

# Systematics and biology of the African genus *Ferraria* (Iridaceae: Irideae)

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## ABSTRACT

Following field and herbarium investigation of the subequatorial African and mainly western southern African *Ferraria* Burm. ex Mill. (Iridaceae: Iridoideae), a genus of cormous geophytes, we recognize 18 species, eight more than were included in the 1979 account of the genus by M.P. de Vos. One of these, *F. ovata*, based on *Moraea ovata* Thunb. (1800), was only discovered to be a species of *Ferraria* in 2001, and three more are the result of our different view of De Vos's taxonomy. In tropical Africa, *F. glutinosa* is recircumscribed to include only mid- to late summer-flowering plants, usually with a single basal leaf and with purple to brown flowers often marked with yellow. A second summer-flowering species, *F. candelabrum*, includes taller plants with several basal leaves. Spring and early summer-flowering plants lacking foliage leaves and with yellow flowers from central Africa are referred to *F. spithamea* or *F. welwitschii* respectively.

The remaining species are restricted to western southern Africa, an area of winter rainfall and summer drought. We recognize three new species: *F. flava* and *F. ornata* from the sandveld of coastal Namaqualand, and *F. parva*, which has among the smallest flowers in the genus and is restricted to the Western Cape coastal plain between Ganzekraal and Langrietvlei near Hopefield. *Ferraria ornata* blooms in May and June in response to the first rains of the season. Among the remaining species, *F. uncinata* subsp. *macrochlamys* is now *F. macrochlamys* and is treated as comprising three subspecies: subsp. *macrochlamys* from central and northern Namaqualand has leaves with thickened, crisped margins; subsp. *kamiesbergensis* from the southern Kamiesberg has leaves with unthickened margins and blades curved in one direction; and subsp. *serpentina* from gravels and sands of coastal Namaqualand has serpentine leaves, also with unthickened margins. Among the remaining species, *F. divaricata* subsp. *arenosa* is now treated as a synonym of *F. divaricata*. Because of our re-interpretation of the type of *F. divaricata*, plants which were called *F. divaricata* subsp. *divaricata* and subsp. *australis* are now treated as synonyms under the name *F. variabilis*.

Flowers of *Ferraria* are unique in Iridaceae in having tepal limbs with crisped margins and a style that divides into flattened branches, each deeply forked with finely fringed adaxial margins. Despite relative floral uniformity, the genus displays a surprising range of discrete pollination systems for so small a genus. Pollinators include Diptera in the families Muscidae, Calliphoridae, and Sarcophagidae (*F. crispa* group); anthophorine and honey bees (*F. ferrariola*); eumenid wasps (*F. divaricata*, *F. macrochlamys*, *F. variabilis*); and Coleoptera in the families Meloidae and Melyridae (*F. uncinata*). Preliminary phylogenetic analysis using plastid DNA regions shows *F. glutinosa* to be sister to an unresolved cluster of southern African species and confirms as plesiomorphic the open branching habit, many-flowered inflorescences and exerted globose capsules that characterize *F. glutinosa* and its immediate allies in subgen. *Glutinosa*.

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## INTRODUCTION

When last revised by De Vos (1979), *Ferraria* Burm. ex Mill. (Iridaceae: Iridoideae) was treated as comprising 10 species: nine native to the southern African winter rainfall zone and a broadly circumscribed *F. glutinosa* (Baker) Rendle, widespread across the summer rainfall interior of southern and tropical Africa. Field work in central and southern Africa in the past 10 years, often in conjunction with studies of pollination biology and examination of herbarium collections, has shown that the taxonomy of the genus needed major adjustment. Some nomenclatural changes have already been published. *F. ovata* (Thunb.) Goldblatt & J.C.Manning was added to the genus (Goldblatt & Manning 2002) after the rediscovery in the wild in 2001 of the plant named *Moraea ovata* by C.P. Thunberg in 1800. Subspecies *macrochlamys* of *F. uncinata* Sweet is now recognized as a separate species (Goldblatt & Manning 2004), and reinterpretation of the type of *F. divaricata* Sweet resulted in plants called *F. divaricata* subsp. *divaricata* and subsp. *australis* M.P.de Vos being referred to a new species, *F. variabilis* Goldblatt & J.C.Manning. Subsp.

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PLATE 1.—*Ferraria*: A, *uncinata* (Clanwilliam, Western Cape) (no. 16); B, *macrochlamys* subsp. *kamiesbergensis* (Kliprand, Northern Cape) (no. 17b); C, *foliosa* (near Elands Bay, Western Cape) (no. 6); D, *variabilis* (Bushmanland, Northern Cape) (no. 14); E, *crispa* (Langebaan, Western Cape) (no. 5); F, *ferrariola* (Bitterfontein, Northern Cape) (no. 11); G, *glutinosa* (northern Namibia) (no. 1); H, *ornata* (near Groen River Mouth, Northern Cape) (no. 10); I, *parva* (Vredenburg, Western Cape) (no. 12); J, *flava* (near Koekenaap, Western Cape) (no. 15).

*arenosa* of *F. divaricata* is now referred to *F. divaricata* (Goldblatt & Manning 2005) and subsp. *aurea* M.P.de Vos is most likely a synonym of the new *F. flava*.

Our examination of herbarium collections (from BM, BOL, K, LISC, NBG, PRE and SAM), photographs and drawings of the tropical African *Ferraria glutinosa* as circumscribed by De Vos (1979), has convinced us that there are at least four clearly defined sets of populations under this name. Mid- to late summer-blooming populations with brown or dull purple flowers with yellow tepal margins and one or two poorly developed basal leaves match the type of *F. glutinosa*, which is from Angola. We refer plants with a fan of up to eight basal leaves and yellow flowers sometimes marked with brown, also blooming in mid- to late summer, to *F. candelabrum* (Baker) Rendle. Among a series of late spring to early summer-blooming (October to mid-December) populations with smaller, dull yellow to buff flowers and lacking foliage leaves on flowering stems, we recognize *F. spithamea* (Baker) Goldblatt & J.C.Manning for plants lacking fringed style branches and tepal limbs with smooth rather than crisped margins. Plants with tepal limbs with minute brown, red, purple or dull green spotting and well-developed fringed style branches represent a fourth species, the earliest name for which is *F. welwitschii* Baker. We cannot exclude the possibility that additional species occur in tropical Africa, but specimens from there have flowers too poorly preserved to be certain.

These changes render De Vos's 1979 account of *Ferraria* of limited practical use. We provide a revision of the genus in which we recognize 18 species, including three new species, *F. flava*, *F. ornata* and *F. parva*, all from the western coastal belt of South Africa. We also reduce De Vos's *F. kamiesbergensis* to subspecific rank in *F. macrochlamys* and describe subsp. *serpentina* of that species. After briefly outlining the morphology of *Ferraria* and what is known about its phylogeny, we propose a new subgeneric classification. We also review the pollination biology of the genus, show how floral morphology is closely correlated with pollination ecology, and conclude with a key and systematic account of the genus.

#### GENERIC RELATIONSHIPS AND GEOLOGICAL AGE

*Ferraria* is a member of the predominantly Old World tribe Irideae (subfam. Iridoideae), which includes the northern hemisphere genus *Iris* L. ( $\pm 280$  spp.) of Eurasia and North America, the largely sub-Saharan African *Moraea* Mill. ( $\pm 200$  spp.), the southern African *Bobartia* L. (15 spp.), and *Dietes* Salisb. ex Klatt (6 spp.), also largely sub-Saharan African, but with one species on Lord Howe Island in the southern Pacific (Mathew 1980; Goldblatt 1990). Additional small genera of the tribe are now no longer recognized. *Hermodactylus* Mill. (1 sp.), *Pardanthopsis* (Hance) Lenz (1 sp.), and *Belamcanda* Adans. (1 sp.) have been shown by molecular study to be nested in *Iris* (Tillie *et al.* 2001), whereas *Barnardiella* Goldblatt (1 sp.), *Galaxia* Thunb. (15 spp.), *Gynandriris* Parlatores (9 spp.), *Hexaglottis* Vent. (6 spp.) and *Homeria* Vent. (32 spp.) are now known to be nested in *Moraea* (Goldblatt 1998; Goldblatt *et al.* 2002) and are included in that genus.

Both morphological analysis and molecular DNA sequences of plastid DNA regions show that *Ferraria* is sister to *Moraea* ( $\pm 210$  species) (Goldblatt 1990; Reeves *et al.* 2001; Goldblatt *et al.* 2002; Goldblatt *et al.* 2008) and this clade is sister to *Dietes/Bobartia*. Using the molecular clock and a combined analysis of four chloroplast DNA regions, preliminary dating estimates showed that *Ferraria* and *Moraea* diverged in the Miocene,  $\pm 25$  mya (Goldblatt *et al.* 2002). Subsequent dating using improved molecular clock analysis techniques indicate that the two genera diverged earlier,  $\pm 30$  mya, therefore in the late Oligocene (Goldblatt *et al.* 2008). *Moraea* is distinguished from *Ferraria* by its bifacial leaf, single internode corms of axillary corm ontogeny, whereas the leaves of *Ferraria* are unifacial and isobilateral, the ancestral type in Iridaceae, its corm consists of multiple internodes and is of axial origin (De Vos 1977).

#### MORPHOLOGY

*Corm*: unmistakable in Iridaceae, relatively large, depressed globose to almost discoid, and lacks tunics when mature. A new corm, produced each season, develops from the base of the flowering stem (De Vos 1977), and is therefore regarded as terminal or axial (sensu Goldblatt *et al.* 2006) in origin. This ontogenetic pattern contrasts with development in the immediately related genus *Moraea*, corms of which are lateral in origin, arising from an axillary bud at the base of the flowering stem (Goldblatt 1976, 1990). Although *Ferraria* corms are described as having tunics, the tunics are membranous and short-lived and are rarely present in mature corms, but in *F. flava* corms carefully removed from the sandy ground have a dark, softly fibrous covering.

Although new corms are produced annually, those of the previous seasons are not completely re-absorbed. Instead, they persist as hard brown discs attached to each other, like a string of large beads behind the current corm. Anatomically, corms lack an organized stele, a feature shared with *Moraea* (De Vos 1977), and as in that genus, new roots emerge from the base of the terminal bud when growth is renewed at the beginning of the wet season. This contrasts with the typical pattern in corm-bearing plants, including Iridaceae subfam. Crocoideae (syn. Ixiodeae), Colchicaceae and Tecophilaeaceae, which have an organized stele and in which the new roots emerge from the base or lower half of the corm (Goldblatt 1990).

*Leaves*: the lowermost foliar organs sheath the emergent shoot and lack blades and are cataphylls. There are usually three present and they are typically pale and membranous. The cataphylls are distinctive in *Ferraria ferrar-iola*, where they consistently turn reddish with pale speckling above ground level, and often also in *F. crispa* and *F. densipunctuata*. In *F. ornata* the uppermost cataphyll develops red pigmentation above the ground. The true foliage leaves have a sheathing base and a unifacial, linear to sword-shaped blade with several to many equal, parallel veins or, in *F. crispa*, *F. foliosa* and *F. schaeferi*, there is a relatively prominent central vein, the pseudomidrib, consisting of a pair of large, opposed, vascular traces (De Vos 1979). Even *F. glutinosa* has, at least anatomically, a

pair of larger vascular traces in the centre of the leaf, but this is not evident in live plants or pressed specimens. Foliage leaves are lacking on the flowering shoots of *F. spithamea* and *F. welwitschii*, and leaves are evidently not normally produced by the flowering stems even after flowering and fruiting are completed. Non-flowering and juvenile individuals produce one large, narrowly sword-shaped leaf and one or two smaller ones on a new shoot produced from the base of the fruiting stalk as capsules mature. *Ferraria glutinosa* may also have a reduced or vestigial basal leaf, but cauline leaves are always present.

The basal leaves (or the juvenile leaves produced by immature plants) differ sharply from the cauline leaves in *Ferraria densesepunctulata*, *F. ferrariola*, *F. ornata* and *F. ovata*. In the last-named species the short, bifacial, broadly ovate cauline leaves contrast with the unifacial, linear basal leaves. In *F. ornata*, juvenile and non-flowering plants produce 3–5 centric, subterete leaves, round to oval in cross section and up to 100 mm long, whereas flowering individuals have shorter falcate-lanceolate and channelled to concave leaves up to 40 mm long, with short or vestigial unifacial tips.

In *Ferraria foliosa* and *F. schaeferi* the basal leaves are thickest in the midline and have the central vein internal to the thickest part of the blade (De Vos 1979). The leaf blade (the unifacial portion of the leaf) of *F. brevifolia* is considerably shorter than the prominent sheaths which together form a tight fan. *Ferraria spithamea* lacks unifacial foliage leaves except in non-flowering individuals; flowering plants bear relatively large sheathing leaves at the base and in axils of the flowering stems, the tips of which are sometimes extended as short, unifacial blades.

Leaf margins may be undifferentiated or are moderately to prominently thickened and hyaline. The hyaline appearance is the result of the thickening of the strand of sclerenchyma, present below the marginal epidermis in leaves of all species. Thickened margins are particularly prominent in *Ferraria macrochlamys* subsp. *macrochlamys* and *F. uncinata*. In *F. uncinata* the margins are also usually moderately to strongly crisped and the marginal thickenings may be slightly irregularly serrate to crenulate. The leaf tips are often slightly hooked, the feature for which *F. uncinata* was named, but the hook is only weakly developed and is not restricted to that species. In *F. macrochlamys* subsp. *macrochlamys* the marginal thickenings are often slightly and minutely pilose (visible under 10× magnification) and usually crisped or at least crenulate. The blades of the basal leaves of *F. macrochlamys* subsp. *serpentina* are slightly curved back on themselves in loose concertina fashion and the margins are not thickened. In contrast, the leaves of *F. macrochlamys* subsp. *kamiesbergensis* all curve gently to the same side, and in some populations, the curvature is particularly pronounced, forming almost a half circle.

Leaf blades of the *Ferraria glutinosa* and *F. crispa* groups have a visible central vein but in *F. divaricata*, *F. ornata*, *F. variabilis* and the *F. ferrariola* and *F. uncinata* groups, the leaves show no external evidence of an enlarged central vein and leaf sections show all vascular traces to be ± the same size in these species (De Vos 1979).

**Flowering stem and inflorescence:** the stem of all species is ± erect, terete and, in well-grown plants, often branched. There are three distinct growth patterns. In subgen. *Glutinosae* (the *Ferraria glutinosa* group), the stem bears well-developed branches and the internodes are sheathed only near their bases. Most other species, e.g. *F. crispa*, *F. ferrariola*, have short, suberect branches crowded in the upper half of the stem, and the internodes are usually enclosed by large leaf sheaths. The cauline leaves may be held ± in two opposed, vertical ranks, or are strongly curved outward in a spirally 2-ranked arrangement in *F. foliosa* and *F. schaeferi*. In subgen. *Glutinosae* the upper nodes and distal portions of the internodes are sticky. In a third growth form, typical of a few species including *F. macrochlamys* and *F. variabilis*, the above-ground part of the stem and internodes are short, and the few branches produced are usually subequal in length and crowded close to the ground, giving the plants a somewhat tufted appearance. *Ferraria ornata* is acaulescent, with the stem entirely underground and the rhipidia are borne at ground level.

The main axis and each branch terminates in a cluster of flowers, a rhipidium, the basic inflorescence unit of all Iridaceae subfam. Iridoideae. This is a laterally compressed monochasial cyme with the main axis collapsed and the flowers enclosed by a pair of opposed, large, ± leaf-like bracts called spathes (Goldblatt 1990). The flowers are borne serially on short pedicels that elongate at flowering so that the flower bud is raised out of the sheathing spathes. Within the rhipidium, each flower, except the first one, is enclosed in a large submembranous bract, which in *Ferraria* can usually be seen to have a pair of weakly defined keels, each often greenish and with a central vascular trace. In subgen. *Glutinosae* the rhipidia usually have at least three and in *F. glutinosa* up to six flowers. All members of subgen. *Ferraria* have just two flowers in each rhipidium. The inner of the two spathes is longer than the outer and is partly to entirely sheathed by the outer spathe. The spathe tips are often slightly hooked and curved inward, a feature weakly developed in most species. A feature of several species, notably *F. crispa* and *F. foliosa*, is the elongation of the inner spathe as the capsules ripen. The enlarging capsule therefore remains enclosed in protective leafy spathe tissue until the aerial parts wither and dry.

**Perianth:** specialized in the family, the *Ferraria* flower embodies several derived features. The inferior ovary is either ovoid and borne on a long pedicel that reaches the tips of the spathes (subgen. *Glutinosae*), or the pedicel reaches to about the middle of the spathes and the ovary is ellipsoid (*F. crispa*, *F. foliosa*, *F. ornata*, *F. ovata*), or fusiform and with a sterile, tubular upper half or beak (*F. schaeferi* and sect. *Macroscyphae* of subgen. *Ferraria*). The ovules are then restricted to the lower part of the ovary. The six tepals are subequal or those of the inner whorl are somewhat smaller. The tepals are clawed and the claws may be relatively short, broad, and slightly ascending to suberect. The claws typically overlap each other and together form a wide to narrow floral cup, whereas the tepal limbs spread horizontally or are slightly reflexed. In *F. ferrariola*, *F. parva* and the *F. uncinata* group, the tepal claws are relatively narrow, comparatively long, and suberect, and then form a narrow cup or



gullet, while the limbs may be distally recurved or the inner tepal limbs may be fully reflexed. In *F. ornata* the lower third of the tepal claws are narrowed with the result that the floral cup has wide gaps or windows alternating with the bases of the claws. The tepal limbs are lanceolate-attenuate and have tightly crisped margins, except *F. spithamea*, in which the margins are plane.

Perianth colour is variable across the genus and is even, within limits, in species. Colours are typically relatively dull, and the margins of the tepal limbs often have a contrasting lighter or darker pigmentation. Because of intraspecific variation it is hard to generalize about colour. *Ferraria glutinosa* has predominantly dark brown (chocolate-coloured) to dull purple tepals (also described as violet), the limbs of which have yellow margins and sometimes yellow markings at the bases of the limbs. *F. welwitschii* has dull yellow to buff tepals with tiny, dark red, brown or dull green spots but the tepal limb margins lack contrasting colour. *F. macrochlamys* and the closely allied *F. brevifolia* consistently have pale, watery yellow tepal limbs with slightly darker margins. Populations of these species differ, if at all, in the colour intensity of the few small spots toward the limb bases. *Ferraria uncinata* usually has deep blue-violet tepal limbs, but populations in the north of its range often have light brown limbs with dark blue spots.

The tepals of *Ferraria crispa*, *F. foliosa*, *F. ornata* and *F. schaeferi* are usually irregularly mottled with dark brown to dull maroon on a paler ground colour. But at least in *F. crispa* and *F. glutinosa* there are individuals with almost uniformly dark brownish tepals with pale, almost golden margins (see figure in Manning *et al.* 2002: 157). Flowers of *F. divaricata* are also dark-coloured, but are not blotched with darker pigment; instead they have dark brown limbs, described in the type description as chocolate-brown, with light brown margins and a pale cup, usually longitudinally streaked with brownish purple or with a single broad longitudinal streak. The series of populations that De Vos (1979) called subsp. *aurea* have flowers with yellow tepals very faintly marked with contrasting colour. *Ferraria variabilis* shows a range of distinctive perianth patterning across its range. In the north, in Namaqualand and southern Namibia, flowers have tepal limbs with a darker band toward the base and are pale brown distally and the margins are the same pale brown. The claws are pale greenish cream with a narrow darker band running down the midline. In the western Karoo flower pigmentation is more variable, with shades of brown or yellow predominating but individual variation is often striking. In the southern Cape and southern Karoo *F. variabilis* has greenish yellow or light to middle brown tepal limbs, usually darker in the midline, and with small or medium-sized spots in the lower third, or when brown, then often with spots irregularly scattered across the limb and the margins sometimes slightly darker coloured. The claws are pale, usually with a darker streak in the midline. Perianth colour can vary as much within a population as across the entire southern Cape and western Karoo.

Perhaps most striking in floral pigmentation, *Ferraria ovata* has yellow tepals with dark brown at the base of the tepal limbs and along the margins and mid-

line (Figure 7). In *F. ferrariola* the tepal limbs range from pale yellow to grey-blue or light turquoise usually with a pale yellow zone toward the base of the outer tepal limbs bearing small dark dots, while the particularly prominent, feathery style branches are grey-blue to pale purple. The smaller, less conspicuous inner tepals are unmarked, often a darker colour, and the limbs are  $\pm$  reflexed, in contrast to the horizontally extended outer tepal limbs.

Each tepal claw bears a nectary, which takes the form of small dark zones or larger shallow depressions covering one third to almost half the claw. Nectaries are largest and most conspicuous in the tropical African species and in those southern African species with a shallow floral cup, as in *Ferraria crispa*, *F. foliosa* and *F. schaeferi* the nectary is paler than the rest of the claw. In contrast, the nectaries of *F. glutinosa* and *F. welwitschii* are dark brown and often wider than high. *F. densepunctulata* and *F. ovata* have small, pale, bilobed or paired nectaries above the tepal bases. In *F. ornata* the nectaries are  $\pm$  white with violet spots and the distal edges are raised into an irregularly lobed crest. Smaller nectaries located close to the tepal base are often not easy to identify, particularly in species with a deep, narrow floral cup. In those species with large nectaries, small droplets of intensely sweet nectar, in excess of 50 % sucrose equivalents, are scattered over the surface, which may coalesce in a pool in the base of the floral cup when the air is moist or after light rain. Nectar of remarkably low sugar concentration, in the range of 5–9 % sucrose equivalents, accumulates in a pool in the relatively deep floral cups of *F. divaricata* and *F. variabilis*. The size and position of nectaries is usually constant, but we have encountered populations of *F. variabilis* with large bilobed nectaries forming pockets in the middle of the outer tepal claws (e.g. Goldblatt & Porter 12977 from the Tankwa Karoo) although the species usually has small dark nectaries close to or at the base of the claws (De Vos 1979).

*Androecium and gynoecium:* the three stamens have filaments united for most of their length in a slender, smooth or rarely puberulous column that reaches to the apex of the floral cup. The upper 1.5–3.0 mm of the filaments are free and diverging. The anthers are either oblong with conventional, parallel thecae (sects. *Glutinosae* and *Ferraria*), or the thecae are held together only at their tips and diverge from the apex after anthesis, usually becoming widely divergent (sect. *Macroscyphae*). The filaments are inserted in a small pocket in the connective  $\pm$  a third of the anther length above the base or, in sect. *Macroscyphae* a short distance below the anther apex.

Pollen is bright orange-red in most species, or occasionally yellow, but *Ferraria flava* consistently has yellow pollen. Pollen of *F. welwitschii* has been described as orange-yellow (Milne-Redhead 2664) or is yellow in photographs we have examined. Anthers shrink a surprising amount, at least a third and up to half their length, after pollen is shed. De Vos (1979) described the pollen grains in some detail: they are always monosulcate with reticulate exine but exhibit no features of taxonomic significance within the genus.

The ovary is borne on a well-developed (subgen. *Glutinosae*) or short pedicel that elongates just before anthesis, thus raising the flower bud above the sheathing inflorescence spathes. The ovary is either narrowly ovate-truncate (subgen. *Glutinosae*) to  $\pm$  fusiform (sect. *Ferraria* except *F. schaeferi*) or in all members of sect. *Macroscyphae* and *F. schaeferi* elongate-fusiform, tapering distally into a slender, sterile tube, the rostrum or beak. Only the middle portion of the wider, lower portion of the ovary then contains ovules. The ovary remains included in the spathes except in subgen. *Glutinosae* and is then held either just below the apex of the inner spathe, or when the ovary is beaked, well within the spathes.

