

**CYANIXIA, A NEW GENUS FOR THE SOCOTRAN
ENDEMIC *BABIANA SOCOTRANA*
(*IRIDACEAE–CROCOIDEAE*)**

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The sub-Saharan and mainly western southern African genus *Babiana* (*Iridaceae–Crocoideae*) is morphologically diverse, containing some 80 species. The Socotran *B. socotrana*, which differs from all other members of the genus *inter alia* in its trisulcate pollen grains, basic chromosome number, $x=10$, corms of axillary origin, and globose, colliculate–tuberculate seeds, is here excluded from *Babiana* and referred to the new genus *Cyanixia*. Other *Babiana* species have monosulcate pollen grains with a two-banded operculum, a basic chromosome number of $x=7$, terminal corm ontogeny, and derived pear-shaped seeds with a smooth glossy surface. *Cyanixia socotrana* was previously assigned to *Babiana* because of superficial similarities in morphology, including plicate leaves and blue flowers, thought at the time to be bilabiate, although now known to be actinomorphic and rotate. DNA sequence analysis using the chloroplast gene *matK* confirms that *Babiana* is a monophyletic assemblage, whereas *B. socotrana* is sister to the *Lapeirousia/Savannosiphon* clade of sub-Saharan Africa. The latter shares axillary corm ontogeny with the southern African *Micranthus*, *Thereianthus*, and *Watsonia*, in contrast to the more common situation in *Crocoideae* (including *Babiana*) in which the corm develops from the base of the flowering stem. The tropical African *Zygotritonia*, which also has axillary corm development, shares with *Cyanixia* a trisulcate pollen grain, but it differs markedly from that genus in its small, zygomorphic flower, undivided style, and basic chromosome number $x=8$. *Cyanixia* is here described as a new monotypic genus of *Crocoideae*, probably most closely allied to *Savannosiphon*, also a monospecific genus.

Keywords. *Babiana*, biogeography, *Crocoideae*, *Cyanixia* gen. nov., *Iridaceae*, Socotra, systematics.

INTRODUCTION

Babiana Ker Gawl. (*Iridaceae–Crocoideae* [syn. *Ixioidae*]), a genus of some 80 species (Lewis, 1959; Goldblatt & Manning, 2000 and unpublished data), is centred in western southern Africa, an area of winter rainfall and summer drought. A few species occur outside this climatic zone, and one, *B. hypogaea* Burch., extends

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to eastern South Africa, Botswana, Namibia, Zambia, and Zimbabwe. *Babiana socotrana* Hook.f., described by J.D. Hooker in 1881 from the Indian Ocean island of Socotra, has long seemed geographically misplaced in *Babiana*, but it was nevertheless included by G.J. Lewis in her 1959 monograph of the genus. As part of a systematic study of *Babiana* begun in 1999, the present authors examined living plants of *B. socotrana* grown at Kirstenbosch Botanical Garden, South Africa (Fig. 1). The vegetative morphology and appearance of the flowers led us to question its generic placement and to examine the taxonomically critical aspects of the plant, including pollen morphology, leaf anatomy, corm ontogeny, and chromosome number. All of these features disagree with *Babiana*, and a DNA sequence study of the genera of *Crocoideae*, using the chloroplast gene *matK*, confirms our conclusion that *B. socotrana* is misallied generically. We describe it here as the new genus *Cyanixia* Goldblatt & J.C. Manning, containing the single species *C. socotrana* (Hook.f.) Goldblatt & J.C. Manning, endemic to Socotra.

MATERIALS AND METHODS

Voucher information for plants studied is given in Table 1.

Cytology

Root tips were harvested from healthy plants (*Miller* 10146) grown at the Royal Botanic Garden Edinburgh (RBGE). Tips were pretreated before spreading on glass slides for chromosome examination using a standard squash technique (Jong, 1993).

Pollen morphology

Pollen grains taken from anthers of fresh flowers (*Lavranos et al.* 30806) were mounted directly on glass slides in Calberla's fluid (Ogden *et al.*, 1974). After about 24 hours exine stains pink and can readily be distinguished from the apertural membrane. Calberla's fluid maintains grains in a hydrated state and preparations last for several weeks, or longer if coverslip edges are sealed using nail varnish.

Leaf anatomy

Portions of fresh leaves (*Lavranos et al.* 30806) were fixed in FAA, stored in 70% ethanol, and when ready for examination dehydrated in a graded ethanol-toluene series and embedded in wax. Sections made at 12µm were double-stained in toluene blue and safranin following established procedures (Rudall, 1983).

Seed morphology

Seeds of two *Babiana* species, representative of the genus as a whole (Table 1), as well as those of *B. socotrana*, were examined using a scanning electron microscope

