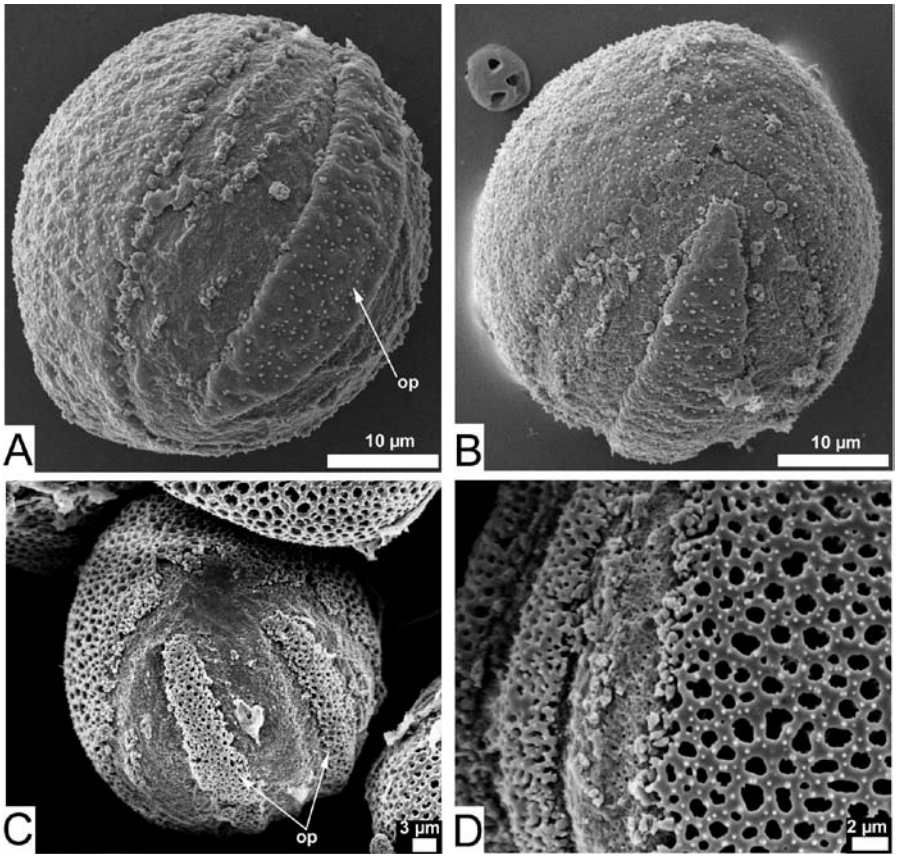

FIGURE 3.—Pollen morphology of *Thereianthus* species. A, B, *T. bracteolatus*: A, aperture with 1-banded operculum (arrowed); B, monosulcate grain with microperforate tectum. C, D, *T. intermedius*: C, aperture with 2-banded operculum (arrowed); D, reticulate exine.

TABLE 1.—Pollen operculum type and exine sculpturing in *Thereianthus*. Square brackets [ ] indicate closely associated operculum bands, and curved brackets () indicate the less common operculum character state

Species	Operculum	Exine sculpturing	Reference or voucher
Sect. *Brevibracteae*			
T. racemosus	2(1)-banded	Reticulate	Goldblatt *et al.* 1991
T. intermedius	2-banded	Reticulate	*Hanekom & Tilney s.n.* (NBG)
T. montanus	[2](1)-banded	Reticulate	*Oliver 12197* (NBG)
T. minutus	[2]-banded	Perforate	Goldblatt *et al.* 1991
T. juncifolius	2-banded	Perforate	Goldblatt *et al.* 1991
Sect. *Thereianthus*			
T. bulbiferus	1-banded	Perforate	*Manning 3212* (NBG)
T. bracteolatus	1-banded	Perforate	Goldblatt *et al.* 1991
T. spicatus	1-banded	Perforate	Goldblatt *et al.* 1991
T. ixioides	1-banded	Perforate	Goldblatt *et al.* 1991
T. elandsmontanus	1-banded	Perforate	*Manning 3213* (NBG)
T. longicollis	1-banded	Perforate	Goldblatt *et al.* 1991

racemosus but the operculum is incompletely 2-banded in *T. minutus* and *T. montanus*. In these two species the operculum is apparently 1-banded but lacks exine along the centre of the operculum in some or all grains, suggesting incomplete fusion of two separate bands (Goldblatt *et al.* 1991).

A 2-banded operculum and perforate exine are likely plesiomorphic conditions for Crocoideae, and more specifically for Watsonieae (Goldblatt *et al.* 1991), suggesting that the species in sect. *Brevibracteae* with reticulate exine as well as those species in sect. *Thereianthus* with 1-banded operculum are derived in these two respects.

MORPHOLOGY AND CLASSIFICATION

Thereianthus is, relative to its size, quite as diverse florally as other genera of Crocoideae (Goldblatt & Manning 2006). Although the reproductive biology remains poorly known, the species display a variety of floral syndromes, including adaptations to short-tongued, generalist, hopliine beetles, and to several variants of long-proboscid fly or butterfly pollination systems. Floral symmetry and perianth tube length are valuable characters for discriminating the species. Vegetative differences also provide critical diagnostic characters. Four types of leaf blade are evident: linear or lanceolate and plane with a single main or primary vein (pseudomidrib) evident but not raised when fresh and without evident secondary veins, the pseudomidrib becoming raised in herbarium material through collapse of the mesophyll tissue (*T. minutus*); linear and plane with more than one ± equally strong primary vein plus secondary veins (*T. bulbiferus, T. intermedius, T. minutus, T. montanus* and *T. racemosus*); linear-filiform and elliptic or terete in section without evident primary vein (pseudomidrib) (*T. bracteolatus* and *T. juncifolius*); and linear-corrugate with several equally strongly thickened and raised primary veins plus secondary veins (*T. elandsmontanus, T. ixioides, T. longicollis* and *T. spicatus*).

The striking variation in capsule shape and especially in seed form that is evident in the genus has remained undocumented until now. The remarkable seeds of *Thereianthus minutus*—fusiform with a long, thread-like chalazal extension—were first noted by Manning & Goldblatt (2004), who mistakenly interpreted the thread-like extension as an elongated funicle. From later examination of freshly opened, mature capsules, we are able to confirm that the thread-like structure represents a prolongation of the chalazal crest and not the funicle. Similar filiform chalazal extensions of variable length also characterize the seeds of *T. intermedius, T. juncifolius* and *T. racemosus* (seeds unknown for *T. montanus*). The thread-like chalazal extension is least developed in *T. racemosus*, in which it is shorter than the seed body and ± straight, but in *T. intermedius*, *T. minutus*, and *T. juncifolius* the extension is two to three times longer than the seed body and sharply bent back ± midway to form a hooked or crook-like extension. The latter two species have fusiform seeds and the chalazal extension extends significantly beyond the seed body before bending back. In these two species the chalazal extensions are largely accommodated in the elongated neck or beak of the flask-shaped capsules. The function of the thread-like extension is unknown.

Variation in pollen morphology in *Thereianthus* was first documented by Goldblatt *et al.* (1991), who discovered two distinct types of operculum and exine sculpturing among the species that they examined. The pollen operculum in *T. bracteolatus, T. ixioides, T. longicollis* and *T. spicatus* was clearly 1-banded but was completely or incompletely 2-banded in *T. juncifolius, T. minutus* and *T. racemosus*. The latter condition was interpreted as basic for the genus. Most species examined had the usual microperforate tectum. The sole exception, *T. racemosus*, had unusual reticulate exine sculpturing, which was also found to characterize all species of *Micranthus*. We have now examined pollen morphology in all *Thereianthus* species.

Thereianthus species fall into two distinct, evidently monophyletic groups on the basis of bract size and venation, seed shape, and pollen operculum condition: the *T. racemosus* group, treated here as sect. *Brevibracteae*, which is characterized by shorter bracts lacking prominent veins, evidently specialized seeds with a filiform chalazal extension (unknown in *T. montanus*), and pollen with a plesiomorphic, 2-banded operculum; and the *T. spicatus* group, treated here as sect. *Thereianthus*, which has larger, prominently veined bracts, seeds with an unspecialized chalazal crest, and apomorphic pollen with a 1-banded operculum. Leaf and bract anatomy, as well as filament orientation and length, further group the

members of sect. *Thereianthus* into two groups, treated here as series. The four species with strongly thickened and raised primary veins and shorter, erect or arcuate filaments comprise ser. *Thereianthus*, and the remaining two species with plane or smooth leaves and longer, declinate filaments comprise ser. *Bracteolatus*.

TAXONOMY

Thereianthus *G.J.Lewis* in Journal of South African Botany 7: 33 (1941). Lectotype: *Thereianthus spicatus* (L.) G.J.Lewis, designated by Goldblatt & Manning: 130 (2008).

Beilia Eckl.: 43 (1827), nom. nud.

Beilia Eckl. ex Kuntze: 305 (1898), nom. illegit. superfl. pro *Paulomagnusia* Kuntze (1891) [= *Micranthus* (Pers.) Eckl., nom. cons.]. Type: *Beilia spicata* (L.) Eckl. ex Kuntze (= *Thereianthus spicatus* (L.) G.J.Lewis).

Watsonia unranked *Beilia* Eckl. ex Baker 16: 158 (1877). Type: *Watsonia punctata* (Andrews) Ker Gawl. (= *Thereianthus bracteolatus* (Lam.) G.J.Lewis).

Watsonia subgen. *Beilia* Eckl. ex Baker: 177 (1892). Lectotype: *Watsonia punctata* (Andrews) Ker Gawl. (= *Thereianthus bracteolatus* (Lam.) G.J.Lewis), here designated.

Etymology: from the Greek, *thereios*, summer, *anthos*, flower.

Deciduous geophytes with globose corm, axillary in origin and rooting from below, tunics of coarsely netted fibres. *Cataphylls* 2. *Leaves* 3 or 4(6), all cauline and superposed, usually ± dry at flowering, lowermost subbasal, longest, inserted on stem above corm but below ground level, blade falcate or linear with margins not thickened, plane and either with definite main or primary vein (pseudomidrib) or with several equally prominent veins, or ± terete, glabrous or rarely scabridulous, usually dry at flowering, upper leaves progressively shorter, uppermost sometimes entirely sheathing. *Stem* usually unbranched, rarely with short branch from upper leaf axil, terete in section. *Inflorescence* a crowded or rarely lax spike, flowers spirally arranged or ± 2-ranked in bud, entire spike loosely spirally twisted at anthesis; bracts firm-textured, short, often overlapping, green below with apices dry and brown or entirely dry, smooth or prominently veined, inner 2-nerved and apically forked but splitting to base as capsule matures, mostly membranous (leathery in *T. juncifolius*). *Flowers* actinomorphic or zygomorphic, long-lived, closing at night, usually blue to purple, rarely white or pinkish, unmarked or lower three tepals with darker markings in lower $^1/_2$, sometimes all tepals with white markings, usually unscented, with nectar from septal nectaries; perianth tube short to elongate, funnel-shaped or cylindric; tepals subequal, ± spreading. *Stamens* unilateral and arcuate or declinate or central and symmetrically arranged; filaments inserted shortly below top of perianth tube, slender, free; anthers linear, dehiscing longitudinally, usually purple. *Ovary* subglobose; style filiform, branches slender and deeply divided, recurved. *Capsules* woody, ovoid to spindle- or flask-shaped, tardily dehiscent. *Seeds* angular-elongate with chalazal crest or narrowly ovoid-fusiform with thread-like or filiform chalazal extension, smooth or wrinkled, matte. *Basic chromosome number*: $x = 10$.

Eleven species, South Africa, restricted to the winter rainfall zone in the southwestern portion of western Cape, mostly in nutrient-poor, stony sandstone soils; two

Key to species

1a Bracts short, 3–8 mm long, uniformly leathery or soft-textured and without prominent veins (sect. *Brevibracteae*):
- 2a Leaf blades filiform-terete; spike lax, bracts distant (lower internodes 3–5 × longer than bracts); inner bracts as long as or slightly longer than outer and similar in texture, both uniformly green with dry, papery apices; tepals ovate-obovate; stamens central . . . . . 5. *T. juncifolius*
- 2b Leaf blades linear to falcate, plane; spike dense, bracts ± imbricate (lower internodes < twice as long as bracts); inner bracts shorter than outer and membranous-papery except along veins; tepals lanceolate; stamens unilateral-arcuate:
  - 3a Perianth tube very short, 1.0–1.5 mm long, included in bracts . . . . . 1. *T. racemosus*
  - 3b Perianth tube longer, 10–30 mm long, exserted from bracts:
    - 4a Bracts 3–5 mm long; perianth tube 10–13 mm long; capsules ovoid, 4–5 mm long; plants of the Cold Bokkeveld, mountains around Ceres, and Piketberg . . . . . 2. *T. intermedius*
    - 4b Bracts (5–)6–8 mm long; perianth tube 20–30 mm long; plants from Grootwinterhoek to Riviersonderend Mtns and Kogelberg:
      - 5a Leaves ± falcate, lowermost mostly 3–7 mm wide and usually much shorter than stem, with evident pseudomidrib but without evident secondary veins, the pseudomidrib raised when dry but secondary veins never raised; perianth magenta or deep pink, anthers pale yellow; filaments 3–4 mm long; capsules flask-shaped, 6–8 mm long . . . . . 4. *T. minutus*
      - 5b Leaves linear, lowermost 2.5–2.8 mm wide and mostly longer than stem, with main and secondary veins raised when dry; perianth and anthers purple; filaments 6–8 mm long; capsules unknown . . . . . 3. *T. montanus*

1b Bracts longer, (7–)8–15 mm long, with prominently raised, closely set veins (sect. *Thereianthus*):
- 6a Leaves leathery without strongly raised veins; perianth tube curved and flowers thus ± nodding; filaments declinate, 6–10 mm long (ser. *Bracteolatus*):
  - 7a Stem developing cluster of large cormels in axil of lowest leaf; leaves linear with evident veins; perianth tube 7–9 mm long; tepals pale to mid-blue with white markings at base, veins not mottled, lateral longitudinal veins with numerous branches in distal half; filaments 6–8 mm long . . . . . 6. *T. bulbiferus*
  - 7b Stem without cormels; leaves terete or elliptic in section, without evident veins; perianth tube (7–)8–10(–15) mm long; tepals purple to violet with prominent, darkly mottled veins, lateral longitudinal veins mostly without branches in distal half; filaments 8–10 mm long . . . . . 7. *T. bracteolatus*
- 6b Leaves striate or corrugate with strongly raised veins; perianth tube straight or slightly curved distally and flowers thus suberect; filaments central or arcuate, 3–5 mm long (ser. *Thereianthus*):
  - 8a Perianth tube 25–40 mm long, > twice as long as tepals . . . . . 11. *T. longicollis*
  - 8b Perianth tube 7–25 mm long, < twice as long as tepals:
    - 9a Perianth tube filiform, tightly clasping style for most of length and then abruptly dilated at mouth; filaments central, symmetrical and completely exposed, blocking mouth of perianth tube . . . . . 9. *T. ixioides*

9b Perianth tube narrowly funnel-shaped or ± cylindrical, not tightly clasping style; filaments arcuate, included within upper part of tube and not blocking mouth:
10a Flowers usually blue, rarely white or pink, lower three tepals with white markings near base outlined distally with dark blue chevron; tepals lanceolate, 3–5 mm wide . . . . . 8. *T. spicatus*
10b Flowers pale flesh-pink with purple tube, lower three tepals marked with purple in basal half; tepals linear, 1.5–3.0 mm wide . . . . . 10. *T. elandsmontanus*

species, *Thereianthus juncifolius* and *T. minutus,* grow in seepages and along streams.

Sect. **Brevibracteae** *Goldblatt & J.C.Manning*, sect. nov.

Plantae foliis filiformibus teretibusque vel lineari-falcatis planisque, cum vel sine nervo principali prominenti sed nunquam fortiter nervatis marginibus non incrassatisque; bracteis brevibus, 3–8 mm longis uniformiter coriaceis vel modice mollibus sine costis prominentibus; seminibus (ubi cognitis) ellipsoideo-fusiformibus cum appendice chalazae gracili vel filiformi, rubro-brunneis, testa longitudinaliter rugosa vel obscure scalariformi; grano pollinis operculo ± 2-vittato, exinio perforato vel reticulato.

Type species: *T. racemosus* (Klatt) G.J.Lewis.

Leaves filiform and terete, or linear to falcate and plane, with or without prominent main vein but never strongly ribbed; bracts short, 3–8 mm long, uniformly leathery or moderately soft-textured, without prominent veins. *Pollen* operculum ± 2-banded, exine perforate or reticulate. *Seeds* (where known) ellipsoid-fusiform with filiform or thread-like chalazal extension, reddish brown, testa sculpturing longitudinally rugose or obscurely scalariform.

1. **Thereianthus racemosus** *(Klatt) G.J.Lewis* in Journal of South African Botany 7: 36 (1941). *Watsonia racemosa* Klatt 15: 354 (1882). Type: South Africa, [Western Cape], 'in montibus ad Vier en Twintig Rivieren', Dec. without year, *Zeyher 1609* (B, holo.; BOL!, GRA, K (2 sheets)!, PRE, SAM (3 sheets)!, iso.).