The slender style, held within the filament column, divides at its apex into three tangentially flattened branches, each divided for more than half its length into a pair of conduplicate lobes or arms that curve outward. The arms consist of an adaxial surface, nearly always deeply and irregularly fringed, and an abaxial surface that arches over the anthers and bears the stigma. The fringes of *Ferraria glutinosa* can be seen under at least 20 $\times$  magnification to be minutely papillate, a feature not or barely developed in other species. In *F. spithamea* the style branches lack the fringes that characterize the rest of the genus.

In subgen. *Glutinosae* and sect. *Ferraria* of subgen. *Ferraria*, the stigma is minute and located at the apex of each stylar arm (see illustrations by De Vos 1979). In sect. *Macroscyphae* (subgen. *Ferraria*) the stigmatic surface consists of an expanded and channelled fold of tissue below the tip of each style arm. The stigmatic surface is unusually large in *F. ferrariola* and arches over the adjacent anther lobe, partly concealing it.

**Capsules and seeds:** capsule shape largely mirrors that of the ovary. Thus, in subgen. *Ferraria* the capsule is  $\pm$  globose-truncate closely resembling that in the related *Bobartia*, the less specialized species of *Dietes* (e.g. *D. bicolor*) and many species of *Moraea*. In *F. crispa*, *F. densepunctulata* and *F. foliosa*, which have a fusiform ovary, capsules are ovoid with a rounded to pointed apex. In those species with a beaked ovary, the beak persists in fruit as a firm extension at the tip of the large, ovoid, seed-bearing portion of the fruit. The capsules are enclosed in the spathes throughout their development in subgen. *Ferraria* but remain exserted in subgen. *Glutinosae* as they ripen.

The relatively large seeds are unique in Irideae in their size, multifaceted shape and distinctive smooth, glossy surface. In most species, seeds are five- or six-sided with the facets separated by raised, somewhat undulate ridges and the individual facets have a  $\pm$  plane to slightly undulate or somewhat wrinkled surface. These seeds are, to some extent, variable in size, even in the same capsules, and  $\pm$  2.5–3.4 mm wide and 3–4 mm at the longest axis. Seed colour ranges from pale to dark brown, with the ridges separating the facets often lighter yellow-brown. The entire seed surface is smooth and glossy without raised cell outlines. De Vos (1979) noted that *F. divaricata* (as subsp. *arenosa*) stands out in having matte, dull brown, globose seeds with a slightly wrinkled,  $\pm$  ruminate sculpturing (called reticulate by De Vos) and fove-

ate epidermal cells, which we have confirmed for one population.

#### CHROMOSOME CYTOLOGY

The basic chromosome number in *Ferraria* (Table 1) is  $\times = 10$  and diploid numbers range from  $2n = 20$  to 60 (Goldblatt 1971; De Vos 1979; Goldblatt & Takei 1997). Most species are paleodiploid but *F. crispa* and *F. schaeferi* have tetraploid and hexaploid populations ( $2n = 40$  and 60) (Table 1). Largely on the basis of their tetraploid chromosome number,  $2n = 40$ , but also a slightly smaller flower, De Vos (1979) segregated the northern populations of *F. crispa* as subsp. *nortieri*. The southern and eastern populations of the species are hexaploid,  $2n = 60$ . The single count for *F. glutinosa* (from Namibia) is tetraploid and *F. variabilis* has diploid and tetraploid populations, the latter in the southern part of its range (and were assigned by De Vos to a separate subsp. *australis* of *F. divaricata*). The southern African *F. flava*, *F. ovata*, *F. ornata*, *F. parva* and the tropical *F. candelabrum* and *F. spithamea* are uncounted.

TABLE 1.—Chromosome numbers of *Ferraria*. Data from Goldblatt (1971), De Vos (1979), and Goldblatt & Takei (1997). *Ferraria candelabrum*, *F. parva*, *F. ornata*, *F. ovata*, *F. spithamea* and *F. macrochlamys* subsp. *serpentina* are uncounted

Species	Diploid chromosome no. $2n$
<i>divaricata</i> (as subspp. <i>aurea</i> and <i>arenosa</i> )	20
<i>crispa</i> (also as subsp. <i>crispa</i> and <i>F. undulata</i> )	60
<i>crispa</i> (as subsp. <i>nortieri</i> )	40
<i>densepunctulata</i>	20
<i>variabilis</i> (as <i>F. divaricata</i> subsp. <i>divaricata</i> )	20
<i>variabilis</i> (as <i>F. divaricata</i> subsp. <i>australis</i> )	40
<i>ferrariola</i> (also as <i>F. longa</i> )	20
<i>flava</i> (as <i>F. divaricata</i> subsp. <i>aurea</i> )	20
<i>foliosa</i>	20
<i>glutinosa</i>	40
<i>kamiesbergensis</i>	20
<i>longifolia</i>	20
<i>macrochlamys</i> subsp. <i>macrochlamys</i>	20
<i>macrochlamys</i> subsp. <i>kamiesbergensis</i>	20
<i>schaeferi</i>	40, 60
<i>uncinata</i>	20
<i>welwitschii</i> (as <i>F. glutinosa</i> )	20

Chromosomes are large, as they are in most genera of subfam. Iridoideae (Goldblatt 1971). The basic karyotype consists of nine acrocentric and one metacentric chromosome pair, reported for *Ferraria welwitschii* (De Vos 1979, as *F. glutinosa*). The southern African species have, in contrast, a derived karyotype of  $10 \pm$  acrocentric chromosomes, some of the smaller pairs tending to metacentric. Within Iridoideae, the karyotype of *F. welwitschii* with its metacentric chromosome pair, most closely resembles that of *Moraea* species that have  $\times = 10$ , the ancestral base number in that genus. Both *Bobartia* and *Dietes*, the two genera immediately related to the *Ferraria*–*Moraea* clade also have  $\times = 10$  (Goldblatt 1971; Goldblatt & Takei 1997) and a karyotype with both acro- and metacentric chromosomes.

## POLLINATION BIOLOGY

Somewhat surprisingly for a small genus with superficially similar flowers, pollination of *Ferraria* is relatively diverse (Goldblatt *et al.* 2009). As was long suspected, the flowers of several species are adapted for pollination by muscid flies, calliphorid flies, flesh flies and other families of Diptera. Vogel (1954), in his seminal survey of pollination systems in the southern African flora, regarded *Ferraria* as a genus adapted for pollination by flies. The basis for this contention appears to have been the reports by Scott Elliot (1891) of visits to *F. crispa* (as *F. undulata*) by two Diptera, the flesh fly *Scathophaga hottentotta* (now *S. stercoraria*) (Sarcophagidae) and the blowfly *Chrysomya regalis* (Calliphoridae). These insects are evidently attracted to the strong, molasses or burnt sugar odour of the flowers (sometimes loosely described as putrid or decaying), combined with a dull, mottled perianth coloration, reminiscent of the flowers of *Orbea* and *Stapelia* species (Apocynaceae). Two populations sampled respectively by R. Raguso (pers. comm. 2009) and R. Kaiser (pers. comm. 2009) both yielded significant amounts of guaiacol, a phenylpropionoid, which has a strong molasses odour. The reward offered is concentrated sugary nectar retained as tiny droplets on the surface of large perigonal nectaries within the floral cup.

*Ferraria densepunctulata*, *F. foliosa*, *F. ovata*, and *F. schaeferi* (all sect. *Ferraria*) share this pollination system, often termed sapromyiophily (Faegri & van der Pijl 1979) and according to the definition, associated with a dull-coloured and often mottled perianth, odours of rotting protein, but without a reward. Clearly, flies are attracted by the appearance and odour of the flowers but in *Ferraria* they are rewarded by concentrated nectar. Four families of Diptera: Calliphoridae (*Chrysomya*), Tachinidae (genus undetermined), Sarcophagidae (*Scathophaga*), and Muscidae (several genera) have now been recorded visiting flowers of this group of species (Goldblatt *et al.* 2009). In fair to warm weather, flowers of these species are rarely without one or more fly visitors, usually carrying dense loads of bright orange pollen covering the dorsal parts of the head and thorax and sometimes the abdomen. The  $\pm$  bitter or aminoid scents produced by the flowers of *F. crispa*, *F. foliosa*, and *F. ovata* are typical of flowers visited by these flies. In contrast, *F. densepunctulata* and *F. schaeferi* flowers have faint, and to the human nose, pleasant floral odours, and visits by the same suite of fly species are as frequent as those to *F. crispa* and *F. foliosa*.

Not all *Ferraria* flowers have this floral presentation and pollination system. Flowers of *F. ferrariola* are specialized in the genus in having a narrow floral cup, 17–20 mm deep, a pale blue-grey or yellow perianth with only the outer tepals bearing nectar guides, nectar of elevated sugar concentration, and typically a faint sweet scent recalling violets mixed with a spicy odour, in some populations recalling vanilla or, in others, bitter almonds. Flowers of some populations appear to be unscented. The flowers are pollinated only by bees, including honey bees, *Apis mellifera*, and long-tongued anthophorines, including *Anthophora praecox* (Goldblatt *et al.* 2009). Observations on the pollination of other bee-pollinated Iridaceae show that anthophorine bees of

several species may visit and successfully pollinate species of *Babiana* and *Gladiolus* (Goldblatt *et al.* 1998, 2001; Goldblatt & Manning 2006) across their ranges, and we conclude that different *Anthophora* species probably visit *F. ferrariola* at other sites across its wide range. Bees climb into the narrow floral cup, evidently in search of nectar and, in doing so, they passively accumulate loads of orange pollen on the dorsal part of the thorax. Visits to a second flower result in the deposition of pollen on the exposed stigmatic surfaces of the style branches.

*Ferraria divaricata* and *F. variabilis*, either have dull-coloured flowers, either uniformly pale to dark brown, speckled or banded with purple, brown or green on a cream to dull yellow background, or in *F. macrochlamys* pale, watery yellow. Floral odour seems to be absent, or is slightly unpleasant, but indefinable. The flowers produce large amounts of nectar of exceptionally low sugar concentration, mostly 3–10 % sucrose equivalents, which accumulates in a pool in the base of a wide, fairly deep floral cup. Flowers of both species are visited by medium-sized to large potter wasps, *Delta* and *Allepipona erythrospina* (Eumenidae) or female masarine wasps (Masarinae), *Jugurtia koeroegabensis* recorded on *F. variabilis* (as *F. divaricata*) and *Ceramius* on *F. macrochlamys* subsp. *kamiesbergensis* in Namaqualand (Gess 1997, reported as *F. divaricata*, now *F. variabilis*). Other potential insect visitors including bees and flies of several families common nearby are not attracted to these flowers. The eumenid wasps, seen only infrequently, display a constant foraging pattern, alighting on flowers of one plant after another. In doing so they become densely covered in pollen on the dorsal part of the head and thorax. Microscopic examination of pollen from captured male and female individuals of *Allepipona* and female *Delta caffer* shows that the only type of pollen they carry is that of *Ferraria*. The reason for visits by wasps is unknown but may simply be for the water content of the nectar rather than the dissolved sugar, although the possible presence of amino acids in the nectar has not been assessed.

One last pollination system in the genus is that reported in *Ferraria uncinata*, which is visited only by small herbivorous beetles, *Iselma planidorsus* (Meloidea), and an unnamed genus of Melyridae (Goldblatt *et al.* 2009). We assume that nectar of moderate sugar concentration is the reward for these insects. We are hesitant to accept these beetles as the legitimate pollinators but these fairly common flower visitors are almost invariably seen on flowers of *F. uncinata*.

Pollen carried by flies, bees, and wasps was always deposited on the dorsal part of an insect's thorax as it enters the floral cup in search of nectar. To date, no insect visitors capable of accomplishing pollen transfer have been recorded on the small, pale, watery, yellow flowers of *Ferraria brevifolia* but we assume the species has the same pollinator as *F. macrochlamys*. The flowers of these species have faintly scented flowers with a narrow floral cup containing dilute nectar, 6–12 % sucrose equivalent. All these species require insect-mediated pollen transfer and our lack of success in locating pollinators remains puzzling.

Nectar sugar chemistry, examined for individuals of four species shows that *Ferraria* species secrete hexose-dominant nectar (Goldblatt *et al.* 2009). This is consistent with nectar sugars of the sister genus *Moraea* (Goldblatt & Bernhardt 1999) and contrasts with nectar sugars of Iridaceae subfam. Crocoideae which are sucrose-rich or sucrose dominant except in a few species adapted to butterfly or sunbird pollinators (Goldblatt *et al.* 1999, 2001; Goldblatt & Manning 2006).

#### HISTORY

The first record of *Ferraria* in the literature is the illustration of *F. crispa* in the celebrated volume, *Flora seu de florum cultura* (Flora of cultivated plants) by the 17th century artist, Giovanni Battista Ferrari (1633). Interestingly the illustration was made from a plant grown in Italy. Ferrari called it '*flos indicus e violaceo fuscus radice tuberosa*' and, unfortunately, did not record the source of his plant. The genus appears in the botanical literature again in Robert Morison's (1680) *Plantarum historiae universalis* as *Gladiolus indicus e violaceo fuscus* and in Olof Rudbeck's (1701) *Reliquiae rudbeckianae* as *Narcissus indicus flore saturate purpureo* but the illustrations in both works appear merely to have been copied from Ferrari's original. *Ferraria* was formally described by Philip Miller (1759a, b), who attributed the name to the Dutch botanist, Johannes Burman. Evidently Burman communicated to Miller his intention to name the genus *Ferraria*, of course, honouring Giovanni Ferrari. Burman's own paper was published two years later (Burman 1761) and included not only an extended botanical description, but woodcut illustrations of two plants, *F. crispa*, and what he called *F. fimbriata*, the identity of which is uncertain. The illustrations are in fact the types of the two species and adequate for the identification of *F. crispa* but not for *F. fimbriata*. We agree with De Vos (1979) that the latter is not *F. crispa*. Our best guess is that the illustration represents what is now *F. divaricata*.

Linnaeus (1759) accepted the genus without citing Miller or Burman, but listed one species, *Ferraria undata*, without description. Later in *Species plantarum* edn 2, Linnaeus (1763) admitted one species, *F. undulata*, thus overlooking Burman's earlier epithet, *F. crispa*, although citing Burman's paper. Linnaeus's *F. undulata* was based on Miller's 1759 illustration and was the name used for the species until the late 20th century when Moore (1974) noted that *F. crispa* has nomenclatural priority.

The distinctive and most unusual looking *Ferraria crispa* was grown in Paris and Vienna in the later 18th century and was illustrated by Jacquin (1770) and Redouté (1802), amongst others. Thunberg (1787) collected *F. crispa* himself and realized it was Linnaeus's *F. undulata*. However, he transferred the species to *Moraea*, which then included such diverse genera as *Bobartia* and *Aristea* (typical *Moraea* species were at the time included in *Iris*). Only two other species of the genus, *F. ferrariola* and *F. ovata*, are known to have been recorded before 1800. Jacquin described *Moraea ferrariola* in 1790, thus following Thunberg's circumscription of that genus. Jacquin's description was based on a plant grown in Vienna, and very likely provided by

Franz Boos and Georg Schol, who collected plants for Jacquin at the Cape in the years 1786 to 1788 (Gunn & Codd 1981). Then, in the 1890s, most likely 1893, Francis Masson, plant collector for the Royal Botanic Gardens, Kew, discovered what we now know to be *Ferraria ovata* in western South Africa. His collection, a dried specimen lacking preserved flowers or corms, was described as *Moraea ovata* by Thunberg (1800).

We owe the restoration of *Ferraria* to Willdenow (1800) for in edn 4 of *Species plantarum* he included *F. undulata* and *F. ferrariola* in the genus, as well as two American species, the superficially similar *F. pavonia*, now *Tigridia pavonia*, and *F. ixioides*, now *Libertia ixioides*. Thunberg's *Moraea ovata* was not included in Willdenow's account (perhaps because of their contemporary publication) and *M. ovata* remained a puzzling species until 1995 when vegetative plants were collected near the Skilpad Reserve in Namaqualand by botanist, Annelise le Roux. Flowering specimens were obtained soon thereafter and the species was found to have a *Ferraria*-like flower. *M. ovata* was transferred to *Ferraria* by Goldblatt & Manning (2002). Salisbury (1796), always a maverick, also recognized *Ferraria* but expanded its circumscription to include species of what are today *Moraea* and *Sisyrinchium* as well as *Iris domestica* (syn. *Belamcanda chinensis*). Ker Gawler (1804, 1827) followed Willdenow in maintaining *Ferraria* but *Tigridia pavonia* and a few of its American allies in the tribes Tigridieae and Trimezieae (species of *Cypella*, *Eleutherine*, *Gelasine*, and *Trimezia*) were sometimes included in *Ferraria*. *Tigridia* had actually been described for Linnaeus fil.'s *Ferraria pavonia* in 1789 (Jussieu 1789) although the species itself was only formally transferred to that genus some years later (De Candolle in Redouté 1802). The separation of *Tigridia* from *Ferraria*, or for that matter *Moraea*, was not universally accepted until late in the 19th century (Molseed 1970).

The early 19th century saw the addition of two new *Ferraria* species: *F. uncinata* (Sweet 1826a) and *F. divaricata* (Sweet 1827) were both grown in England from corms or seeds collected by Walter Synnot, landdrost (magistrate) at Clanwilliam from 1821 to 1825. Four more species were described in the latter half of the 19th century by J.G. Baker (1878), notably *Ferraria glutinosa* and its allies, *F. candelabrum* and *F. spithamea*, all from Angola and based on collections by the Austrian Friedrich Welwitsch in the years 1855–1861, and all were initially referred to *Moraea* by Baker who evidently did not see their resemblance to the southern African *Ferraria* species (Baker 1877, 1896). This error was most likely due to the condition of the specimens, the flowers of which are poorly preserved. In 1892, Baker described another Angolan species, *F. welwitschii*, this time as referred to the genus. Based not on herbarium material but on an illustration of a plant grown in England, the drawing with some parts painted in watercolour, showed clearly the hallmarks of *Ferraria*, fringed style crests, a floral cup and crisped and undulate tepal limb margins. It was left to J.B. Rendle (1899) to transfer to *Ferraria*, Baker's other tropical species. Baker (1876) also described what is now *F. macrochlamys* but included it in *Lapeirousia*. The species was based on a poor herbar-



ium specimen in the Kew Herbarium, originally owned by William Forsyth and probably collected by William Paterson in the 1780s, though this is no more than surmise.

Several more species were added in the later 19th and early 20th centuries but most are synonyms of those already described. In 1920, Kurt Dinter added *Ferraria schaeferi* based on collections from southern Namibia  $\pm$  1912–1913, unaware that the species had first been recorded by J.-F. Drège in 1820. G.J. Lewis added *Ferraria brevifolia* and *F. foliosa* in 1954 and M.P. de Vos, in her revision of the genus, added *F. densepunctulata* and *F. kamiesbergensis*. De Vos recognized just 10 species and four subspecies (14 taxa). De Vos unfortunately misunderstood the tropical African species and included the four we recognize here in *F. glutinosa*, following Carter's (1963) lead. Our revision reverses this action, and we now admit 18 species and two subspecies (20 taxa) in *Ferraria* assigned to two subgenera and three sections.

#### PHYLOGENY AND EVOLUTION

De Vos (1979) considered the morphologically and geographically isolated *Ferraria glutinosa* (in which she included all four tropical African species we recognize), the least specialized member of the genus in the light of its open branching growth form, cluster of basal leaves differentiated from the bract-like cauline leaves, multi-flowered inflorescences, and globose, truncate ovary. These features seem intuitively to be ancestral, recalling species of the related genus *Moraea*. Molecular studies of the genera of the Iridaceae using plastid DNA sequences confirm that *Ferraria* and *Moraea* are immediately related (Goldblatt *et al.* 2002, 2008). The genera share apomorphic astelic corms that produce roots from the base of the terminal bud, unique in the Iridaceae, and also have flowers with the filaments partly united, whereas other African genera of Irideae and *Iris* itself, have free filaments as their ancestral condition.

DNA sequences of 12 *Ferraria* species, using the plastid DNA regions *trnL-F* and *rbcL* (unpublished data), confirm our intuitive hypothesis about relationships within the genus. *Ferraria glutinosa* is sister to the remaining species in the data set, which did not include any other tropical African species. The relationships among these species is largely unresolved, leaving us with the conclusion that *F. glutinosa* (and presumably the morphologically similar tropical species) are taxonomically and geographically isolated species that evolved before the establishment of the present southern African winter rainfall climate. This in turn is consistent with the most recent molecular clock estimates of the divergence of *Moraea* and *Ferraria*  $\pm$  30 mya (Goldblatt *et al.* 2008), during the later Oligocene, when the African climate become increasingly dry and seasonal, but with summer precipitation. This period coincides with the establishment of circum-Antarctic oceanic circulation and the strengthening of the cold Benguela current along the southwestern African coast. Although still under a summer rainfall regime, seasonal aridity is believed to have caused the reduction of forest in favour of open grass-dominated habitats (Raven & Axelrod 1974; Coetzee 1993). Such a regime would have encour-

aged the evolution of geophytic plants, which survive periods of drought using underground storage organs that enable them to rapidly sprout and flower when suitable growing conditions return.

The onset of a winter rainfall regime in southern Africa probably dates from the beginning of the Pliocene,  $\pm$  6 mya, and this is when we assume that a recent burst of radiation occurred in *Ferraria* in the south, associated with summer drought and cool, wet, winter conditions. We infer that the resulting species we see today are too recent to have accumulated sufficient DNA sequence diversity to be successfully resolved in phylogenetic studies of two chloroplast DNA regions we utilized for our molecular study.

For the present, except for the position of *Ferraria glutinosa* (and we infer, the other tropical species) as sister to the remaining species confirmed by DNA sequence studies, we are left with morphology as a guide to the phylogeny of the genus. Outgroup comparison reveals two major specializations in the *Ferraria* species of the southern African winter rainfall zone: an ovary with a sterile tubular tip, the beak (and associated beaked capsule); and divergent anther lobes. The first of these is present in the species of sect. *Macroscyphae* (subgen. *Ferraria*) of De Vos plus *F. schaeferi*, and divergent anther lobes are restricted to that section, although the expression of the character is delayed in *F. ferrariola* and *F. parva*, in which it is expressed in older flowers, after dehiscence of the anther lobes and sometimes only on the second day of anthesis.

We propose a revised infrageneric classification of *Ferraria* based first on the molecular data, supplemented by the morphological variation evident in the ovary and anthers. Thus we recognize two subgenera, subgen. *Glutinosae*, for the tropical species and subgen. *Ferraria* for the remaining species, all of winter rainfall southern Africa. We endorse De Vos's two sections, *Ferraria* and *Macroscyphae*, the first for species with parallel anther lobes, broad, spreading tepal claws and a relatively wide floral cup, and except for *F. schaeferi*, a subacute capsule apex lacking a beak. Sect. *Macroscyphae* always has anther lobes joined only at the tips and usually widely divergent (rarely sub-parallel), a beaked ovary, and except in *F. divaricata* and *F. variabilis*, suberect tepal claws that form a narrow floral cup. In sect. *Macroscyphae* we recognize three informal series, *Macroscyphae*, *Subdivaricatae* and *Uncinatae*.

#### SYSTEMATICS

***Ferraria* Burm. ex Mill.**, Figures of plants, vol. 2: 187, t. 280 (1759a) and The gardeners dictionary, edn 7 (1759b); De Vos: 327–375 (1979). Type species: *Ferraria foliis lanceolatis* ... (= *F. crispa* Burm.).