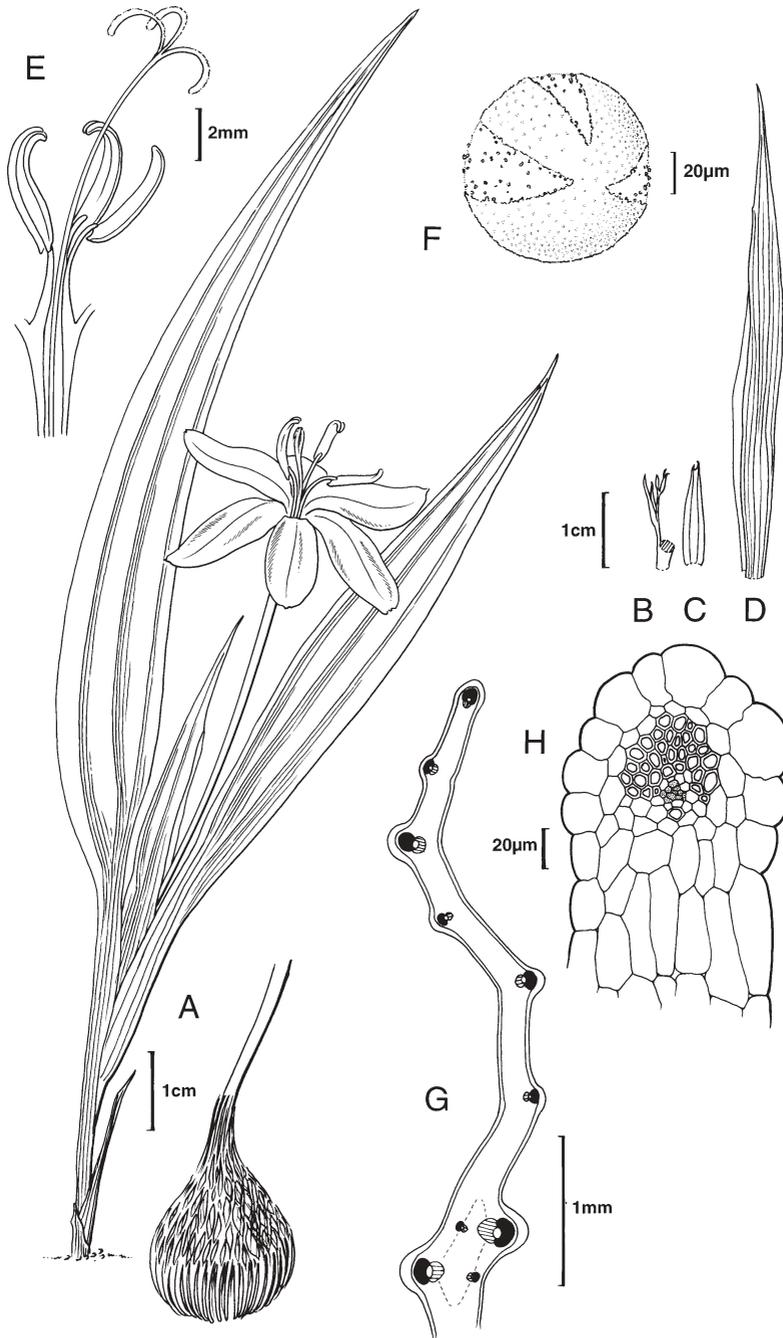


FIG. 1. Morphology and anatomy of *Cyanixia socotrana*. A, whole plant and corm; B, spike (lower flower excised); C, inner bract; D, outer bract; E, detail of stamens, style, and style branches; F, pollen grain; G, transverse section of half a leaf blade (sclerenchyma cap solid black, xylem parallel lines); H, detail of leaf margin, showing marginal epidermis and subepidermal sclerenchyma cap associated with a marginal vein. Drawn by John Manning.

TABLE 1. Collection data for the plants studied (acronyms indicate herbarium in which voucher is housed)

Species	Study site	Voucher
Seed morphology and corm morphology:		
<i>Babiana curviscapa</i> G.J. Lewis	S Africa, N Cape, Kamiesberg	Goldblatt & Manning 10007 (MO, NBG)
<i>B. mucronata</i> (Jacq.) Ker Gawl.	Western Cape, Olifants River valley	Goldblatt & Manning 10937 (MO, NBG)
<i>Cyanixia socotrana</i>	Socotra, Hamaderoh ridge	Lavranos <i>et al.</i> 30806 (MO)
Cytology:		
<i>Cyanixia socotrana</i>	Socotra, limestone plateau above Noged plains	Miller s.n. RBG Edinburgh 1996/2351 (E)
DNA:		
<i>Anomatheca laxa</i> (Thunb.) Goldblatt		Chase I-1 (K)
<i>Aristea glauca</i> Klatt		Goldblatt 9500 (MO)
<i>Babiana ambigua</i> (Roem. & Schult.) G.J. Lewis		Goldblatt 11464 (MO)
<i>B. attenuata</i> G.J. Lewis		Goldblatt & Manning 11323 (MO)
<i>B. crispa</i> G.J. Lewis		Goldblatt & Manning 11077 (MO)
<i>B. cuneata</i> Goldblatt & Manning ms		Goldblatt & Manning 11457 (MO)
<i>B. curviscapa</i> G.J. Lewis		Goldblatt & Manning 11326 (MO)
<i>B. ecklonii</i> Klatt		Goldblatt & Manning 9958 (MO)
<i>B. fimbriata</i> Klatt		Goldblatt 11452 (MO)
<i>B. framesii</i> L. Bolus		Nanni s.n. (MO)
<i>B. leipoldtii</i> G.J. Lewis		Goldblatt 11416 (MO)
<i>B. lineolata</i> Klatt		Goldblatt 11631 (MO)
<i>B. lobata</i> G.J. Lewis		Goldblatt & Manning 9901 (MO)
<i>B. melanops</i> Goldblatt & Manning ms 1		Goldblatt 11577 (MO)
<i>B. melanops</i> Goldblatt & Manning ms 2		Goldblatt & Manning 10239 (MO)
<i>B. minuta</i> G.J. Lewis		Lewis 2322 (NBG)
<i>B. nana</i> (Andr.) Spreng.		Goldblatt 11549 (MO)
<i>B. odorata</i> L. Bolus		Goldblatt & Manning 11418 (MO)
<i>B. papyracea</i> Goldblatt & Manning ms		Goldblatt 11611 (MO)
<i>B. patersoniae</i> L. Bolus		Goldblatt & Manning 9954 (MO)
<i>B. pubescens</i> (Lam.) G.J. Lewis		Goldblatt & Manning 9907 (MO)
<i>B. purpurea</i> (Jacq.) Ker Gawl.		Goldblatt 11533 (MO)
<i>B. pygmaea</i> (Burm.f.) N.E. Br.		Goldblatt & Manning 11415 (MO)
<i>B. regia</i> (G.J. Lewis) Goldblatt & Manning ms		Goldblatt & Manning 11558 (MO)