Plants 130–250 mm high. *Corm* globose, ± 10 mm diam.; tunics of moderately fine-textured to coarsely netted fibres, sometimes forming short neck. *Cataphylls* dry and papery, reddish brown. *Stem* erect or flexed slightly outward above sheath of second leaf, unbranched or very rarely with short branch from upper leaf axil, 0.8–1.0 mm diam. below spike. *Leaves* (3)4(5), lowermost inserted below ground, blade reaching base of spike or not, drying from tip at flowering, linear or falcate, 60–130(–190) × 1–3(–4) mm, thick-textured, plane with main vein not thickened or raised when fresh and usually without evident secondary veins, rarely with 1 secondary vein visible on each side, upper 3 leaves cauline with lower 2 inserted on lower $^1/_3$ of stem, sheathing for $^1/_2$ to $^2/_3$ length with blades 20–40 mm long, uppermost leaf entirely sheathing, well separated from spike, all sheaths shortly imbricate or uppermost a little distant. *Spike* erect, moderately densely 5–25-flowered; bracts shortly imbricate, outer 3–5 mm long, up to 1 internode long, acute, green below or entirely brown and leathery with narrow membranous margins and papery tip, without evident veining, inner ± as long or slightly longer, notched apically, ± membranous with narrow brown zone along veins. *Flowers* suberect, pale blue, lower three tepals white at base with purple median chevron in lower $^1/_4$, strongly honey-scented; perianth sub-actinomorphic, funnel-shaped; tube straight, 1.0–1.5 mm long, narrowly funnel-shaped, included in bract; tepals elliptical-oblanceolate, subequal, spreading and slightly cupped, 7–9 × 3–4 mm. *Stamens* unilateral but laterals slightly spreading; filaments arcuate, 3–4 mm long, exserted 1.5–2.5 mm from tube; anthers 4–5 mm long, dark blue; pollen pale blue. *Ovary* ovoid, ± 2 mm long; style arching over stamens, dividing between base and middle of anthers, branches 2.0–2.5 mm long, divided for ± $^1/_2$ their length. *Capsules* ovoid, 4–5 × 2.5–3.0 mm. *Seeds* ovoid, ± 1 mm long, with ± straight, thread-like chalazal extension ± 0.5 mm long, reddish brown. *Flowering time*: Dec. Figure 4.

Distribution and ecology: *Thereianthus racemosus* appears to be restricted to the Voorberg (also known as the Twenty Four Rivers Mtns) above Porterville (Figure 5), where it occurs on seasonally moist or marshy, sandy flats in restioid communities. Most collections are from the Suurvlakte in the Grootwinterhoek Wilderness Area. It is an obligate pyrophyte, flowering only in the summer following a burn.

The short-tubed, pale blue flowers are strongly honey-scented and are evidently adapted to a variety of short-tongued pollinators, including various Hymenoptera, Lepidoptera, and Coleoptera. Goldblatt *et al*. (1998) reported pollination of *T. racemosus* by the hopliine beetle, *Khoina bilateralis*, in the Grootwinterhoek Wilderness area.

Diagnosis and relationships: the short floral bracts, 3–5 mm long, and the very short perianth tube, 1.0–1.5 mm long, and well included within the bracts, are diagnostic for the species. Uniquely for the genus, the flowers are fragrant and strongly honey-scented. The narrow, leathery leaves with ± distinct main vein but usually without evident secondary veins, the very short capsules, small seeds, 1.0–1.5 mm long, and reticulate pollen exine suggest that the species is most closely allied to *Thereianthus intermedius* from the Cold Bokkeveld. That species has darker blue flowers with a much longer perianth tube, 10–13 mm long, and seeds with the chalazal extension longer than the seed body.

History: the species was first collected by botanical collector Carl Ludwig Zeyher, who was active in the Western Cape in the first half of the nineteenth century. Although the type collection is not dated, Zeyher appears to have collected on the Twenty Four Rivers Mtns only once, in 1831, when he made a rich haul of specimens from the mountains around Tulbagh in the company of his sometime partner Christian Frederick Ecklon (Glen & Germishuizen 2010), and the species was probably discovered then. It has since been collected just a handful of times on the same mountains, always following veld fires.

FIGURE 4.—*Thereianthus racemosus*. A–D, *Goldblatt 10454*: A, whole plant; B, flower, front view; C, flower, side view; D, details of stamens and stigma. E, F, *Manning 3289*: E, capsule; F, seed. Scale bar: A–C, 10 mm; D, 3 mm; E, 2 mm; F, 0.5 mm. Artist: John Manning.

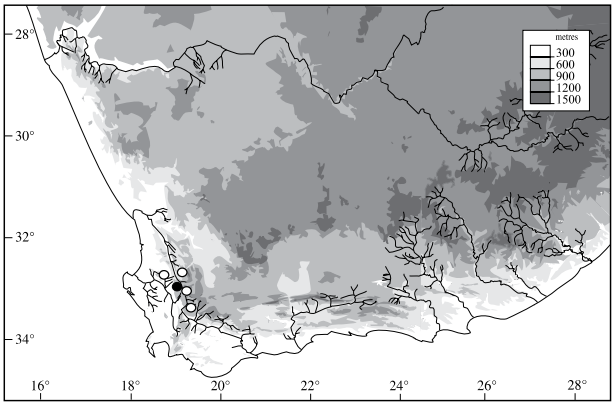

FIGURE 5.—Known distribution of *Thereianthus racemosus*, ●; *T. intermedius*, ○.

Additional specimens examined

WESTERN CAPE.—3319 (Worcester): Twenty Four Rivers Mtns above Porterville, (–AA), 16 Dec. 1949, *Esterhuysen 16620* (BOL); Groot Winterhoek Wilderness Area, (–AA), 14 Dec. 1995, *Steiner 3061* (NBG); near Groot Winterhoek Forest Station, (–AA), 27 Dec. 1995, *Goldblatt 10454* (MO, NBG); Grootwinterhoek Wilderness Area, Suurvlakte, (–AA), 8 Jan. 2010 (fr.), *Manning 3289* (NBG).

2. **Thereianthus intermedius** *J.C.Manning & Goldblatt,* nom. et stat. nov., *T. lapeyrousioides* var. *elatior* G.J.Lewis in Journal of South African Botany 7: 38 (1941). Type: South Africa, [Western Cape], Ceres Hills, Jan. 1892, *L. Guthrie 2208* (BOL, holo.!).

Plants 200–350 mm high. *Corm* globose, ± 10 mm diam.; tunics of fine-textured, netted fibres accumulating with age and forming neck around base of stem. *Cataphylls* dry and papery, reddish brown. *Stem* erect, flexed slightly outward above sheath of second leaf, unbranched, 1.0–1.5 mm diam. below spike. *Leaves* (3)4, lowermost inserted below ground, blade reaching base of spike or not, drying from tip at flowering, linear, 70–150 × 2–3 mm, thick-textured, with main vein ± evident but not thickened or raised when fresh, plus a pair of secondary veins, upper (2)3 leaves cauline with lowermost (1)2 inserted on lower $^1/_3$ of stem, sheathing for $^1/_2$ to $^2/_3$ length with blades 30–60 mm long, uppermost leaf entirely sheathing or with short blade up to 20 mm long, well separated from spike, all sheaths shortly imbricate or uppermost a little distant. *Spike* erect, moderately densely 12–40-flowered; bracts not or scarcely imbricate, outer 3–5 mm long, up to 1 internode long, obtuse, brown and leathery with narrow membranous margins, without evident veining, inner ± as long or slightly longer, notched apically but sometimes splitting to base after fertilization by enlarging capsule, ± membranous with narrow brown zone along veins. *Flowers* suberect, violet (rarely pale blue), lower three tepals whitish at base with purple or dark blue median chevron in lower $^1/_4$; perianth subactinomorphic; tube straight or slightly arching in upper ± 3 mm, 10–13 mm long, cylindrical and widening slightly in upper ± 3 mm; tepals narrowly oblanceolate, subequal, spreading and slightly cupped, 10–11 × 3.0–3.5 mm. *Stamens* unilateral; filaments erect, ± 7 mm long, exserted ± 4 mm from tube; anthers purple, 4–5 mm long; pollen violet. *Ovary* ovoid, 2.0–2.5 mm long; style arching over stamens, dividing below base of anthers, branches ± 2.5 mm long, divided for ± $^1/_2$ their length. *Capsules* ovoid, 4–5 × 3–4 mm. *Seeds* ovoid, ± 1.5 × 1.0 mm, with thread-like chalazal extension up to 3 mm long abruptly reflexed from near middle, reddish brown, testa striate-rugulose. *Flowering time*: Dec. Figure 6A–F.

Distribution and biology: originally recorded from two unlocalized collections made near Ceres (Lewis 1941), *Thereianthus intermedius* has now also been collected in the Cold Bokkeveld at the headwaters of the

FIGURE 6.—A–F: *Thereianthus intermedius*, *Hanekom & Tilney s.n.* A, whole plant; B, half flower; C, outer bract; D, inner bract; E, capsule; F, seeds. G–J: *T. montanus*, *Oliver 12197*. G, whole plant; H, flower, front view; I, half flower; J, outer (left) and inner (right) bracts. Scale bars: A, B, G–J, 10 mm; C–E, 2 mm; F, 0.5 mm. Artist: John Manning.

Olifants River and at high elevations on Zebrakop in the Piketberg (Figure 5). In the north it has been collected from the farms Elandskloof and Kunje along the eastern foot of the Cold Bokkeveld Mtns, with another collection from Visgat on the western edge of the Skurweberg, and in the south from Castle Rocks at the western edge of the Hex River Mtns above Ceres. It is restricted to seasonally waterlogged or marshy, sandy flats dominated by restioids, between ± 500 and 1 000 m, and flowers only after fire.

We assume that the moderately long-tubed flowers are pollinated by various long-tongued insects, including anthophorine bees (Apidae: Anthophorinae) and butterflies.

Diagnosis and relationships: *Thereianthus intermedius* is recognized by its linear leaves, 2–3 mm wide, elongate spike with short floral bracts, 3–5 mm long, and violet (pale blue on Piketberg) flowers with moderately long floral tubes, 10–13 mm long, and slightly longer than the tepals. The leaves have an additional pair of secondary veins, one running on each side of the central vein close to the leaf margin, and the spike is moderately dense, with the bracts shorter than or scarcely as long as the internodes. The small, ovoid capsules, 4–5 mm long, contain distinctive seeds, with an ovoid seed body and long, thread-like chalazal extension ± twice as long as the seed body and sharply bent backwards along the length of the seed.

Thereianthus intermedius is most likely to be confused with *T. minutus*, which has similar plane leaves (but with the pseudomidrib much less distinct), short bracts, and long-tubed flowers. It differs most obviously from *T. minutus* in its purple or blue (vs magenta or deep pink) flowers with a shorter floral tube (10–13 mm vs 20–30 mm), shorter bracts (3–5 mm vs 6–8 mm) and in its smaller capsules (ovoid and 4–5 mm long vs flask-shaped and 6–8 mm long) capsules containing ovoid (vs fusiform) seeds. The distribution of the two species is complementary, with *T. intermedius* ranging from the Cold Bokkeveld to the Skurweberg, the western Hex River Mtns and Piketberg (Figure 5), and *T. minutus* distributed from the Grootwinterhoek Mtns above Tulbagh through the Franschhoek and Du Toitskloof Mtns to the Kogelberg and western end of the Riviersonderend Mtns (Figure 7).

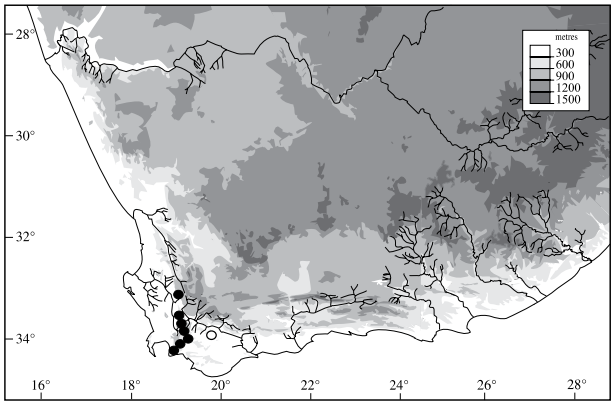

FIGURE 7.—Known distribution of *Thereianthus minutus*, ●; *T. montanus*, ○.

History: the species seems to have been first collected by botanist Louise Guthrie in January 1892, and has been recorded only sporadically since then, most recently by local landowner Louis Hanekom, who noticed it flowering for the first time on his Farm Kunje in Dec. 2009 after the extensive wildfire that swept the area in the summer of 2008/09. He passed the plants on to Jeanetta Tilney, who has been documenting the species on her property on Middelberg Pass for some years and who in turn brought it to our attention.

Thereianthus intermedius was first described as var. *elatior* of *T. lapeyrousioides* [now *T. minutus* (Klatt) G.J.Lewis (Goldblatt 1989)], distinguished from the typical variety by its taller stature (240–460 mm high), slightly longer, narrower leaves, and longer, more floriferous (12–40-flowered) spike with shorter bracts ± 5 mm long (Lewis 1941). Subsequently, Manning & Goldblatt (2004) argued that collections of *T. minutus* from Bainskloof displayed the full range of variation in these features and concluded that var. *elatior* could not be recognized at any taxonomic level. The recent collection of fresh material of the plants from the Farm Kunje shows that we were wrong and that other, more significant differences not identified by Lewis (1941) exist between the two taxa, justifying their recognition as distinct species. These include perianth colour, floral tube length, shape and size of the capsule, seed shape and pollen exine sculpturing.

Etymology: *Thereianthus intermedius* approaches *T. minutus* in its seeds with filiform chalazal extension but resembles *T. racemosus* in its short capsules and reticulate pollen sculpturing, and we thus propose the name *T. intermedius* in recognition of its somewhat intermediate character.

Additional specimens seen

WESTERN CAPE.—3218 (Clanwilliam): Piketberg, SW slopes of Zebrakop, (DA–DB), 4 Jan. 1995, *Goldblatt & Manning 10168* (MO). 3219 (Wuppertal): Elandskloof, marshy places, 3000′ [915 m], (–CA), 18 Dec. 1948, *Levyns 9349* (BOL). 3319 (Worcester): Visgat, upper Olifants River Valley, (–AA), 28 Dec. 1946, *Esterhuysen 13435* (BOL, NBG, PRE); Ceres, 1700′ [518 m], (–AD), Jan. 1903, *Bolus 8342* (BOL, PRE); Ceres, (–AD), Jan. 1929, *Thode A2287* (NBG, PRE); Ceres, (–AD), Jan. 1932, *Leslie s.n. NBG46/32* (BOL); Ceres, Castle Rocks, *vlakte* [flats] on NE slopes, abundant after fire, 3800′ [1 158 m], (–AD), 14 Jan. 1960, *Esterhuysen 28430* (BOL, MO).

3. **Thereianthus montanus** *J.C.Manning & Goldblatt* in Bothalia 34: 103 (2004). Type: South Africa, Western Cape, Riviersonderend, Pilaarkop, ridge WNW of peak, 31 Jan. 2004, *E.G.H. Oliver 12197* (NBG, holo.!; MO, iso.!).

Plants 200–350 mm high. *Corm* globose, 7–10 mm diam.; tunics of fine-textured, netted fibres accumulating with age and forming neck around base of stem. *Stem* erect, flexed outward above sheath of second leaf, unbranched, 1.0–1.5 mm diam. below spike. *Cataphylls* dry and papery, reddish brown. *Leaves* 3 or 4, lowermost inserted below ground, blade reaching or exceeding spike, linear, 150–300 × 2.5–2.8 mm, thick-textured, with main vein evident but not thickened or raised when fresh, plus 1 or 2 evident secondary veins on each side, upper 2 or 3 leaves cauline with lower 1 or 2 inserted on lower $^1/_3$ of stem, sheathing for $^1/_2$ to $^2/_3$ length with short

blades 15–25 mm long, uppermost leaf well separated from spike, short and entirely sheathing, all sheaths distant. *Spike* erect, compact, densely 7–10-flowered; bracts imbricate, outer 6–8 mm long, obtuse to truncate, green and leathery below, dry and brown in upper $^1/_2$, ± 2 internodes long, inner ± 1.5 mm shorter than outer, notched apically, brown and papery with narrow darker zone along veins. *Flowers* suberect, purple, lower three or all tepals each with spear-shaped, purple median streak near base, throat and lower part of tube white; perianth subactinomorphic, salver-shaped; tube straight or slightly arching in upper ± 5 mm, 22–27 × 1.2–1.5 mm, cylindrical and widening slightly in upper ± 5 mm; tepals spreading and slightly cupped, narrowly elliptical to lanceolate, subequal, 9–15 × 3.5–5.0 mm. *Stamens* unilateral; filaments erect, 6–8 mm long, exserted 3–4 mm from tube; anthers 4–5 mm long, purple; pollen violet. *Ovary* ovoid, 2.0–2.5 mm long; style arching over stamens, dividing between base and middle of anthers, branches ± 2.5 mm long, divided for ± $^1/_2$ their length. *Capsules and seeds* unknown. *Flowering time*: late Jan.–Feb. Figure 6G–J.

Distribution and biology: Thereianthus montanus is known from a single population on steep, south-facing slopes of Pilaarkop in the Riviersonderend Mtns (Figure 7). Plants are scattered in moist, loamy soil in short, grassy fynbos at an altitude of ± 1 500 m.

The long-tubed, violet flowers appear to be adapted for pollination by long-proboscid flies or butterflies (Manning & Goldblatt 2004), and accumulate nectar only in the lower few millimetres, which is consistent with pollination by long-proboscid insects with mouthparts 20–25 mm long.

Diagnosis and relationships: *Thereianthus montanus* is distinguished by its linear leaves without thickened or raised main vein when fresh, although the mesophyll tissue collapses on drying to leave the central and secondary veins apparently raised in herbarium specimens, and compact spikes of salver-shaped, purple flowers with slender perianth tube 22–27 mm long and purple anthers. It is most likely to be confused with long-tubed *T. minutus* with similarly long-tubed flowers and which has been recorded from the western Riviersonderend Mtns, but this species is generally shorter, mostly 100–200 mm tall, with a broader, mostly falcate lower leaf, (1.5–)3.0–7.0 mm wide and rarely reaching the base of the spike, and with a prominent pseudomidrib but inconspicuous secondary veins. On drying, the main vein in the leaves of *T. minutus* becomes raised through collapse of the surrounding blade tissue but the secondary veins are never pronounced. The flowers in *T. minutus* are a distinctive magenta colour, with yellow anthers. Unfortunately fruits and seeds are not known in *T. montanus* and so cannot be compared with the distinctive flask-shaped capsules and fusiform seeds with thread-like chalazal extension of *T. minutus*. The two species differ in pollen exine sculpturing. *T. minutus* has an unspecialized perforate pollen exine, unlike the unusual reticulate pollen exine of *T. montanus*, which suggests that its closest allies are actually *T. racemosus* from Grootwinterhoek and *T. intermedius* from the Cold Bokkeveld, being the only other two species in the genus with reticulate exine.