Named for the 17th century artist, Giovanni Ferrari, whose illustrated works were much celebrated by contemporaries; his *Flora seu de florum cultura* (Flora of cultivated plants) included the first illustration of *Ferraria*, *F. crispa*, drawn from plants grown in Italy.

Revisionary accounts: De Vos in Journal of South African Botany 45: 295–375 (1979).

Small to medium-sized seasonal perennials. *Corm* depressed-globose, consisting of several internodes, producing roots from terminal bud, lacking tunics when mature. *Leaves* several, lower 3 or 4 lacking blades, thus cataphylls, foliage leaves with isobilateral, sword-shaped to linear, unifacial blades, sometimes not produced on flowering stem, basal one or more and largest, progressively smaller above, becoming bract-like at distal nodes. *Flowering stem* aerial or largely to entirely underground, usually branched, branches often short and crowded distally. *Inflorescence* a 2- or several-flowered rhpidium; spathes green, often leafy, enclosing flower buds, inner always longer than outer, margins free to base. *Flowers* radially symmetric, fugaceous or lasting 2 days, often dull-coloured, usually cream-coloured to buff or brownish, sometimes yellow, rarely blue-violet, spotted and blotched dark brown, green or purple, without scent or scented with sweet, spicy or rotting odours; tepals free, clawed, those of outer whorl slightly to significantly larger than inner, claws forming a wide or narrow cup or shallow basin, limbs spreading to slightly reflexed, margins crisped, the tips attenuate and twisted, producing nectar from nectaries at base or middle of claws, distal edges of nectaries lobed in *F. ornata*. *Stamens* symmetrically arranged; filaments united in lower

± two thirds in a smooth column, free and diverging in upper third or quarter; anthers appressed to style branches, lobes joined to connective but not to each other, parallel and ± contiguous or widely diverging, rarely subparallel but not contiguous. *Ovary* included or exerted from spathes, often with sterile beak; style enclosed by filament column, dividing at column apex into short branches, each forked into flattened, diverging, conduplicate arms, each usually prominently fringed on adaxial margin, rarely fringes vestigial or absent (*F. spithamea*), stigmatic surface terminal on style branches or on grooved lobe below tip of abaxial margin. *Capsules* globose-truncate, ovoid or ellipsoid, then often beaked. *Seeds* angular, mostly 5- or 6-sided, facets separated by winged angles, facets ± smooth or wrinkled, in one species ± globose and reticulate. *Basic chromosome number*  $\times = 10$ .

Species: 18, dry parts of central and southwestern Africa, with a centre along the southern African west coast and near interior, and four species extending from interior southern Africa through Namibia to Angola, Congo, Zambia, Zimbabwe and Malawi in dry grassland, generally favouring sandy soils, occasionally rocky habitats or seasonally wet sites.

### Key to species

- 1a Anthers with filament insertion in lower third and lobes parallel and usually contiguous above filament insertion when fully dehiscent; capsules globose- to ovoid-truncate or acute or beaked in one species; perianth with tepal claws usually forming a shallow cup and bearing prominent nectaries  $\frac{1}{3}$  to  $\frac{1}{2}$  as long as claw; stigmas minute, terminal on apices of style branch arms (subgen. *Glutinosae* and sect. *Ferraria*):
  - 2a Upper internodes below flower clusters with sticky exudate; ovary ovoid, short, < 10 mm long; capsules ovoid to globose and truncate (subgen. *Glutinosae*):
    - 3a Leaves several (up to 8) in basal fan; rhpidia with outer spathe  $\frac{1}{3}$  to  $\frac{1}{4}$  as long as inner ..... 2. *F. candelabrum*
    - 3b Leaves absent at base of flowering stem or 1–4 basal; rhpidia with outer spathe  $\frac{1}{3}$  to slightly more than  $\frac{1}{2}$  as long as inner:
      - 4a Flowers brown or dark purple, sometimes marked with yellow near tepal limb bases; tepal limbs often with buff to yellow margins; flowering plants usually with 1–4 basal foliage leaves, or foliage leaves reduced; filament column 8–11 mm long; flowering (Dec.–)Jan.–Mar.(–May) ..... 1. *F. glutinosa*
      - 4b Flowers yellow to buff, limbs sometimes speckled with brown, dark red, purple or dull green spots; tepal limb margins not contrasting in colour; flowering plants lacking foliage leaves at base and branches subtended by sheathing leaves without blades; filament column 5.0–7.5 mm long; flowering (Sept.–)Oct. to Dec.(–early Jan.):
        - 5a Tepal limbs speckled with dark colour and margins obviously crisped; style branch arms prominently fringed ..... 4. *F. welwitschii*
        - 5b Tepal limbs uniformly yellow and margins plane or slightly undulate; style branch arms entire (not fringed) and arching outward ..... 3. *F. spithamea*
  - 2b Plants ± acaulescent or stem aerial, then upper internodes below flower clusters not sticky; ovary ± fusiform, > 10 mm long; capsules usually ovoid, rounded at apex or with short sterile beak (sect. *Ferraria*):
    - 6a Stem aerial, slender with internodes partly exposed; basal leaves linear to falcate, with blades usually < 5 mm wide:
      - 7a Plants ± acaulescent; tepal claws narrow in lower third, thus forming a windowed cup; nectaries concave, at apex of narrow part of claw and with raised and lobed to fringed distal edge ..... 10. *F. ornata*
      - 7b Plants with aerial stems; tepal claws broad and not abruptly narrowed in lower part, cup not windowed; nectaries relatively large, in centre of tepal claws and without raised distal edges:
        - 8a Cauline leaves lanceolate-attenuate; flowers grey or blue-green with minute brown, maroon or violet speckling; nectaries yellowish green ..... 9. *F. densepunctulata*
        - 8b Cauline leaves ovate-cucullate; flowers yellow with brown margins and a few conspicuous spots; nectaries cream-coloured streaked maroon ..... 8. *F. ovata*
    - 6b Stem stout, mostly covered by leaf bases; leaves sword-shaped to falcate, with blades > 5 mm wide:
      - 9a Ovary with short tapering beak, ± 8 mm long; tepals 22–25(–30) mm long, pale yellow with dark brown margins and blotches, often coalescing in outer quarter; flowers sweetly scented ..... 7. *F. schaeferi*
      - 9b Ovary fusiform, without tapering beak; tepals 25–35 mm long; flowers variously coloured, usually dark maroon or purple with paler margins or cream-coloured to pale yellow and variously striped and blotched, with an unpleasant, burnt-sugar or putrid scent:
        - 10a Blades of basal leaves with slightly thickened zone in middle and prominent central vein; leaves 2-ranked ..... 5. *F. crispa*
        - 10b Blades of basal leaves much thickened in middle but with weakly developed central vein; leaves spirally 2-ranked ..... 6. *F. foliosa*
  - 1b Anthers with filament insertion in upper third and lobes held together only at tips, usually widely divergent when fully dehiscent, rarely sub-parallel but not contiguous (not always so in freshly opened flowers); capsules always prominently beaked; perianth with tepal claws forming deep, narrow or wide cup; stigmas consisting of groove below tips of style branch arms (sect. *Macrosphyphae*):
    - 11a Floral cup widening substantially toward apex, rim ± as wide or wider than depth of cup:
      - 12a Flowers small, sweetly, slightly clove-scented; floral cup ± 8 mm deep, ± 7 mm wide at rim; outer tepals 18–22 mm long; filament column ± 6 mm long ..... 12. *F. parva*
      - 12b Flower relatively large, unscented or faintly unpleasantly scented; floral cup 12–15 mm deep, 13–20 mm wide at rim; outer tepals 30–45 mm long; filament column 8–13 mm long:

- 13a Plants usually subcaulescent and stem mostly covered by sheathing parts of leaves; flowers lasting 2 days; seeds (4)5(6)-sided, facets separated by raised angles, surface smooth ..... 14. *F. variabilis*  
 13b Plants with aerial stem and branching only distally; flowers lasting a single day; seeds  $\pm$  globose, surface matte ..... 13. *F. divaricata*  
 11b Flowers with narrow cup, sides  $\pm$  erect (rim of cup  $\frac{1}{2}$  to  $\frac{2}{3}$  as wide as depth of cup):  
 14a Stem produced well above ground; basal leaves sharply distinct from cauline leaves and with internodes partly exposed; flowers with floral cup 17–20 mm deep; outer tepals 30–40 mm long ..... 11. *F. ferrariola*  
 14b Stem not or only shortly extended above ground (unless growing in shade); basal leaves often hardly distinct from cauline leaves (or from spathes enclosing flower clusters); floral cup 10–12 mm deep; outer tepals 25–35 mm long:  
 15a Basal leaves broad, leathery-succulent, 8–20 mm wide, cauline leaves and spathes different from basal leaves; flowers lasting a single day, deep yellow; anthers and pollen yellow ..... 15. *F. flava*  
 15b Basal leaves hardly distinct from cauline leaves, rarely exceeding 12 mm wide, flowers lasting two days, watery yellow, blue or shades of beige to cream-coloured dotted with blue spots; anthers and pollen usually orange to  $\pm$  red:  
 16a Flowers usually predominantly blue to violet with dull yellow-green to khaki margins, occasionally tepal limbs pale bluish or cream-coloured, then speckled dark blue; margins of at least lowermost leaves conspicuously thickened, hyaline and partly crisped and undulate; marginal thickenings smooth ..... 16. *F. uncinata*  
 16b Flower pale watery yellow with darker yellow to buff or khaki margins; leaf margins either thickened then lower leaves with margins plane or serrulate to crenate, or sometimes slightly crisped or unthickened and margins plane; marginal thickenings when present often shortly velvety:  
 17a Basal leaves with extended, lanceolate to linear blades longer than sheaths ..... 17. *F. macrochlamys*  
 17b Leaves with short, oblique, ovate blades less than half as long as sheaths ..... 18. *F. brevifolia*

A. Subgen. **Glutinosae** (*M.P.de Vos*) Goldblatt & J.C.Manning, subgen. & comb. nov. Sect. *Glutinosae* M.P.de Vos: 329 (1979). Type: *Ferraria glutinosa* (Baker) Rendle.

Plants with open, aerial branching system and stem sticky below nodes. *Rhipidia* with > 2 and up to 6 flowers each. *Flowers* with tepal claws forming a wide cup, bearing prominent nectaries with dry nectar; filaments inserted in lower third of anthers; anther lobes parallel and contiguous above filament insertion when fully dehiscent. *Ovary* exserted, ovoid; stigmas minute, terminal on apices of style branch arms. *Capsules* globose- to ovoid-truncate.

1. *Ferraria glutinosa* (Baker) Rendle, in W.P.Hiern, Catalogue of the African plants collected by Dr. Friedrich in 1853–61, vol. 1,2: 27 (1899); De Vos: 329 (1979); Goldblatt: 11 (1993). *Moraea glutinosa* Baker: 271 (1878). Type: Angola, Huila, near Lopollo, Ferrão da Sola, February and April 1860, *Welwitsch 1543* (BM, holo.!, K!, LISU, P!, iso.).

*F. bechuanica* Baker: 344 (1898). Type: Bechuanaland [Botswana], Ngamiland, Kalahari Desert near Manumwe, 'flowers chocolate with yellow fringe', 26 Feb. 1897, *Lugard 237* (K, holo.!).

*Moraea randii* Rendle in Rand: 144 (1898). *Ferraria randii* (Rendle) Rendle: 54 (1905). Type: Southern Rhodesia [Zimbabwe], Bulawayo, Jan. 1898, *Rand 223* (BM, lecto.! here designated; BR, iso.).

*F. viscaria* Schinz: 77 (1900). Type: South West Africa [Namibia], Omupanda, *Wulphorst 45* (Z, holo.).

?*Moraea malangensis* Baker: 862 (1901). Type: Angola, Malange, without date, *Expedition von Mechow 386* (B, holo., no longer extant, R. Vogt pers. comm.).

Plants mostly 400–600 mm high. *Stem* exposed above sheaths of lower leaves, with 1(2) branches from upper nodes, branches rarely also branched; distal 5–6 mm of upper internodes sticky, often with sand adhering. *Leaves* at base solitary or up to 4, sometimes basal leaf poorly developed; blades linear, straight, 4–6(–10) mm wide, with visible central vein, cauline leaves moderately well developed, often longer than basal leaf, progressively reduced above and then largely sheathing. *Rhipidia* 4–6-flowered; inner spathe 30–42 mm long, outer entirely sheathing, usually  $\pm \frac{1}{2}$  to  $\frac{1}{3}$  as long as inner. *Flowers* on pedicels slightly longer than spathes, lasting a single day, usually dark brown to dull purple or maroon; tepal limbs with pale yellow to gold margins,

sometimes limbs marked or sparsely spotted yellow near base or with large irregular brown blotches on pale background; claws brown or yellow streaked with purple or brown, odourless; tepals diverging, claws forming wide basin  $\pm$  10 mm deep, 15–18 mm wide at rim, limbs spreading  $\pm$  horizontally to reflexed; margins crisped; nectaries dark brown, 1.5  $\times$  2.0 mm, 3–4 mm above claw bases; outer tepals 23–33  $\times$   $\pm$  10 mm, claws usually slightly longer and  $\pm$  as wide as limbs; inner tepals slightly smaller, claws tapering to narrow base. *Stamens* with filaments united in a minutely puberulous column 8–11 mm long, free in upper 1.5–2.0 mm; anther thecae diverging below, parallel above filament insertion, 5–6 mm long before anthesis, 3–4 mm long after anthesis, dark brown; pollen orange. *Ovary* narrowly ovoid, usually exserted, 5–7 mm long; style branches 2 mm long, dividing into diverging, prominently fringed arms 2–3 mm long, fringes smooth or minutely papillate, 4–5 mm long; stigmas terminal on tips of style arms. *Capsules* ovoid- to globose-truncate, mostly 12–18 mm long. *Seeds* glossy, brown, 4–5 mm at longest axis,  $\pm$  5-sided, facets separated by raised ridges, facet surfaces wrinkled. *Flowering time*: mostly Jan.–Mar., occasionally later. Figure 1; Plate 1G.

**Distribution and biology:** *Ferraria glutinosa* occurs across a wide belt of summer rainfall southern and central Africa; it is relatively common across Botswana and northern Namibia from where it extends northward to southern Angola, and westward to the North-West Province of South Africa and western Zimbabwe, but with an isolated record from Malawi (Figure 2). We have seen no collections from Zambia, where it is likely to occur. *F. glutinosa* is usually found in sandy ground with the corms deeply buried, but sometimes in rocky places. Several collections specifically mention white sand habitats and others red sand.

**Diagnosis and relationships:** *Ferraria* species in tropical Africa and summer rainfall southern Africa differ from all species of the southern African winter rainfall zone in their open-branching habit, stems with sticky exudate below the nodes, rhipidia with several (usually 4–6) flowers, and subglobose, flat-topped capsules. The genus in tropical Africa is, nevertheless, unusually variable as regards plant height, presence or absence of foliage leaves on the flowering stem, proportions of the

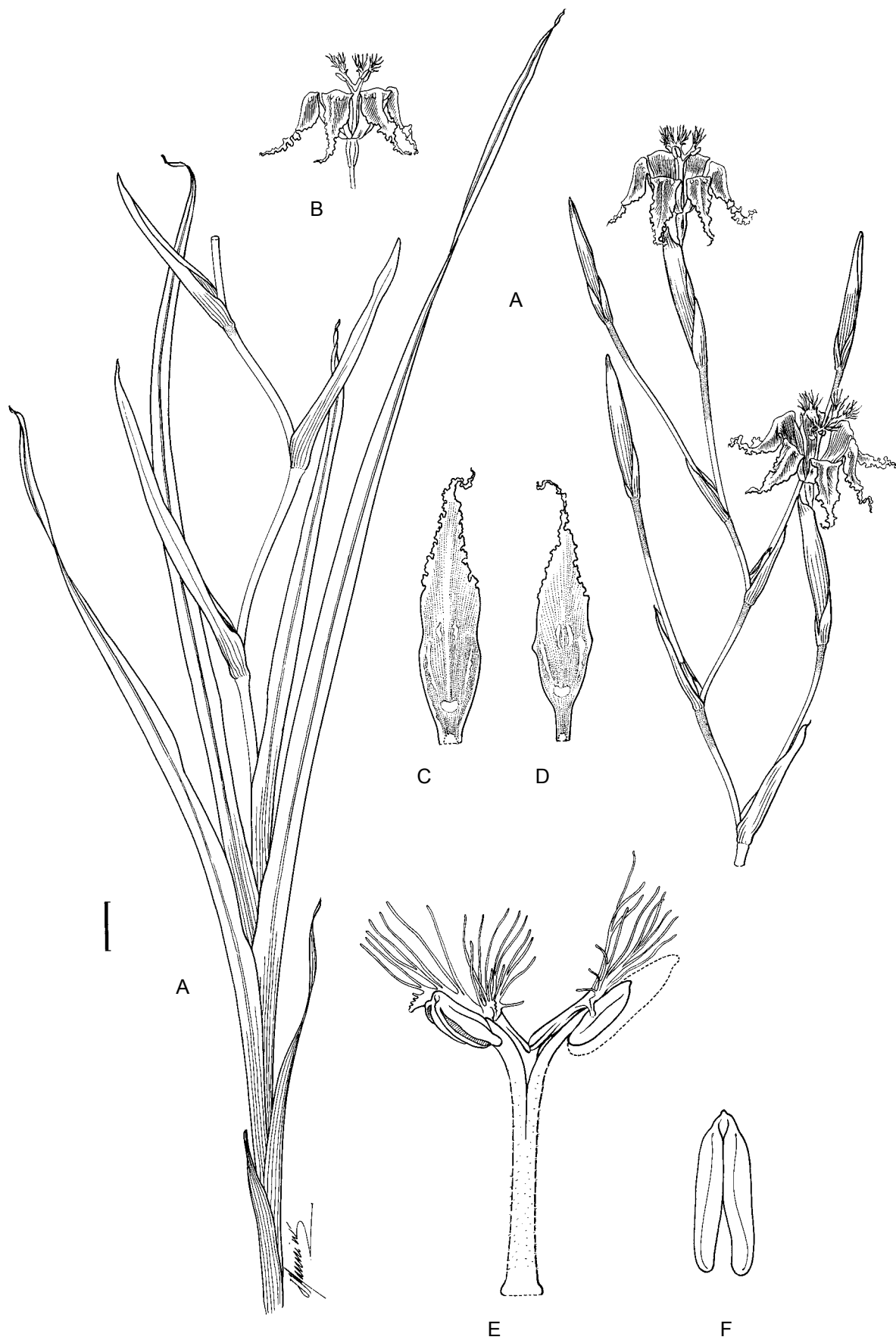


FIGURE 1.—*Ferraria glutinosa*. A, flowering stem; B, flower, side view; C, outer tepal; D, inner tepal; E, staminal column and style, undeveloped anther indicated by broken line; F, anther. Scale bar: A, B, 10 mm; C, D, 5 mm; E, F, 1.5 mm. Artist: John Manning.

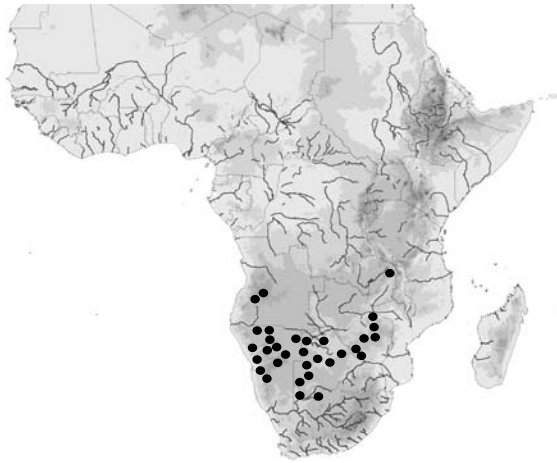


FIGURE 2.—Known distribution of *Ferraria glutinosa*.

inner and outer rhipidial spathes, and flower colour and patterning. It is not altogether surprising then, that 12 species have been described for the area between North-West Province of South Africa and western Angola, southern Congo and Zimbabwe. *Ferraria glutinosa*, based on *Moraea glutinosa*, one of the first four of these named species, was first collected by Friedrich Welwitsch in western Angola in the years 1855–1861, and is the name used until now for all populations of *Ferraria* in tropical Africa (De Vos 1979; Goldblatt 1993).

Three other Welwitsch collections of *Ferraria* from Angola formed the basis for *Moraea andongensis*, *M. candelabrum* and *M. spithamea*, named by J.G. Baker (1878) at the same time as *F. glutinosa*. Five more species were subsequently described by Baker (1892, 1901), four from Angola and one from Botswana (then Bechuanaland); one more species was described from Namibia (Schinz 1900); one from Zimbabwe (Rendle in Rand 1898); and one from Congo (Bulus 1932a). Five of these were placed in the synonymy of *Ferraria glutinosa* by Carter (1963), who suggested that the Namibian *F. viscaria* was probably also conspecific. Following Carter's lead, De Vos (1979) treated all 12 named species from tropical Africa as synonyms of *F. glutinosa*. Her taxonomy was uncritically accepted by Goldblatt (1993) for *Flora zambesiaca* and by Geerinck (2005) for *Flore d'Afrique Centrale*.

We have examined most of the available herbarium collections of tropical African *Ferraria* and conclude that recognition of a single tropical species does not reflect the extent of the variation among *Ferraria* populations there. Most importantly, there are two major vegetative types, one with only short sheathing leaves produced by the flowering stem in plants flowering mainly in October to mid-December, and another with at least one and up to eight well-developed basal leaves with unifacial blades and a relatively prominent central vein in plants flowering in (December) January to March. In the light of the variation, which is closely correlated with flower size and colouring, tepal patterning, relative proportions of the inner and outer inflorescence spathes, flowering time, and partly with geography, we propose an alternative taxonomy, recognizing four species, thus to a large extent validating Baker's (1878) original interpretation of *Ferraria* in tropical Africa.

*Ferraria glutinosa*, largest-flowered of the tropical species, is distinguished by the presence of several foliage leaves with well-developed blades, at least one of which is basal, and dark brown to purple flowers. Several specimens have the basal leaf virtually vestigial, but longer cauline leaves (e.g. Eyles 8543). Also exceptional are collections from Gweru [Gwelo] and Lomagundi in Zimbabwe (Holland s.n.; Rutherford-Smith 593), which respectively have three or six basal leaves. The inner inflorescence spathes are (30–)35–42 mm long, with the outer half or sometimes only one third as long. The brown to dark purple (also described as brown-violet, bright mauve or dark maroon) flowers have tepal limbs edged with yellow, sometimes also marked with yellow, and are produced mainly from January to March. The plants described as *F. bechuanica* from Botswana by Baker (1898), *Moraea randii* by Rendle (in Rand 1898) from Zimbabwe, and *F. viscaria* from Namibia by Schinz (1900) are the same species, but we note that the flowers of the last-named, *F. viscaria*, were described as yellow. We also provisionally include *F. malangensis* (Baker 1901) in *F. glutinosa* because its flowers were described as violet, but details of the leaves and flowering time, essential for confident identification, are not known. The type at the Berlin Herbarium is evidently lost (R. Vogt pers. comm. 2008).

Like the other species of *Ferraria* from tropical Africa, *F. glutinosa* is remarkable in having sticky internodes, a feature absent in the southern African winter rainfall species of the genus, but present in a few species of related genera of the southern African *Moraea* (only subgen. *Visciramosa*) and two species of *Bobartia* (Strid 1974; Goldblatt 1986). Rand (1898) noted that ants are trapped in the sticky exudate and suggested that this was a defence against these insects, which we assume might consume nectar, the reward for legitimate pollinators.