TABLE 1. (Cont'd)

Species	Study site	Voucher
<i>B. ringens</i> (L.) Ker Gawl.		Goldblatt s.n. no voucher
<i>B. rubrocyanea</i> (Jacq.) Ker Gawl.		Goldblatt & Manning 11555 (MO)
<i>B. sambucina</i> (Jacq.) Ker Gawl.		Goldblatt 11465 (MO)
<i>B. scabrifolia</i> Brehm ex Klatt		Goldblatt & Manning 11322 (MO)
<i>B. scariosa</i> G.J. Lewis		Goldblatt 11614 (MO)
<i>B. sinuata</i> G.J. Lewis		Goldblatt & Manning 9610 (MO)
<i>B. spathacea</i> (L.f.) Ker Gawl.		Goldblatt & Manning 11521 (MO)
<i>B. stricta</i> (Aiton) Ker Gawl.		Goldblatt 11434 (MO)
<i>B. torta</i> G.J. Lewis		Goldblatt & Manning 11374 (MO)
<i>B. aff. torta</i> G.J. Lewis		Goldblatt & Manning 11334 (MO)
<i>B. truncata</i> G.J. Lewis		Goldblatt & Manning 11367 (MO)
<i>B. vanzyliae</i> L. Bolus		Goldblatt 11401 (MO)
<i>B. villosa</i> (Aiton) Ker Gawl.		Goldblatt 11426A (MO)
<i>B. villosula</i> (Gmel.) Ker Gawl. ex Steud.		Goldblatt 11312 (MO)
<i>Chasmanthe aethiopica</i> (L.) N.E. Br.		Chase I-3 (K)
<i>Crocoshia mathewsiana</i> (L. Bolus) Goldblatt ex M.P. de Vos		Goldblatt & Manning 9830 (MO)
<i>Crocus pulchellus</i> Herb.		Chase I-19 (K)
<i>Cyanixia socotrana</i>		Lavrano 30806 (MO)
<i>Devia xeromorpha</i> Goldblatt & J.C. Manning		Snijman & Manning 1194 (MO)
<i>Dierama robustum</i> N.E. Br.		Goldblatt & Manning 9536 (MO)
<i>Duthieastrum linifolium</i> (M.P. de Vos) M.P. de Vos		Manning 2235 (MO)
<i>Freesia alba</i> Baker		Goldblatt 5293 (MO)
<i>Geissorhiza heterostyla</i> L. Bolus		Goldblatt & Manning 9668 (MO)
<i>Gladiolus papilio</i> Hook.f.		Goldblatt & Manning 9841 (MO)
<i>Hesperantha pseudopilosa</i> Goldblatt		Goldblatt & Manning 9677 (MO)
<i>Ixia latifolia</i> D. Delaroché		Goldblatt & Manning 9594 (MO)
<i>Lapeirousia neglecta</i> Goldblatt & J.C. Manning		Goldblatt & Manning 9489 (MO)
<i>Melasphaerula ramosa</i> (Burm.f.) Ker Gawl.		Goldblatt s.n. (MO)
<i>Micranthus junceus</i> N.E. Br.		Chase I-156 (K)
<i>Nivenia corymbosa</i> Baker		Goldblatt s.n. (MO)
<i>Pillansia templemanni</i> L. Bolus		Bean s.n. (MO)
<i>Radinosophon lomatensis</i> N.E. Br.		Goldblatt & Porter s.n. (MO)
<i>Romulea monadelpha</i> (Sweet) Baker		Goldblatt 6230 (MO)
<i>Savannosophon euryphylla</i> (Harms) Goldblatt & Marais		Bolnick s.n. (MO)
<i>Sparaxis variegata</i> (Sweet) Goldblatt		Goldblatt 2460 (MO)

TABLE 1. (*Cont'd*)

Species	Study site	Voucher
<i>Syringodea bifucata</i> M.P. de Vos		Davidson 3108 (MO)
<i>Thereianthus racemosus</i> (Klatt)		Goldblatt 10454 (K)
G.J. Lewis		
<i>Tritonia disticha</i> Baker		Goldblatt & Manning 9545 (MO)
<i>Tritoniopsis unguicularis</i> (Lam.)		Goldblatt 9486 (MO)
G.J. Lewis		
<i>Watsonia angusta</i> Ker Gawl.		Goldblatt 6904 (MO)
<i>Xenoscapa fistulosa</i> (Spreng. ex Klatt)	Goldblatt & J.C. Manning	Chase 11508 (K)

following standard procedures (e.g. Goldblatt & Manning, 1991; Goldblatt *et al.*, 1991).

Corm ontogeny

Origin of the new season's corm was determined by examining corms of living plants (Table 1) at the end of the growing season.

DNA sequencing

Total DNA was extracted according to Reeves *et al.* (2001) and the plastid *matK* exon was amplified according to Soltis & Soltis (1998). DNA sequences were aligned by eye, reaching 1984 characters of which 205 were excluded since no satisfactory alignment could be performed (the aligned matrix is available from V.S. and J.D.). Bootstrap resampling was performed using PAUP 4.0b6 (Swofford, 2001) and consisted of 500 replicates using the tree bisection–reconnection swapping algorithm with 10 trees held at each replicate. See Table 1 for voucher data.