History: a single flowering stem of the species was first collected by botanists Ted and Inge Oliver in February 1999, and the type material was collected by Ted Oliver from the same locality five years later, in January 2004.

Additional specimen examined

WESTERN CAPE.—3419 (Caledon): Riviersondered Mtns, Pilaarkop, ridge WNW of peak, ± 1 500 m, (–BB), 26 Feb. 1999, *E.G.H. & I.M. Oliver 11228* (NBG).

4. **Thereianthus minutus** *(Klatt) G.J.Lewis* in Journal of South African Botany 7: 43 (1941). *Watsonia minuta* Klatt: 353 (1882). Type: South Africa, [Western Cape], Tulbagh Waterfall, *Ecklon & Zeyher Irid. 189* (B, lecto.!, designated by Goldblatt 19: 143 (1989); MO!, S!, SAM!, isolecto.) [Syntype: South Africa, [Western Cape], Dutoitskloofberge am Wasserfall, *Drège 1551* (B 'Herb. Lübeck', believed destroyed)].

Watsonia lapeyrousioides Baker: 178 (1892). *Thereianthus lapeyrousioides* (Baker) G.J.Lewis 7: 38 (1941). Type: South Africa, [Western Cape], clivis montium inter Villiersdorp & French Hoek [Franschhoek], Nov. 1879, *Bolus 5251* (BOL, lecto.!, here designated; K, isolecto.!) [Syntype: South Africa, [Western Cape], Du Toitskloof, without date ['1840' on specimen], *Drège s.n.* (K[*K320511*]!, ?SAM[*SAM21067*]!].

Plants 100–200(–300) mm high. *Corm* globose, 7–10 mm diam.; tunics of fine-textured, netted fibres, sometimes accumulating with age and forming short neck around base of stem. *Stem* usually inclined but flexed outward above sheath of second leaf and then erect, unbranched, 0.8–1.5 mm diam. below spike. *Cataphylls* dry and papery, reddish brown. *Leaves* 3 or 4(–6), lowermost inserted below ground, blade mostly much shorter than spike, rarely exceeding it, mostly falcate, rarely linear-arcuate, (30–)40–100(–350) × (1.5–)3–7 mm, thick-textured, with main vein evident but not raised when fresh (becoming raised when dry), plus 1 or 2 evident secondary veins on each side, upper leaves cauline with lower 1 or 2 inserted on lower $^1/_3$ of stem, sheathing for $^1/_2$ to $^2/_3$ length with blades 20–40 mm long, uppermost leaf well separated from spike, short and entirely sheathing, all sheaths shortly imbricate or distant. *Spike* erect, compact, moderately densely (3–)5–10(–20)-flowered; bracts shortly imbricate, outer (5–)6–8 mm long, obtuse to truncate, green and leathery below, dry and brown in upper $^1/_2$, ± 1.5 internodes long, inner ± 1.0–1.5 mm shorter than outer, notched apically, brown and papery with narrow darker zone along veins. *Flowers* suberect, dark pink to magenta, lower three tepals usually with darker median mark near base, throat white; perianth subactinomorphic, salver-shaped; tube straight, 20–30 × 1.2–1.5 mm, widening gradually and evenly from base; tepals spreading and slightly cupped, elliptical to oblanceolate, subequal, 7–10 × 2–4 mm. *Stamens* unilateral; filaments erect, 3–4 mm long, exserted ± 2 mm from top of tube; anthers 3–4 mm long, pale yellow; pollen cream-coloured. *Ovary* ovoid, 2.0–2.5 mm long; style arching over stamens, dividing just below or just above base of anthers, branches ± 4 mm long, divided for ± $^1/_2$ their length. *Capsules* flask-shaped, 6–8 mm long. *Seeds* fusiform, 1.5–2.0 mm long, with chalazal extension up to 4 mm long, thus ± twice as long as seed body, sharply bent back ± midway and hooked or crook-like, sometimes twisting around adjacent seeds, reddish brown,

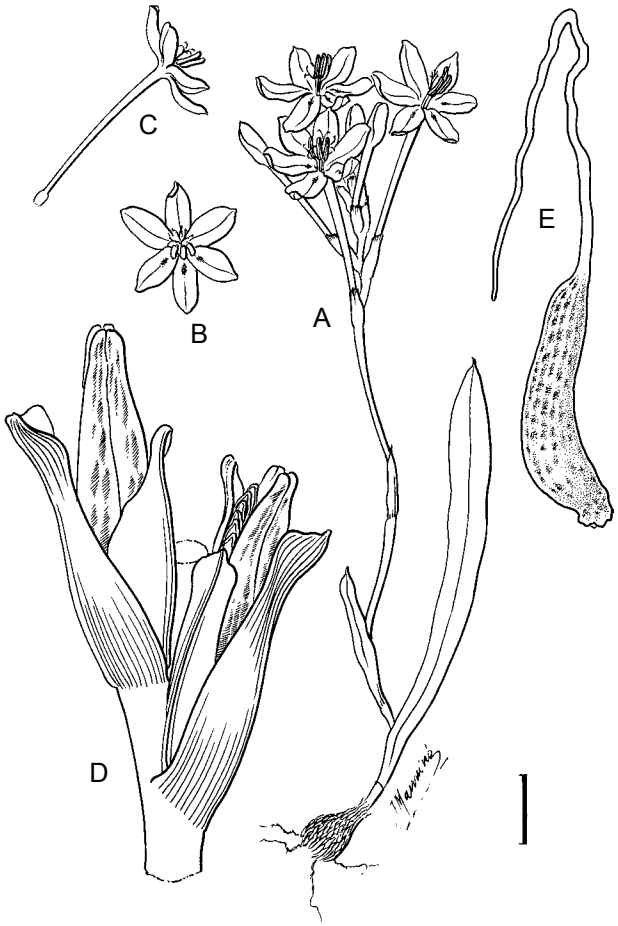

FIGURE 8.—*Thereianthus minutus*. A–C, *Goldblatt & Manning 9505*: A, whole plant; B, flower, front view; C, flower, side view. D, E, *Manning 3327*: D, capsules; E, seed. Scale bar: A–C, 10 mm; D, 2 mm; E, 0.5 mm. Artist: John Manning.

longitudinally rugulose. *Flowering time*: Dec.–Jan., rarely as early as late Oct. Figure 8.

Distribution and ecology: endemic to the mountains in the extreme southwestern part of Western Cape, from above Porterville southwards to the Kogelberg and western Riviersonderend Mtns (Figure 7). *Thereianthus minutus* is restricted to moist habitats such as rock ledges, damp cliffs and streamsides, growing in flushes, peaty seepages and mossy turf. Fires are necessary for flowering to occur in plants on deeper, more heavily vegetated soils but in exposed habitats plants flower regularly without burning.

The long-tubed, magenta flowers are consistent with pollination by long-proboscid flies and we have observed visits to the species by *Philoliche rostrata* (Tabanidae) above Tulbagh Waterfall in December 2010.

Diagnosis and relationships: *Thereianthus minutus* is distinguished by its mostly falcate, relatively broad lower leaf blade, mostly 3–7 mm wide, with a pronounced main vein, and dark pink to magenta flowers with perianth tube 20–30 mm long. On drying and in herbarium material the pseudomidrib becomes raised through collapse of the surrounding mesophyll tissue but the secondary veins remain inconspicuous. The short bracts, 5–8 mm long, without prominent veins are typical of sect. *Brevibracteae* but the pale yellow anthers are unusual in the genus and found elsewhere only in *T. juncifolius* (sect. *Brevibracteae*) and *T. bracteolatus* (sect. *Thereianthus*). It is most likely to be confused with *T. intermedius* and *T. montanus*, both of which have similar long-tubed flowers but of the more typical blue to purple colour and with purple stamens. The three species have complementary ranges: *T. intermedius* from the Piketberg, Cold Bokkeveld and Skurweberg has a perianth tube 10–13 mm long, shorter bracts 3–5 mm long, and smaller, ovoid capsules 4–5 mm long; *T. montanus* from the eastern Riviersonderend Mtns has similar bract and perianth tube dimensions but longer filaments, 6–8 mm long and exserted 3–4 mm from the tube, and mostly narrower leaves, 2.5–2.8 mm wide, with the main and also secondary veins becoming raised on drying and in herbarium material. *T. montanus* is generally a taller species, 200–300 mm tall, with the lower leaf longer than the spike. In addition, the perianth tube in *T. montanus* is virtually cylindrical throughout, widening only in the upper 5 mm, unlike the tube in *T. minutus*, which is slightly narrower below but widening gradually and evenly towards the top.

The fruit and seeds of *Thereianthus montanus* are unfortunately not known but the flask-shaped capsules of *T. minutus* are distinctive, as are the fusiform seeds with long, thread-like chalazal extension ± twice as long as the seed body. The placenta is restricted to the lower portion of the capsule and the tapered neck or beak accommodates the chalazal extensions of the seeds.

History: *Thereianthus minutus* was first collected by the botanical collectors Christian Frederick Ecklon and Carl Ludwig Zeyher at Tulbagh Waterfall, possibly in 1831 when they visited this site (Glen & Germishuizen 2010), and almost contemporaneously by the naturalist and traveller Carl Drège, who found it in the Du Toitskloof Mtns sometime between 1826 and 1834. The date 1840 marked on the type collection at Kew is not the date of collection as Drège returned to Europe in 1834 (Glen & Germishuizen 2010), and is probably the date that the specimen was offered for sale and acquired by the herbarium. These two collections formed the basis of both *Watsonia minuta* Klatt (1882) and *W. lapeyrousioides* Baker (1892). At the time of her revision of *Thereianthus*, Lewis (1941) had not been able to identify Klatt's *W. minuta* and although she transferred the name to *Thereianthus* she treated the taxon as a doubtful species, possibly near *T. racemosus*, based on Klatt's curious and quite mistaken description of the perianth tube as a mere 4 mm long. She accordingly recognized *T. lapeyrousioides* as a separate species. Ironically, and quite inexplicably, she overlooked the significance of the *Ecklon & Zeyher 189* syntype of *W. minuta* at SAM, which she cited under *T. lapeyrousioides* and which would have established the identity of Klatt's species. It was left to Goldblatt (1989) to recognize that this was the earliest name for the species.

The Ecklon & Zeyher collections were distributed under the unpublished name *Beilia triticea* Eckl. (now applied to *Thereianthus bracteolatus*), while the *Drège* material was misidentified as *Anomatheca juncea* (Ker Gawl.) Ker Gawl. (= *Freesia verrucosa*). Plants from the Cold Bokkeveld, treated by Lewis (1941) as *T. lapey-*

rousioides var. *elatior* G.J.Lewis, are recognized here as a distinct species, *T. intermedius*.

Additional specimens examined

WESTERN CAPE.—3318 (Cape Town): Jonkershoek Mtns, (–DD), 1826, *Marloth s.n.* (PRE); Jan. 1888, *Marloth s.n.* (NBG); Jonkershoek State Forest, Stellenboschberg, (–DD), 8 Dec. 1975, *Haynes 1180* (NBG); Stellenbosch, Swartboskloof, (–DD), 25 Oct. 1960, *Van der Merwe 23-94* (NBG, PRE). 3319 (Worcester): Winterhoeksberg, (–AA), Nov., *Ecklon & Zeyher Irid. 188* (72.11) (MO); Tulbagh, Watervalsberge, east of Suurvlakte Falls, (–AC), 29 Dec. 2000, *Hansford 22* (NBG); lower Wellington Sneeukop, (–CA), 23 Dec. 1945, *Esterhuysen 1254* (BOL); Bain's Kloof [Bainskloof], (–CA), 12 Nov. 1896, *Schlechter 9126* (BOL, MO, PRE); 28 Nov. 1926, *Grant 2648* (BOL, MO); 27 Nov. 1939, *Bond 5* (NBG); 17 Jan. 1945, *Compton 16922* (NBG); 9 Nov. 1946, *Compton 18682* (NBG); 6 Nov. 1948, *Acocks 15238* PRE); Nov. 1949, *Stokoe s.n. SAM60115* (SAM); Dec. 1957, *Loubser 866* (NBG); 24 Nov. 1979, *Goldblatt 5221* (PRE); 27 Nov. 1990, *Steiner 2265* (MO, NBG); Baviaanskloof, above pools in middle of valley, (–CA), 12 Jan. 1993, *Goldblatt & Manning 9505* (MO); (–CA), 15 Jan. 2011 [fruiting], *Manning 3327* (NBG); Wolwekloof Forest Reserve, (–CA), 20 Oct. 1946, *Barker 4249* (NBG); Limietberg, (–CA), 28 Nov. 1982, *Esterhuysen 35830* (MO, PRE), *Jackson s.n.* (NBG); Slanghoek Mtns, Witte River Valley, (–CA), Nov. 1922, *Thorne SAM46563* (SAM), 21 Nov. 1943, *Wasserfall 614* (NBG), 28 Dec. 1975, *Esterhuysen s.n.* (MO); Du Toit's Kloof, (–CA), Jan. 1880, *Bolus 5497* (BOL); 10 Dec. 1945, *Esterhuysen 12369* (BOL); Dec. 1949, *Stokoe s.n.* (NBG, *SAM60114*); Rawsonville, veld opposite Farm Gevonden, (–CA), 3 Nov. 1962, *Walters 912* (NBG); Du Toitskloof Mtns, Elandsberg catchment, (–CC), 29 Dec. 2000, *Low 6770* (NBG); Slanghoek Valley, The Cossacks, (–CC), 16 Dec. 1997, *Oliver 11004* (NBG); Paarl, Haalhoek Spitzkop, (–CC), 2 Jan. 1947, *Esterhuysen 13528* (BOL, NBG), 19 Dec. 1981 *Esterhuysen 35731* (BOL, MO); Wemmershoek area, Klein Drakenstein Mtns above Zachariashoek, (–CC), 1 Jan. 1983, *Oliver 7928* (NBG, PRE); French Hoek [Franschhoek], (–CC), 23 Dec. 1895, *Bolus 4010* (MO, NBG, PRE), Jan. 1949, *Stokoe s.n. SAM60178* (SAM); Franschhoek Pass, Adolph's Kop, (–CC), 15 Dec. 1944, *Esterhuysen 11047* (BOL, PRE); western Riviersonderend Mtns, 26.4 km west of Olifantsberg, (–CD), 18 Dec. 2007, *Helme 5172* (NBG). 3418 (Simonstown): Jonkershoek Valley, near top of Kurktrekker, (–BB), 1 Dec. 1989, *Oliver 9352* (NBG); Kogelberg Forest Reserve, near Rooiels, (–BD), 11 Nov. 1952, *Rycroft 1354* (NBG). 3419 (Caledon): Villiersdorp, (–AB), 23 Nov. 1930, *Nel s.n.* (NBG).

5. **Thereianthus juncifolius** *(Baker) G.J.Lewis* in Journal of South African Botany 7: 37 (1941). *Morphixia juncifolia* Baker: 238 (1876a). *Watsonia juncifolia* (Baker) Baker: 178 (1892). *Freesia juncifolia* (Baker) Klatt in T.A.Durand & Schinz 5: 188 (1894). *Lapeirousia juncifolia* (Baker) N.E.Br.: 194 (1931). Type: South Africa, [Western Cape], without precise locality or date, [Piquetberg Div. fide Baker (1896)], *Zeyher 1619* (K [*K320516 ex herb. Wallich*], lecto.!, here designated; BOL!, K (3 sheets)!, S!, SAM! (2 sheets), isolecto.) [The Herb. Wallich duplicate is selected as lectotype from among four duplicates at Kew as having been available to Baker at the time and as bearing the inscriptions '*Morphixia juncifolia* Baker' and 'Type'].

Anomatheca calamifolia Klatt: 355 (1882), nom. superfl. pro *Morphixia juncifolia* Baker (1876b). Type: South Africa, [Western Cape], Twenty Four Rivers, *Zeyher* [as *Drège*] *1619* (S, 'Herb. Klatt', holo.!; BOL!, K (3 sheets)!, S!, SAM (2 sheets)!, iso.).

Ixia zeyheri Baker: 166 (1892), nom. superfl. pro *Morphixia juncifolia* Baker (1876a) [based on the same type]. Type: South Africa, [Western Cape], without precise locality or date, *Zeyher 1619* (K [*K320516 ex herb. Wallich*], lecto.!, here designated; BOL!, K (3 sheets)!, S!, SAM (2 sheets)!, isolecto.).

Slender plants 120–200(–300) mm high. *Corm* globose, 5–10 mm diam.; tunics of fine-textured, netted fibres, accumulating with age and forming thick neck up to 60 mm long around base of stem. *Stem* flexed outward above sheath of second leaf and then erect, unbranched or rarely with short branch from axil of uppermost scale-leaf, 0.5–1.0 mm diam. below spike. *Cataphylls* dry and papery, reddish brown, uppermost long and reaching to lower leaf blade. *Leaves* (3)4, lowermost inserted below ground, blade mostly reaching to spike or exceeding it, filiform-terete, 150–500 × 0.5–1.5 mm, thick-textured, striate with slightly raised veins when dry, upper leaves cauline with lower 1 or 2 inserted on lower $^1/_3$ of stem and mostly imbricate with lowermost sheathing for < $^1/_2$ length with blades (20–)40–100 mm long, uppermost 1 or 2 leaves scale-like and entirely sheathing, inserted ± midway between foliage leaves and spike and well separated from spike. *Spike* erect, elongate, laxly (2)3–10-flowered, lower internodes 3–5(–7) × longer than bracts but progressively shorter acropetally and uppermost internodes ± as long as bracts; bracts not imbricate, outer 3–5 mm long, acute to truncate, soft-textured and green with papery brown tips, inner slightly longer than outer and similar in texture, acute or truncate. *Flowers* suberect, purple to lilac with white throat; perianth actinomorphic, salver-shaped; tube straight, 11–18 mm long, widening gradually and evenly from base, 1.0–1.5 mm diam. at mouth; tepals spreading and slightly cupped, ovate or obovate, subequal, 10–15 × 3.5–6.0 mm. *Stamens* central; filaments erect, 4–6 mm long, exserted 3–4 mm from tube; anthers 3–4 mm long, lilac or pale yellow; pollen lilac or cream-coloured. *Ovary* ovoid, ± 1.5 mm long; style central, dividing between base and middle of anthers, branches ± 3 mm long, divided for > $^1/_2$ their length, spreading or recurved. *Capsules* flask-shaped, 9–15 mm long. *Seeds* fusiform, 6–7 mm long, with chalazal thread ± 13 mm long, thus ± twice as long as seed body, sharply bent back ± midway and hooked or crook-like, sometimes twisting around adjacent seeds, reddish brown, longitudinally rugulose. *Flowering time*: Dec.–Feb., rarely to Mar. Figure 9.