The fairly open branching pattern of the tropical species is also quite different from the crowded, short branches of other species of *Ferraria* and this, as well as the ovoid-truncate capsule and several-flowered rhipidia suggest an ancestral position in the genus. The morphological indicators of its unspecialized status are confirmed by molecular analysis using plastid DNA sequences, which places *F. glutinosa* as sister to the winter rainfall southern African species of the genus that were included in a preliminary analysis.

Both the common tropical African *Ferraria welwitschii* and the related but rare *F. spithamea* are smaller plants, notable for lacking foliage leaves on flowering plants. They also have flowers somewhat smaller than in *F. glutinosa*, with yellow to buff tepals (in *F. welwitschii* with the limbs marked throughout with small brown to dark red spots, more densely so on the claws), and large dark brown nectaries ± in the middle of the claws (illustrated in Geerinck 2005: plates 9A, B, as *F. glutinosa*). The rhipidia typically have the outer spathe slightly more than half to two thirds as long as the inner. Both these species bloom mainly in November to mid-December, but have been recorded in flowering as early as October.

The corms of *Ferraria glutinosa* are eaten raw or roasted by the Kwanyama Ovambo, according to the



ethnobotanist Robert Rodin (1985). Except for its value as an occasional ornamental in the garden or in containers, we know of no other human use of this or any other *Ferraria* species. It is noteworthy in the context of Rodin's statement about the edibility of corms, that Mannheim *et al.* (2008) report that *Ferraria glutinosa* is poisonous to stock, with symptoms including anorexia, increased heart rate, rapid respiration, diarrhoea and apathy. Post mortem signs are cyanosis, hyperaemia of the lung, and bloody inflammatory areas of the stomach and intestine. No southern African species is known to be toxic and we have seen cattle grazing on *F. divaricata*, but evidently not relishing it, for animals rarely took more than a mouthful before moving on.

### Representative specimens

ANGOLA.—Huila: without precise locality or date, *Dekindt* 493 (LISC) [specimen incomplete and without base]. Huambo: Chianga,  $\pm 1\ 700$  m, 3 Nov. 1962, *Teixeira & Andrada* 6525 (LISC). Cunene: Cuvelai, 11 Dec. 1972, *Menezes* 4270 (LISC).

BOTSWANA.—1825 (Panda-ma-Tenga): 13 km toward Jolies Pan, flowers yellow, (–DC), 23 Dec. 1996, *Bryns* 6972 (NBG). 2033 (Chibabava): near Kwebe Hills, (–CA), Dec. 1898, *Lugard* 282 (K). 2121 (Ghanzi): Groot Laagte (East) fossil river valley, (–AD), 16 Mar. 1980, *Smith* 3176 (MO, PRE, SRGH). 2322 (Kang): Phuduhudu, (–DD), 12 Dec. 1989, *Barnard* 499 (PRE). 2421 (Tshane): Kalahari Park, SW of Ritchie's Pan, white sand savanna, (–AC), Mar. 1979, *Van der Walt* 5807 (PRE).

MALAWI.—Northern:  $\pm 10$  km north of Mpherembe, sand at edge of thicket, brown with yellow centre, 1 180 m, 7 Feb. 1987, *La Croix* 957 (MO).

NAMIBIA.—1915 (Okakuejo): Ovamboland, Oshikango, brown-purple with yellow spots, 1 May 1973, *Rodin* 9360 (MO, WIND). 1917 (Tsumeb): Tsumeb, 25 Jan. 1911, *Dinter* 1840 (SAM). 1920 (Tsumkwe): 6 km east of Tsumkwe along Botswana border, white sand, (–DA), 13 Jan. 1971, *Giess, Watt & Syman* 11027 (PRE); 157 miles [251 km] east of Grootfontein, Simkue, (–DA), 16 Jan. 1958, *Story* 6156B (PRE, with colour slides). 2017 (Waterberg): Otjiwarongo, turn-off to Waterberg, (–DA), 24 Mar. 1987, *Maggs* 83 (WIND). 2115 (Karibib): Donkerhuk 91, sandy ground, (–DD), 2 Mar. 1965, *Barnard* 79 (PRE); Erongo Siding, deep Kalahari sand, (–DB), 22 Apr. (fr.), *Bean, Vlok & Viviers* 1837 (BOL, MO); Namibrand, Altenbronn, (–DD), 10 Mar. 1964, *Seydel* 264 (B). 2117 (Otjosondou): Waterberg, Quickborn, (–AA), 30 Mar. 1930, *Bradfield* 146 (PRE). 2118 (Steinhausen): 15 km along Kapps Farm road, Steinhausen to Windhoek, sandy plain, (–CC), Mar. 1988, *Goldblatt & Manning* 8805 (MO). 2216 (Otjimbingwe): dry rocky slopes of Kupferberg Pass, SW of Windhoek, (–DB), 21 Mar. 1988, *Goldblatt & Manning* 8843 (MO, WIND). 2217 (Windhoek): Farm Frauenstein, (–AD), 18 Jan. 1976, *Giess* 13901 (WIND); Goreangab Dam near Windhoek, (–CA), 21 Feb. 1965, *Giess* 8395 (NBG); Lichtenstein, (–CC), 20 Jan. 1923, *Dinter* 4311 (B). 2219 (Sandfontein): east of Gobabis, farm road between Farm Isabella and Farm Etna, (–AD), 8 Mar. 2002, *Bartsch* 503 (WIND). 2316 (Nauchas): Khomas, Farm Lichtenstein North, rock outcrop, (–DD), 3 Mar. 2002, *Mannheimer* 1732B (WIND). 2317 (Rehoboth): Rehoboth, (–AC), 13 Apr. 1911, *Dinter s.n.* (SAM).

ZIMBABWE.—Mazoe, Umvukwes, 5000 ft [1 525 m], Ruorka Ranch, 17 Dec. 1952, *Wild* 3911 (MO, K, PRE, SRGH). Lomagundi, Dyke near Rod Camp Mine, flowers yellow, spotted purple, 22 Feb. 1961, *Rutherford-Smith* 593 (K). Mangula Township, 17 Dec. 1961, *Jacobsen* 1990 (PRE). Plumtree, Jan. 1936, *Eyles* 8543 (K) [without basal foliage leaves]. Gwelo, 29 Dec. 1929 (cultivated at Kirstenbosch), *Holland s.n.* (BOL as *National Botanic Gardens* 92/28, K). Matobo, Farm Besna Kobila, grassland, Dec. 1955, *Miller* 3215 (PRE).

NORTHERN CAPE.—2723 (Kuruman): Kuruman, Esperanza, (–AD), Apr. 1940, *Esterhuysen* 2219 (BOL); Kormutsethla, (–BB), 2 Feb. 1934, *Cross* 1088 (PRE).

**2. *Ferraria candelabrum* (Baker) Rendle**, Catalogue of the African plants collected by Dr. Friedrich in 1853–61, vol. 1, 2: 27 (1899). *Moraea candelabrum* Baker: 271 (1878). Type: Angola, Huila, Morro de

Lopollo, Apr. 1860, *Welwitsch* 1544 (BM, lecto!), designated by De Vos, 1979: 331; K!, LISU, iso.).

?*Moraea andongensis* Baker: 271 (1878). *F. andongensis* (Baker) Rendle: 27 (1899). Type: Angola, Pungo Andongo, Mutollo near Pedras de Guinga, marshy, low grassland, Jan. (fr. Mar.), *Welwitsch* 1532 (BM, lecto!), designated by De Vos: 331 (1979); K!, LISU, iso.).

*M. kitambensis* Baker: 575 (1898). Type: Angola, Bangala, Kitamba, on Cuango River, in swamp, 1880, *Buchner* 679 (B, holo., no longer extant (R. Vogt pers. comm); K, iso!, fragment and drawing of B specimen).

Plants mostly 600–800 mm high. *Stem* enclosed below by overlapping leaf bases, exposed above, branched from upper nodes, branches sometimes 2(3) per node, and primary branches themselves often 1(2)-branched; upper nodes and distal parts of internodes sticky, often with sand adhering. *Leaves* at base 5–8,  $\pm$  narrowly sword-shaped-linear, straight, 8–10 mm wide, with visible central vein; margins not thickened; cauline leaves well developed, shorter than basal, progressively reduced above and becoming largely sheathing and bract-like. *Rhipidia* at least 3- or 4-flowered; inner spathe 28–32 mm long, outer entirely sheathing, usually  $\pm \frac{1}{3}$  ( $-\frac{1}{4}$ ) as long as inner. *Flowers* on pedicels slightly longer than spathes, ?lasting a single day, brown with yellow markings or pale yellow, evidently odourless; tepals ascending with claws forming a cup 11–12 mm deep,  $\pm 9$  mm wide at rim, limbs  $\pm$  spreading,  $\pm 10$  mm long, margins crisped; nectaries not evident; outer tepals 20–25 mm long, claws 11–13 mm long, inner tepals slightly smaller, claws tapering to narrow base. *Stamens* with filaments united in a column  $\pm 11$  mm long, free in upper  $\pm 1.5$  mm; anther thecae  $\pm$  parallel,  $\pm 3$  mm long, shorter after anthesis. *Ovary* usually exserted, narrowly ovoid,  $\pm 3$  mm long; style branches  $\pm 1.5$  mm long, dividing into diverging, prominently fringed arms  $\pm 2$  mm long; stigmas terminal on tips of style arms. *Capsules* globose-truncate,  $\pm 8$  mm long. *Seeds* unknown. *Flowering time*: Feb.–Apr., possibly also in Jan.

*Distribution and biology*: known to us from just four collections, none with well-preserved flowers, *Ferraria candelabrum* is recorded from central Angola and adjacent western Zambia (Figure 3). Plants grow in rocky, well-drained sites. Collections usually mention hilly places, but the type of the synonym, *Moraea kitambensis*

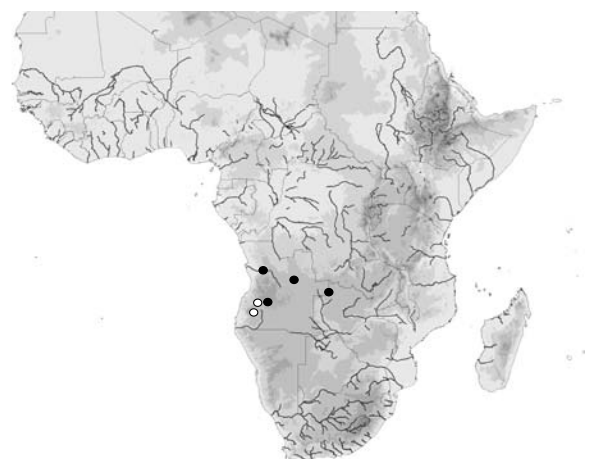


FIGURE 3.—Known distribution of *Ferraria spithamea*, ○; *F. candelabrum*, ●.

sis, is said to be from a swampy place (which seems unlikely). The type of *Moraea andongensis*, provisionally assigned here, is from marshy, low grassland.

**Diagnosis and relationships:** none of the collections of *Ferraria candelabrum* has well-preserved flowers but the colour was described as yellow in the type collection, brownish in one other, and buff with dark brown stripes and spots in a third. Despite the lack of precise floral details, the vegetative habit is unique among the tropical African species. Plants stand up to 800 mm high, and have a basal fan of several (up to 8) long, relatively soft-textured leaves. The stem is branched repeatedly, the branches terminating in unusually slender rhipidia about 30 mm long. Notably the outer of the two rhipidial sheaths is  $\frac{1}{3}$ – $\frac{1}{4}$  as long as the inner, giving the plants a distinctive appearance. *Ferraria candelabrum* is no doubt closely allied to the widespread subtropical African *F. glutinosa* and was included in that species by De Vos (1979). The unusually narrow rhipidia and short outer spathe makes the species easy to recognize. Unlike *F. candelabrum*, *F. glutinosa* has a single or rarely up to three basal leaves, sometimes poorly developed at flowering, a stem usually with the primary branches themselves only occasionally branched and large capsules 12–18 mm long, compared to capsules  $\pm$  8 mm long, known only from the somewhat atypical collection from Lubango in Angola (De Menezes 1661).

We provisionally place *Ferraria andongensis* in the synonymy of *F. candelabrum*. Although flowering in January and fruiting in March, plants of the type collection are much less robust, at most only 300 mm tall, and have only one basal leaf and a second, well-developed cauline leaf, both with narrow blades,  $\pm$  2.5 mm wide. The outer inflorescence spathes are short, about a third as long as the inner, and this as well as the small capsules are consistent with *F. candelabrum*. Welwitsch, in his notes, described the flowers as dull sulphur-yellow. The anthers are short,  $\pm$  2 mm long. Little more can be deduced from the type material.

#### Representative specimens

ANGOLA.—Huila: Lubango, on plateau of Ponta do Lubango, 11 Apr. 1965, De Menezes 1661 (LISC).

Also known from Angola from the types of the species cited above.

ZAMBIA.—Northwestern: Mwinilunga District: Ikelenge, Milomba Hill, among rocks, 1 440 m, 22 Feb. 1995, Zimba *et al.* 632 (MO, PRE); Mwinilunga, base of Kalene Hill, 1 400 m, sandy bank, flowers buff with dark brown stripes and spots, 22 Feb. 1975, Hooper & Townsend 327 (K).

### 3. *Ferraria spithamea* (Baker) Goldblatt & J.C.Manning, comb. nov.

*Moraea spithamea* Baker in Transactions of the Linnean Society, London, ser. 2, Botany 1: 271 (1878). Type: Angola, sandy places about Humpata and Lopollo, Oct. 1859 (fl. and fr.), Welwitsch 1547 (BM, lecto!, designated by De Vos: 331 (1979); K, iso!).

Plants mostly 100–160 mm high. *Stem* exposed above sheaths of cauline leaves; upper nodes and distal parts of internodes sticky, often with sand adhering, 2 or 3 internodes long, with a branch at each node, thus 2- or 3-branched. *Leaves* of flowering plants absent at base, borne at aerial nodes, partly sheathing, channelled throughout, 20–40 mm long; leaves of vegetative plants unknown. *Rhipidia* at least 3-flowered; inner spathe

25–30 mm long, outer entirely sheathing,  $\pm$  half as long as inner. *Flowers* on pedicels as long or slightly longer than spathes, ?lasting a single day, yellow, marked with brown spots toward base of tepals, tepals ascending, claws forming a cup,  $\pm$  8 mm deep,  $\pm$  7.5 mm wide at rim, limbs spreading, margins slightly undulate (not crisped); nectaries  $\pm$  1.5 mm diam., in lower third of outer tepal claws, in middle of inner tepal claws, colour unknown; outer tepals  $\pm$  20 mm long, inner  $\pm$  18 mm long. *Stamens* with filaments united in column  $\pm$  8 mm long, free in upper  $\pm$  1 mm; anther thecae parallel or diverging basally,  $\pm$  3 mm long. *Ovary* oblong to narrowly ovoid,  $\pm$  3 mm long, included or exerted 2–3 mm at anthesis; style branches  $\pm$  1.3 mm long, dividing into two divergent, entire arms  $\pm$  2 mm long; stigmas terminal on style arms. *Capsules* globose-truncate,  $\pm$  5 mm long, exerted from spathes, smooth. *Seeds* unknown. *Flowering time*: Oct.–Dec.

**Distribution and biology:** *Ferraria spithamea* is a narrow endemic of the highlands of southwestern Angola (Figure 3). Its habitat is described as thorny thicket in sand, or among rocks.

**Diagnosis and relationships:** poorly understood, *Ferraria spithamea* is known to us from just two collections, the type and one other, both from southwestern Angola. The species is recognized primarily by the entire, arching style arms, without the fringes characteristic of other species of the genus, but also by the pale yellow flowers with the tepal limbs at best undulate, and not crisped as they are in other species. Plants lack foliage leaves at flowering and we assume the foliage leaves are developed later in the season from separate shoots. The growth form is thus exactly as in the fairly widespread tropical African *F. welwitschii* but that species differs in the slightly smaller flowers, also yellow to buff, but with the tepal limbs and distal parts of the claws liberally scattered with minute dark spots. Normally a taller plant, *F. welwitschii* may reach 350 mm, therefore about twice as tall as *F. spithamea* and, typical of *Ferraria*, it has crisped tepal limb margins and prominently fringed style arms. We have relied in part for the description of the flowers of *F. spithamea* on Welwitsch's notes which describe the yellow tepal colour (*flava*) marked from the middle to the base with small dark marks (*parvis nigris picta*).

The lack of style branch fringing and tepal limbs without crisped margins are anomalous in *Ferraria* but the vegetative form, distally sticky internodes and distinctive corm, leave us in no doubt that the species is correctly assigned to the genus.

#### Representative specimen

ANGOLA.—Huila: Sa de Bandeira, Bata-Bata, 6 Dec. 1961, Santos 657 (LISC).

4. *Ferraria welwitschii* Baker, Handbook of the Irideae 74 (1892). Type: Angola, locality unknown, cultivated in England (Hort. Saunders), Welwitsch s.n. (K, holo.! drawing only with tepal painted in watercolour).

?*Moraea viscosa* R.C.Foster: 48 (1936), as a new name for *M. aurantiaca* Baker: 575 (1898), nom. illegit. non A. Dietrich: 485 (1832). Type: Angola, Malange, Oct. 1879, Expedition von Mechow 303 (B, holo.! (fragment), K, drawing!).

*Moraea aurantiaca* Baker: 575 (1898). Type: Angola, Malange, October 1879, *Expedition von Mechow 303* (B, holo.! (fragment), K, drawing!).

*F. hirschbergii* L.Bolus: 57 (1932a). Type: Congo, [Shaba], near Lubumbashi (Elisabethville), *von Hirschberg s.n.*, cultivated at National Botanic Gardens, Kirstenbosch, 615/29 (BOL, holo.!; K (two sheets)!, SAM, iso.!).

Plants (120–)180–350 mm high. *Stem* exposed above sheaths of lower leaves; upper nodes and distal parts of internodes sticky, often with sand adhering. *Leaves* of flowering plants sheathing, occasionally with short blades shorter than sheaths; of vegetative plants (1)2, narrowly sword-shaped, straight or falcate, 1.5–3.0 mm wide, with visible main vein. *Rhipidia* 4- or 5-flowered; inner spathe 20–34 mm long, outer entirely sheathing, mostly  $\frac{1}{2}$  to  $\pm \frac{2}{3}$  as long as inner, 10–17 mm. *Flowers* on pedicels  $\pm$  as long as spathes, lasting a single day, pale to dull yellow to buff (?also orange) with brown to dark red or dull green spots on limbs and distal part of claws, evidently odourless, tepals ascending, claws forming a cup, 7–9 mm deep,  $\pm$  7 mm wide at rim, limbs spreading to reflexed up to 40°, margins crisped; nectaries dark brown,  $\pm 1.5 \times 2$  mm,  $\pm$  in centre of claws; outer tepals  $15\text{--}20 \times \pm 5$  mm, inner 14–20 mm long. *Stamens* with filaments united in a column 5.0–7.5 mm long, free in upper 1.0–1.5 mm; anther thecae parallel or diverging basally, 1.5–2.5 mm long, slightly shorter after anthesis. *Ovary* usually exserted, oblong to narrowly ovoid, 2–3 mm long; style branches 1.5–2.0 mm long, dividing into diverging, fringed arms; stigmas terminal on style arms. *Capsules* globose-truncate, mostly 5–7 mm long, exserted from spathes, smooth or minutely warty (Mendes 1957). *Seeds* angular,  $\pm$  prismatic, 3 mm long, glossy, brown with pale, raised angles,  $\pm$  5-sided, facet surfaces undulate to wrinkled. *Flowering time*: mostly Oct. to early Dec.(early Jan.).

*Distribution and biology*: *Ferraria welwitschii* occurs across a wide belt in central Africa from the Malange highlands in west-central Angola, across Zambia to southern Congo and Zimbabwe (Figure 4). Records indicate that plants grow on the margins of open woodland, often in rocky ground and in fairly moist habitats, including riverbanks and dambos.

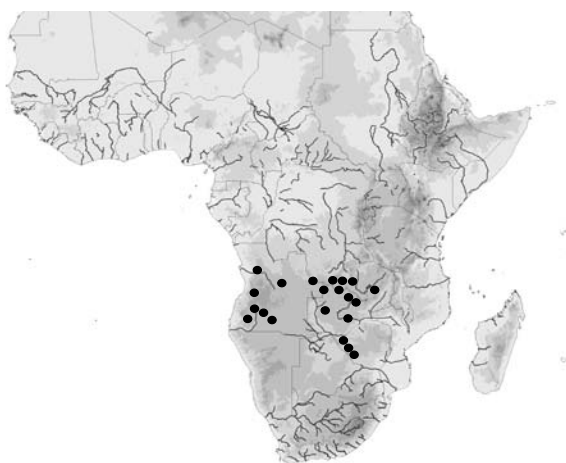


FIGURE 4.—Known distribution of *Ferraria welwitschii*.

*Diagnosis and relationships*: the type collection of *Ferraria welwitschii* is a pencil drawing of a plant cultivated in Britain, with one of the tepals coloured. The plant evidently stood  $\pm 300$  mm high, lacked developed basal foliage leaves and had flowers with reflexed, dull yellow tepal limbs covered with fine, dark brown spots. Friedrich Welwitsch is believed to have collected the plant but the original locality is not recorded. Plants matching this collection, although not always as tall, have been recorded widely across Angola, Zambia, Congo and parts of Zimbabwe, always flowering early in the wet season, October to mid-December, and consistently lacking well-developed foliage leaves. Even those specimens in fruit (e.g. *Cruse s.n.* from Zambia collected in late December) lack foliage leaves; other collections (e.g. *Mendes 1957* from Angola in fruit in January) have short, narrow foliage leaves emerging at the base, evidently representing late-developing foliage leaves on a shoot lateral to the main axis. It is clear that flowering plants do not produce leaves later in the season but rely on the stems and sheathing leaves for photosynthesis and production of storage carbohydrates for the new corms developed after flowering. This pattern recalls tropical African *Gladiolus unguiculatus* Baker; flowering and fruiting specimens of this species have short or vestigial foliage leaves but plants remain green even after the capsules have ripened and the seeds are shed in December (Goldblatt 1996). Corms of both species eventually produce new foliage leaves from shoots lateral to the fruiting axis, after the capsules have ripened. Vegetative specimens of *F. spithamea* have one or more well-developed leaves and one or two smaller leaves in a basal tuft.

Evidently the closely allied *Ferraria spithamea* from southwestern Angola has a similar growth form, but the yellow tepals lack the characteristic small dark spots, have at best undulate margins (never crisped), and the style branches lack the feathery fringes of all other *Ferraria* species.

The inclusion of *Ferraria welwitschii*, and for that matter *F. spithamea*, in the larger-flowered *F. glutinosa* (e.g. Carter 1963; De Vos 1979; Geerinck 2005), a taller, more robust plant with brown or purple (to maroon) or sometimes partly yellow flowers, and often bears one or more foliage leaves and well-developed cauline leaves on flowering individuals, now seems mistaken. The flowers of *F. glutinosa* have tepal limbs edged in yellow and bloom mainly from January to March, rarely in late November or December. Colour photographs in *Flore d'Afrique Centrale* (Geerinck 2005) show the flower form, colour and patterning of *F. welwitschii* clearly and they contrast starkly with photographs of *F. glutinosa* (e.g. *Story 6165B* PRE; Mannheimer *et al.* 2008) and our illustration of the species (Figure 1). We include *F. hirschbergii* in the synonymy of *F. welwitschii*, the type of which closely matches that species. We provisionally also include a second heterotypic synonym, *Moraea aurantiaca*, in *F. welwitschii*. The type, at the Berlin Herbarium, is fragmentary, but consists of an apparently leafless plant without flowers, but with small rounded capsules. We assume the species was called *aurantiaca* because the flowers were orange (or thought to be so) but the basis for this is not evident to us. Duplicates of

the type collection, if they exist, may help establish the identity of this name. The flowering time, October, and absence of leaves are consistent with our provisional assignment to *F. welwitschii*.