RESULTS

Cytology

Examination of mitotic metaphase shows a chromosome number of $2n=20$ in *Cyanixia socotrana*. The karyotype consists of one long pair of acrocentric chromosomes and nine much shorter acrocentric pairs. The karyotype is strongly asymmetric (*sensu* Stebbins, 1950) and bimodal.

Leaf anatomy

The leaf blade is slightly plicate in transverse section, lacking a pseudomidrib but with one to three primary veins each separated by two or three secondary veins

(Fig. 1G). The epidermal cells are thin-walled and rectangular in transverse section except over the vascular bundles where they are round in section. The mesophyll cells are somewhat elongated across the leaf axis and chlorenchymatous except in the thicker region of the pseudomidrib where they are rounded and parenchymatous. The leaf margins bear a marginal vascular bundle with a sclerenchyma cap at the phloem pole, immediately adjacent to the marginal epidermis (Fig. 1H). The vascular bundles are in two incomplete rows on the angles of the zig-zags formed by the plicate folding. The largest bundles are at the primary veins where they occur in an opposing or oblique pair, accompanied by a single small or tertiary bundle on each side of the pair. The bundles between the primary veins are smaller and are not opposite but arranged in an alternating series of two or three adjacent bundles on one side followed by a similar number on the opposite side. Sclerenchyma caps are present at the phloem poles of all vascular bundles, typically separated from the epidermis by a single hypodermal layer. Although valuable for assessing some generic relationships in *Iridaceae* (Goldblatt, 1990a; Rudall & Goldblatt, 1991), the leaf anatomy of *Cyanixia* conforms to the putative ancestral type for subfamily *Crocoideae* in all aspects apart from being plicate.

Pollen morphology

The pollen grains of *Cyanixia socotrana* are remarkable in the *Iridaceae* in being asymmetrically 3-sulcate. The globose grains, 68–72µm in diameter, have three elliptical sulci running almost their full length. The sulci are not equidistant from one another: the exine between consists of two narrow bands and a broad one (Fig. 1F). The exine is perforate and micropunctate, the plesiomorphic and most common state in *Crocoideae* (Schulze, 1970; Goldblatt *et al.*, 1991). The apertural membrane has a distinct margin and small fragments of exine scattered over the surface. The plesiomorphic condition of pollen grains in *Crocoideae* is monosulcate with a pair of narrow exine bands lying parallel to the long axis of the aperture, sometimes described as an operculum (Goldblatt *et al.*, 1991). This pollen type is the only one known in *Babiana* (Goldblatt *et al.*, 1991 and unpublished data), whereas the pollen of *Cyanixia* recalls that of the tropical African genus *Zygotritonia* Mildbr. (also subfamily *Crocoideae*) which is likewise 3-sulcate but with more or less symmetrical apertures (Goldblatt *et al.*, 1991). Like most other *Crocoideae* the exine of *Zygotritonia* is perforate and micropunctate.

Seed morphology

Seeds of *Cyanixia* (Fig. 2D) are more or less globose with a somewhat flattened chalazal end and measure c.2 × 1.8mm. The surface is smooth in outline but slightly and irregularly wrinkled. The surface cells are clearly delineated, and colliculate to more or less tuberculate. The outer surface is rough (Fig. 2E) and covered with small platelets. Seeds of the two *Babiana* species sampled (Fig. 2A–C), *B. curviscapa*