Distribution and ecology: a mainly montane species occurring from the southern Cedarberg through the Olifants River Mtns to the Skurweberg north of Ceres, with a disjunction to the Hottentots Holland, Kogelberg and Klein River Mtns in the south, and also recorded on the lower southern slopes of the Riviersonderend Mtns (Figure 10). The species is thus apparently absent from the mountains between Ceres and Stellenbosch. Plants are restricted to seeps, streamsides, drainage lines and marshy ground, and may be locally abundant, mostly between 500 and 1 000 m but to near sea level along coastal ranges. The leaves are still green and fresh at flowering. As in most species in the genus, flowering is stimulated by fire.

The long-tubed, salver-shaped, purple flowers suggest pollination by long-proboscid flies, possibly Bombyliidae or Tabanidae, and butterflies but we have not observed any visits.

Diagnosis and relationships: one of the most distinctive members of the genus, *Thereianthus juncifolius* is characterized by its slender habit, filiform-terete leaves, 0.5–1.5 mm diam., and very lax spike of salver-shaped, purple flowers with slender tube 11–18 mm long and ovate-obovate tepals. The lower flowers are well sepa-

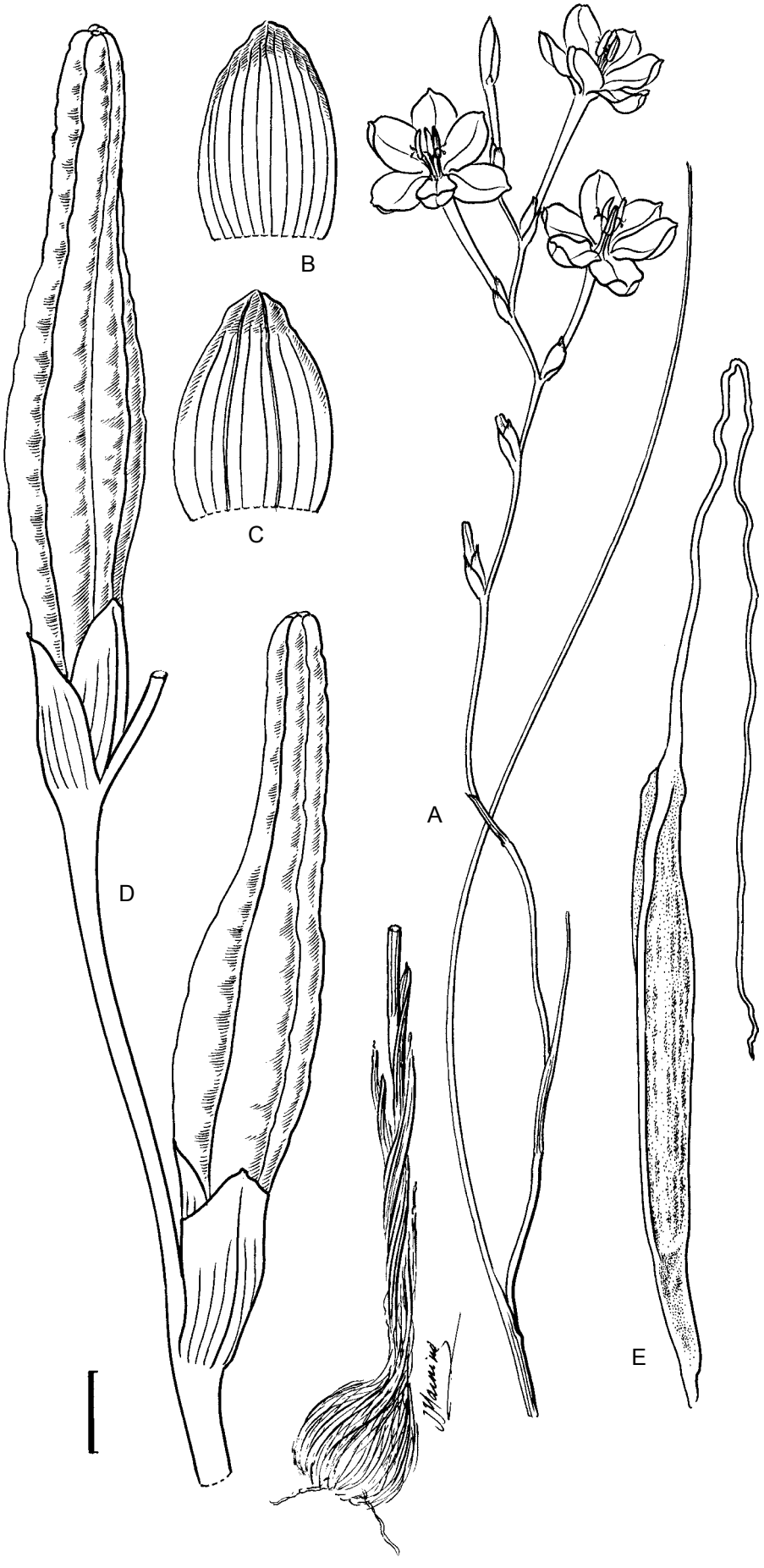

FIGURE 9.—*Thereianthus juncifolius*, *Manning 3329*. A, whole plant; B, outer bract; C, inner bract; D, capsules; E, seed. Scale bar: A, 10 mm; B–D, 2 mm; E, 0.5 mm. Artist: John Manning.

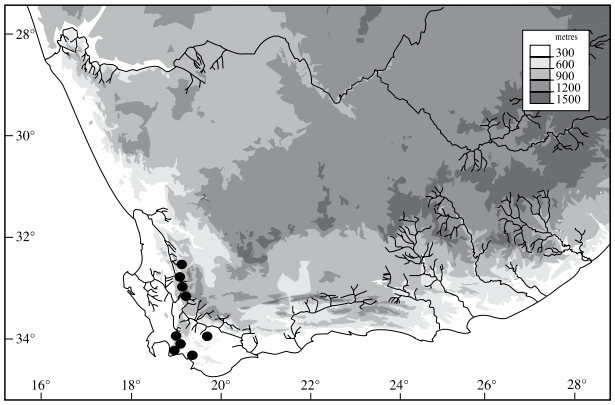

FIGURE 10.—Known distribution of *Thereianthus juncifolius*, ●.

rated from one another by internodes three to five times longer than the bracts. The species is also distinctive in its bracts, the inner as long as or slightly longer than and similar in texture to the outer, both soft-textured and green throughout except for the brown, papery tips. In all other species the inner bracts are shorter than the outer and membranous or papery except along the veins. The capsules are markedly flask-shaped with a narrow, tapering neck and fusiform seeds with a long, filiform chalazal extension ± twice as long as the seed body. The placenta is restricted to the lower portion of the capsule and the tapered neck or beak accommodates the chalazal extensions of the seeds, which extend up the neck of the capsule to the apex and then flex sharply back towards the seed body. This combination of unusual characteristics sets the species apart from others in the genus but the flask-shaped capsules and the seeds with long, filiform chalazal extensions indicate a close alliance with *T. minutus*.

History: the unusual morphology of the species caused a great deal of uncertainty about its generic position among early workers. The lax spike and salver-shaped flowers determined its initial description in the genus *Morphixia* (Baker 1876a) but the subsequent realization of the taxonomic importance of divided style branches encouraged various authors to place it in all possible genera with this character, namely *Watsonia* (Baker 1892), *Freesia* (Klatt 1894) and *Lapeirousia* (Brown 1931). Although Baker (1892) initially misunderstood the affinities of *Thereianthus juncifolius*, he rapidly appreciated its relationship to other species in the genus by including it with them in subgen. *Beilia* of *Watsonia*. His simultaneous redescription of the species as *Ixia zeyheri*, based on the same collection, is best viewed as an aberration since none of the herbarium material seen by him bears this name. Klatt's (1882) independent description of the species in the genus *Anomatheca* Ker Gawl., again based on the same collection by Zeyher, anticipates his later inclusion of that genus in *Freesia*.

Additional specimens examined

WESTERN CAPE.—3219 (Wuppertal): S Cedarberg, Sneeuberg, (–AC), 1 Mar. 1947, *Esterhuysen 13842* (BOL); Algeria Forest Station, Sneeuberg, 4200–4800′ [1 280–1 460 m], (–AC), 5 Feb. 1982, *Viviers 121* (NBG); Apollo Mtn., Kromrivier Valley, 1 340 m, (–AC), 24 Jan. 1986, *Taylor 11482* (NBG); Elandskloof, Hexberg slopes, marshy site, (–CA), 12 Dec. 1982, *Esterhuysen 35847A* (MO); Keerom, E foot of Twenty Four River Mtns [Olifantsrivierberge], (–CC), 3 Dec. 1950, *Esterhuysen 17863* (BOL, NBG); Grootfontein, next to Ratelrivier, (–CC), 12 Dec. 1982, *Van Zyl 2418* (NBG); Koue Bokkeveld, Skoongesig, Fonteinbult, (–CC), 29 Dec. 1978, *Hanekom 2573* (MO, PRE); Grootwinterhoek Forest Station, rocky flats, along stream, (–CC), 27 Dec. 1995, *Goldblatt 10455* (MO); 3319 (Worcester): mtns near Porterville, (–AA), Nov. 1912, *Edwards s.n. BOL16150* (BOL); Groot Winterhoek Forestry Station, 650 m, (–AA), 2 Dec. 1983, *De Kock 52* (NBG); Groot Winterhoek, road to De Tronk at Groot Kliphuis river crossing, (–AA), 10 Dec. 2007, *Helme 5091* (NBG); eastern slopes of Witsenbergen, (–AA), Dec. 1919, *Andreae 178* (NBG); Skurfdebergen near Wagensboom River, (–AB), 27 Jan. 1897, *Schlechter 10169* (BOL); Schurfteberg Pass, (–AB), 20 Dec. 1944, *Compton 16799* (NBG). 'Worcester, beim Waterfall,' (–AC), Dec. *Ecklon & Zeyher Irid. 297* (1.12) (MO). 3418 (Simonstown): margins of streams flowing into Buffels River near Pringle Bay, (–BD), 27 Jan. 1936, *Pillans 8185* (BOL); Betty's Bay, (–BD), 10 Feb. 1956, *Levyns 10451* (BOL); marsh on mtns behind Rooiels–Stalberg–Pringle E Peak, (–BD), 10 Jan. 1971, *Esterhuysen 32561* (BOL, MO); Kogelberg, (–BD), 16 Jan. 1944, *Esterhuysen 10010* (BOL); mtns north of Palmiet River Mouth, (–BD), 26 Jan. 1947, *Esterhuysen 13667* (BOL, NBG); mtns above Betty's Bay, marshy slopes in valley at base of Platberg, (–BD) 27 Jan. 1980, *Esterhuysen 35387* (BOL, MO); Kogelberg State Forest, Oudebosch, 80 m, (–BD), 20 Jan. 1992, *Kruger 302* (MO, NBG). 3419 (Caledon): Hottentots Holland Mtns, east of Landdroskop Hut, (–AA), 6 Jan. 2000, *Oliver & Oliver 11470* (NBG); Grabouw, (–AA), Jan. 1943, *Stokoe s.n. SAM55716* (SAM); Nuweberg Forest Reserve, slopes of Landdrost kop, damp gully above path to Somerset Sneeukop, (–AA), 11 Jan. 1987 *Goldblatt 8351* (MO); Aries Kraal, (–AA), 1 Jan. 1945, *Compton 16851* (NBG); Lebanon, (–AA), Jan. 1968, *Kruger 640* (NBG); Highlands Forest Reserve, hiking trail, marshy places, (–AC), 29 Jan. 1987 *Goldblatt 8469* (MO); summit of Klein River Mtns, Bellevue, (–AD), 2 Feb. 2008, *Helme 5322* (NBG); Vogelgat, N of Mt Frustration, (–AD), 1 Mar. 1987, *Williams 3785* (NBG); Vogelgat, Rock-in-the-Path, (–AD), 1 Feb. 1986, *Williams 3643* (NBG); Hermanus, Fernkloof Nature Reserve, 400′ [122 m] (–AD), 21 Jan. 1981, *Orchard 583* (MO); Greyton, foot of Riviersonderend Mtns, (–CA), 16 Jan. 1988, *Oakes s.n.* (NBG).

Sect. **Thereianthus**

Leaves linear or falcate, plane and either leathery without raised veins or strongly ribbed or corrugate with prominently raised veins, or ellipsoid in section; bracts (7–)8–15 mm long, closely and prominently veined with raised veins (sclerenchymatous phloem caps prominent). *Pollen* operculum 1-banded, exine perforate. *Seeds* (where known) ellipsoid-ovoid and angled, without chalazal extension, brown to blackish.

Ser. **Bracteolatus** *J.C.Manning & Goldblatt*, ser. nov.

Lamina foliorum non costata nec corrugata sine nervis prominentibus vel incrassatis, floribus actinomorphis tepalis patentibus et tubo curvato, staminibus ± declinatis.

Type species: *Thereianthus bracteolatus* (Lam.) G.J.Lewis.

6. **Thereianthus bulbiferus** *Goldblatt & J.C.Manning*, sp. nov.

Plantae 140–200 mm altae, cormo globoso 10–15 mm diam., tunicis fibrosis crassis interdum infra unguiscentibus, caule usitate eramoso cormelos 5–7 in axilla folii infimi facienti, foliis 4, infimo lineari-falcato, 70–120 × (1.5–)2–3 mm, coriaceis, spica erecta dense 7- ad 15-flora, bracteis breviter imbricatis, bractea externa 7–9(–10) mm longa interna quam $^{1}/_{2}$ ad $^{3}/_{4}$ plo breviore, floribus coeruleis tepalis inferioribus prope basin nota alba mediana munitis, perianthio actinomorpho, tubo

7–9 mm longo infundibuliformi, tepalis subaequalibus vel interioribus pauce latioribus oblanceolatis patentibus parum cupulatis (10–)13–20 × 3–6 mm, staminibus ± declinatis, filamentis 6–8 mm longis ± 5–6 mm ex tubo exsertis, antheris 4 mm longis purpureis, ramis styli profunde furcatis 3–5 mm longis.

TYPE.—Western Cape, 3319 (Worcester): Bo-Hermon, Elandsberg Nature Reserve, alluvial flats near river, after fire, (–AC), 7 Nov. 2010, *J.C. Manning 3312* (NBG, holo.; MO, iso.).

Plants 140–200 mm high. *Corm* globose, 10–15 mm diam.; tunics of coarsely netted fibres, sometimes forming claws below, accumulating with age and forming short neck around base of stem. *Stem* erect, flexuous or flexed outward only above sheath of second leaf, usually unbranched, rarely with short branch from upper leaf axil, 2.0–2.5 mm diam. below spike, developing conspicuous cluster of 5–7 cormels, each 3–4 mm diam., in axil of lowest leaf. *Cataphylls* dry and papery, reddish brown. *Leaves* 4, lowermost inserted below ground, blade reaching base of spike or not, ± dry at flowering, linear-falcate, often sinuous-twisted, 70–120 × (1.5–)2–3 mm, leathery, with 3 ± equally distinct veins or with main vein slightly more distinct, not thickened or raised when fresh but prominent when dry, upper 3 leaves cauline with lower 2 inserted on lower $^1/_3$ of stem and sheathing for ± $^1/_2$ length, sheaths shortly imbricate, blades 50–70 × 3–4 mm, uppermost leaf a little distant from lower leaves and well separated from spike, usually with short blade 20–50 mm long, rarely almost entirely sheathing. *Spike* erect, densely 7–15-flowered; bracts imbricate for ± $^1/_2$ their length, outer 7–9(–10) mm long and up to two internodes long, obtuse or truncate, either green below or entirely brown and leathery, conspicuously and closely veined, with narrow membranous margins, inner bract $^1/_2$ to $^3/_4$ as long as outer, bifid, ± membranous with narrow brown zones along veins. *Flowers* patent, pale to mid-blue, lower three tepals with white median mark near base; perianth actinomorphic; tube slightly curved, 7–9 mm long, funnel-shaped, exserted 2–5 mm beyond bracts; tepals oblanceolate, subequal or inner slightly broader, spreading and slightly cupped, (10–)13–20 × 3–6 mm. *Stamens* ± declinate; filaments 6–8 mm long, exserted ± 5–6 mm from tube; anthers all facing upwards or median (lower) facing downwards or outwards, 4 mm long, purple; pollen lilac. *Ovary* obovoid, 2.0–2.5 mm long; style ± deflexed to lie beneath stamens, dividing at middle of anthers, branches 3–5 mm long, divided to near base. *Capsules* ovoid, 6 × 3 mm long, slightly shorter to slightly longer than bract. *Seeds* subglobose-angled, 1.5–2.0 mm long, chalaza ± excavated, yellowish brown, obscurely scalariform-rugulose. *Flowering time*: Nov. (early Dec.). Figure 11.

Distribution and ecology: a local endemic between Piketberg and Wellington, *Thereianthus bulbiferus* is most common along the western foot of the Elandskloof Mtns near Hermon, where it is known from several populations on Elandsberg Nature Reserve (Figure 12). The southernmost population near Agter Paarl, known only from a single specimen collected over forty years ago, is now likely extinct through agriculture. Plants at Elandsberg Nature Reserve grow on seasonally moist or wet alluvial flats, primarily in Swartland Alluvial Fynbos (Mucina & Rutherford 2006) communities but extending into adjacent Swartland Alluvial Renosterveld. Flowering is most prolific after fire but occasional individuals will flower in open or cleared spaces in the intervening years. The species co-occurs throughout its range with *T. spicatus*, which favours drier soils. At Elandsberg, *T. bulbiferus* occurs as single-species communities on the lower, moister flats but on the slopes, where it is restricted to drainage lines, it interdigitates with *T. spicatus* growing on adjacent drier sites. The single collection from near Agter Paarl (*Thompson 622*) is a mixed gathering comprising a single stem of *T. bulbiferus* and two stems of *T. spicatus*, suggesting that the two species grew in close proximity there too, and both species have also been collected on the Piketberg, although in different localities.