### Representative specimens

ANGOLA.—Huila: Ganguelas, Vila Artur de Paiva, banks of the Cubango, 1 450 m, 4 Jan. 1960, *Mendes 1957* (fr.), (LISC, MO); Huambo, outskirts of Nova Lisboa, 1 750 m, 8 Nov. 1970, *da Silva 3340* (K, LISC, PRE); Caala to Cuima, 26 Nov. 1959, *Stopp 122* (K). Lubango, Hoque, on road to Dinde, 5 km, 9 Nov. 1962, *De Menezes 340* (K, LISC, PRE). Cuanza Sul: Cela-Cassamba,  $\pm$  1 350 m, 28 Sept. 1963, *Texeira & All 7396* (LISC).

CONGO.—Shaba: Lubumbashi, woodland and savanna, 1 300 m, 6 Dec. 1968, *Lewalle s.n.* (MO); near Lubumbashi, banks of the Nat-webo, 25 Oct. 1970, *Lisowski 108* (B, BR, K); Lubumbashi, Paturage de la Karavia, Nov. 1933, *Quarré 3633* (BR).

ZAMBIA.—Northwestern: Mwinilunga: Kalenda Ridge, W of Matonchi Farm, stony ground, 8 Oct. 1937 (fr. 16 Dec. 1937), *Milne-Redhead 2664* (K).

ZAMBIA.—Western: Luano Forest Reserve, Chingola, in granite rocks, 19 Nov. 1961, *Linley 218* (K, MO, PRE, SRGH).

ZAMBIA.—Copperbelt: Kitwe, dambo margin, 13 Dec. 1959, *Fanshawe 5314* (K, NDO); Mufulira, dambo, 10 Nov. 1947, *Cruse 92* (K), late Dec. 1947 (fr.), *Cruse s.n.* (K); Kawambwa Dist., 900 m, by M'bereshi River, 2 Dec. 1961, *Richards 15485* (K); Mazabuka, Ridge-way road, 2 Dec. 1931, *Central research station 541* (K, PRE). Mumbwa Dist., 30 miles [48 km] west of Kafue Hoek pontoon on road to Mankoya, 21 Nov. 1959, *Drummond & Cookson 6734* (K, MO, PRE, SRGH).

ZIMBABWE.—Bulawayo, 25 Dec., 'brown flowers', *Norman R44* (K); Matobo, Paddocks, black land, Dec. 1931, *Rattray 440* (K); Farm Shumbashaba, among rocks, Dec. 1954, *Miller 2569* (K); Gokwe, Charama road fly gate 4 miles [6 km] north of Gokwe, 2 Jan. 1963, *Bingham 393* (PRE).

### B. Subgen. *Ferraria*

Plants acaulescent or with aerial stems with relatively short branches enclosed by leaf sheaths. *Stem* not sticky below nodes. *Rhipidia* with only 2 flowers each. *Flowers* with tepal claws widely diverging, forming a shallow cup, with large nectaries with non-fluid nectar, or forming a deep, wide to narrow cup with small nectaries and with fluid nectar; filaments inserted in lower third or near apex of anthers; anther lobes parallel and usually contiguous above filament insertion or lobes not contiguous and usually widely diverging when fully dehiscent. *Ovary* included, ellipsoid, with or without sterile beak; stigmas minute, terminal on apices of style branch arms, or larger, on lobes below style arm tips. *Capsules* ovoid-oblong and obtuse or with prominent beak.

#### B1. Sect. 1. *Ferraria*

*Flowers* with tepal claws widely diverging, forming a shallow cup, with large nectaries with non-fluid nectar; filaments inserted in lower third of anthers; anther lobes parallel and contiguous above filament insertion. *Ovary* ellipsoid, sometimes with sterile beak; stigmas minute, terminal on apices of style branch arms. *Capsules* ovoid-oblong and obtuse or with prominent beak.

5. *Ferraria crispa* *Burm.* in *Nova acta physico-medico Academiae Caesareae Leopoldino-Carolinae germanicae naturae curiosorum* 2: 199 (1761); De Vos: 338 (1979). Type: South Africa, without precise locality, illustration in Burman, *Nova acta physico-medico*

*Academiae Caesareae Leopoldino-Carolinae germanicae naturae curiosorum* 2: 199, t. 3, fig. 1 (1761).

*F. undulata* L.: 1353 (1763), nom. illegit. superfl. pro *M. crispa* *Burm.f. Moraea undulata* (L.) Thunb.: no. 14 (1787). Type: South Africa, without locality or collector, illustration in Miller: 187, t. 280 (1759a), lecto., here designated.

*F. ensiformis* Mill. (1768), nom. superfl. pro *F. crispa* *Burm.* Type: not designated.

*F. obtusifolia* Sweet: t. 148 (1826b). Type: illustration in Sweet, l.c. (1826b).

*F. major* Eckl.: 18 (1827), nom. nud.

*F. vandermerwei* L.Bolus: 276, fig. D (1932b). Type: South Africa, [Western Cape], near Swellendam, cultivated in Cape Town, Sept.–Oct. 1932, *Van der Merwe s.n. BOL20168* (BOL, holo.).

*F. crispa* subsp. *nortieri* M.P.de Vos: 338 (1979), syn. nov. Type: South Africa, [Western Cape], heights north of Verlorenvlei, 28 Aug. 1976, *De Vos 2366* (NBG, holo.).

See De Vos (1979: 338) for additional synonymy.

Plants usually robust, (300–)450–1 500 mm high. *Stem* much branched in upper half, sheathed by leaf bases below; cataphylls and bases of leaf sheaths often speckled pale on red background. *Leaves* several, linear to sword-shaped, (4–)6–12 mm wide, basal leaves longest, with visible main vein. *Rhipidia* 2-flowered; spathes green with membranous margins, inner 45–65 mm long, outer  $\pm$  half as long, usually entirely sheathing. *Flowers* on pedicels 40–60 mm long, lasting a single day, variously pale yellow to beige with brown to dull purple mottling and brown margins to predominantly brown with pale yellow margins, strongly scented, odour reminiscent of caramel or molasses, tepals widely diverging, forming a shallow bowl 6–8 mm deep, 13–18 mm wide at mouth, nectary  $\pm$   $\frac{1}{2}$  length of claw, sometimes slightly longer, limbs spreading horizontally; outer tepals 28–35 mm long, claws 8–12 mm long, limbs to 25 mm long, inner tepals slightly shorter and narrower. *Stamens* with filaments united in smooth column  $\pm$  6 mm long, free in upper 3 mm; anthers  $\pm$  3 mm long, thecae parallel, shortly apiculate; pollen orange. *Ovary* spindle-shaped, not beaked, included in spathes, 12–20 mm long; style branches  $\pm$  4 mm long, forked in upper half, divided into diverging arms; 4–5 mm long, prominently fringed; stigmas terminal on style arms. *Capsules* ovoid to oblong, 15–25 mm long, obtuse or pointed at apex. *Seeds* angular, mostly 5-sided,  $\pm$  4 mm long, facets slightly wrinkled. *Flowering time*: Aug.–Oct. Plate 1E.

*Distribution and habitat*: *Ferraria crispa* is best known as a coastal species and it is common along the Western Cape coast in rocky sites from Lambert's Bay to Hermanus; it also occurs sporadically further east along the coast at least to Herold's Bay near George (Figure 5). Showing a striking ecological shift, it also grows in montane habitats, sometimes along streams in deep, coarse sand, or on seasonally moist south-facing slopes, from Pakhuis Pass in the north through the Witteberg and Swartberg to Georgida in the Baviaanskloof Mtns of Eastern Cape. Usually fairly robust in stature, plants of montane populations can reach a remarkable 1.5 m in height, more than has been recorded in any coastal population of the species. Unlike the coastal populations which flower annually, the montane populations of *F. crispa* flower well only in late spring following a wild fire the previous summer.

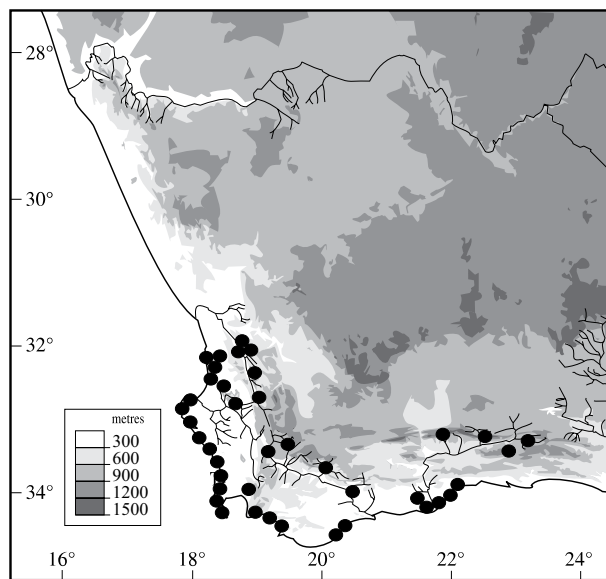


FIGURE 5.—Known distribution of *Ferraria crispa*.

Long known by the later synonym, *Ferraria undulata* L., dating from 1763 (e.g. Baker 1892, 1896), the species was first described by Johannes Burman in 1761 as *F. crispa*. It is the most well-known species of the genus and the name *F. crispa* (or *F. undulata*) is often carelessly applied to other members of the genus. The species is best recognized by the habit, with stems produced well above the ground and bearing numerous branches crowded in the upper half of the stem, combined with a flower with a wide, shallow cup and an ovoid capsule lacking a beak. The sword-shaped lower leaves and the shorter cauline leaves have a definite main vein and form two-opposed vertical ranks. The strongly scented flowers have tepals speckled or blotched dark brown to dull purple on a cream-coloured to pale yellowish background, or occasionally predominantly dark brown, but whatever the dominant colour, the crisped margins are a pale colour, sometimes almost golden when the tepals are otherwise brown. More important than their colour and patterning, which is quite variable, the tepals form a wide, fairly shallow cup and each claw has a large nectary, often covering almost half the surface. The nectaries produce minute droplets of concentrated nectar scattered over the entire surface.

De Vos (1979) recognized the northern populations of *Ferraria crispa* as subsp. *nortieri* because of their pale green rather than slightly glaucous leaves, slightly smaller flowers, the perianth with a cup  $\pm 8$  mm deep and  $\pm 10$  mm wide at the rim, and the ovary less than 20 mm long. The inner tepals are also slightly narrower,  $\pm 6.5$  mm wide versus  $\pm 10$  mm wide in the typical subspecies. The distinction is less clear than De Vos indicated and we prefer not to recognize these northern populations formally. Notably, all plants of subsp. *nortieri* for which chromosome numbers are available, are tetraploid,  $2n = 40$ , whereas populations assigned to subsp. *crispa* to the south and in the southern Cape mountains are hexaploid,  $2n = 60$ . The smaller flower dimensions, and smaller pollen grain size noted by De Vos, seem directly correlated with the lower ploidy level in these northern populations.

The ecological range of *Ferraria crispa*, as noted above is remarkable. We have looked in vain for differences between the coastal populations that favour rocky outcrops and those from montane sandy slopes and in the absence of any morphological distinction, apart from greater height in the latter plants, they remain the same taxon.

#### Representative specimens

WESTERN CAPE.—3218 (Clanwilliam): 2 km from Lambert's Bay to Vredendal, (–AB), 5 Sept. 1976, *De Vos* 2374 (NBG); Pakhuis Pass, road to Klein Kliphuis, (–BB), 4 Sept. 1976, *De Vos* 2368 (NBG). 3317 (Saldanha): Bobbejaankop, Saldanha, (–BB), 2 Sept. 1974, *De Vos* 2323 (NBG). 3318 (Cape Town): entrance to West Coast National Park, calcareous slope, (–AA), 4 Aug. 2001, *Goldblatt & Manning* 11665 (MO); Dassen Island, (–AC), Jan. 1926 (fr.), *Lang sub Marloth* 6696 (PRE); Robben Island, (–CC), *Walgate* 496 (NBG); Spieka near Klipheuwel, (–DA), 10 Sept. 1975, *Thompson* 2617 (NBG). 3319 (Worcester): Hex River Pass, (–BD), 26 Sept. 1951, *Barker* 7454 (NBG). 3320 (Montagu): Montagu Baths, (–CC), Oct. 1921, *Page* 74 (PRE). 3321 (Ladismith): Swartberg Mtns, road to Gamkakloof, deep sand along stream, burned last summer, (–BD), *Goldblatt & Porter* 11858 (MO, NBG); Kamkaberg Nature Reserve, (–CB), 15 Aug. 1983, *Cattell & Cattell* 298 (NBG). 3322 (Oudtshoorn): Swartberg Mtns, Meiringspoort, (–BC), *Loubser sub De Vos* 2351 (NBG). 3418 (Simonstown): Strandfontein, (–AB), 18 Sept. 1942, *Compton* 13705 (NBG). 3419 (Caledon): Kleinmond, (–AC), *De Vos* 2360 (NBG); Hermanus, (–AC), Nov. 1921 (fr.), *Rogers* 22619 (PRE); Fernkloof Nature Reserve, (–AD), 2 Oct. 1984, *Drewe* 154 (MO). 3420 (Bredasdorp): De Hoop, (–AD), 13 Sept. 1979, *Burgers* 2217 (NBG). 3421 (Riversdale): Stilbaai, hill near tennis courts, (–AD), 23 Nov. 1978 (fr.), *Bohnen* 4651 (NBG, PRE); 1 mile [1.6 km] N of Gouritz River mouth, (BD), 18 Sept. 1968, *Mauve* 4755 (PRE).

EASTERN CAPE.—3323 (Willowmore): Georgida, (–AD), Oct. 1930, *Fourcade* 4411 (NBG).

6. *Ferraria foliosa* G.J.Lewis in *Annals of the South African Museum* 40: 117 (1954); De Vos: 366 (1979). Type: South Africa, [Western Cape], near Elandsbaai [Elands Bay], 12 Sept. 1955, *Lewis* 2301 (SAM60809, holo.!; SAM (two sheets)!, STE!, PRE!, iso.).

Plants 300–800 mm high. *Stem* leafy and much-branched, branches rotated in clockwise fashion. *Leaves*: basal (and juvenile) with linear blades diamond-shaped in cross section, thickened in midline,  $\pm 8$ –10 mm wide, main vein hardly evident below thickened midline; cauline leaves falcate, channelled below, distally horizontal, main vein often not evident, arranged in a two-ranked spiral. *Rhipidia* 2-flowered; inner spathe 48–50 mm long, often prominently inflated, outer 28–30 mm long, sheathing below, diverging in upper half, hooked at tips. *Flowers* on pedicels 17–20 mm long, lasting a single day, dull maroon to purple or dark brown, usually with darker purple-maroon blotches, margins pale brown, claws usually maroon speckled with white, putrid- or molasses-smelling, tepal claws broad, forming a wide cup, 7.5–8.0 mm deep, 13–18 mm wide at rim, nectaries pale green, heart-shaped, prominent,  $\frac{1}{3}$  to  $\frac{1}{2}$  as long as claw, limbs  $\pm$  spreading; outer tepals 33–40 mm long, inner tepals 28–35 mm long, claws of both whorls 9–10 mm long. *Stamens* with filaments united in a column 8–11 mm long, free in upper 1.5–2.5 mm; anthers  $\pm 3.5$  mm long before anthesis, thecae parallel; pollen orange. *Ovary* spindle-shaped, not beaked, included, 15–20 mm long; style branches  $\pm 4.5$  mm long, diverging, with prominently fringed arms; stigmas terminal on style arms. *Capsules* ellipsoid, 28–35 mm long, round



at apex. *Seeds* angular,  $\pm$  5-sided,  $\pm$  3 mm long, facets slightly wrinkled, light brown, shiny. *Flowering time*: late Aug.–Oct. Plate 1C.

**Distribution and biology:** the vegetatively distinctive *Ferraria foliosa* is restricted to dunes and sandy beaches along the Atlantic coast of Northern and Western Cape of South Africa (Figure 6). Plants have been recorded from near Hondeklip Bay in the north to near Velddrif in the south, where it overlaps the range of *F. crispa*. The latter favours rocky sites in contrast to the deep sands, mostly in strandveld close to the sea shore in which *F. foliosa* grows. The dull purple-brown flowers have a strong unpleasant, molasses-like or putrid odour and attract numerous flies which successfully accomplish cross pollination.

Vegetatively, *Ferraria foliosa* can be recognized by the long, linear basal leaves much thickened in the midline, thus diamond-shaped in cross section (see De Vos 1979), and sometimes dry by flowering time. The basal leaves differ markedly from the shorter, wider cauline leaves, the blades of which are also thickened in the middle and arch outward, ultimately spreading horizontally. Successive leaves are opposed but collectively the leaves have a spirally two-ranked arrangement. This is also reflected in the short lateral branches, which are crowded in the upper half of the stem, the successive ones rotated slightly in a clockwise direction. The flowers differ little from those of closely related *F. crispa* in their darkly mottled pigmentation, broad tepal claws with large nectaries, and wide, shallow floral cup. Whereas the flowers of *F. crispa* are usually shades of dull yellow, buff and brown, those of *F. foliosa* are mottled dull purplish, or brownish maroon on a paler grey-purple background.

In her key to the species, De Vos (1979) distinguished *Ferraria foliosa* and *F. schaeferi* from *F. crispa* by the leaf blades having numerous parallel veins rather than a single prominent vein. That distinction seems to us to poorly reflect their morphology, for the blades of *F. foli-*

*osa* are so thickened and leathery that no veins are evident except for the main vein in the centre of the thickened blade. *Ferraria foliosa* is better distinguished from *F. crispa* by the spirally rotated leaves and branches, and secondarily by the duller flower coloration, the background tinged with purple and the mottling a maroon to dull purple in *F. foliosa* that contrasts with the dark brownish or dull yellow colouring on a pale cream-coloured background, or brown with yellow margins in *F. crispa*. The cream-coloured perianth covered with dark speckles and prominently beaked ovary, immediately separate *F. schaeferi* from *F. foliosa*. The species appears to have first been collected by Harry Bolus near Velddrif in 1892, but that specimen was overlooked by Lewis and was referred to *F. crispa* by De Vos in her account of *Ferraria*.

#### Representative specimens

**NORTHERN CAPE.**—3017 (Hondeklipbaai): Farm Avontuur, 3 km E of Hondeklipbaai [Hondeklip Bay], (–AD), 25 Aug. 1986, *Le Roux & Lloyd 260* (NBG); sandy slopes above lighthouse at Groen River Mouth, (–DC), 25 Aug. 2002, *Goldblatt & Porter 12113* (MO); Groen River Mouth, above highwater mark, (–DC), 29 Aug. 1977, *De Vos 2396* (PRE).

**WESTERN CAPE.**—3117 (Lepelfontein): Brand-se-Baai, (–BD), 23 Aug. 1993, *De Villiers 121* (PRE). 3118 (Vanrhynsdorp): Olifants River, dunes at river mouth, (–CA), 8 Oct. 1983, *O'Callaghan 649* (NBG). 3218 (Clanwilliam): Otterdam, Lambert's Bay, (–AB), 6 Sept. 1953, *Compton 24162* (NBG); sandy slope south of Leipoldville, Elandsbaai [Elands Bay] road, (–AD), 15 Sept. 2001, *Goldblatt & Porter 11886* (MO, NBG); sandy flats along coast between Nuwedam and Soutkloof, S of Elandsbaai [Elands Bay], (–AD), 5 Oct. 2004, *Goldblatt & Porter 12619* (MO, NBG); Elands Bay, sand below Bobbejaankop, (–AD), 28 Aug. 1976, *De Vos 2365* (NBG); Dwarskersbos, strandveld, (–CA), 7 Oct. 2004, *Goldblatt & Porter 12636* (NBG); dunes at mouth of Berg River, (–CC), Oct. 1892, *Bolus 6301* (BOL, NBG, PRE).

**7. *Ferraria schaeferi* Dinter** in Repertorium Novae Species Regni Vegetabilium 16: 339 (1920); De Vos: 344 (1979). Type: South West Africa [Namibia], Klinghardt Mtns, Dreikugelberg, 14 Aug. 1913, *Schäfer 562* (B, neo.), designated by De Vos 1979: 344).

Plants 200–500 mm high. *Stem* sheathed by leaf bases, branching repeatedly in upper axils, branches rotated in clockwise spiral; with corm bearing long runners from base, each terminating in a small corm. *Leaves* with overlapping sheaths; blades thick and leathery, thickened in midline and main vein usually evident, arranged in a two-ranked spiral, spreading horizontally above, 12–20 mm wide. *Rhipidia* 2-flowered; spathes firm, leafy in texture, with translucent membranous upper margins, inner 50–60 mm long, outer somewhat shorter, sheathing only near base, arching outward in upper half. *Flowers* on pedicels 40–50 mm long, lasting a single day, creamy yellow with small to large brown spots, margins dark brown, usually sweetly scented (of violets), tepal claws broad, forming a wide cup,  $\pm$  8 mm deep, 12–15 mm wide at rim, with brownish purple, heart-shaped nectaries in lower half,  $\pm$   $\frac{1}{2}$  as long as claw; outer tepals  $\pm$  25 mm long, inner tepals 22–24 mm long, claws of both whorls  $\pm$  8 mm long. *Stamens* with filaments united in a column  $\pm$  7.5 mm long, free in upper 2 mm; anther thecae parallel,  $\pm$  5 mm long at anthesis, later shrinking; pollen dull brown to orange. *Ovary* spindle-shaped, 20–25 mm long, tapering to a slender beak,  $\pm$  8 mm long, included; style branches  $\pm$

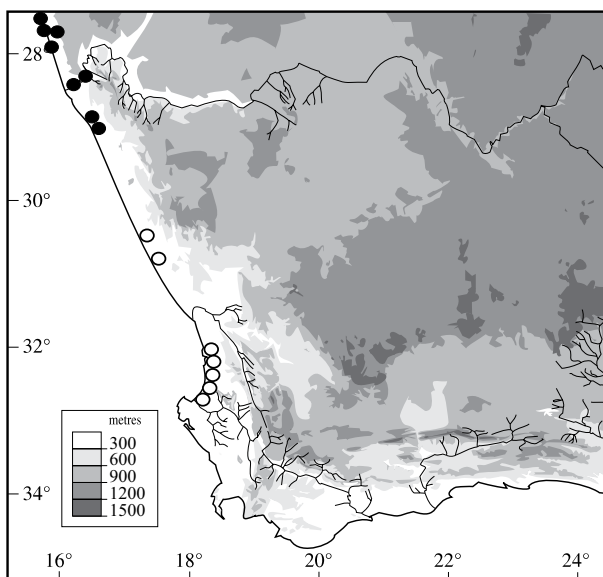


FIGURE 6.—Known distribution of *Ferraria foliosa*, ○, *F. schaeferi*, ●.

2 mm long, diverging into prominently fringed arms  $\pm$  2 mm long; stigmas terminal on style arms. *Capsules*  $\pm$  ellipsoid, 20–25 mm long, excluding beak. *Seeds* light brown, glossy, 5- or 6-angled, facets  $\pm$  smooth. *Flowering time*: mid-Jul.–Sept.