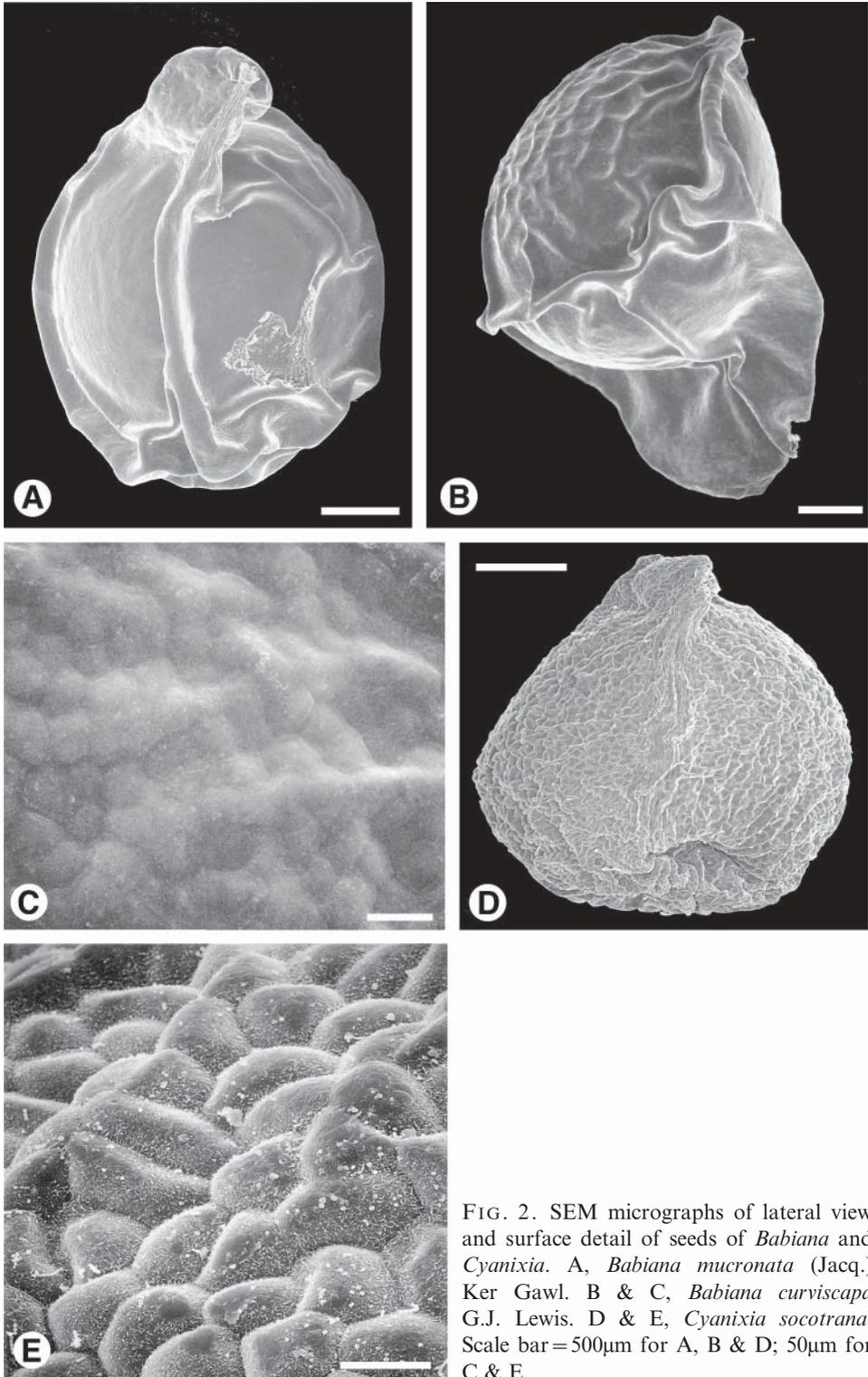


FIG. 2. SEM micrographs of lateral view and surface detail of seeds of *Babiana* and *Cyanixia*. A, *Babiana mucronata* (Jacq.) Ker Gawl. B & C, *Babiana curviscapa* G.J. Lewis. D & E, *Cyanixia socotrana*. Scale bar = 500 μ m for A, B & D; 50 μ m for C & E.

and *B. mucronata*, differ substantially from those of *Cyanixia*, which are pear-shaped in outline, $3-3.5(-4) \times 2-2.5$ mm, with well-developed ridges of seed coat tissue enclosing a rounded seed body. The narrow part of the seed at the micropylar end is composed entirely of seed coat. The surface is lightly rugose or, on some facets, virtually smooth. The surface cells are not delineated but are covered by a glossy, translucent surface layer. There is a weak distinction at the slightly flattened chalazal end of the seed.

Corm ontogeny

New corms develop entirely from an axillary bud, as described for *Watsonia* Miller and *Micranthus* (Pers.) Eckl. (de Vos, 1977). In the plants examined, new corms had developed from more than one of the axillary buds as a means of vegetative reproduction. Axillary corm development (de Vos, 1977; Goldblatt, 1990a) can be recognized by the position of the new corm which develops entirely from an axillary bud near the base of the flowering stem. In the alternative mode of corm ontogeny, which we call terminal development, the new corm is largely formed from tissue at the base of the current flowering stem and it incorporates axillary buds at the lower nodes. As a result, the flowering stem is attached to the new corm near its apex, lateral to the terminal shoot. The site of attachment can often be recognized by a small scar or pit adjacent to the terminal shoot. Terminal corm development occurs in the majority of genera of *Crocoideae*, including *Babiana*.

DNA sequencing

The results of a preliminary DNA sequence analysis of a range of *Iridaceae* genera, including 24 of the 28 genera of *Crocoideae* and 35 species of *Babiana*, using the chloroplast gene *matK* are presented in Fig. 3. In the bootstrap consensus tree the monophyly of *Babiana* is strongly supported (bootstrap support [BS] 100%) in relation to the taxa analysed when *Cyanixia socotrana* is excluded. The latter is sister to *Lapeirousia* Pourr./*Savannosiphon* Goldblatt & Marais on a well-supported clade (BS 97%), which is sister to *Watsonia*/*Pillansia* L. Bolus plus *Micranthus*/*Thereianthus* G.J. Lewis. All of these are exclusively southern African. The combined clade of these six genera plus *C. socotrana* has moderate support (BS 74%). Other features of the phylogeny do not concern us here but we note that subfamily *Crocoideae* (including all the genera between *Romulea* Maratti and *Anomatheca* Ker Gawl. on the tree) is a strongly supported clade (BS 100%). This result supports that of Reeves *et al.* (2001) for *Crocoideae* using three chloroplast DNA regions, *rbcL*, *trnL*, and *rps4*.

DISCUSSION

Cyanixia socotrana was discovered in February 1880, in the hills southwest of Galonsir, in the course of I.B. Balfour's pioneering exploration of Socotra in