Visits by monkey beetles (Coleoptera: Hopliini) have been observed at Elandsberg Nature Reserve (unpublished obs.) but the relatively short-tubed flowers produce nectar and are probably also visited by anthophorine bees.

Diagnosis and relationships: *Thereianthus bulbiferus* is diagnosed by its leathery leaves without raised central and secondary veins when fresh, the lower leaf mostly characteristically falcate or arcuate and often sinuous-twisted, and by the moderately dense spikes of blue flowers with relatively short, funnel-shaped perianth tube, 7–9 mm long exserted up to 5 mm beyond the bracts, actinomorphic perianth with white markings at the base of all the tepals, and ± declinate stamens and style. Flowers with declinate stamens are found elsewhere in sect. *Thereianthus* only in *T. bracteolatus*, and in both species the perianth tube is curved so that the flowers face sideways rather than upwards. Both species also have inconspicuously veined leaves. The seeds, with an unusual chalazal depression or small excavation rather than crest, are distinctive for *T. bulbiferus*.

Thereianthus bulbiferus is unique in the genus in producing a cluster of cormels from the axil of the lowermost leaf. These cormels, 3–4 mm diam., are present at flowering time, and although they may be lost from some pressed specimens, their presence can be readily inferred by the split in the leaf sheath through which they protruded. Florally, the species is distinguished from *T. bracteolatus* by the light to mid-blue perianth with white markings on all tepals, which are inconspicuously veined, the outer longitudinal veins ± evenly branched along their entire length. The flowers of *T. bracteolatus*, in contrast, are dark blue to purple without evident white markings but with the longitudinal veins splashed or spotted with purple. The outer longitudinal veins in this species are typically only weakly branched in the distal half so that the tepals appear to be parallel-veined from the base.

All other members of sect. *Thereianthus* have strongly and closely ribbed leaves, and mostly arcuate stamens (except *T. ixioides*, which has symmetrical stamens). Fresh leaves of the members of the *T. spicatus* alliance have the veins separated from one another but as the leaves dry and shrink, the veins become closely appressed, leaving no gaps between them. The leaves of *T. bracteolatus* and *T. elandsmontanus*, in contrast, are ±

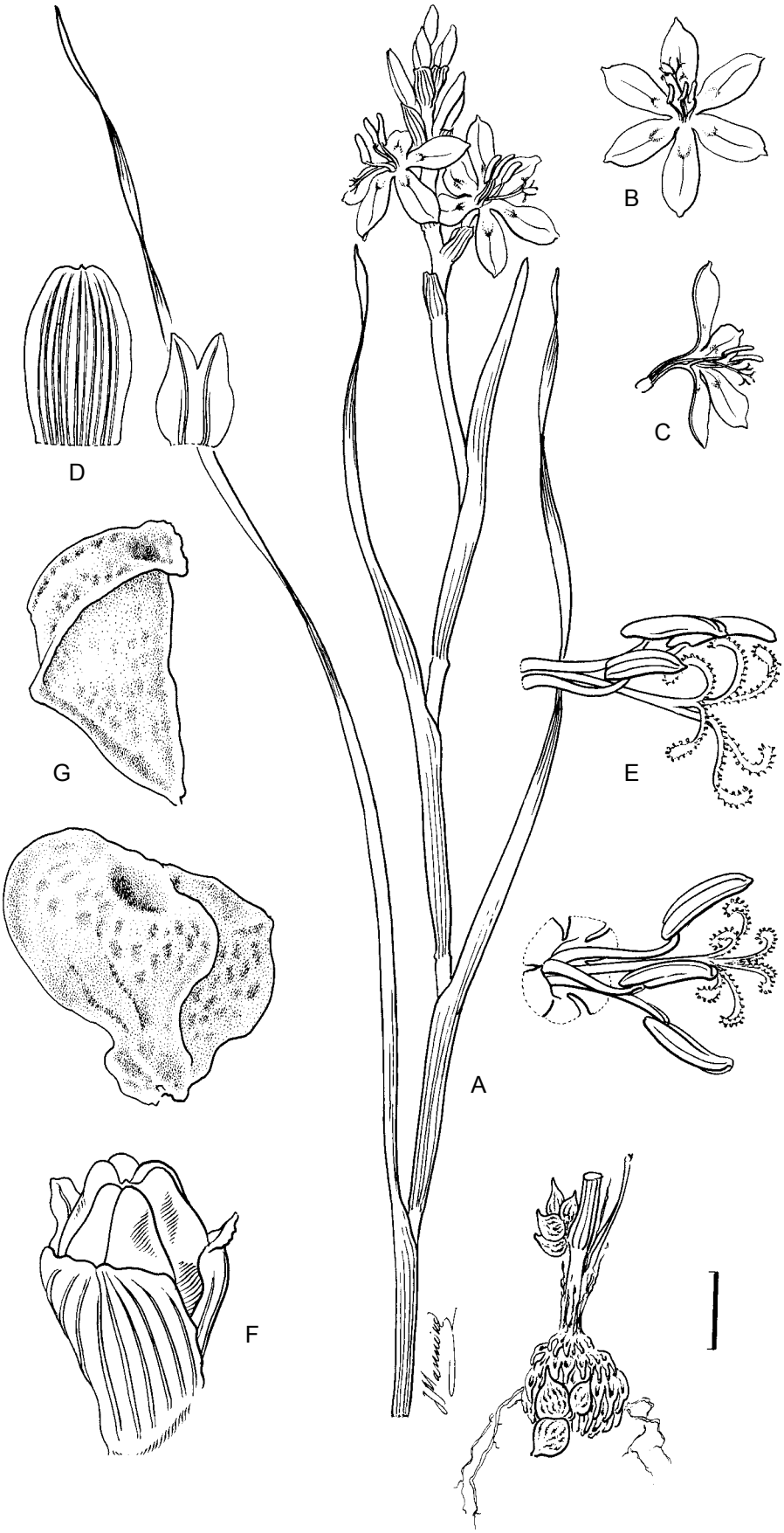

FIGURE 11.—*Thereianthus bulbiferus, Manning 3312*. A, whole plant; B, flower, front view; C, half flower; D, outer (left) and inner (right) bract; E, details of stamens and stigma; F, capsule; G, seeds. Scale bar: A–C, 10 mm; D, E, 3 mm; F, 2 mm; G, 0.5 mm. Artist: John Manning.

smooth and leathery when fresh and although the veins become evident as the leaf dries, they remain separated from one another by intervening blade tissue and by lower order veins.

History: although collected on two separate occasions several decades ago, *Thereianthus bulbiferus* was confused with both *T. bracteolatus* and *T. spicatus*, and it was only in 2010 when we were able to properly

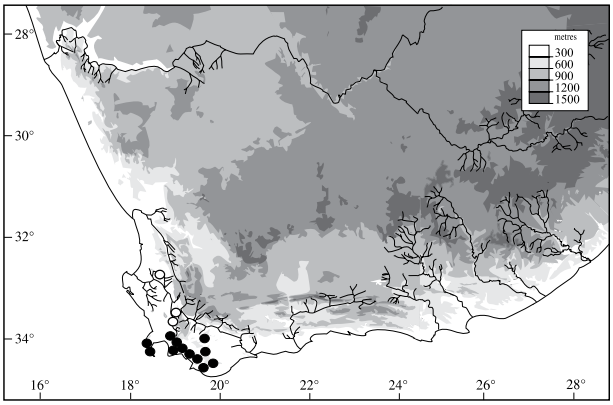

FIGURE 12.—Known distribution of *Thereianthus bracteolatus*, ●; *T. bulbiferus*, ○.

examine living plants in the field at Elandsberg Nature Reserve that it became clear that they represent a distinct species.

Etymology: the specific epithet alludes to the characteristic cormels on the lower part of the stem.

Additional specimens examined

WESTERN CAPE.—3218 (Clanwilliam): Piketberg, Sandleegte [Buglerspost, at top of Versveld Pass], 2400' [730 m], (–DC), 3 Dec. 1973, *Linder 130* (BOL). 3318 (Cape Town): Pause's plot on Protea F.U.C. road off Agter-Paarl road, (–CB), 2 Dec. 1968, *Thompson 622A* (NBG). 3319 (Worcester): Bo-Hermon, Elandsberg Nature Reserve, Vervlak, sandstone flats burned in Mar., (–AC), Nov. 1999, *Manning s.n.* (NBG); 7 Nov. 1999, *Parker 390* (NBG).

7. **Thereianthus bracteolatus** *(Lam.) G.J.Lewis* in Journal of South African Botany 7: 42 (1941). *Gladiolus bracteolatus* Lam.: 725 (1788). Type: South Africa, without precise locality, said to have been collected by *Sonnerat s.n.* (P: Herb. Lamarck, holo.!).

Ixia punctata Andrews: t. 177 (1801). *Watsonia punctata* (Andrews) Ker Gawl.: 229 (1804). *Gladiolus punctatus* (Andrews) Roem. & Schult.: 425 (1817). Type: South Africa, 'Cape of Good Hope', said to have been collected and sent by G. Hibbert, illustration in Andrews, *The botanist's repository* 3: t. 177 (1801).

Gladiolus subulatus Vahl: 97 (1805), nom. illegit. superfl. pro *G. bracteolatus* Lam. (1788). *Watsonia subulata* Klatt, nom. nov. pro *G. subulatus* Vahl, nom. illegit. et superfl. pro *G. bractolatus* Lam. Type: South Africa, without precise locality or date, *Bulow s.n. C1000844* (C, holo.!).

Gladiolus triticeus Thunb.: 194 (1807). *Watsonia triticea* (Thunb.) Spreng.: 150 (1824). *Beilia triticea* (Thunb.) Eckl.: 43 (1827). *Micranthus triticeus* (Thunb.) Heynh.: 405 (1847). *Watsonia punctata* var. *triticea* (Thunb.) Baker: 177 (1892). *Beilia spicata* var. *triticea* (Thunb.) Kuntze: 305 (1898). Type: South Africa, without precise locality, *Thunberg s.n. UPS-THUNB1084* (UPS-THUNB, holo.!).

Plants (80–)150–200(–300) mm high. *Corm* globose, 10–15 mm diam., developing several large cormels at base; tunics of coarsely netted fibres, thickened and forming woody claws below, accumulating with age and forming collar up to 20 mm long around base of stem. *Stem* erect, flexuous or flexed outward only above sheath of second leaf, unbranched, (1.5–)2.0–2.5 mm diam. below spike. *Cataphylls* dry and papery, reddish brown. *Leaves* 4(5), lowermost inserted below ground, blade reaching base of spike or not, ± dry at flowering, linear, elliptic or terete in section, 70–170 × 0.5–1.5(–2.0) mm, leathery, with 3 ± equally distinct veins or with main vein slightly more distinct, not thickened or raised when fresh but prominent when dry, upper 3(4) leaves cauline with lower 2 inserted on lower $^1/_3$ of stem and sheathing for ± $^1/_2$ length, sheaths usually shortly imbricate, blades 50–70 mm long, uppermost leaf a little distant from lower leaves and well separated from spike, entirely sheathing or with short blade 20–50 mm long. *Spike* erect, densely 7–15(–30)-flowered; bracts imbricate for ± $^1/_2$ their length, 8–10(–12) mm long and ± two internodes long, outer entirely brown and leathery, obtuse or truncate (rarely apiculate), conspicuously and closely veined, with narrow membranous margins, inner $^1/_2$ to $^3/_4$ as long as outer, bifid, ± membranous with narrow brown zones along veins. *Flowers* ± patent, purple to violet with dark blotches and streaks on longitudinal veins and especially midline; perianth actinomorphic; tube slightly curved, (7–)8–10(–15) mm long, funnel-shaped, usually exserted 2–6(–10) mm beyond bracts, rarely just included; tepals oblanceolate, subequal or inner slightly broader, spreading and slightly cupped, (10–)11–17 × 3–6 mm. *Stamens* unilateral, ± declinate, sometimes weakly so and then ± central; filaments 8–10 mm long, exserted ± 6–8 mm from tube, usually flexed sharply upwards apically; anthers all facing upwards, usually white (rarely purple), 4–6 mm long; pollen white (rarely brown when anthers purple). *Ovary* obovoid, 2.0–2.5 mm long; style ± deflexed to lie beneath stamens, dividing opposite middle of anthers, branches 3–5 mm long, divided to near base. *Capsules* ovoid, ± 6 mm long. *Seeds* subglobose- or ellipsoid-angled, ± 2 mm long, chalaza truncate, brown, testa colliculate. *Flowering time*: late Nov.–early Jan. Figure 13A–G.

Distribution and ecology: the only species of *Thereianthus* on the Cape Peninsula*, T. bracteolatus* occurs from the Peninsula and Stellenbosch along the coastal ranges of the Hottentots Holland, Kogelberg and Klein River/Babilonstoring Mtns to Bredasdorp in the east, with isolated records from near Caledon (Drayton Siding) and the lower slopes of the Riviersonderend Mtns above Greyton (Figure 12). Somewhat surprisingly, the species has not been recorded from the Caledon Swartberg. Although there is an early record, *Zeyher 1608* (SAM), from the Twenty Four Rivers Mtns near Porterville, the species has never been re-collected here and as this collection is a mixed one that includes a stem of *T. longicollis*, which is known from this location, the association of *T. bracteolatus* with the locality is probably an error.

The species is locally common after fire on sandy flats and lower slopes below 1 000 m, although plants will also flower in cleared places along roads in the absence of fire. The distribution of *Thereianthus bracteolatus* largely overlaps with that of *T. spicatus*, with the notable exception of the Cape Peninsula where only *T. bracteolatus* is found, but *T. spicatus* favours more stony sites and often heavier soils. We have encountered both species growing adjacent to each other at Kogelberg, with *T. bracteolatus* on damper soils and flowering in December and *T. spicatus* immediately adjacent on rocky slopes and flowering in January.

The purple or violet flowers with a relatively short perianth tube are evidently adapted to pollination by various nectar-feeding bees.

FIGURE 13.—*Thereianthus bracteolatus*. A–E, *Goldblatt 9032*: A, whole plant; B, flower, side view; C, outer tepal; D, inner tepal; E, details of stamens and stigma. F, G, *Rodgers 2829*: F, capsule; G, seeds. *T. spicatus*. H–J, *Goldblatt 6837*: H, whole plant; I, flower, front view; J, flower, side view. K, L, *Goldblatt & Manning 9567*: K, capsules; L, seed. Scale bars: A, B, H–J, 10 mm; C, D, F, K, 2 mm; E, 3 mm; G, L, 0.5 mm. Artist: John Manning.

Diagnosis and relationships: *Thereianthus bracteolatus* is unmistakeable when seen alive, with very narrow leaves, 0.5–1.5(–2) mm diam., and terete or elliptic in section, and dense spikes of sideways-facing, deep purple or violet flowers with curved perianth tube (7–)8–10(–15) mm long, and relatively long, unilateral, declinate stamens. The flowers, which lack nectar guides, have darkly pigmented veins, giving them a characteristic blotched-striate appearance. Although Lewis (1941) noted that the branching pattern of the veins was distinctive for the species, this difference is not evident in all plants. Like other species in the genus, each tepal has three primary longitudinal veins but unlike other species, the lateral veins are often only branched in the basal half so that the tepals appear to be ± parallel-veined for most of their length. In the other species the veins are not darkly pigmented and thus not evident, and the lateral longitudinal veins are ± evenly branched throughout their length.

Perianth tube length is somewhat variable, usually 8–10 mm but 10–15 mm long in an isolated population at Drayton Siding east of Caledon (*Goldblatt 394*). The anthers and pollen are usually white but plants from

the Silvermine area of the Cape Peninsula have purple anthers with brown pollen. Another isolated population, from the lower slopes of the Riviersonderend Mtns above Greyton (*Esterhuysen 20763*), has stamens that are less obviously declinate than usual but matches the species in vegetative and other floral characters, including the distinctive tepal venation. This population may repay further consideration.

The smooth leaves and especially the declinate stamens (but not the characteristic tepal venation) are both shared with *Thereianthus bulbiferus* from gravelly flats between Malmesbury and Paarl. This species has pale to mid-blue flowers with distinct white blotches at the base of each tepal, and shorter filaments, 6–8 mm long. Most characteristically, the plants develop a cluster of cormels in the axil of the lower leaf, whereas cormels in *T. bracteolatus* are developed at the base of the parent corm. Although *T. bracteolatus* is sometimes confused with *T. spicatus*, especially in the dried state when details of the perianth coloration and stamen orientation are obscured, the two are readily distinguished by the difference in leaf texture: leathery and terete or elliptic in section without raised veins in *T. bracteolatus* versus plane and ribbed or corrugate with raised veins in *T. spicatus*. Living plants of *T. spicatus* are readily separated by their blue (rarely white or pink) flowers with white markings on the lower three tepals outlined with a purple chevron and lacking darker venation, the ± straight or distally curved perianth tube, 12–25 mm long, and the much shorter, arcuate filaments, 3–4 mm long.

History: the second species of *Thereianthus* to be described after *T. spicatus, T. bracteolatus* was named in the genus *Gladiolus* by French biologist J.P.B. Lamarck (1788) from specimens said to have been collected by naturalist and draughtsman Pierre Sonnerat, who could only have collected this material in 1773, on the outgoing leg of his voyage to Isle de France (now Mauritius). This name was overlooked by the English botanical artist and engraver, Henry Andrews (1801), who described *Ixia punctata* from plants cultivated in London that had been sent to collector and botanical patron G. Hibbert from the Cape of Good Hope. In continental Europe, the species was described under the name *Gladiolus triticeus* for a third time a few years later by Thunberg (1807), based on his own collections from the Cape. At the time, Thunberg expressed doubt as to whether his species was truly different from *G. spicatus* L. (i.e. *T. spicatus*) and must have appreciated the similarity between these species, ultimately to be treated in a separate genus. J.G. Baker (1892) subsequently treated Thunberg's name as a variety of Andrew's species, which had by now been transferred to *Watsonia* as *W. punctata* (Andrews) Ker Gawl. The nomenclature was clarified by Lewis (1941), who correctly identified Lamarck's name as the earliest for the species, and also established the genus *Thereianthus* for plants until then treated as subgen. *Beilia* of *Watsonia*.