*Distribution and biology*: favouring deep sands, mainly along the coast, or a short distance inland, *Ferraria schaeferi* extends from near Lüderitz Bay in south-western Namibia in the north, to the coast at Grootmis in Northern Cape, South Africa in the south (Figure 6). The type locality, the Klinghardt Mtns of southwestern Namibia, lies some 40 km inland, which is somewhat unusual but we have also seen *F. schaeferi* growing near Brandkaros east of Alexander Bay, some 30 km inland, along the Orange River. There is also an early record of the species at Arrisdrif (Marloth 12391), even further inland, so *F. schaeferi* is not restricted to near-coastal habitats. The inland stations benefit from coastal fog, the additional precipitation allowing this otherwise coastal species to extend into the interior.

Unlike the flowers of the related species, *Ferraria crispa* and *F. foliosa*, those of *F. schaeferi* sometimes have, at least to the human nose, a pleasant, sweet scent reminiscent of violets, but with a slightly sour undertone. We have noted in cultivated plants that some have sweeter-scented flowers at cool temperatures, whereas others smell putrid both at cooler and warm temperatures. Whatever the scent, the flowers of *F. schaeferi* are visited exclusively by a range of small and large fly species, mostly of the families Muscidae and Calliphoridae that forage on the droplets of sweet nectar on the nectaries.

*Diagnosis and relationships*: with a basic floral morphology very much like that of *Ferraria crispa* and *F. foliosa*, *F. schaeferi* has widely spreading tepals, the broad claws of which form a shallow cup,  $\pm$  8 mm deep and some 12 mm wide at the rim. The tepal claws bear large heart-shaped nectaries, while the limbs have a creamy pale yellow ground colour speckled with small dark brown spots, the same colour as the crisped margins. In vegetative form, *Ferraria schaeferi* most closely resembles *F. foliosa* which also has the leaves and branches arranged in a two-ranked spiral, and the leaf blades are similarly thick and leathery with a weakly defined central vein. In addition to the differently coloured perianth, the ovary and capsule have a pronounced beak up to 8 mm long, that readily separates *F. schaeferi* from *F. foliosa*. In its normally sandy habitat, plants spread vegetatively on long runners produced from the base of the stem that can extend below the ground a metre or more from the parent plant, each terminating in a corm.

Although first collected in October 1830 on the south side of the Orange River by the important early plant explorer in South Africa, J.F. Drège (*Drège s.n.*, P), *Ferraria schaeferi* is based on an early 20th century collection made about 1912 to 1913 by the medical doctor, Fritz Schäfer, who worked on the Lüderitz Bay–Keetmanshoop railway in the then German colony of South West Africa (Gunn & Codd 1981), now Namibia. Schäfer made two collections in the Klinghardt Mtns in the Namib Desert south of Lüderitz Bay, and these specimens formed the basis for Dinter's description of *F. schaeferi*. The broad similarity of the plant to *F. crispa*

led 19th century botanists to overlook the Drège collection, which lacks flowers, but has the characteristic beaked capsules that mark *F. schaeferi* unmistakably.

#### Representative specimens

NAMIBIA.—2615 (Lüderitz): Kosisberge, (–AA), 8 Sept. 1929, Dinter 6689 (B); Lüderitzbucht, (–AC), Sept. 1917, Nobel s.n. (SAM12783); Kowis Mtns, east of Lüderitz, 644 m, (–AA), 15 Aug. 2001, Smook 11394 (PRE); east of Grosse Bucht, wind farm site, (–CC), 21 Sept. 2001, Mannheimer & Burke 1703 (WIND). 2715 (Bogenfels): south Namib opposite Possession Is., (–AA), 10 Oct. 1976, De Vos 2379 (NBG); Granietberg near Bogenfels, (–AA), Aug. 1911, Schaefer 14 (sub Marloth 5249) (PRE); Buchubergen, (–DD), 9 Aug. 1929, Dinter 6584 (B). 2816 (Oranjemund): rocky outcrop before Schakel Mtn among quartzite stones, (–BA), 31 Jul. 1977, Muller 752 (WIND).

NORTHERN CAPE.—2816 (Oranjemund): Beauvallon, sanddune, (–DA), 22 Aug. 2001, Goldblatt & Porter 11739 (MO); 19 Jul. 2002, Manning 2746 (NBG). 2817 (Vioolsdrif): stony gravel flats near Arrisdrif, banks of Orange River, (–AC), 31 Aug. 1925, Marloth 12391 (PRE). 2916 (Port Nolloth): 5 km E of Port Nolloth, (–BC), 22 Aug. 2001, Goldblatt & Porter 11734A (MO). 2917 (Springbok): Grootmis, sanddune, (–CA), Oct. 1977, De Vos 2391 (NBG).

8. *Ferraria ovata* (Thunb.) Goldblatt & J.C.Manning in Novon 12: 461 (2002). *Moraea ovata* Thunb.: 186 (1800). Type: South Africa, [Northern Cape,] Namaqualand, near Kooksfontein [as Koksfontein, also Cocksfonteyn], (now Soebatsfontein), without date, probably in 1793, Masson s.n. UPS-THUNB1225 (UPS-THUNB, holo!).

Plants often small, (40–)100–200 mm high. *Stem* erect, unbranched, lower half partly exposed. *Leaves*: basal and juvenile with short, linear blades, up to 45  $\times$  2 mm; cauline entirely bifacial, broadly ovate to rotund, amplexicaul, 15–18 mm long, spreading, concave; margins membranous, often reddish. *Rhipidia* 2-flowered; spathes leafy, green, often brown at tips, inner 18–20 mm long, outer 12–20 mm long, sheathing in lower half, arching outward above. *Flowers* on pedicels 7–12 mm long, lasting a single day, pale yellow with brown spots in midline and base of limbs, margins closely crisped, dark brown, acrid-smelling, tepal claws broad, 7–8 mm long, forming a cup  $\pm$  7 mm deep,  $\pm$  8 mm wide at rim, nectaries  $\pm$  2 mm long, above base of claws,  $\pm$  2  $\times$  2 mm, paired or bilobed, greenish, tepal limbs spreading; outer tepals 17–20 mm long, limbs 8–12 mm long, inner slightly smaller than outer. *Stamens* with filaments united in a column 7–8 mm long, free in upper 1 mm; anther thecae parallel,  $\pm$  2 mm long; pollen orange. *Ovary* included, spindle-shaped,  $\pm$  6 mm long, without beak; style branches  $\pm$  2 mm long, diverging into prominently fringed arms; stigmas terminal on style arms. *Capsules* ovoid (mature capsules and seeds unknown). *Flowering time*: Jun.–Jul. Figure 7A–E.

*Distribution and biology*: found on granitic slopes and clay-loam flats, *Ferraria ovata* is restricted to central Namaqualand, South Africa, where it has been recorded from a few isolated sites from Soebatsfontein in the north to the low hills of the southern Kamiesberg between Kliprand and Bitterfontein (Figure 8). Plants typically grow in gritty granitic gravel among rocks that protect the corms from predation. Like those of other species of sect. *Ferraria*, the flowers of *F. ovata* seem adapted for pollination by muscid and blowflies.

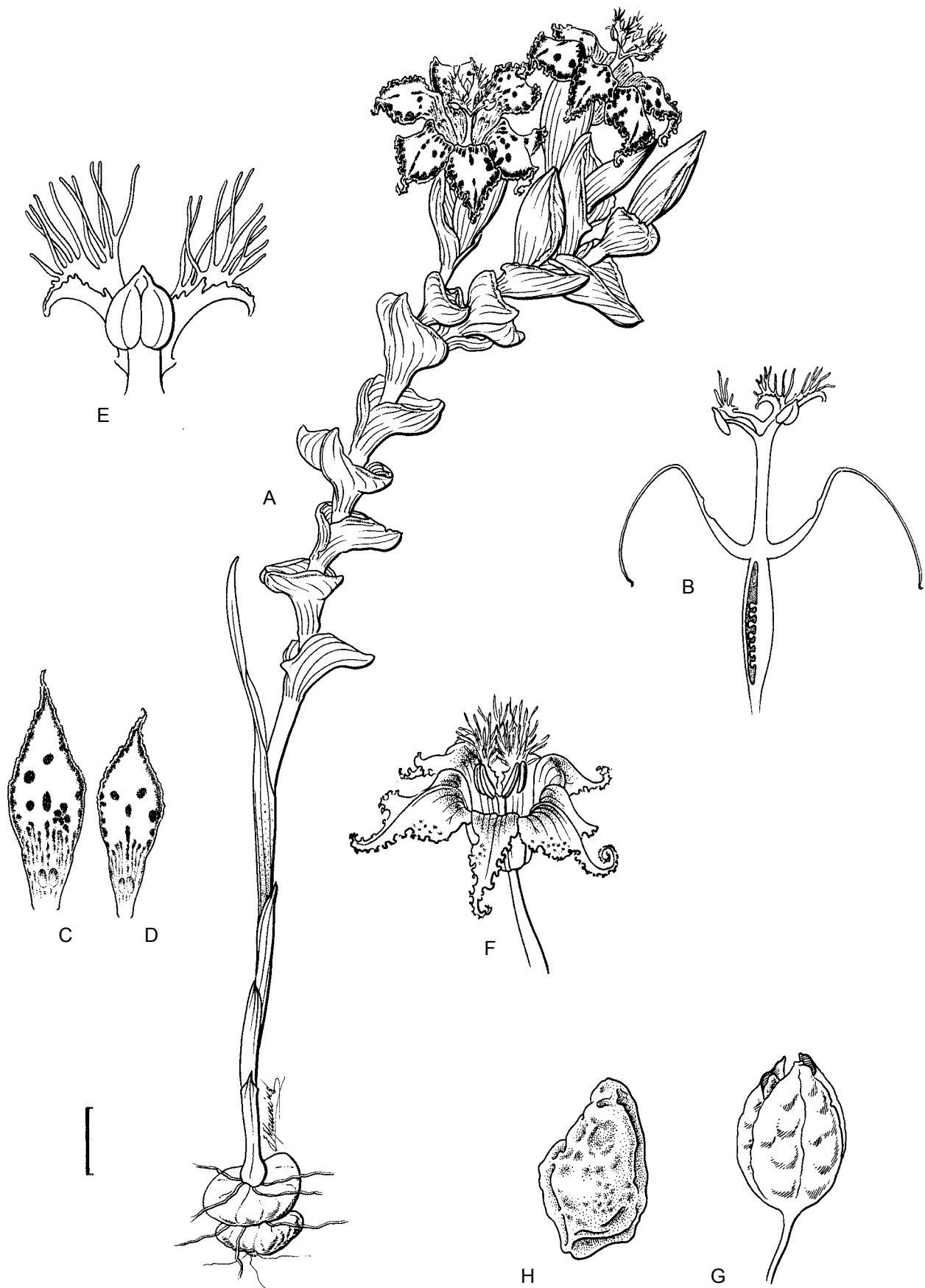


FIGURE 7.—A–E, *Ferraria ovata*: A, whole plant; B, half-flower; C, outer tepal; D, inner tepal; E, anther and style branches. F, *Ferraria variabilis*: flower. G, H, *F. densepunctulata*: G, capsule; H, seed. Scale bar: A, C, D, F, G, 10 mm; B, 5 mm; E, 2 mm; H, 1.5 mm. Artist: J.C. Manning.

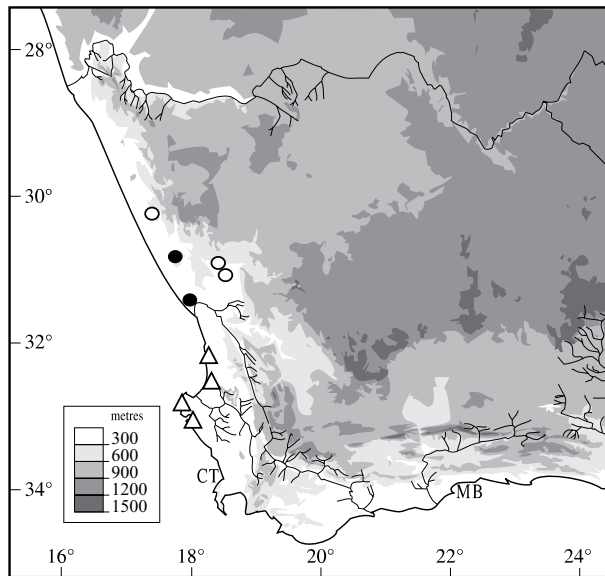


FIGURE 8.—Known distribution of *Ferraria densepunctulata*, △; *F. ovata*, ○; *F. ornata*, ●.

**Diagnosis and relationships:** the parallel anthers, wide and shallow tepal cup, spindle-shaped ovary without a beak, and stigmas terminal on the style arms, show that *Ferraria ovata* belongs in sect. *Ferraria*. It most closely resembles the coastal species *F. densepunctulata*, which also has dimorphic basal and cauline leaves, a sparsely branched or unbranched stem, and the relatively small bilobed or paired nectaries located well above the base of the tepal claws. It is one of three winter flowering species in the genus, the others being the coastal species, *F. densepunctulata* and *F. ornata*.

**History:** one of the rarest species of the genus, *Ferraria ovata* was first collected in the 1790s, probably in 1793, by the Royal Botanic Gardens Kew collector, Francis Masson, and not again for over 200 years. The species was described as *Moraea ovata* by Thunberg in 1800, based on Masson's collection, which was in fruit and without corms. Plants were rediscovered in 1995 by botanist, Annelise le Roux, who collected a sterile specimen near Soebatsfontein in central Namaqualand. A later record by P. Desmond and party, also sterile, finally led us to a site with plants in bloom near Kliprand, east of Bitterfontein (Manning 2350), in June 2001, when it became clear that the plants represented an unknown species of *Ferraria* (Goldblatt & Manning 2002).

#### Representative specimens

**NORTHERN CAPE.**—3017 (Hondeklipbaai): Namaqualand, Farm Doornfontein 464, Steenkamp Kraal, sandy loam slope, (–BA), 2 Sept. 1995 (sterile), *Le Roux* 4658 (JONK).

**WESTERN CAPE.**—3018 (Kamiesberg): Farm Gannabos, 25 km from Bitterfontein on road to Kliprand, granite outcrops, (–CD), 10 Aug. 2000 (fr.), *Goldblatt & Manning* 11373 (MO, NBG), 10 Jun. 2001, *Manning* 2350 (MO, NBG); Knersvlakte, Farm Steenbokskraal, (–CD), 20 Aug. 1999 (fr.), *National Geographic-IPC Expedition* 115 (NBG).

**9. *Ferraria densepunctulata* M.P.de Vos** in *Journal of South African Botany* 45: 346 (1979). Type: South Africa, [Western Cape], Elandsbaai [Elands Bay], 14 Jun. 1974, *Loubser sub De Vos* 2317 (STE, holo.!; PRE, iso.).

Plants slender, mostly 120–250 mm high. *Stem* several-branched in upper half, lower half of stem partly visible; leaf sheaths and cataphylls often flushed red with pale spotting. *Leaves*: basal with long compressed-cylindrical blades, loosely 2-ranked, 3–5 mm wide, with narrow hyaline to reddish margins; cauline leaves shorter, spreading outward, tips often hooked; juvenile leaves in a 2-ranked cluster, up to 6, terete, hollow, dark green. *Rhipidia* 2-flowered; spathes green with narrow membranous margins either pale or flushed red; inner 40–50 mm long, outer  $\pm$  25 mm long, sheathing below, diverging and hooked distally. *Flowers* on pedicels slightly shorter to  $\pm$  as long as spathes, lasting two days, pale greenish to grey-blue, outer tepals densely speckled with small maroon to purple or dark blue spots, inner tepal limbs maroon to purple or dark blue blotch in lower  $\frac{1}{2}$ , faintly spice-scented, tepal claws forming a shallow cup,  $\pm$  9 mm deep, 15–20 mm wide at rim; nectaries bilobed, above base of outer tepal claws, in midline of inner tepal claws, tepal limbs spreading horizontally, undulate or only slightly crisped; outer tepals  $25\text{--}30 \times 11\text{--}13$  mm, inner tepals  $20\text{--}23 \times \pm 10$  mm, claws of both whorls  $\pm 10$  mm long, inner much narrower than outer. *Stamens* with filaments united in a column 8–10 mm long, free in upper  $\pm 2$  mm; anther thecae parallel,  $\pm 4$  mm long before anthesis; pollen orange or dull yellow. *Ovary* sometimes exserted, spindle-shaped, 12–15 mm long, without obvious beak but without ovules in upper 3–4 mm; style  $\pm 10$  mm long, style branches  $\pm 3$  mm long, divided in upper  $\frac{1}{3}$  into diverging, fringed arms; stigmas terminal on style arms. *Capsules* ovoid, 15–25 mm long, apex subacute. *Seeds* pale glossy brown,  $\pm 3$  mm diam., 5-sided with facets slightly wrinkled. *Flowering time*: May–Jul. Figure 7G, H.

**Distribution and biology:** *Ferraria densepunctulata* grows in rocky or calcareous sandy sites along the Western Cape coast of South Africa, from Lambert's Bay in the north to Langebaan in the south (Figure 8). At Jacobsbaai near Saldanha, plants grow in limestone pavement. The spice-scented flowers are pollinated by a range of short-tongued flies.

**Diagnosis and relationships:** early flowering and relatively rare, *Ferraria densepunctulata* was only described in 1979 by M.P. de Vos, and until she began her study of the genus, the species was known from just three collections, the first made by C.L. Leipoldt in June 1941 in the hills at Langebaan, south of Saldanha, still the most southerly record. The species is distinctive in the narrow basal leaves, oval in cross section, and rather different from the shorter, broader cauline leaves, and in the unusually coloured flowers, minutely dark blue to purple spotted on a pale greenish to grey-blue background, but with the limbs of the inner tepals so densely speckled as to appear solidly coloured, either maroon or dark slate blue. The flowers are also unusual in the genus in having the tepal limb margins undulate instead of closely crisped. The small bilobed nectaries are located at the base of the outer tepals but in the midline of the inner tepal claws, the lower halves of which are linear and  $\pm 1$  mm wide. Like other members of sect. *Ferraria*, the stigmas are terminal on the arms of the style branches and the ovary is not beaked as in all but *F. schaeferi* of the section. The flowers are unique in the section in last-

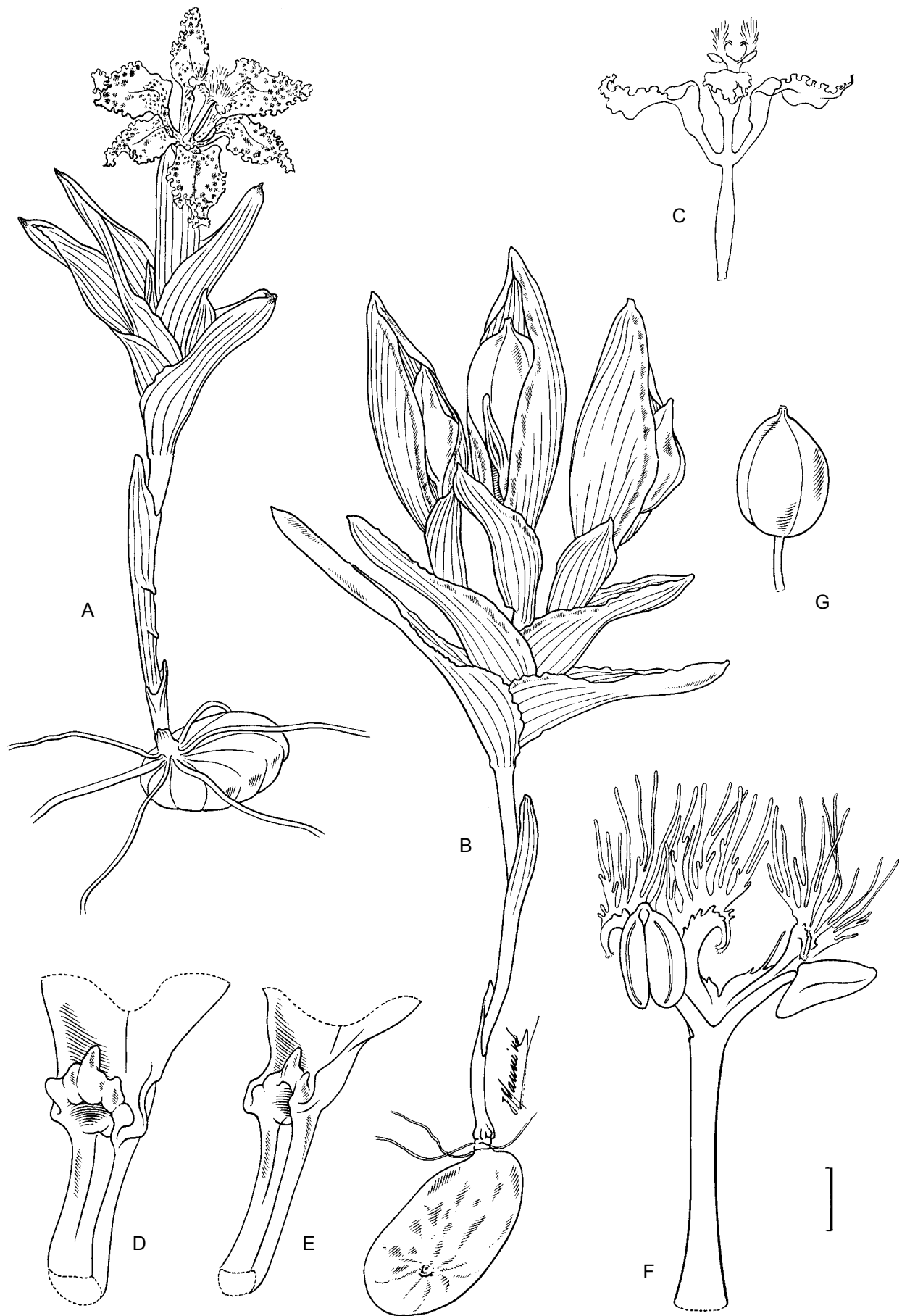


FIGURE 9.—*Ferraria ornata*, Manning 3174. A, flowering plant; B, fruiting plant; C, outline side view of flower; D, claw of outer tepal; E, claw of inner tepal; F, staminal columns and style; G, capsule. Scale bar: A–C, G: 10 mm; D, E, 0.5 mm; F, 1.5 mm. Artist: J.C. Manning.



ing two days instead of a single day. The leaves of non-flowering plants are so strikingly different from those of mature, flowering individuals that they appear to represent a different species. Four to six in number, they are held in a close, 2-ranked fan and the blades are dark green, terete and hollow.

The early flowering habit of *Ferraria densepunctulata* is now known to be matched in the genus by *F. ornata* and *F. ovata*, both of which also have the narrow basal leaves differentiated from the shorter and broader cauline leaves.

#### Representative specimens

WESTERN CAPE.—3217 (Vredenburg): Jacobsbaai, in limestone pavement, (–DD), Aug. 2007 (fr.), Goldblatt & Manning 12914A (MO); Cape Columbine, hill adjacent to lighthouse, in sand with limestone gravel, (–DD), 8 Sept. 2009, Goldblatt & Porter 13285 (MO, NBG). 3218 (Clanwilliam): Langdam, near Lambert's Bay, (–AB), Jun. 1974, De Vos 2298 (NBG); Elands Bay, near school, (–AB), 17 May 1966, Pamphlett 98 (NBG); Farm St Helenafontein, sandy ground, (–DB), 11 Sept. 2008 (fr.), Goldblatt & Porter 13111 (MO, NBG). 3318 (Cape Town): Langebaan, hills behind hotel, (–AA), Jun. 1941, Leipoldt 3844 (BOL).