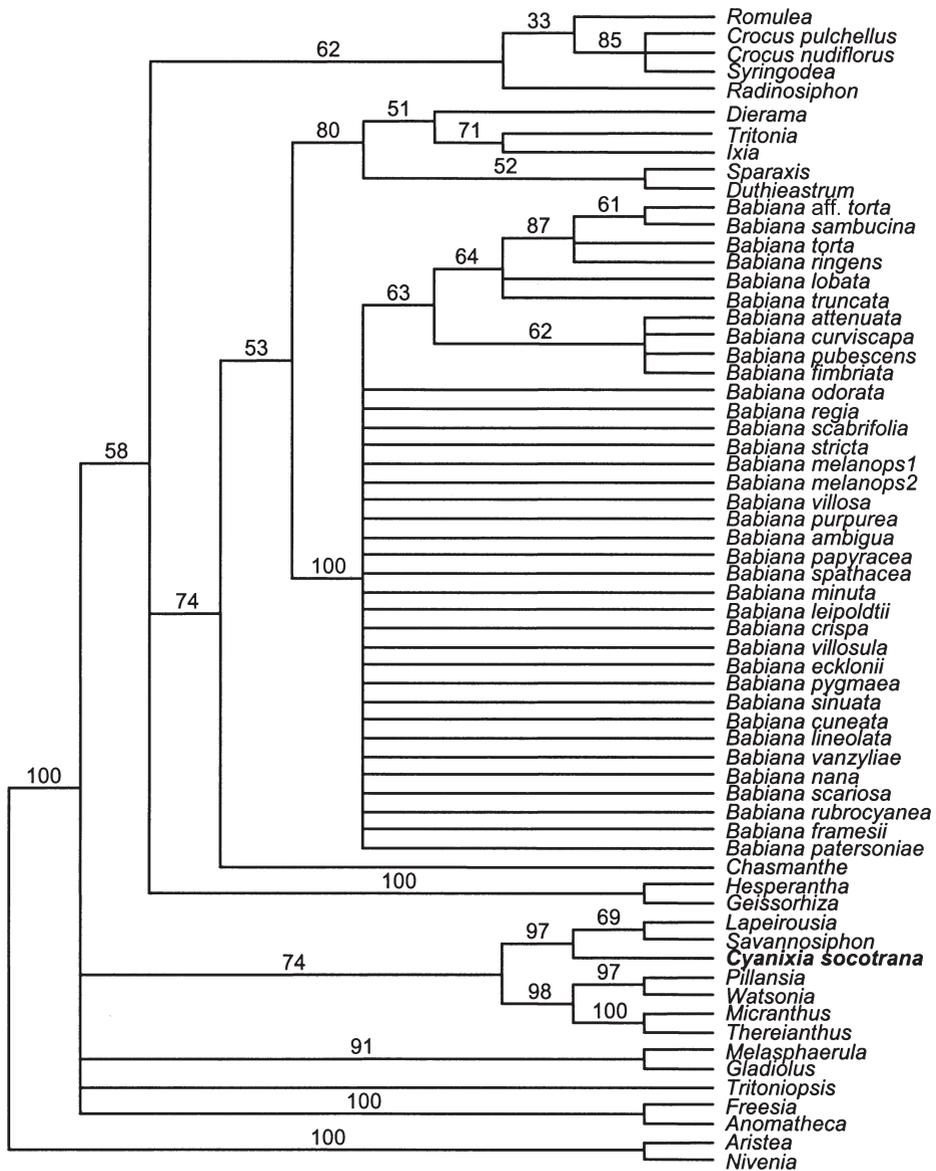


FIG. 3. Bootstrap consensus tree for selected *Iridaceae* taxa showing the position of *Cyanixia socotrana* as sister to *Savannosiphon/Lapeirousia* and unrelated to *Babiana* s.s. Bootstrap values above 50% are indicated on the branches; *Aristea* and *Nivenia* were used as outgroups following Reeves *et al.* (2001).

1879–80. It was grown in Britain from corms sent to the Royal Botanic Gardens, Kew, and flowered there in September 1880. It was painted for an article in *Curtis's Botanical Magazine* (1881) in which it was described and therein referred to the southern African genus *Babiana* (Hooker, 1881; Balfour, 1888). We learn little more than this in Balfour's 'Botany of Socotra' (1888) or from Forbes's *The Natural*

History of Socotra and Abd-el-Kuri (1903) except that it grows on limestone slopes at c.540m and on granite rocks and ledges in the Hajhir (Haggeher) mountains at c.900m.

The original reasons for placing *C. socotrana* in *Babiana* were based solely on gross overall morphological similarity, particularly the pleated leaf blades set obliquely on the sheaths. Although characteristic of *Babiana*, this leaf form is also found in two other African genera, *Savannosiphon* (one species) and *Zygotritonia* (four species), as well as in some species of *Crocoshmia* Planchon (eight species), all in the same subfamily of *Iridaceae* (Goldblatt, 1990a,b; Rudall & Goldblatt, 1991). While the stems, leaves, and bracts of *Babiana* are usually hairy to some degree (Lewis, 1959), Hooker (1881) noted that *B. socotrana* was glabrous throughout; he also described the flowers as having the limbs (i.e. tepals) distinctly two-lipped. All the flowers we have examined, alive and in photographs (Mackintosh-Smith, 1999; A.G. Miller, pers. comm.), are perfectly actinomorphic and rotate, with equally spreading, subequal tepals, and are by no means bilabiate. We suspect the two-lipped appearance of the perianth seen by Hooker may have been a result of distortion in the bud (see illustration in Hooker, 1881). Lewis (1959) included *B. socotrana* in her monograph of *Babiana* and expressed no misgivings about its placement in section *Babiana*, although she made no suggestion about its possible relationships.

The taxonomically important features of *C. socotrana*, most notably pollen grains, seed morphology, corm tunics and corm ontogeny, all differ fundamentally from those of other *Babiana* species and lead us to the conclusion that this species does not belong in *Babiana*, and we describe it as the new genus *Cyanixia*. Typically in *Iridaceae*, the taxonomic characters recognized as critical are all highly consistent within genera. In addition, chromosome base number, at least in most genera of *Crocoideae*, is constant (Goldblatt & Takei, 1993). Differences in most of these features are therefore regarded as signals of distant relationship and we conclude that *Babiana* and *Cyanixia* are not closely allied although both certainly belong in *Crocoideae*.