Additional specimens examined

WESTERN CAPE.—3318 (Cape Town): Table Mountain, (–CD), Jan. 1898, *Thode 6017* (NBG), Dec. 1950, *Pillans 10276* (MO); Cape Peninsula, Camps Bay, (–CD), Dec. without year, *Zeyher 5038* (SAM); 5 July 1943 [fr.], *Barker 2416* (NBG); above S end of Kirstenbosch, (–CD), 28 Nov. 1953, *Esterhuysen 22404* (BOL); Kenilworth, (–CD), Dec. without year, *Bolus 3305* (NBG); Kenilworth Race Course, (–CD), 11 Dec. 1969, *Esterhuysen 32359* (BOL, MO, NBG); near Stellenbosch, (–DD), Dec. 1924, *Rogers 28929* (BOL, NBG). 3319 (Worcester): Franschhoek Pass, east side, (–CC), 26 Nov. 1939, *Compton 8185* (NBG). 3418 (Simonstown): Vlaggenberg [Vlakkenberg], (–AB), 1 Jan. 1896, *Wolley Dod 345* (BOL); Bergvliet Farm, (–AB), 16 Dec. 1976, *Purcell 152* (SAM); Constantia Nek, (–AB), 24 Jan. 1929, *Gillett 3365* (BOL, NBG); Steenberg Plateau, (–AB), Dec. 1944, *Lewis 56067* (SAM); Silvermine Valley, (–AB), Dec. 1944, *Lewis 56066* (SAM); mntns above Muizenberg, (–AB), Jan. 1881, *Bolus 3305* (BOL, NBG); Red Hill, (–AB), 21 Dec. 1963, *Taylor 5616* (NBG); Farm Buffelsfontein W of Redhill, (–AB), 17 Dec. 1984, *Snijman 833* (NBG); Patreis Vlei [Patrys Vlei], (–AD), 3 Jan. 1941, *Salter 8586* (BOL, NBG); Cape Point Reserve, sandy plain on Circular Drive, (–AD), 31 Dec. 1989, *Goldblatt* 9032 (MO); Cape Point, (–AD), 1 Jan. 1968, *Taylor 7267* (NBG); Steenbras, (–BB), Dec. 1945, *Lewis 58735* (SAM); Palmiet River Valley, (–BD), Nov. 1944, *Lewis 56408* (SAM); between Kogel Baai and Rooi Els, (–BD), Nov. 1945, *Lewis 58736* (SAM); Kogelberg State Forest, Palmiet River Valley, (–BD), 29 Nov. 1991, *Kruger 97* (NBG); Palmiet River Mouth, (–BD), 7 Dec. 1962, *Grobler 71* (NBG). 3419 (Caledon): Aries Kraal, (–AA), 18 Nov. 1944, *Leighton 808* (BOL); 18 Nov. 1944, *Leighton 3361* (NBG); Lebanon Forest Reserve, (–AA), 14 Jan. 1971, *Haynes 510* (NBG); Grabouw near Palmiet River, (–AA), Dec. 1899, *Bolus 3305* (BOL); Bot River, (–AC), 9 Dec. 1951, *Taylor 3810* (NBG); Honingklip, (–AC), without date, *Taylor 5119* (NBG); Hermanus Mtn, (–AD), 26 Dec. 1943, *Leighton 357* (BOL); Hermanus, Rotary Way, (–AC), 8 Jan. 1975, *Walters 1452* (NBG); Hermanus, Vogelgat Nature Reserve, (–AD), 7 Jan. 1984, *Burman 1273* (BOL); Fernkloof Nature Reserve, 500 m, (–AD), 2 Jan. 1976, *Orchard 359* (MO, NBG); top of Shaw's Pass, (–AD), Jan. 1957, *Lewis 63514* (BOL); foothills of River Sonder End [Riviersonderend] Mtns, (–BA), Apr.–May 1950 [fr.], *Lewis 2280* (SAM); Zonder End [Riviersonderend], (–BA), without date, *Barnard 448* (SAM); Riviersonderend Mtns near Greyton, (–BA), 30 Nov. 1952, *Esterhuysen 20763* (BOL, MO, NBG); Caledon, Drayton Siding, (–BA), 16 Dec. 1968, *Goldblatt* (BOL); north end of Akkedisberg Pass, fynbos slopes, burned last summer, (–BC), 19 Nov. 1979, *Goldblatt 5186* (MO); Elandskloof, (–BD), 17 Dec. 1896, *Schlechter 9765* (BOL, MO); between Gansbaai and Baardscheerdersbos, (–DA), 11 Nov. 1980, *Snijman 380* (NBG); between Wolvengat and Elim, Farm 239, (–DA), 25 Nov. 2000, *Mucina 251100/5* (NBG); Bredasdorp, plateau on mountain top, (–DB), 19 Dec. 1930, *Galpin 22442* (BOL). *Doubtful locality*: 3319 (Worcester): Twenty Four Rivers, (–AA), without date, *Zeyher 1608* [excluding single specimen of *T. longicollis* as indicated] (SAM).

Ser. **Thereianthus**

Leaves ribbed or corrugate, with thickened and raised veins. *Flowers* suberect with ± straight tube; perianth actinomorphic or more usually zygomorphic. *Stamens* arcuate, rarely central.

8. **Thereianthus spicatus** *(L.) G.J.Lewis* in Journal of South African Botany 7: 39 (1941). *Gladiolus spicatus* L.: 37 (1753). *Ixia spicata* (L.) Willd.: 200 (1797), hom. illegit. non Burm.f. (1768). *Gladiolus alopecuroides* Pers.: 46 (1805), nom. illegit. pro *Gladiolus spicatus* L. et hom. illegit. non L. (1756). *Micranthus spicatus* (L.) Heynh.: 405 (1847). *Paulomagnusia spicata* (L.) Kuntze: 702 (1891). *Beilia spicata* (L.) ex Kuntze: 305 (1898) [*Beilia spicata* (L.) Eckl. nom. inval.]. Type: from South Africa without any details ex Herb. van Royen (?L, not found). Neotype, designated here: South Africa, [Western Cape], Jonkershoek Valley, contour path below Berg River Neck, 29 Dec. 1989, *Goldblatt & Manning 9028* (NBG, neo.; K, MO, PRE, iso.).

Thereianthus spicatus var. *linearifolius* G.J.Lewis: 40 (1941). Type: South Africa, [Western Cape], mountains near Franschhoek, *Salter 2973* (BOL, holo.!).

Gladiolus rubens Vahl: 98 (1805). *Watsonia rubens* (Vahl) Ker Gawl.: sub t. 1072 (1807). Type: South Africa, not cited, probably at C.

Plants (150–)200–500(–600) mm high. *Corm* globose, 10–20 mm diam.; tunics of coarsely netted fibres, thickened and claw-like at base, accumulating with age and forming neck up to 20 mm long around base of stem. *Stem* erect or flexed outward above sheath of second leaf, unbranched or rarely with short branch from axil of uppermost leaf, 1.5–3.0 mm diam. below spike. *Cataphylls* dry and papery, reddish brown. *Leaves* 4(5), lowermost inserted below ground, blade reaching or exceeding spike (rarely shorter than spike), ± dry at flowering, linear, (100–)200–250 × 1–2(–4) mm, closely 3–5(–7)-ribbed, glabrous or minutely scabridulous along ribs and margins, upper 3 leaves cauline, second and third leaves usually ± imbricate and enveloping stem but uppermost leaf distant, blades successively shorter, uppermost leaf only rarely reaching base of spike, entirely sheathing or with short blade 20–60 mm long. *Spike* erect, densely (3–)6–20(–30)-flowered; bracts imbricate for $^{1}/_{2}$ to $^{2}/_{3}$ length, (7–)8–13(–15) mm long and two or three internodes long, outer acute, either green below or entirely brown and leathery, conspicuously and closely veined, with narrow membranous margins, inner slightly shorter, bifid, ± membranous with narrow brown zones along veins. *Flowers* suberect, mostly pale to mid-blue, rarely white or pink, lower three tepals each with white marking near base outlined distally with purple chevron; perianth subactinomorphic or weakly zygomorphic; tube ± straight or slightly curved outwards in distal 3 mm, (12–)15–18(–25) mm long, 1.0–1.5 mm diam. at mouth, ± dilated gradually and evenly from base to tip, exserted 6–15 mm beyond bracts, 0.8–1.8 × as long as tepals; tepals elliptical-oblanceolate, inner three slightly smaller, spreading and slightly cupped, 10–18 × 3–5 mm. *Stamens* arcuate; filaments 3–4 mm long, exserted 2 mm from tube; anthers 4–5 mm long, purple; pollen purple. *Ovary* obovoid, 2.0–2.5 mm long; style arching above anthers, dividing at ± middle of anthers, branches 4–5 mm long, divided to near base. *Capsules* narrowly ovoid, 6–7 × 3 mm. *Seeds* ellipsoid-angled, ± 2 mm long, black or brown, testa striate-colliculate. *Flowering time*: (Nov.) Dec.–Jan., rarely into early Feb. Figure 13H–L.

Ecology and distribution: the most common species in the genus, *Thereianthus spicatus* is distributed along the coastal mountains and foothills in the southwestern part of Western Cape, from Piketberg and Porterville southwards to the Palmiet River Mouth and onto the lower slopes of the Riviersonderend Mtns but is absent from the Cape Peninsula (Figure 14). The species is mostly found on sandstone slopes but also grows on shale bands and on granite, from near sea level to over 1 000 m. Flowering is strongly stimulated by fire but plants will bloom in older, open veld and in fire-breaks.

Flower colour is somewhat variable in the species, usually mid- to deep blue but sometimes white or pink. Although the different forms are often mixed, there is an altitudinal component to perianth colour in populations in the Jonkershoek Valley, where the proportion of white flowers increases with elevation. The relatively great variation in perianth tube length suggests adaptation to the local pollinator fauna. Mostly 15–20 mm long, the perianth may be as long as 25 mm in plants from Grootwinterhoek (*Helme 5141*) and in Idas Valley, Stellenbosch (*Levyns 1458*), and as short as 12 mm around Somerset West (*Martley s.n. BOL22440, Schlechter 7245*). Leaf width in the species is mostly 1–2 mm but plants with broader leaves, 3–4 mm wide, are known from Bainskloof, Stellenbosch, Kuils River and Somerset West. A collection of unusually delicate plants, with small tepals 8 mm long (*Esterhuysen 22748*) from Bailey's Peak matches the species in other respects, notably the ribbed leaves, and perianth tube 15–20 mm long, and we regard it as a local, montane form.

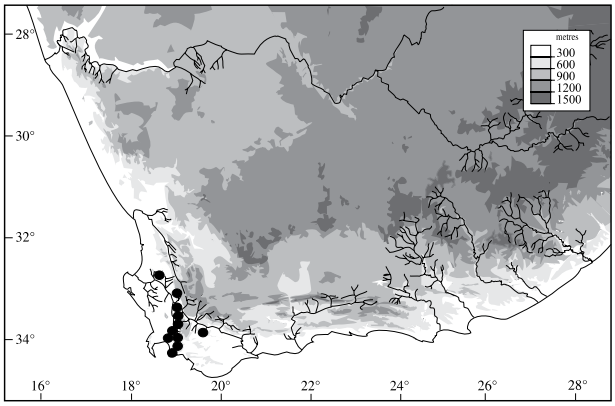

FIGURE 14.—Known distribution of *Thereianthus spicatus*, ●.

The moderately long-tubed flowers are evidently adapted to pollination by correspondingly long-tongued insects, and we have seen the species being visited by the butterfly *Cynthia cardui* (Nymphalidae) at Jonkershoek. The perianth tube is narrowed towards the base, and nectar wells up for some distance into the tube, where it is accessible to long-tongued anthophorine bees as well, which probably also play a role in pollination.

Diagnosis and relationships: the central species in series *Thereianthus, T. spicatus* is distinguished from the other members of the genus with strongly ribbed leaves (*T. elandsmontanus, T. ixioides* and *T. longicollis*) by flowers with a moderately long perianth tube, (12–)15–18(–25) mm long, usually curved outwards slightly near the tip and dilating gradually and evenly from base to apex. The tepals are relatively large, elliptical-oblanceolate, 10–18 × 3–5 mm, and the stamens are arcuate, with filaments 3–4 mm long. Although usually glabrous, the leaves in some plants are scabridulous along the ribs and margins. This is especially evident in the collection from Piketberg but occurs sporadically elsewhere as well.

Perianth length is more variable in this species than in others, and longer-tubed forms are sometimes misidentified as *Thereianthus longicollis*—both species have been collected in the mountains above Tulbagh Waterfall and above Saron. We have seen both in the field and there is no doubt that they are distinct. Longer-tubed plants of *T. spicatus*, such as those from the Grootwinterhoek Mtns above Porterville with tubes reaching to 25 mm long, are distinguished from *T. longicollis* by their proportionally larger tepals, always less than twice as long as the tube. The critical differences separating *T. spicatus* from the closely allied *T. ixioides* and also from *T. bracteolatus* (ser. *Bracteolatus*), with which it has been confused in the past, are discussed under those species.

History: the earliest known species in the genus, *Thereianthus spicatus*, was first named in the genus *Gladiolus* (Royen 1740; Linnaeus 1753) but subsequently transferred to various other genera, including *Ixia* L., *Watsonia*, *Micranthus* and the invalidly published *Beilia* (Ecklon 1827). This reflects the uncertainty about generic circumscriptions that prevailed for many years. The original collector and date of collection are unknown but the species was evidently cultivated in the botanical gardens at Leiden, The Netherlands, in the 1740s. Forms with narrower leaves were distinguished by Lewis (1941) as var. *linearifolius* but this distinction has no taxonomic merit (Manning & Goldblatt 2004), with individual collections showing a range of leaf widths from 1–3 mm (e.g. *Esterhuysen 13673*).

Nomenclatural note: the species was based by Linnaeus (1753) on the polynomial *Gladiolus foliis linearibus, caule simplicissimo, floribus spicatus* (Royen 1740) but no specimen under this inscription could be located at Leiden (G. Thijsse pers. comm. Nov. 2010) and must be presumed lost—types of the other three *Gladiolus* species listed by Royen (1740) are all at Leiden. Possibly, therefore, no authentic material was available to Linnaeus. A specimen with the binomial *G. spicatus* in the Linnean Herbarium (LINN 59.3) and inferred to have come from Traugott Gerber (fl. 1739–1741) by Jackson (1912), was regarded by Jarvis (2007) as original material. Critically, however, this specimen does not match the protologue, having just a single sheathing leaf, and it cannot therefore be considered to be original material. Although it was identified as the holotype by Manning & Goldblatt (2004), their designation is not nomenclaturally effective in lacking a definitive phrase designating it as a lectotype (Jarvis 2007; Art. 9.21: McNeill *et al.* 2006). Significantly, the specimen is not in fact *T. spicatus* as currently understood, being a species of *Gladiolus*, evidently *G. communis*. The current taxonomic association of the name can be traced to Thunberg (1807) (*UPS-THUNB1072*) but the basis for this remains unknown. We designate a neotype here to fix its application in this sense.