#### 10. *Ferraria ornata* Goldblatt & J.C.Manning, sp. nov.

Plantae acaulescentes usitate 50–80 mm altae, foliis 4 vel 5 amplexicaulibus concavo-lanceolatis ad  $40 \times 15$  mm, lamina folii basalis 5–10 mm longa subtereti ad cylindrica, spathis coriaceis glaucis marginibus translucentibus spatha interna 40–50 mm longa externa 20–30 mm longa extrinsecus arcuata, floribus albis tepalis basi pallide flavis, limbis unguibusque brunneis maculatis inodoris, marginibus undulatis crispisque, nectaribus bilobis in medio unguum marginibus distalibus cristis prominentibus, tepalis inaequalibus externis  $\pm 19 \times 10$  mm unguibus  $\pm 8$  mm longis  $\pm 2$  mm latis ad basem, internis  $\pm 13 \times 6$  mm unguibus  $\pm 6.0$  longis  $\pm 1.5$  mm latis ad basem, columna filamentorum  $\pm 8$ –9 mm longa, antheris  $\pm 3$  mm longis brunneis lobis paralleli, ovario fusiformi incluso 10–12 mm longo, ramis styli fimbriatis.

TYPE.—Northern Cape, 3017 (Hondeklipbaai): central Namaqualand, sandy slopes 10 km inland from Groen River mouth, Farm Van Zylsrus, 500 m along dirt track N of main road, strandveld in deep sand, (–DC), 2 Jun. 2008, Manning 3174 (NBG, holo.; MO, iso.).

Plants acaulescent, congested, 50–80 mm high. *Stem* 2–4-branched; replacement corms not present at flowering, developing later; cataphylls (usually only uppermost) turning red above ground. *Leaves* 4 or 5, amplexicaul, lanceolate-concave, up to  $40 \times 15$  mm, glaucous with purple tips; margins reddish membranous, finely crisped, basal leaf with blades only 5–10 mm long, subterete to cylindrical, obtuse-apiculate, 3–4 mm diam.; non-flowering plants with 1–3(–5) leaves; blades suberect or falcate, subterete or cylindrical,  $\pm$  quadrangular to round in section, 60–80  $\times$  2–4 mm, obtuse-apiculate, glaucous with purple apex and sheath, sheath margins and veins abaxially minutely hairy. *Rhipidia* 2-flowered; spathes leathery, glaucous, with translucent, membranous margins, inner 40–50 mm long, outer much smaller, 20–30 mm long, sheathing in lower half, arching outward. *Flowers* on pedicels 30–40 mm long,

lasting a single day, white with base of tepal limbs yellow, limbs finely brown-spotted basally and with fewer, larger brown spots distally, margins finely crisped, yellow and brown, claws streaked with brown, unscented, with bilobed, concave nectaries in middle of claws, distal nectary margin prominently crested, pale lilac with purple streaks, tepal claws narrowed below, forming a windowed cup 7–8 mm deep and  $\pm 10$  mm wide at rim, limbs spreading or slightly reflexed; tepals unequal, outer  $\pm 19 \times 10$  mm with claws ascending,  $\pm 8$  mm long, narrowed below and  $\pm 2$  mm wide, inner  $\pm 13 \times 6$  mm with claws  $\pm 6$  mm long, narrow proximal part  $\pm 1.5$  mm wide. *Stamens* with filaments united in column 8–9 mm long, free in upper  $\pm 2$  mm; anthers diverging, thecae parallel,  $\pm 3$  mm long, brown; pollen orange. *Ovary* included, spindle-shaped, 10–12 mm long; style branches diverging, deeply divided into diverging, fringed arms; stigmas terminal on style arms. *Capsules* broadly ovoid, 14–18 mm long, tapering to acute tip. *Seeds* irregularly 5(6)-sided,  $\pm 3 \times 2$  mm, facets separated by pale straw-coloured, wavy ridges, facet surfaces usually  $\pm$  plane and dark brown. *Flowering time*: May to early Jun. Figure 9, Plate 1H.

*Distribution and biology*: *Ferraria ornata* is known from two extended populations, one on slopes above the lower Groen River in central Namaqualand and the other west of Koekenaap in southern Namaqualand, some 120 km to the south. It occurs on sandy ground in sandveld (Figure 8). At its northern site on the northern bank of the Groen River,  $\pm 10$  km inland from the Atlantic coast, plants occur in localized colonies in deep, gritty, sandy soil in Namaqualand Strandveld vegetation among succulent shrubs, including *Othonna cylindrica* and *O. coronopifolia*. The plants appear to be habitat specific and were not located in patches of Namaqualand Coastal Fynbos that interdigitate with the strandveld. Plants flower early in the season, after the first rains, in May or June, and last a single day, opening  $\pm 08:00$  and collapsing  $\pm 16:00$ . Branches are produced in the upper one or two leaf axils, which extend the flowering period for some weeks, possibly into early July in years of favourable rainfall. Juvenile and non-flowering plants produce a tuft of cylindrical leaves quite different from those on flowering individuals. Replacement corms of flowering individuals are absent at flowering and develop later as the capsules ripen.

The species was discovered by Cape Town ecologist, Rupert Koopman, who collected a fruiting specimen in spring 2007. The locality was visited in the following winter in a year of poor rainfall but we were able to locate a single flowering individual for description and illustration.

*Diagnosis and relationships*: stemless, and with the tepal claws unusually narrow in the lower part, thus forming a windowed cup, *Ferraria ornata* is easily recognized by its small size, flowering individuals standing only 50–80 mm high. The flowers are unique in the fleshy crests bordering the distal margins of the nectaries, which are situated in the middle of the tepal claws, and which secrete miniscule quantities of sticky, sweet nectar. The flowers appear scentless to the human nose. The short, concave cauline leaves of flowering plants stand in marked contrast to the long, centric leaves of

non-flowering individuals. Both the early flowering and unusual, concave cauline leaves of flowering plants suggest it is most closely allied to *F. ovata*, which has a similar growth strategy of early flowering and small, concave cauline leaves on a taller flowering stem.

#### Additional specimens

NORTHERN CAPE.—3017 (Hondeklipbaai): same locality as type collection, Aug. 2007 (fr. and sterile), *Koopman s.n.* (NBG).

WESTERN CAPE.—3118 (Vanrhynsdorp): Farm Kommandokraal west of Koekenaap, sandveld,  $\pm 80$  m, (–CA), 9 Sept. 2008 (fr.), *Goldblatt & Porter 13098* (K, MO, NBG, PRE).

B2. Sect. **Macroscyphae** Baker in Journal of the Linnean Society 16: 106 (1877); De Vos: 349 (1979). Type species: *Ferraria divaricata* Sweet (lectotype designated by De Vos 1979: 350).

*Flowers* with tepal claws forming a deep, wide or narrow cup containing fluid nectar; filaments inserted near apex of anthers; anther lobes when fully dehiscent usually widely divergent, rarely parallel but never contiguous. *Ovary* always with sterile beak; stigmas on lobes below apices of style branch arms. *Capsules* with prominent beak.

#### Series Subdivaricatae

11. ***Ferraria ferrariola*** (Jacq.) Willd., Species plantarum edn 4, 3: 581 (1800); De Vos: 350 (1979). *Moraea ferrariola* Jacq.: (1790). Type: South Africa, without precise locality or collector, illustration in Plantarum rariorum horti caesarei schoenbrunnensis 4: 24, t. 450 (1804).

*F. viridiflora* Andrews: 285 (1803) [*F. viridis* Ker Gawl. (1804) orth. var.]. Type: South Africa, collected by W. Synnot, without precise locality, illustration in The botanist's repository 4: t. 285 (1803); no preserved material known.

*F. longa* Barnes: 313 (1930). Type: South Africa, [Northern Cape], Nieuwoudtville, cultivated at Kirstenbosch, Jul. 1930, *P. Ross-Frames s.n.* BOL19720 (BOL, holo.).

Plants slender, mostly 150–250 mm high. *Stem* sheathed below by mottled cataphylls and leaf sheaths; lower internodes usually partly exposed, usually branched in upper  $\frac{1}{2}$ . *Leaves*: basal linear, unifacial, usually slightly longer than stem, mostly 2–3 mm wide, main vein usually well delineated; cauline leaves markedly shorter and broader than basal leaves and resembling spathes. *Rhipidia* 2-flowered; spathes glaucous or pale green, with broad transparent margins, inner 45–60(–70) long, often inflated, outer  $\pm \frac{1}{2}$  to  $\frac{2}{3}$  as long, sheathing below, diverging in upper half and  $\pm$  hooked at tips. *Flowers* on pedicels 20–30 mm long, lasting two days, greenish blue, grey-blue, or pale watery yellow to pale green, usually with darker spots and streaks on outer tepal limbs, faintly sweet- or spice-scented, sometimes odourless, tepal claws forming a narrow, closed cup, 17–20 mm deep,  $\pm 12$  mm wide at mouth; nectaries small, at base of tepals; outer tepals (30–)35–40 mm long, claws fairly narrow, 17–20 mm long, inner slightly shorter and narrower, limbs of outer  $\pm$  spreading, inner usually reflexed. *Stamens* with filaments united in a column 14–19 mm long, free in upper 1–2 mm; anther thecae initially parallel,  $\pm 4$  mm long at anthesis, later diverging and shrinking to almost 2 mm. *Ovary* spindle-shaped, 20–25 mm long, with sterile beak,

(5–)8–12 mm long; style branches  $\pm 2.5$  mm long, dividing into diverging, fringed arms,  $\pm 2.5$  mm long; stigmas irregularly shaped lobes in middle of style arms, arching over anthers. *Capsules* ovoid-oblong, 14–20(–25) mm long, beak (5–)8–12 mm long. *Seeds* mostly 5-sided,  $3.0\text{--}3.5 \times 2.5\text{--}3.0$  mm, smooth, shiny, brown, facets separated by prominent, pale wavy ridges, facets light yellow-brown with surfaces smooth or slightly wrinkled. *Flowering time*: Jun.–Aug. Plate 1F.

*Distribution and biology*: usually in rocky sites, the relatively common *Ferraria ferrariola* is found on granite and sandstone slopes, or in sandy ground usually not far from rock outcrops. Its range extends from the Richtersveld in northern Namaqualand to the Bokkeveld and Olifants River Mtns as far south as Clanwilliam (Figure 10). The floral cup contains nectar of moderately high sugar concentration. The scented flowers, which last two days, appear attractive to bees, the only recorded floral visitors (Goldblatt *et al.* 2009). These include honey bees, *Apis mellifera*, and *Anthophora* species, which visit the flowers to forage for nectar, and during their visits accomplish pollination.

*Diagnosis and relationships*: *Ferraria ferrariola* is readily recognized by the linear basal leaves, quite different from the shorter cauline leaves, the stem usually partly exposed, and the red-flushed and white-speckled cataphylls and sheath of the lowermost leaf. The large flowers have a deep and relatively narrow floral cup, 17–20 deep and  $\pm 12$  mm wide at the mouth. The flowers are usually shades of turquoise-grey to pale slate-blue with a pale yellow nectar guide lightly speckled with darker colour on the limbs of the outer tepals (Manning *et al.* 2002: 157). The flowers have a faint sweet odour, often with spicy overtones of almond or cinnamon or vanilla, unique in the genus.

The relationships of *Ferraria ferrariola* are evidently with sect. *Macroscyphae* with which it shares the divergent anther lobes and large stigma lobes below the tips of the style arms, as well as a prominently beaked ovary.

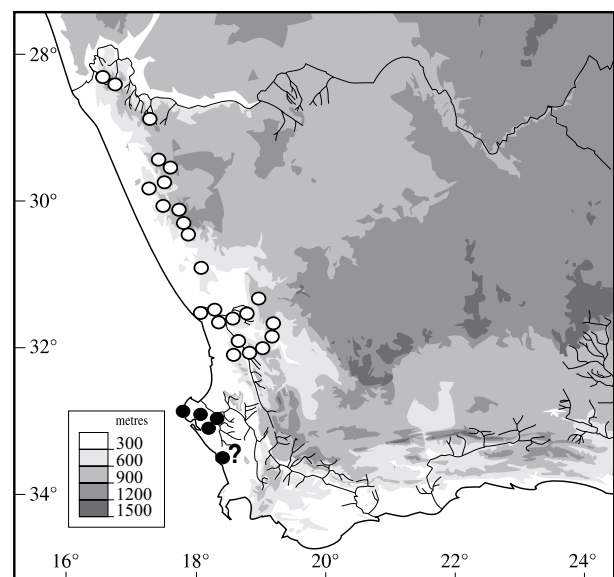


FIGURE 10.—Known distribution of *Ferraria ferrariola*, O; *F. parva*, ●.

The sharp dimorphism between the basal and cauline leaves does not occur in other species of the section, but is found in *F. densepunctulata* and *F. ovata* of sect. *Ferraria*, and in *F. glutinosa* of subgen. *Glutinosae*. These species are, however, otherwise very different in having flowers with the tepal claws forming a wide, shallow cup, anthers with parallel lobes, small stigmatic surfaces terminal on the style arms, and an ovary lacking a beak.

In our Western Cape Wildflower Guide (Manning & Goldblatt 1996: 51) we misidentified as *Ferraria ferrariola* the photograph of a second species, *F. parva*, described here as new. Whereas the two have flowers of similar shape, divaricate anthers, and a narrow floral cup, those of *F. parva* are much smaller, with a floral cup,  $\pm 6$  mm deep, and outer tepals 18–22 mm long, compared to (30–)35–40 mm in *F. ferrariola*. The sheaths and cataphylls of *F. parva* also lack the red flush and white speckling so characteristic of *F. ferrariola*.

#### Representative specimens

NORTHERN CAPE.—2817 (Vioolsdrif): Richtersveld, Kodaspiek, stony clay loam, (–AA), 2 Sept. 1977, *Oliver, Toelken & Venter* 395 (PRE); Armanshoek, moist gorge, (–AC), Aug. 1995, *Williamson & Williamson* 5647 (NBG); stony flats  $\pm 4$  km N of Eksteenfontein, (–CD), 23 Aug. 2001 (fr.), *Goldblatt & Porter* 11755 (MO). 2917 (Springbok): granite dome W of Springbok, (–DB), 21 Aug. 2002, *Goldblatt & Porter* 12085 (MO). 3017 (Hondeklipbaai): Kamieskroon, (–BB), 24 Jul. 1941, *Compton* 11110 (NBG); flats east of Karkams on Tweerivieren road, (–BD), 21 Aug. 2001, *Goldblatt & Porter* 11723 (MO). 3119 (Calvinia): Nieuwoudtville Wildflower Reserve, dolerite rocks, (–AC), 11 Aug. 1983, *Perry & Snijman* 2276 (NBG); Botterkloof Pass, (–CA), 12 Aug. 1983, *Van Wyk* 1453 (NBG); top of Botterkloof, (–CC), 28 Jul. 1948, *Lewis* 1992 (SAM).

WESTERN CAPE.—3018 (Kamiesberg):  $\pm 9$  km N of Bitterfontein, (–CC), 20 Aug. 2001, *Goldblatt & Porter* 11713A (MO). 3118 (Vanrhynsdorp): Holrivier, stony hills, (–AD), 11 Aug. 1970, *Hall* 3730 (NBG); Farm Kliphoeck, 10 miles [16 km] east of Doringbaai, (–CC), 12 Aug. 1970, *Hall* 3743 (NBG). 3218 (Clanwilliam): Pakhuis Pass, west end, (–BB), 23 Aug. 1966, *Barker* 10454 (NBG); Clanwilliam, 350 ft [106 m], (–BB), 22 Aug. 1896, *Schlechter* 8597 (PRE). 3219 (Wuppertal): between Pakhuis and Botterkloof, 2 km past Bidouw turn-off, (–AA), 4 Sept. 1976 (fr.), *De Vos* 2369 (NBG).

#### 12. *Ferraria parva* Goldblatt & J.C.Manning, sp. nov.

Plantae usitate 80–150 mm altae, foliis unifacialibus, basalibus 2–3 linearibus 3–5 mm latis, caulibus lanceolatis 4–6 mm latis, spathis pallidis viridibus interne 45–65 mm longis, externe  $\pm$  dimidio longiore interne, floribus atroflavis ad pallide caeruleo-viridibus atromaculatis, marginibus crispis bubalinis, tepalis exterioribus 18–22 mm longis, columna filamentorum  $\pm 6$  mm longis, antheris  $\pm 3$  mm longis lobis divaricatis.

TYPE.—Western Cape, 3217 (Vredenburg): sandveld west of Vredenburg, north side of Saldanha highway, opposite cemetery, under shrubs and restios, (–DD), 19 Sept. 2007, *Goldblatt & Manning* 13000 (NBG, holo.; MO, iso.).

Plants mostly 80–150 mm high, not including basal leaves. Stem branched near base and in upper part, lower  $\frac{1}{2}$  often partly exposed; cataphylls and sheath of lowermost leaf pale. Leaves unifacial, basal 2 or 3  $\pm$  linear, usually exceeding spathes, 3–5 mm wide, upper leaves subtending branches lanceolate, spreading, shorter and wider than basal, mostly 4–6 mm wide, margins and

main vein not evident when alive; non-flowering plants with 2 or 3 linear leaves, oval in cross section, without differentiated margins or main vein. *Rhipidia* 2-flowered; spathes pale green, apices slightly hooked, inner 45–65 mm long, often inflated with age, margins transparent, outer spathe  $\pm \frac{1}{2}$  as long as inner, often diverging in upper  $\frac{1}{3}$ . Flowers on pedicels 18–20 mm long, lasting 2 days, spotted with dark brown in a dull yellow, light red-brown or pale greenish blue background, margins crisped, buff to khaki, sweetly scented of a mix of jasmine and coconut, tepal claws forming a narrow cup  $\pm 8$  mm deep,  $\pm 7$  mm wide at rim; outer tepals 18–22  $\times$  8–10 mm, claws 7–8 mm long with a pouch-like bilobed nectary in lower midline; inner tepal slightly shorter and  $\pm \frac{1}{2}$  as wide, limbs slightly reflexed, inner more so than outer. Stamens with filaments united in a column  $\pm 6$  mm long, free in upper  $\pm 1.5$  mm; anther thecae initially parallel, later divaricate,  $\pm 3$  mm long at anthesis, later  $\pm \frac{2}{3}$  as long. Ovary fusiform, 12–15 mm long, with a sterile beak up to 7 mm long; style branches  $\pm 2$  mm long, forked in upper  $\frac{1}{2}$ , prominently fringed; stigmas narrow, at lateral ends of style branches, arching forward. Capsules ovoid-oblong, 15–20 mm long, with beak up to 2–7 mm long. Seeds angular, smooth, shiny, golden brown, mostly 5-sided, facets smooth or slightly wrinkled. Flowering time: late Aug.–mid-Sept. Figure 11, Plate 11.

*Distribution and biology:* *Ferraria parva* is a surprising discovery—plants grow close to Saldanha and Vredenburg, an area believed to be well-explored botanically. Clearly rare, the species is restricted to sandveld and limestone fynbos on the Western Cape coast between Bokbaai and Vredenburg and the Berg River near Langrietvlei (Figure 10). Plants grow in deep sandy ground, sometimes over limestone, or in cracks in limestone or calcrete pavement. The flowers last two days and have a sweet scent reminiscent of a mix of jasmine and coconut or, less often, a somewhat sour, unpleasant odour. The floral cup contains moderately sweet nectar of mean 24.2 % sucrose equivalents. Pollination biology is unknown but, like its closest relative, *F. ferrariola*, the flowers appear adapted for pollination by bees foraging for nectar. At the type site we noticed plants had been well pollinated. Unfortunately, many plants in the small population had been uprooted and the corms eaten, presumably by porcupines. Apart from the type site, incidentally, the only known locality for *Romulea elliptica* M.P.de Vos, just one other record of the species was known before 2007, made in 1940 by W.F. Barker ‘on the road to Ganzekraal’ (probably the farm southwest of Darling near Bokbaai). Collecting in the Saldanha area in 2008 showed the species to be fairly common in the immediate area of Vredenburg and Saldanha, both on limestone and in sandy ground. The single flower of the Ganzekraal collection is poorly preserved but is comparable in size and has the divaricate anthers and general appearance of *F. parva*.

*Diagnosis and relationships:* we first encountered *Ferraria parva* in 1995 while taking photographs for the *West Coast Wildflower Guide* (Manning & Goldblatt 1996) and included therein a photograph of the species misidentified as *F. ferrariola*. Later, during our study of *Ferraria*, it became clear that this

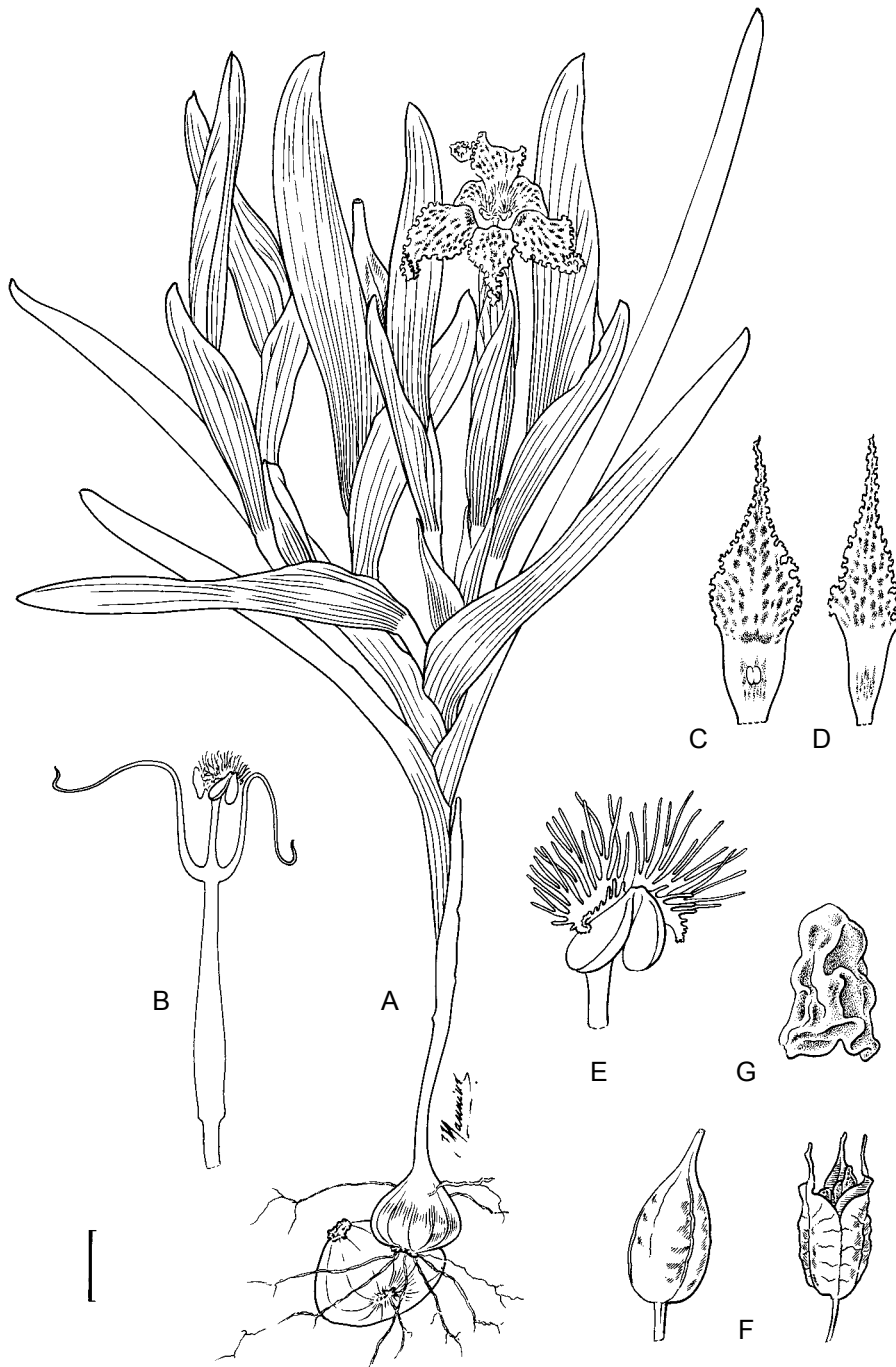


FIGURE 11.—*Ferraria parva*, Goldblatt & Manning 13000. A, flowering plant; B, half flower; C, outer tepal; D, inner tepal; E, anther and single style branch; F, capsules, undehiscent (left) and dehiscent (right); G, seed. Scale bar: A, F, 10 mm; B–D, 5 mm; E, G, 2 mm. Artist: J.C. Manning.

was not *F. ferrariola*, which is a Namaqualand plant that extends south only as far as Clanwilliam, but an unknown species. After repeated searches at the same site, we re-collected the species in September 2007. The flower is similar to *F. ferrariola* in basic structure: it has a narrow floral cup and tepals with slightly reflexed limbs but the flower is less than half the size of those of *F. ferrariola*, the tepals just 18–22 mm long, the floral cup  $\pm$  8 mm deep and filament column  $\pm$  6 mm long, compared with outer tepals (30–)35–40 mm long, a floral cup 17–20 mm deep and a filament column 14–19 mm long of *F. ferrariola*. The cataphylls and sheath of the basal leaf of *F. parva* are uniformly coloured in contrast to the speckled and usually red-flushed cataphylls and sheaths of *F. ferrariola*.