As outlined above, *Cyanixia* differs significantly from *Babiana* in chromosome base number, $x=10$, trisulcate pollen grains, the axillary ontogeny of the corm, the netted corm tunics, and seed morphology. The globose colliculate (to tuberculate) seeds of *Cyanixia*, with the slightly flattened chalazal end, resemble those of *Lapeirousia* (Goldblatt & Manning, 1992) and *Savannosiphon* (noted here for the first time) and to a lesser extent *Geissorhiza* Ker Gawl. and *Hesperantha* Ker Gawl. (Goldblatt & Wagner, 1984; Goldblatt & Manning, unpublished data). Seeds of *Babiana* are unique in the *Iridaceae* in being pear-shaped, smooth and glossy, and in the slightly folded seed coat that is loosely wrinkled.

The morphological indications that *Cyanixia socotrana* does not belong in *Babiana* are unambiguously supported by molecular analysis. In the consensus tree (Fig. 3) *C. socotrana* is sister to *Lapeirousia* plus *Savannosiphon*, which it resembles in several morphological features, particularly axillary corm development, globose seeds with a colliculate surface, and lightly plicate leaf blades. The

polyaperturate pollen of *Savannosiphon* (Goldblatt *et al.*, 1991) appears to represent an autapomorphy for the genus and thus provides no useful information about relationships. The evident sister relationship between *Lapeirousia/Savannosiphon* and *B. socotrana* is supported strongly enough that we take this topology as conclusive evidence for their relationship. This clade is sister to the exclusively southern African lineage that includes *Pillansia*, *Watsonia*, *Micranthus*, and *Thereianthus*. Significantly, these six genera together with *Cyanixia* stand out in subfamily *Crocoideae* as the only members currently known to have axillary corm development (de Vos, 1977; Goldblatt, 1990a,b), although the condition in the Cape genus *Tritoniopsis* L. Bolus is still uncertain. Based on corm ontogeny and, with minor exceptions, deeply divided style branches, five of these genera (*Lapeirousia*, *Micranthus*, *Savannosiphon*, *Thereianthus*, and *Watsonia*) were included in tribe *Watsonieae* of the *Crocoideae* (then called *Ixioideae*) by Goldblatt (1990a).

The sixth genus, *Pillansia*, was assigned its own tribe *Pillansieae* because of its peculiar panicle-like inflorescence, leaves without a midrib and with margins lacking subepidermal sclerenchyma, and undivided style branches (Goldblatt, 1990a,b). In the light of molecular data this latter decision appears mistaken. *Pillansia* almost certainly belongs with the *Watsonia* group of genera and its morphological peculiarities must be viewed as derived within *Watsonieae* rather than as ancestral. It is noteworthy that *Pillansia* also falls together with *Micranthus* and *Thereianthus* in the less resolved (for *Crocoideae*) three-gene phylogeny of the genera of *Iridaceae* (Reeves *et al.*, 2001).

Cyanixia socotrana cannot be included in *Lapeirousia*, despite the shared karyotype of $x=10$ which is common, and possibly ancestral, in that genus (Goldblatt & Takei, 1993), because *Lapeirousia* has flat-based corms with tunics that are more or less woody or composed of closely compressed fibres, and slender style branches that are, with few exceptions, deeply divided (Goldblatt, 1972, 1990b). The monotypic *Savannosiphon*, although it also has divided style branches, has corms with rounded bases and lightly pleated leaves and may be most closely related to *Cyanixia*; however, the basic chromosome number in *Savannosiphon* is $x=8$, which contrasts with $x=10$ for *Cyanixia*. Furthermore, the pollen grains of *Savannosiphon* are polyaperturate (Goldblatt *et al.*, 1991), again differing significantly from the 3-sulcate grains of *Cyanixia*. *Savannosiphon* is readily distinguished at the macro-morphological level by its white, long-tubed flowers with included stamens and deeply divided style branches.

A closer relationship to the exclusively tropical African *Zygotritonia* seems less likely. *Zygotritonia* has short-tubed, zygomorphic flowers and an undivided style, but shares with *Cyanixia* apomorphic 3-sulcate pollen grains (de Vos, 1982; Goldblatt *et al.*, 1991). The similarity in the pollen of the two genera is striking, but a difference in chromosome number, $x=10$ in *Cyanixia*, $x=7$ in *Zygotritonia* (Goldblatt, 1989), as well as flowers which differ in the taxonomically important style branches (and other characters), appears to rule out the possibility. Unfortunately, *Zygotritonia* has not yet been included in molecular phylogenetic studies. Its seeds have not been described in detail before, but those of *Z. nyassana* Mildbr. are

globose to ellipsoid with flattened sides and a smooth matte surface. The surface cells are clearly delineated and foveate. They are thus rather different from those of the *Cyanixial/Lapeirousial/Savannosiphon* clade which have a differentiated, flat chalazal end and surface cells with domed outer walls, usually colliculate or occasionally tuberculate. The affinities of *Zygotritonia* remain obscure and await further investigation. It is, however, noteworthy that it too probably has axillary corm ontogeny. Herbarium specimens of two species, *Z. bongensis* (Pax) Mildbr. and *Z. hysterantha* Goldblatt, show newly developing corms attached to axils just above the base of the flowering stem, which itself shows no sign of producing a new corm as would be expected if corm development were basal.

There seems no doubt that *Babiana socotrana* must be removed from *Babiana*. The only treatment that seems appropriate at present is that it be referred to a new genus which we here call *Cyanixia*.

SYSTEMATICS

***Cyanixia* Goldblatt & J.C. Manning, gen. nov.**

Planta decidua, cormo globoso evolutione axialiter, tunicis fibrosis reticulatis, caule aerali, laevi, foliis paucis distichis, laminis leviter plicatis, inflorescentia spicata, floribus actinomorphis rotatis caeruleis, tubo perianthii cylindrico, tepalis subaequalibus patentibus, staminibus symmetricalibus antheris linearibus, granis pollinis 3-sulcatis exinis perforatis, ovario glabro, stylo filiformi trifurcato, ramis filiformibus divergentibus, seminibus globosis rugosis, numero chromosomatum $x=10$.