Additional specimens examined

WESTERN CAPE.—3218 (Clanwilliam): Piketberg, suurvlakte [west of Avontuur near top of Versveld Pass], 780 m, (–DC), 23 Dec. 1973, *Linder 187* (BOL). 3318 (Cape Town): Paarl Mtn, near top, (–DB), 2 Dec. 1929, *Grant 5027* (BOL, MO); Penhill, Eersterivier, (–DC), 10 Dec. 1977, *Raitt 288* (NBG); Kuils River, (–DC), Dec. 1931, *Basson s.n. BOL2430* (BOL); Joostenberg, (–DD), 14 Nov. 1965, *Lewis 6222* (NBG); Jonkershoek, (–DD), 11 Dec. 1975, *Kruger 119* (NBG); Jonkershoek Valley, below Berg River Nek, (–DD), 29 Dec. 1989, *Goldblatt 9028* (MO, NBG); Jonkershoek, Swartboskloof, (–DD), 5 Dec. 1960, *Van der Merwe 24-43* (NBG); 15 Jan. 1988, *Forsyth 504* (NBG); Jonkershoek, Dwarsberg, (–DD), 9 Feb. 1959, *Rycroft 2147* (NBG); Stellenboschberg above Coetzenberg, (–DD), Nov. 1992, *De Vos 2739* (NBG); Stellenbosch, Idas Valley, (–DD), 5 Dec. 1925, *Levyns 1458* (BOL). 3319 (Worcester): Groot Winterhoek, road to De Tronk at Groot Kliphuis river crossing, (–AA), 10 Dec. 2007, *Helme 5141* (NBG); Tulbagh, Watervalberge, east of Suurvlak Falls, (–AC), 29 Dec. 2000, *Hansford 21* (NBG); Elandsberg Nature Reserve, Bosplaas trek, (–AC), 18 Nov. 1996, *Parker 114* (NBG); Bainskloof Mtns, Bailey's Peak, (–CA), 21 Feb. 1954, *Esterhuysen 22748* (BOL); Bainskloof, (–CA), 1 Jan. 1941, *Kies s.n. NBG62273* (NBG); Limietberg, (–CA), 6 Jan. 1983, *Goldblatt 6837* (MO, NBG); Wemmershoek Mtns, April Peak, (–CC), 15 Dec. 1940, *Esterhuysen 4098* (BOL); Klein Drakenstein Mtns, upper Kasteelkloof, (–CC), 9 Jan. 1969, *Kruger 879* (NBG); Du Toitskloof, (–CC), Jan. 1882, *Tyson 905* (SAM); 1 Jan. 1950, *Hall 285* (MO, NBG); Elandspad Catchment in Agtertafelberg Kloof, (–CC), 28 Dec. 2000, *Low 6769* (NBG); Zachariaskloof Catchment, (–CC), 28 Dec. 1978, *Kruger 1777* (NBG); Franschhoek Pass, (–CC), Dec. 1929, *Thode A2223* (NBG); 17 Jan. 1939, *Gillett s.n. NBG62371* (BOL, NBG); 25 Jan. 1933, *Pillans 7624* (BOL). 3418 (Simonstown): Somerset West, (–BA), Dec. 1930, *Martley s.n. BOL22440* (BOL); Somerset West, Schaapenberg, (–BA), 14 Nov. 2006, *Helme 4097* (NBG); Helderberg Nature Reserve, Porcupine Buttress, (–BB), 3 Dec. 1993, *Runnalls 639* (NBG); Sir Lowry's Pass, (–BB), 15 Jan. 1896, *Schlechter 7245* (BOL); Dec. 1899, *Bolus 4210* (BOL); 19 Dec. 1942, *Compton 14222* (NBG); near foot of Sir Lowry's Pass, (–BB), 27 Jan. 1993, *Goldblatt & Manning 9567* (MO, NBG); Steenbrasdam, (–BB), 22 Dec. 1983, *De Kock 73* (NBG); Steenbras Forest Reserve, (–BB), 24 Jan. 1951, *Barker 7211* (BOL, NBG); Elgin Forest Reserve, (–BB), Jan. 1951, *Lewis 2906* (SAM); Kogelberg Forest Reserve, Blousteenberg, (–BD), 22 Dec. 1969, *Boucher 972* (NBG); Betty's Bay, (–BD), 13 Dec. 1973, *Vogts s.n. NBG173047* (NBG); Harold Porter Reserve, (–BD), 22 Nov. 1963, *Topper s.n. NBG70755* (NBG); Kogelberg, Oudebosch, (–BD), Dec. 1952, *Stokoe s.n. NBG173067* (NBG); slopes above Palmiet River Mouth, (–AC), 20 Dec. 1934, *Salter 5180* (BOL); 26 Jan. 1947, *Esterhuysen 13673* (BOL, NBG). 3419 (Caledon): Aries Kraal, (–AA), 30 Dec. 1944, *Compton 16823* (NBG); sandy plateau above Viljoens pass, (–AA), 31 Jan. 1986, *Goldblatt 7627* (MO); Palmiet River Mtns, (–AC), Jan. 1947, *Stokoe s.n.* (MO); Genadendal, (–BA), 28 Dec. 1894, *Guthrie 3584* (NBG).

9. **Thereianthus ixioides** *G.J.Lewis* in Journal of South African Botany 7: 41 (1941). Type: South Africa, [Western Cape], Bain's Kloof [Bainskloof] at summit, 8 Dec. 1934, *T.M. Salter 5117* (BOL, holo.!).

Watsonia filifolia E.Mey. in Drège: 82 (1843), nom. nud. [South Africa, Du Toitskloof, without date, *Drège s.n.* (MO)]. *Watsonia punctata* var. *filifolia* E.Mey. ex Baker: 16: 159 (1877), nom. nud.

Plants 250–500 mm high. *Corm* globose, 12–20 mm diam.; tunics of coarsely netted fibres, thickened and claw-like at base, accumulating with age and forming short neck around base of stem. *Stem* erect or flexed outward above second sheath, unbranched, 1.0–1.5 mm diam. below spike. *Cataphylls* dry and papery, reddish brown. *Leaves* 4(5), lowermost inserted below ground, blade reaching or exceeding spike, green or dry at flowering, linear, 200–400 × 1.0–2.0 mm, closely 3-ribbed, upper 3(4) leaves cauline, sheaths of all except uppermost ± imbricate, blades successively shorter, up to 150 mm long, uppermost leaf entirely sheathing, distant from next lower and separated from base of spike. *Spike* erect, compact, densely 6–12-flowered; bracts imbricate for $^{1}/_{2}$ to $^{2}/_{3}$ length, 8–13 mm long and two or three internodes long, outer acute or obtuse, either green below or entirely brown and leathery, conspicuously and closely veined, with narrow membranous margins, inner slightly shorter, bifid, ± membranous with narrow brown zones along veins. *Flowers* suberect, white to pale mauve (rarely mid-blue), unmarked or lower three tepals each with purple marking near base (rarely ± all tepals marked); perianth actinomorphic; tube straight, 7–12(–15) mm long, 0.5–1.0 mm diam. at mouth, filiform and tightly clasping style throughout, abruptly expanded in distal 1 mm, exserted 1–9 mm beyond bracts, 0.5–1.0 × as long as tepals; tepals elliptical-oblanceolate, spreading and slightly cupped or flat, 12–15 × 4–6 mm. *Stamens* central, erect or diverging apically with anthers spreading; filaments 3–4 mm long, swollen slightly at base and occluding mouth of perianth tube; anthers 5–7 mm long, lilac or pale yellow; pollen cream-coloured. *Ovary* obovoid, 2.0–2.5 mm long; style central, dividing between base and middle of anther, branches ± 3–4 mm long, divided to near base. *Capsules* ovoid, 7–10 × 3–5 mm. *Seeds* ellipsoid-angled, 2–3 mm long, yellowish brown testa striate-colliculate. *Flowering time*: late Nov.–Dec. or early Jan. Figure 15.

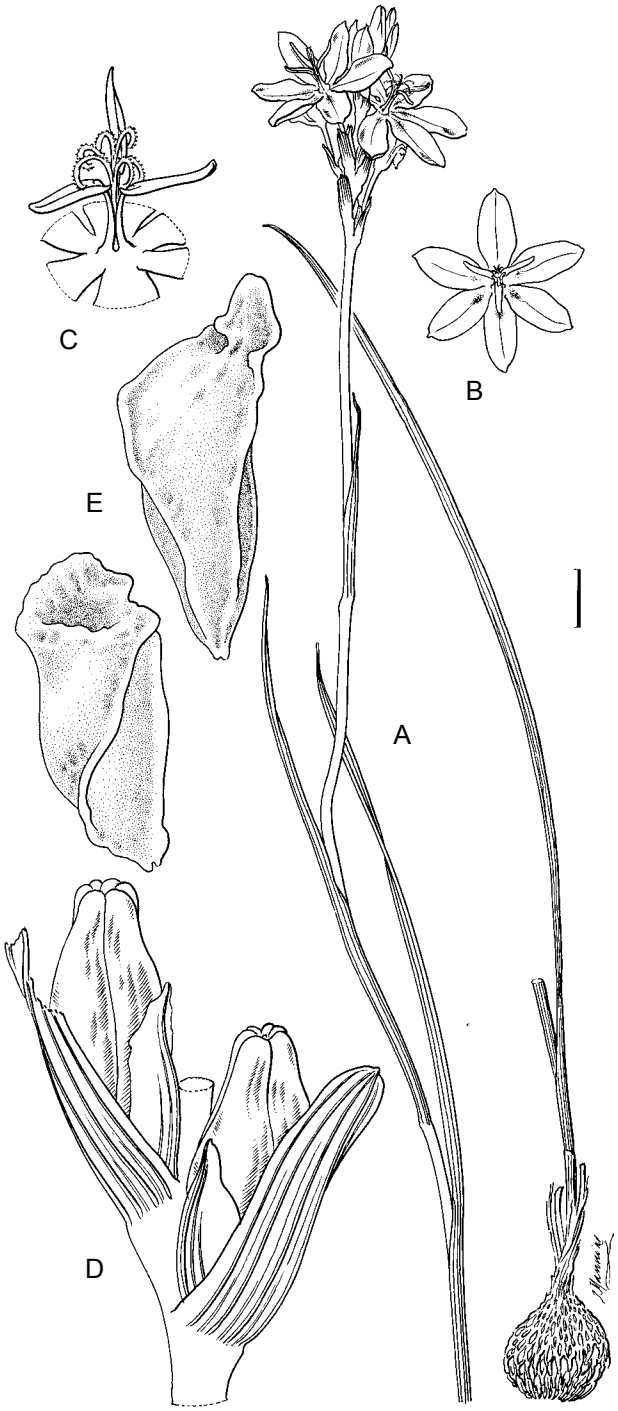

FIGURE 15.—*Thereianthus ixioides*. A–C, *Manning 2198*: A, whole plant; B, flower, front view; C, details of stamens and stigma. D, E, *Manning 3326*: D, capsules; E, seeds. Scale bar: A, B, 10 mm; C, 3 mm; D, 2 mm; E, 0.5 mm. Artist: John Manning.

Distribution and ecology: *Thereianthus ixioides* is a narrow endemic of the mountains between Wellington and Franschhoek, with most collections predictably from the Bainskloof and Du Toitskloof Passes that traverse the Limietberg and Klein Drakenstein Mtns respectively, and from the Zachariaskloof catchment in the Wemmershoek Mtns (Figure 16). Plants are locally common on cooler, south-facing sandstone slopes at mid altitudes, mainly around 1 000 m, often in seasonally damp places, along drainage lines or water courses. Flowering is stimulated by fire but plants also bloom in open veld several years old.

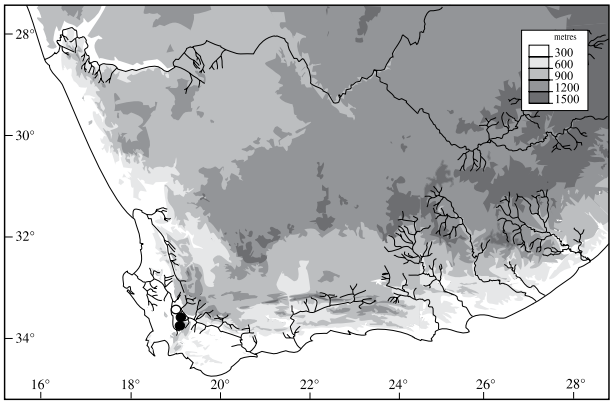

FIGURE 16.—Known distribution of *Thereianthus ixioides*,●; *T. elandsmontanus*, ○.

The compact spikes of white to lilac (rarely blue), actinomorphic flowers are probably adapted to a generalist pollination system and visited by a variety of insects. The filiform perianth tube clasps the style tightly for most of its length, with the mouth occluded by the swollen bases of the filaments. Each flower produces only trace amounts of nectar, which rises to the mouth of the filiform perianth tube through capillary action, where it can be accessed by insects with short mouthparts. The flowers have a remarkable similarity in shape, colour and markings to those of *Ixia metelerkampiae*, another local endemic of the mountains near Wellington and visits by the hopliine beetle (Scarabaeidae: Hopliini), *Peritrichia* sp., to both species were reported by Goldblatt *et al.* (2000). Visits by hopliine beetles (*Heterochelus* sp.) have also been observed at Franschhoek Pass (R. Saunders, pers. comm. Jan. 2011), and pollination by these beetles may be the primary strategy.

Diagnosis and relationships: *Thereianthus ixioides* is recognized by its compact, subcapitate spike of actinomorphic, white or pale lilac (rarely mid-blue) flowers with filiform, straight perianth tube 7–12(–15) mm long and up to 1 mm diam., tightly clasping the style for most of its length and abruptly dilated only in the distal 1 mm, with the filaments thus completely exserted. The stamens are symmetrically arranged, with ± horizontally spreading anthers, and the filaments occlude the mouth of the perianth tube. It has been confused with *T. spicatus* but that species has a mostly longer, ± cylindrical perianth tube (12–)15–25 mm long that is evenly and gradually dilated from the base and not tightly clasping the style, and unilateral, arcuate stamens, with the base of the filaments shortly included within the top of the perianth tube and not occluding the mouth.

History: *Thereianthus ixioides* appears to have been first collected in Du Toitskloof by botanical collector Johann Franz Drège, who was active in the southwestern Cape from 1826–1834. This material was distributed under the name *Watsonia filifolia* E.Mey., and although published by Meyer (Drège 1843), the name was not accompanied by a description and is thus nomenclaturally illegitimate. It was later treated as a variety of *T. spicatus* by Baker (1877) under the name *W. punctata* var. *filifolia*. Our association of the name *W. filifolia* with *T. ixioides* is based on a duplicate of the Drège collection bearing this name in the herbarium of the Missouri

Botanical Garden (MO). The species was re-collected from the same locality half a century later in 1882 by the botanist William Tyson. His material, also identified as *Watsonia punctata* (now *T. bracteolatus*), raised no interest. The next collection, that of Adele Grant made in Bainskloof in 1926 was, however, recognized as representing a new species of *Watsonia* (the genus to which species of *Thereianthus* were then customarily referred), an opinion that was confirmed when T.M. Salter, specialist on the genus *Oxalis*, also came across it in Bainskloof in December 1934. The species was subsequently described by Lewis (1941) in her newly established genus *Thereianthus*, based largely on Salter's ample material, and remained the most recent species to be recognized in the genus for more than half a century (Manning & Goldblatt 2004).

Additional specimens examined

WESTERN CAPE.—3319 (Worcester): Bain's Kloof [Bainskloof], (–AC), 26 Nov. 1926, *Grant 2644* (BOL, MO); Dec. 1957, *Loubser 865* (NBG); Limietberg, north of Bain's Kloof [Bainskloof], 3000' [914 m], (–CA), 6 Jan. 1983, *Goldblatt 6837* (MO, NBG); Bainskloof, just before summit, (–AC), 26 Nov. 1998, *Manning 2198* (NBG); Baviaanskloof, above pools in middle of valley, (–CA), 15 Jan. 2011 [fruiting], *Manning 3326* (NBG); Klein Drakenstein, Haalhoek Spitzkop, (–CC), 2 Jan. 1947, *Esterhuysen 13541* (BOL); Klein Drakenstein Mtns, 1.5 km SE Hugenootskop, (–CC), 14 Jan. 2007, *Helme 4510* (NBG); Du Toitskloof, (–CC), Oct.–Jan, without year [1826–1834], *Drège s.n.* (MO); 1882 [without month], *Tyson 904* (SAM); Dec. 1950, *Lewis 2292* (SAM); 10 Dec. 1950, *Barker 7166* (NBG); Dec. 1951, *Stokoe s.n. SAM63513* (SAM); Wemmershoek Valley, Dec. 1944, *Lewis 849* (SAM); Wemmershoek, (–CC), 14 Dec. 1940, *Esterhuysen 4039* (BOL); Haalsneeuwkop, 4000' [1 220 m], (–CC), Dec. 1944, *Stokoe s.n. SAM56189* (SAM); near Pofadder Pool on Elandspad River, (–CC), 24 Nov. 1985, *Fischer s.n. NBG133017* (NBG); Du Toitskloof Mtns, Elandspad catchment in Agtertafelberg Kloof, 1 020 m, (–CC), 28 Dec. 2000, *Low 6773* (NBG); Zachariashoek, Kasteelkloof catchment, (–CC), 2100' [640 m], 14 Dec. 1972, *Smith 69* (NBG); 30 Dec. 1982, *Viviers 1122* (NBG); Zachariashoek catchment, (–CC), 18 Dec. 1969, *Haynes 260* (NBG).

10. **Thereianthus elandsmontanus** *Goldblatt & J.C.Manning*, sp. nov.

Plantae 140–240 mm altae, cormo globoso 10–15 mm diam., tunicis fibrosis crassis, caule erecto eramoso, cataphyllis papyraceis rubro-brunneis, foliis 4, infimum sub terra insertum laminis linearibus 3- vel 4-nervosis, spica erecta dense 7- ad 15-flora, bracteis imbricatis 8–10(–13) mm longis, bractea externa infra viridi vel omnino brunnea coriacea, interna pauciter breviore, floribus cremeis ad pallide carneis tepalis inferioribus in medio marroninis striatis, perianthio leviter zygomorpho, tubo (17–) 20–23 mm longo cylindrico, tepalis lineari-oblanceolatis patentibus pauciter cupulatis 12–15 × 2–3 mm, staminibus unilateralibus arcuatis, filamentis 4–5 mm longis ex tubo 2–3 mm exsertis, antheris 4 mm longis atropurpureis, styli ramis fere ad basem furcatis ± 3 mm longis.

TYPE.—Western Cape, 3319 (Worcester): Bo-Hermon, Elandsberg Nature Reserve, Slangkop, low sandstone ridge, two years after fire, (–AC), 7 Nov. 2010, *J.C.Manning 3313* (NBG, holo.; MO, iso.).

Plants 140–240 mm high. *Corm* globose, 10–15 mm diam.; tunics of coarse, matted fibres, accumulating with age and forming short neck around base of stem. *Stem* erect, unbranched, ± 1.5 mm diam. below spike. *Cataphylls* dry and papery, reddish brown. *Leaves* 4, lowermost inserted below ground, blade exceeding spike, ± dry at flowering, linear, 200–250 × 2–3 mm, closely 3- or 4-ribbed, upper 3 leaves cauline, sheaths ± imbricate and enveloping entire stem, blades successively shorter, up to 100 mm long, uppermost leaf sheath ± reaching to base of spike, with short blade 20–30 mm long. *Spike* erect, densely 7–15-flowered; bracts imbricate for $^{1}/_{2}$ to $^{2}/_{3}$ length, 8–10(–13) mm long and two or three internodes long, outer acute, either green below or entirely brown and leathery, conspicuously and closely veined, with narrow membranous margins, inner bract slightly shorter, bifid, ± membranous with narrow brown zones along veins. *Flowers* suberect, cream-coloured to pale flesh-pink, flushed purple on tube, lower three tepals with median linear maroon streak extending halfway along blade; perianth weakly zygomorphic; tube slightly curved outwards in distal 3 mm, (17–)20–23 mm long, ± 1.5 mm diam. at mouth, ± cylindrical but widening slightly distally, exserted 13–15 mm beyond bracts; tepals linear-oblanceolate, inner three slightly smaller, spreading and slightly cupped, 12–15 × 1.5–3.0 mm. *Stamens* arcuate; filaments 4–5 mm long, exserted 2–3 mm from tube; anthers 4 mm long, blackish purple; pollen purple. *Ovary* obovoid, 2.0–2.5 mm long; style arching above anthers, dividing between base and middle of anthers, branches, ± 3 mm long, divided to near base. *Capsules* narrowly ovoid, 5–7 × 3 mm. *Seeds* ellipsoid-angled, ± 2 mm long, yellowish brown, testa striate-colliculate. *Flowering time*: Nov. Figure 17.