Type: *Cyanixia socotrana* (Hook.f.) Goldblatt & J.C. Manning (= *Babiana socotrana* Hook.f.).

Deciduous geophyte with globose corm rooting from below; corm axillary in origin, with tunics of reticulate fibres. *Stem* aerial, terete, smooth, sheathed below ground by membranous cataphylls. *Leaves* few, distichous; the lower two or three as cataphylls without blades; foliage leaves unifacial, more or less sword-shaped to lanceolate, without obvious midrib; blades lightly plicate, with a major vein at each fold. *Inflorescence* a spike, the flowers spirally arranged; *bracts* green, leaf-like, the inner much shorter than the outer, forked apically. *Flowers* actinomorphic, rotate, blue, presence of nectar unknown; *perianth tube* elongate-cylindric, straight, widening slightly towards apex; *tepals* nearly equal, spreading. *Stamens* symmetrically arranged, ascending; *filaments* inserted in mouth of tube; *anthers* exerted, linear; pollen 3-sulcate, exine perforate. *Ovary* smooth; *style* filiform, straight, exerted, dividing distally into three short, slender branches. *Capsules* unknown; *seeds* globose, slightly flattened at chalazal end, lightly rugose; surface cells colliculate to more or less tuberculate. Basic chromosome number $x=10$.

Distribution. A single species from Socotra.

Etymology. The name is a compound derived from *cyanos* (blue) and *Ixia*, a genus in the same subfamily of the *Iridaceae* which the flowers broadly resemble.

Cyanixia socotrana (Hook.f.) Goldblatt & J.C. Manning, **comb. nov. Fig. 1.**

Type: Socotra, without precise locality, ii 1880, *Balfour* 249 (holo. K!).

Syn.: *Babiana socotrana* Hook.f., Curtis's Bot. Mag. 37 (ser. 3): pl. 6585 (1881); G.J. Lewis, J. S. African Bot., Suppl. 3: 91 (1959).

Plant 8–10cm high. *Corm* 15–20mm diam., the tunics of coarse fibres forming an open network, dark brown. *Stem* erect, short, unbranched. *Leaves* 3–5, lanceolate, 5–11 × 0.7–1cm, acuminate, lightly scabrid-papillate. *Spike* usually 1–2-flowered; bracts green, 2.5–7cm long, with long leafy cusps, the inner shorter than the outer. *Flowers* pale blue-violet, paler towards the centre, evidently unscented; *perianth tube* c.30mm long, slender; *tepals* c.2.5mm long, lanceolate-elliptic. *Filaments* suberect, 3mm long; *anthers* linear, 3mm long, blue. *Style* dividing opposite middle of anthers, with slender branches c.3mm long. *Capsules* unknown; *seeds* more or less globose, c.2 × 1.8mm, flattened at chalazal end; surface colliculate to tuberculate.

Additional specimens examined. SOCOTRA. Jebel Ma'lih, limestone hills, Miller, Bazar'a, Guarino & Kassim 10146 (E, K); Hamaderoh ridge, Lavranos *et al.* 30806 (MO).

Ecology. Widespread and locally abundant on the limestone plateaus and less commonly on the granite of the Haggeher mountains, 500–900m.

KEY TO THE GENERA OF *WATSONIEAE*

(Genera in subfamily *Crocoideae* with axillary corm development,
and style branches usually deeply divided)

- 1a. Style branches simple, notched apically, or style undivided _____ 2
- 1b. Style branches each divided for half their length _____ 4
- 2a. Leaves flat, without obvious midrib; flowers orange, sessile or on short stalks in much-branched pseudopanicles; pollen grains monosulcate; basic chromosome number $x=20$ _____ **Pillansia**
- 2b. Leaves lightly pleated; flowers variously coloured (blue, red, pink to purple), never orange, sessile in spikes; pollen grains 3-sulcate _____ 3
- 3a. Style undivided; perianth bilabiate, tepals unequal, the dorsal largest and hood-like; basic chromosome number $x=7$ _____ **Zygotritonia**
- 3b. Style divided into three branches; perianth radially symmetric, tepals subequal; basic chromosome number $x=10$ _____ **Cyanixia**
- 4a. Stems compressed and angled or winged; seeds globose, chalazal end sunken 5
- 4b. Stems terete; seeds angular, angles sometimes extended into wings, chalazal end a prominent crest _____ 6

- 5a. Corms bell-shaped with flat base; leaves flat or corrugate; pollen grains monosulcate with two-banded operculum _____ **Lapeirousia**
- 5b. Corms globose, rounded at base; leaf blades lightly plicate; pollen grains polyaperturate _____ **Savannosiphon**
- 6a. Basal leaves 2 or more in a distichous fan; leaf blades flat, relatively broad, margins often \pm thickened; flowers never blue or purple; basic chromosome number $x=9$ _____ **Watsonia**
- 6b. Basal leaf 1; leaf blades terete, if flat then narrow and without thickened margins; flowers purple or blue to nearly white; basic chromosome number $x=10$ _____ 7
- 7a. Flowers <12mm long, in dense distichous spikes; bracts with broad membranous margins; pollen grains zonosulcate, without operculum; exine reticulate _____ **Micranthus**
- 7b. Flowers 20–60mm long, in spiral spikes; bracts without membranous margins; pollen grains (as far as known) monosulcate with two-banded operculum; exine perforate _____ **Thereianthus**

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