Distribution and ecology: *Thereianthus elandsmontanus* is known from a single small population on Slangkop, a low sandstone ridge on Elandsberg Nature Reserve near the foot of the Elandskloof Mtns near Hermon (Figure 16). Just a couple of dozen individuals were found. Although only discovered two years after a fire had cleared the site, it is clear that the species also flowered in the first year after the burn since one of the individuals had the remains of a previous flowering stem still associated with the corm.

The moderately long-tubed, cream-coloured to flesh-pink flowers with conspicuous narrow, maroon markings on the lower three tepals bear a striking resemblance to those of several co-occurring species of Iridaceae, notably *Lapeirousia anceps* (L.f.) Ker Gawl. and *Tritonia undulata* (Burm.f.) Baker, that are adapted to pollination by long-proboscid tabanid flies in the genus *Philoliche*, and it is likely that *Thereianthus elandsmontanus* is also a member of this pollination guild.

Diagnosis and relationships: *Thereianthus elandsmontanus* is distinguished from the other ribbed-leaved species in the genus (ser. *Thereianthus*), by its cream-coloured to pale flesh-pink flowers with moderately long tube, 17–23 mm long and 1.5–1.8 × as long as the narrow, ± linear tepals which are 1.5–3.0 mm wide, the lower three each with a conspicuous maroon median streak extending over the lower half. Unfortunately the flowers do not retain their colour in the herbarium, drying bluish lilac. *T. elandsmontanus* is most likely to be confused with *T. spicatus*, which has a tube of similar length and which also occurs at Elandsberg Nature Reserve but this species has blue (rarely white or pink flowers) with broader, lanceolate tepals, 3–5 mm wide, the lower three marked with a white flash at the base

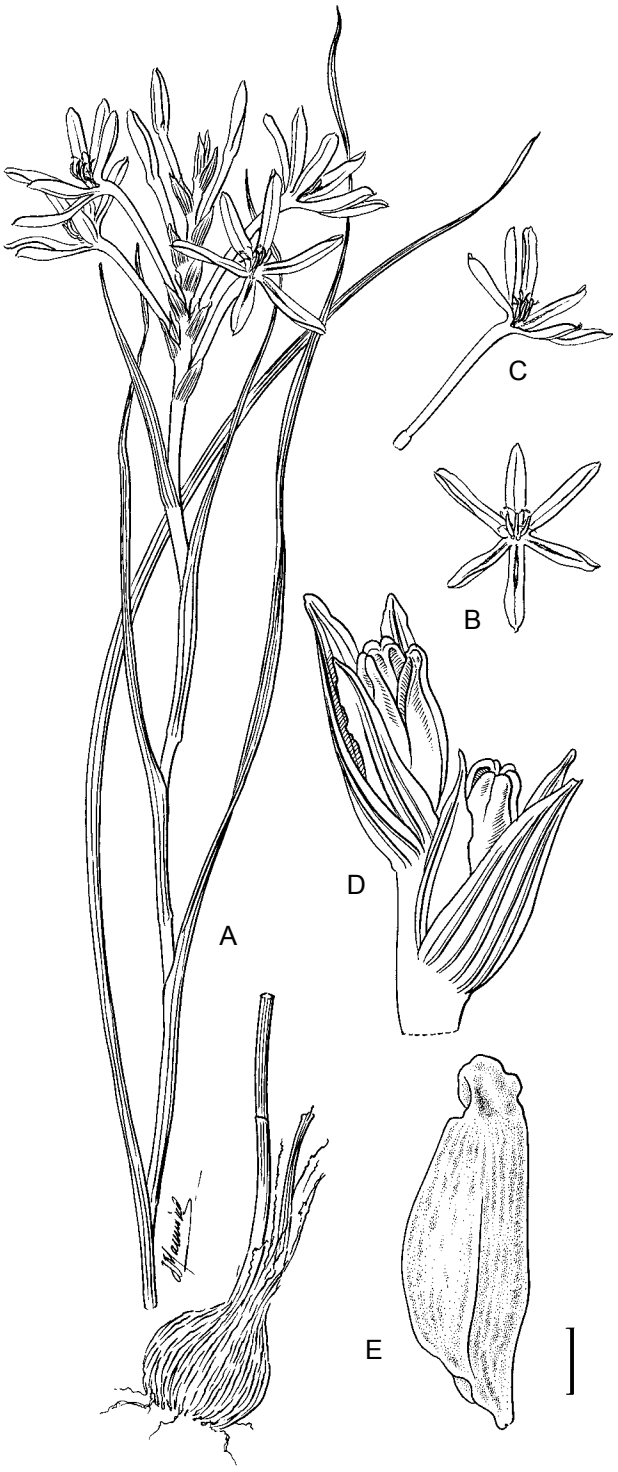

FIGURE 17.—*Thereianthus elandsmontanus, Manning 3313*. A, whole plant; B, flower, front view; C, flower, side view; D, capsules; E, seed. Scale bar: A–C, 10 mm; D, 2 mm; E, 0.5 mm. Artist: John Manning.

bordered distally by a small blue chevron, and slightly shorter filaments, 3–4 mm long vs 4–5 mm long. Although these differences may seem minor, we are familiar with both species on the reserve and are convinced that they are distinct. Another related species, *T. longicollis* from the nearby Saronsberg and Elandskloof Mtns, has a much longer tube, 25–40 mm long and 2.0–2.5 × longer than the tepals, the lower three of which are marked with a dark, transverse chevron. The leaves in *T. elandsmontanus* are often slightly broader than in *T. longicollis*, 2–3 mm vs 1–2 mm, with 3 or 4 vs consistently 3 raised veins. We considered the possibility that the Elandsberg plants might be an isolated, short-tubed form of this species, possibly recognizable at subspecific rank but the consistent morphological and ecological differences between them suggest that recognition at species level is more appropriate. Typical *T. longicollis* is a montane species and the clear separation in tube length between it and *T. elandsmontanus* argues for complete genetic isolation between them.

History: the most recently discovered species in the genus, *Thereianthus elandsmontanus* was collected for the first time in November 2010 on a low sandstone ridge on Elandsberg Nature Reserve. This ridge has been explored botanically since 1996 by the owners of the property, Dale and Elizabeth Parker, but the species was only noticed when it flowered in response to a controlled burn of the ridge in early 2008.

Etymology: the name derives from the Elandsberg Nature Reserve, where the species appears to be endemic.

11. **Thereianthus longicollis** *(Schltr.) G.J.Lewis* in Journal of South African Botany 7: 39 (1941). *Watsonia longicollis* Schltr.: 106 (1900). Type: South Africa, [Western Cape], Tulbagh Waterfall, in saxosis, ± 1200' [365 m], 10 Nov. 1896, *R. Schlechter 9055* (B, holo.; BOL!, GRA!, MO!, PRE! (4 sheets), iso.).

Watsonia punctata var. *longicollis* Baker: 177 (1892). Type: South Africa, [Western Cape], Worcester [District], *Zeyher s.n. K400455* (K, holo.!).

Plants 150–350 mm high. *Corm* globose, 10–15 mm diam.; tunics of coarsely netted fibres, thickened and claw-like at base, accumulating with age and forming short neck around base of stem. *Stem* erect, unbranched, ± 1.5 mm diam. below spike. *Cataphylls* dry and papery, reddish brown. *Leaves* 4, lowermost inserted below ground, blade reaching or exceeding spike, ± dry at flowering, linear, 200–250 × 1–2 mm, closely 3-ribbed, upper 3 leaves cauline, sheaths ± imbricate and enveloping entire stem or slightly distant, blades successively shorter, up to 150 mm long, uppermost leaf sheath reaching to base of spike or separated from it, with short blade 20–60 mm long. *Spike* erect, densely 7–15(–20)-flowered; bracts imbricate for $^{1}/_{2}$ to $^{2}/_{3}$ length, 8–12(–17) mm long and two or three internodes long, outer acute, either green below or entirely brown and leathery, conspicuously and closely veined, with narrow membranous margins, inner slightly shorter, bifid, ± membranous with narrow brown zones along veins. *Flowers* suberect, white or pale pink to purple-pink with purple tube, lower three tepals each with purple chevron or diamond-shaped markings near base; perianth weakly zygomorphic; tube slightly curved outwards in distal 3 mm, 25–40 mm long, ± 2 mm diam. at mouth, ± cylindrical but dilated slightly distally, exserted 20–30 mm beyond bracts, 2.0–2.5 × longer than tepals; tepals oblong-oblanceolate, inner three slightly smaller, spreading and slightly cupped, 12–17 × 2.5–5.5 mm. *Stamens* arcuate; filaments 6 mm long, exserted 3 mm from tube; anthers 4–6 mm long, purple; pollen purple. *Ovary* obovoid, 2.0–2.5 mm long; style arching above anthers,

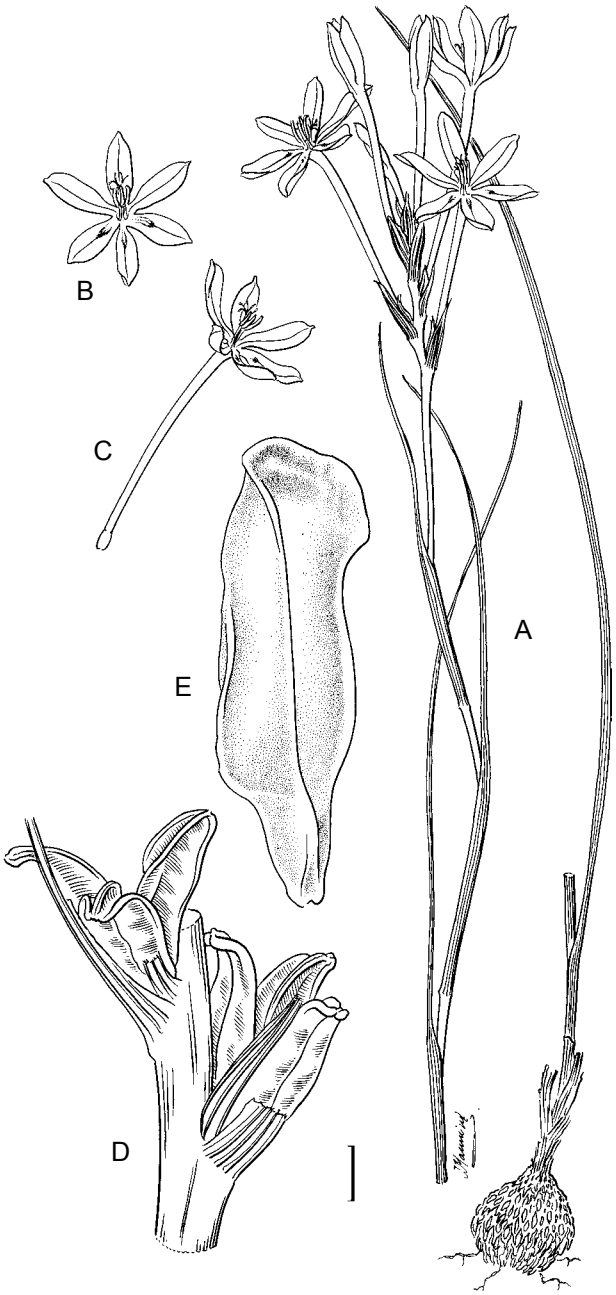

FIGURE 18.—*Thereianthus longicollis, Manning 3325*. A, whole plant; B, flower, front view; C, flower, side view; D, dehisced capsules; E, seed. Scale bar: A–C, 10 mm; D, 2 mm; E, 0.5 mm. Artist: John Manning.

dividing at ± middle of anthers, branches ± 4–5 mm long, divided to near base. *Capsules* narrowly ovoid, 6–7 × 2.5–3.0 mm. *Seeds* ellipsoid-angled, ± 2.5 mm long, yellowish brown, testa striate-colliculate. *Flowering time*: mostly mid-Nov.–late Dec. Figure 18.

Distribution and ecology: *Thereianthus longicollis* is a narrow endemic of the mountains between Porterville and Wolseley (Figure 19), thus including the southern end of the Grootwinterhoek Mtns, Saronsberg and the Elandskloof Mtns. The species has been collected several times at the type locality near the Tulbagh Waterfall but is otherwise known from just a few records to the north above Saron and Porterville, and most recently from Elandsberg Nature Reserve on the lower western slopes of the Elandskloof Mtns. Plants grow in sandy gravel or loamy ground on rocky sandstone slopes, and flower regularly in open proteoid or restioid fynbos.

The very long-tubed, pink or purple-pink flowers with purple markings on the lower three tepals have the stereotypical adaptations for pollination by long-proboscid flies. At or near the type locality above Tulbagh Waterfall we observed pollination visits by the tabanid fly, *Philoliche rostrata*, the proboscis of which measured ± 40 mm, a close match to the tube length in *Thereianthus longicollis*. At this site other representatives of this pollination guild included *T. minutus*, *Geissorhiza confusa* (Iridaceae) and a long-tubed and large-flowered race of *Lobelia coronopifolia* (Lobeliaceae) with a pink corolla.

Diagnosis and relationships: *Thereianthus longicollis* is separated from all other species in the genus by its unusually long perianth tube, 25–40 mm long and 2.0–2.5 times longer than the tepals. The species could only be confused with longer-tubed forms of *T. spicatus*, which have also been recorded from the mountains above Porterville and which we have seen ourselves above Tulbagh Waterfall but the perianth tube in *T. spicatus* is shorter, mostly less than 20 mm long (rarely up to 25 mm) and always less than twice as long as the tepals, and also narrower, at most 1.5 mm diam. at the mouth. A second species in ser. *Thereianthus* with long-tubed flowers, *T. elandsmontanus* from the foothills of the Elandskloof Mtns, has a consistently shorter perianth tube, 17–23 mm long, narrower tepals 2–3 mm wide, with the lower half largely covered by linear purple markings, and often broader leaves with 3 or 4 ribs (see that species for further discussion).

History: *Thereianthus longicollis* was first encountered by botanical collectors Christian Frederick Ecklon and Carl Ludwig Zeyher, who were active in the Cape Colony through the middle of the nineteenth century (Glen & Germishuizen 2010). Their material from Tulbagh Waterfall was distributed under the name *Watsonia* (*Beilia*) *triticea* (now *T. bracteolatus*) and the taxon was first formally recognized as a long-tubed variant of *T. bracteolatus* under the name *Watsonia punctata* var. *longicollis* by Baker (1892, 1896). Although no material was initially listed under this variety, Baker (1896) later cited *Zeyher s.n.* under this name, thereby typifying it unambiguously against a specimen bearing that inscrip-

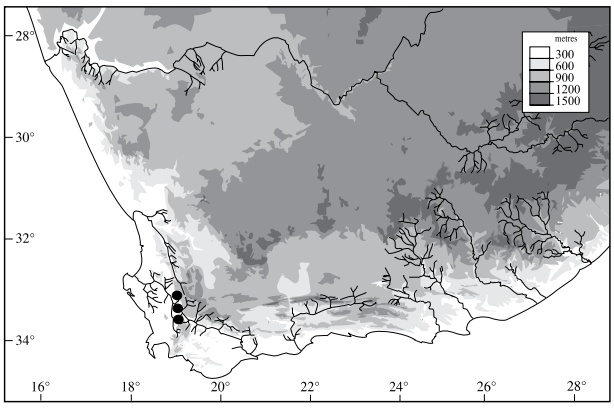

FIGURE 19.—Known distribution of *Thereianthus longicollis*, ●.

tion at the Kew Herbarium, which had been acquired on 1 April 1865 from H.G. Reichenbach. The species was subsequently re-collected at Tulbagh Waterfall on 10 November 1896 by botanist Rudolph Schlechter, who realized that Baker was incorrect in associating the plants with *T. bracteolatus* and described it as a distinct species under the name *W. longicollis*, citing only his collection. Although the labels on his specimens indicate that Schlechter had initially intended to recombine Baker's variety at specific rank, the name as later published is presented as a new species and we treat it as such.

Additional specimens examined

WESTERN CAPE.—3319 (Worcester): Twenty Four Rivers, (–AA), without date, *Zeyher 1608* [only one of the specimens as indicated on sheet] (SAM); De Hoek Estate, near Saron, (–AA), Nov. 1941, *Stokoe s.n. SAM55617* (SAM); slopes of Great Winterhoek Mtns near Saron, (–AA), Nov. 1941, *Stokoe s.n.* (BOL); Porterville, plateau above [Farm] Gelukwaards, (–AA), Dec. 1910, *Edwards 80* (BOL); Bo-Hermon, Elandsberg Nature Reserve, lower slopes of Elandskloof Mtns at southern boundary of farm at end of fence-road, (–AC), 5 Dec. 2010, *Manning 3325* (NBG); Tulbagh Waterfall, (–AC), Nov. without year, *Ecklon & Zeyher s.n. SAM70719* (SAM); 16 Nov. 1941, *Compton 12413* (NBG); [Elandskloof Mtns], Ontongsberg [Ontongskop], lower slopes, (–AC), 16 Nov. 1941, *Isaac s.n.* (BOL); Voëlvleiberge [Elandskloofberge], ascent to Protea plain, (–AC), 29 Dec. 2000, *Hansford 20* (NBG).

EXCLUDED SPECIES

Beilia spicata var. *brevifolia* Kuntze: 305 (1898). Type: South Africa, [Western Cape], Mowbray bei Capstadt, collector and date unknown (specimen not located). The brief description of this taxon '*foliis brevibus 1–2 cm latis acuminatis*' and its collection at Mowbray, a suburb of Cape Town, make it certain that it is not *Thereianthus spicatus*, which has much narrower leaves and is absent from the Cape Peninsula. The only possibility in *Thereianthus* is thus *T. bracteolatus* but the broad leaves are inconsistent with this species as well and suggest that it might be a species of *Watsonia* but its identity remains unclear.

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