#### Representative specimens

WESTERN CAPE.—3217 (Vredenburg): sandveld west of Vredenburg, (–DD), 29 Aug. 1995, Goldblatt & Manning 10271 (MO); limestone-topped hill north of Saldanha, (–DD), 13 Sept. 2008, Goldblatt & Porter 13117 (MO, NBG, PRE). 3218 (Clanwilliam): *Eriocephalus*-dominated sandveld on Farm Brakfontein (Nuweland) south of Langrietvlei, (–CC), 6 Sept. 2008, Goldblatt & Porter 13077 (K, MO, NBG, PRE, S); sandveld near Langebaanweg Fossil Park, (–CC), Goldblatt & Porter 13150 (MO, NBG). 3318 (Cape Town): road to Ganzekraal, (–?DB), 15 Sept. 1940, Barker 730 (NBG).

#### Series *Macroscyphae*

13. *Ferraria divaricata* Sweet in British flower garden: t. 192 (1827); De Vos: 354 (1979). Type: South Africa, without precise locality, collected by W. Synnot, illustration in British flower garden: t. 192 (1827) (no preserved material known).

*F. divaricata* subsp. *arenosa* M.P.de Vos: 358 (1979). Type: South Africa, [Western Cape], Clanwilliam, Nardouw Pass, Farm de Lille, Oct. 1973, *Van Breda sub De Vos 2295* (NBG, holo.!, PRE, iso.!).

Plants (250–)350–500 mm high. *Stem* well developed, much-branched distally. *Leaves* sword-shaped to linear, 6–15 mm wide, often with a slightly raised main vein, glaucous, margins sometimes slightly raised, basal leaves longest, cauline leaves progressively shorter above and becoming spathe-like. *Rhipidia* 2-flowered; spathes glaucous, with broad membranous margins, inner 70–85 mm long, outer  $\pm$  half as long as inner, sheathing entirely or in lower two thirds, then often slightly S-shaped. *Flowers* on pedicels 6–15 mm long, lasting one day, variously dark chocolate to golden brown, crisped part of margins concolourous or paler, claws pale, streaked with fine longitudinal lines or with a broad median darker centre, forming a cup, 14–18 mm deep, 15–18 mm wide at rim; outer tepals (30–)35–44  $\times$  14–16 mm, inner tepals (28–)36–38  $\times$  8–10 mm, claws of both whorls (13–)16–19 mm long; nectaries at base of claws,  $\pm$  black or pale yellow-green, 1.3–4.0 mm long. *Stamens* with filaments united in a column 11–13 mm long, free and arching outward in upper  $\pm$  3 mm; anther thecae usually widely diverging, initially  $\pm$  4 mm long, shrinking after dehiscence; pollen orange. *Ovary* fusiform, 33–42 mm long including beak 15–20 mm long; style branches  $\pm$  2 mm long, dividing into diverging, prominently fringed arms  $\pm$  4 mm long; stigmas on small lobes below tips of style arms, arching over anthers. *Capsules* 15–22 mm long (excluding beak 15–20 mm long). *Seeds* globose,  $\pm$  3 mm diam., pale matte brown, surfaces lightly wrinkled in  $\pm$  ruminant pattern, epidermal cells foveate. *Flowering time*: mainly late Sept. to early Nov.

*Distribution and biology*: *Ferraria divaricata* extends along the west coast and coastal mountains of Northern Cape and Western Cape, South Africa, from near Komaggas in northern Namaqualand southward to the Cape Flats (Figure 12). Plants grow in deep sandy soils, in sandveld or marginal fynbos habitats. The flowers,

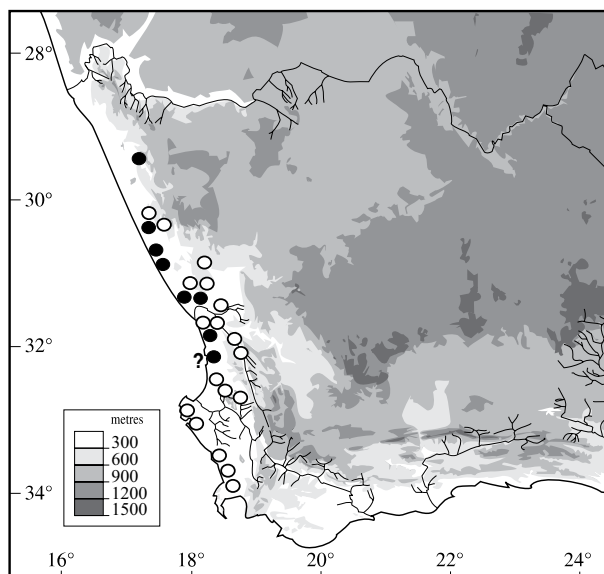


FIGURE 12.—Known distribution of *Ferraria divaricata*, O; *F. flava*, ●.

with a relatively wide, deep floral cup, contain quantities of dilute nectar, seldom more than 8 % sucrose equivalents. This dilute nectar is remarkable as it is an unlikely reward for any potential pollinator. Like its relative, *F. variabilis*, which has a similar floral cup and dilute nectar, the flowers are visited only by vespid and masarine wasps (Eumenidae) (Goldblatt & Manning 2006).

*Diagnosis and history*: the name *Ferraria divaricata* has been generally applied to the low-growing, usually  $\pm$  tufted plant, mostly 100–200 mm tall, now *F. variabilis*, from southwestern Namibia, the Upper Karoo, Namaqualand and Western Cape. This species also has divaricate anthers and pale brown to yellowish tepals with the limbs either speckled or marked with a dark brown to blackish purple band of solid colour at the base and the claws forming a deep floral cup. De Vos (1979) associated the name *F. divaricata* with the northerly populations of *F. variabilis*, which she divided into four subspecies.

Examination of the type, a watercolour illustration in *The British flower garden* led us (Goldblatt & Manning 2004) to question De Vos's interpretation (Goldblatt & Manning 2005) of subsp. *divaricata*. The height, said to be 18 inches (450 mm), the longer basal leaves with a slightly raised central vein and appearing slightly striated when dry as the leaf veins become raised above the surrounding leaf tissue and differentiated from the cauline leaves, plus the exposed stem and uniformly chocolate-brown tepal limbs, seem to us to accord best with the plant De Vos called *F. divaricata* subsp. *arenosa*. This attribution also seems reasonable on circumstantial grounds, for plants depicted in the type illustration were collected (presumably as seed) by Walter Synnot, magistrate (*landdrost*) at Clanwilliam from 1821 to 1825. Synnot collected plants in the Clanwilliam District and nearby (Gunn & Codd 1981), where subsp. *arenosa* is found but there is no evidence that he collected in Namaqualand where subsp. *divaricata sensu* De Vos occurs. This generally tufted plant has flowers with a solid, dark band of colour on the lower half of the tepal limbs. De Vos's two tufted subspecies, subsp. *divaricata* and subsp. *australis*, seem best treated as one species, *F. variabilis*. The fourth subspecies, subsp. *aurea*, is here associated with the new *F. flava*.

The vegetative differences outlined above and the associated different patterns of tepal marking are substantial and are correlated with differences in the seeds. Whereas most *Ferraria* species have brown seeds, compressed by pressure into 5 or 6 smooth, flattened facets separated by thickened ridges, the seeds of plants called subsp. *arenosa* and subsp. *aurea* are globose with reticulate/foveate sculpturing (De Vos 1979). Seeds rarely vary within a species so that differences in seed morphology usually have strong taxonomic significance. Another difference between the last two subspecies is that their flowers last a single day but two days in subsp. *divaricata* and subsp. *australis*.

As here understood, *Ferraria divaricata* is a plant of deep sands or stony sandstone slopes, extending from near Komaggas in northern Namaqualand to the Cape Flats close to Cape Town. Populations extend inland as far as Vanrhynsdorp and the northeastern slopes of the



Piketberg (60–70 km inland). As in most *Ferraria* species, floral pigmentation patterns and colour are variable. The tepal limbs are uniform in colour, except for the margins, and range from light to chocolate-brown with paler margins, or are dull yellow-brown, then with little or no colour difference at the margins. The tepal claws are cream-coloured to palest yellow with fine, dark, longitudinal streaks and usually a dark median stripe.

The Cape Town botanist, H.M.L. Bolus, annotated collections of *Ferraria divaricata* from Langebaan, north of Cape Town, *F. langebaanensis*, but did not publish the name (De Vos 1979).

#### Representative specimens

**NORTHERN CAPE.**—3017 (Hondeklipbaai): 1.2 km east of Oubees/Wildepaardehoek boundary, 4.7 km E of Springbok–Soebatsfontein road, (–BA), 15 Oct. 1986, *Le Roux & Lloyd 664* (NBG); 38 km from Garies to Wallekraal, (–BC), 4 Sept. 1977, *Drijfhout sub De Vos 2399* (NBG); without precise locality: between Komaggas and Soebatsfontein, 9 Sept. 1950, *Barker 6740* (NBG).

**WESTERN CAPE.**—3118 (Vanrhynsdorp): 16 km north of Strandfontein, front of sand dune, (–CA), 12 Sept. 1975, *De Vos 2356* (NBG); west of Koekenaap, Farm Kommandokraal, (–CA), Sept. 2008, *Goldblatt & Porter 13188* (NBG); Ratelfontein, Olifants River Mtns, (–DC), 6 Oct. 2004, *Goldblatt & Porter 12630* (MO). 3218 (Clanwilliam): northeastern slopes of the Piketberg,  $\pm$  28 km north of town, (–DA), 28 Sept. 2001, *Goldblatt & Manning 11931* (MO, NBG). 3318 (Cape Town): Farm Osfontein east of Saldanha and north of Langebaan, calcareous sand and limestone, (–AA), Nov. 1976, *Boucher s.n.* (PRE); Silwerstroomstrand, (–CA), 20 Nov. 1974, *De Vos 2339* (NBG); Bellville, University of Western Cape campus, (–DC), 10 Nov. 1976, *De Vos 2385* (NBG).

**14. *Ferraria variabilis* Goldblatt & J.C.Manning** in *Bothalia* 35: 73 (2005). Type: South Africa, [Northern Cape,] Nieuwoudtville, Klipkoppies, lower slopes, 15 Sept. 1961, *Barker 9537* (NBG, holo.!, MO, iso.!).

*F. antherosa* Ker Gawl.: t. 751 (1804), nom. illegit. superfl. pro *F. viridiflora* [as *F. viridis*] Andrews (= *F. ferrariola* (Jacq.) Willd.). Type: South Africa, without precise locality or collector, illustration in Curtis's Botanical Magazine 19: t. 751 (1804).

*F. divaricata* subsp. *australis* M.P.de Vos: 359 (1979). Type: South Africa, [Western Cape,] Karoo Garden, Whitehill, 17 Sept. 1945, *Compton 17412* (NBG, holo.!).

Plants 60–200(–300) mm high. *Stem* often branched just above base, branches crowded and  $\pm$  equal in length, often forming small tufts. *Leaves* sword-shaped to linear, usually  $\pm$  as long as stem, sometimes up to twice as long, (2–)3–15(–22) mm wide, mostly sub-basal, without visible midrib, often slightly striate, margins often slightly thickened, rarely obscurely crisped, sheaths usually overlapping and concealing stem. *Rhipidia* 2-flowered; spathes glaucous green, inner mostly 60–75 mm long, outer slightly shorter to  $\pm$  as  $\frac{1}{2}$  as long, entirely sheathing or arching outward in distal third. *Flowers* on pedicels 10–15 mm long, lasting 2 (rarely 3) days, predominantly pale to dull yellowish to pale or middle brown, or dull grey-blue, limbs with solid dark brown to blackish purple at base, or with scattered dark spots, margins darker or paler in colour, claws uniformly pale or with dark longitudinal streaks or with a broad darker median streak, forming a floral cup 12–15 mm deep, 13–15 mm wide at rim, usually slightly putrid smelling, nectaries usually basal, rarely in pouches in centre of claws, pale or dark-coloured; outer tepals 30–40(–45)  $\times$  10–15 mm, claws 10–15 mm long; inner tepals

25–40(–45)  $\times$  8–10 mm. *Stamens* with filaments united in a column 8–13 mm long, free and arching outward in the upper 2–4 mm; anthers 3.5–5.0 mm long before anthesis, shorter after dehiscence, thecae joined only at apices, usually widely diverging but sometimes almost parallel. *Ovary* fusiform, 15–20 mm long, with a sterile beak 5–8 mm long; style branches 2–3 mm long, dividing into diverging, prominently fringed arms,  $\pm$  4 mm long; stigmas on small lobes below tips of style arms and arching over anthers. *Capsules* ellipsoid, 30–50 mm long. *Seeds* rounded, usually angled by pressure, coat dull and slightly wrinkled. *Flowering time*: Aug.–Nov. Figure 7F, Plate 1D.

**Distribution and biology:** most widespread of the southern African species, *Ferraria variabilis* extends from southern Namibia to Oudtshoorn including Bushmanland and the Great Karoo and as far east as Upington and Britstown, but is absent from the western coastal forelands of Western Cape Province (Figure 13). Plants grow in a variety of habitats including shale flats, granite outcrops, and deep sands. As described in more detail above and elsewhere (Goldblatt & Manning 2006; Goldblatt *et al.* 2009), the flowers are adapted for pollination by mud wasps (Vespidae): the only pollinating insects recorded on *F. variabilis* are species of *Allepipona* and *Delta* (Eumeninae), and *Jugurtia* (Masarinae). A previous report of pollination of *F. variabilis* by the masarine wasp, *Ceramius* (Goldblatt *et al.* 2009), is incorrect: that record is for *F. macrochlamys* subsp. *kamiesbergensis*.

**Diagnosis and relationships:** *Ferraria variabilis* is morphologically fairly coherent in including plants with relatively few branches crowded near the base, and rarely higher than 200 mm. Plants thus form low tufts unless growing under shrubs when they may be taller. The flowers are fairly large and the broad tepal claws form a deep, relatively wide bowl in which nectar of low sugar concentration accumulates in a pool. The spreading tepal limbs vary considerably in colour and marking. In the north of its range, in Namaqualand and southern Namibia, flowers have light brown tepal limbs with a

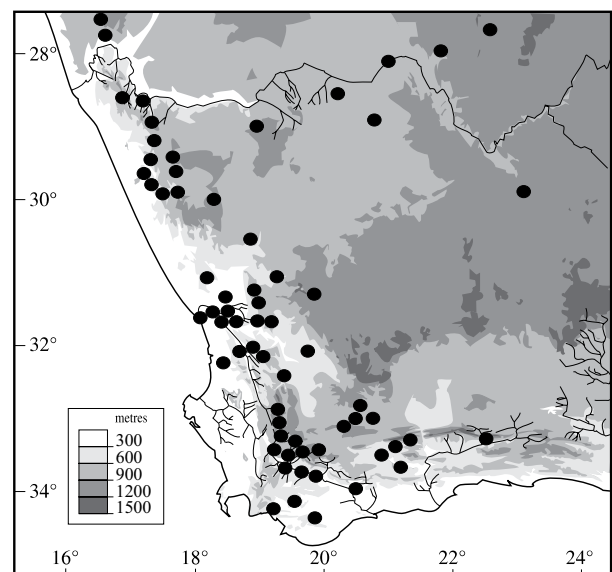


FIGURE 13.—Known distribution of *Ferraria variabilis*.

dark purple longitudinal band toward the base and light brown margins, while the claws are pale greenish cream with a narrow darker band running down the midline. The nectaries in the northern populations are fairly large and green or less often purple-black. In the western and southern Karoo and the southern Cape, populations have greenish yellow or pale to middle brown tepal limbs, usually darker in the midline, and with small or medium-sized spots in the lower third or when brown then often with spots irregularly scattered across the limb and the margins sometimes slightly darker coloured. The claws are pale, usually with a darker streak in the midline and have a small dark nectary at the base or on the inner tepals, shortly above the base. Perianth colour can vary as much within a population as across the entire southern Cape and western Karoo.

Scent is also variable and difficult to describe. In the protologue of *Ferraria antherosa*, an illegitimate, superfluous name but applicable to *F. variabilis*, Ker Gawler (1804) described the scent as reminiscent of green olives, whereas we have noted both a slightly putrid smell or a faint, sweet odour in different populations. Scent characteristics are dependent on temperature and the condition of the plants, so that little can be said with certainty except that odours slightly unpleasing to the human nose are characteristic of the species.

A notable variant of *Ferraria variabilis* occurs in the Olifants River Valley and adjacent mountains, represented by Goldblatt & Porter 12210, and possibly De Vos 2389; leaves are broader and more succulent than those found elsewhere. The best-developed leaves are 20–22 mm wide (versus typically 4–12 mm for most other populations), and the rest of the plant is also larger, thus the outer spathes are 50–70 mm long and the inner may reach 85 mm. Plants form circular mats in stony ground, which suggest spreading by vegetative means. De Vos (1979: 355) found that her collection from the Gifberg, was triploid ( $2n = 30$ ) and she speculated that it was a hybrid between *F. divaricata* subsp. *divaricata* (i.e. the diploid northern form of *F. variabilis* with  $2n = 20$ ) and subsp. *australis* (the southern tetraploid form with  $2n = 40$ ), both of which occur on the lowlands below the Gifberg (and have similarly narrow leaves less than 10 mm wide). Polyploidy and hybrid vigour seem unlikely to explain the gross differences in leaf width and thickness of the plants in question. More likely, they represent a local variant of *F. variabilis* and deserve further investigation. Plants from Boklands-kloof near Lokenburg (Acocks 19736) in the Bokkeveld Mtns have subspathulate leaves with the blades shorter than the sheaths and 15–18 mm at the widest point. The blade margins are also strongly thickened, the thickenings partly wavy to slightly crisped and the apices are hooked. These plants appear vegetatively very unusual; unfortunately the flowers are poorly preserved and colour was not noted on the label. Revisiting Lokenburg in 2008 we found plants with such leaves but the flowers were quite typical of *F. variabilis*.

Some collections of *Ferraria variabilis* from southwestern Namibia, the Richtersveld and Bushmanland have long, narrow leaves exceeding the stems and only 2–3 mm wide (e.g. Mittendorf 43; Mostert 1415), so different from the spathes, that the plants appear to repre-

sent another species. Flowers and other features correspond closely to *F. variabilis* from this, the northwestern and northeastern extremities of its range.

Populations of *Ferraria variabilis* from the Tanqua Basin and nearby (e.g. Goldblatt & Porter 12977, MO, NBG, PRE) stand out in having the nectaries located in prominent pouches in the middle of the tepal claws, rather than at the claw bases. The anthers in the Tanqua Basin populations and others from nearby (e.g. Jackson s.n. NBG, from Wuppertal; Compton 17412, NBG, from Whitehill, incidentally the type of *F. divaricata* var. *australis*) have the anther lobes held  $\pm$  parallel, although joined together only at the tips, as they are in plants from other parts of the range that have widely diverging anther lobes.

*History:* as discussed above under *Ferraria divaricata*, this name was applied in part by De Vos (1979) to what we here call *F. variabilis*. A taller species, *F. divaricata* is based on a painting of a plant about 450 mm high, most likely collected in the Clanwilliam District. It has large flowers with dark brown tepal limbs except for the paler margins, large anthers with widely divaricate lobes, orange pollen, and long basal leaves with a grey bloom. That plant corresponds to what De Vos called *F. divaricata* subsp. *arenosa*, which we considered best treated as a separate species that now bears the name *F. divaricata* (Goldblatt & Manning 2005). The only epithet that can be applied with some degree of certainty to *F. divaricata* subsp. *divaricata sensu* De Vos is the nomenclaturally illegitimate *F. antherosa*, a species based on a plant of uncertain provenance, and painted from a specimen that flowered in England in 1804. The flowers most closely match those of northern populations of low-growing, more or less tufted plants which De Vos distinguished in *F. divaricata* by tepal markings of solid colour and the claws with large green nectaries. The name *F. antherosa* is, however, superfluous because Ker Gawler also cited as a synonym *F. viridis* Andrews, an orthographic variant of *F. viridiflora* (= *F. ferrariola*), published in 1803. *Ferraria divaricata* subsp. *divaricata sensu* De Vos was named *F. variabilis* by Goldblatt & Manning (2005). The epithet reflects the variability in tepal colour and marking across its range, and even within populations. *Ferraria atrata* Loddiges (1828) may be this species but the description, accompanying the illustration, and a fragment at the Kew Herbarium that may be the type, are inadequate to identify the plant. It can even be argued that the species lacks a description, for the text associated with the painting contains no truly descriptive information. It is impossible even to determine whether the anther lobes are parallel or divergent.

*Ferraria divaricata* subsp. *australis* was described by De Vos (1979) for populations that have tepals speckled and streaked and small dark-coloured nectaries at the tepal bases, contrasting with subsp. *divaricata* (as she understood it), which has tepals with solid patterns of colour and larger, pale greenish nectaries. We find the distinction less clear in the field: plants with some tepal streaking or spots have large nectaries and there seems to be a cline from the northwest to the southeast of the range of plants with increasing degrees of tepal spotting and

decreasing size of the nectaries. Some northern populations with tepals marked with solid bands of colour also have fairly small nectaries. Currently, subsp. *australis* is included in the synonymy of *F. variabilis*.

#### Representative specimens

NAMIBIA.—2715 (Bogenfels): Klinghardt Mtns, near ephemeral pan, (–BC), 22 Sept. 1996, *Mannheimer & Mannheimer 271* (PRE, WIND). 2716 (Witputz): Sperrgebiet, SE side of Auros Mtns, in red sand, 644 m, (–CB), 11 Aug. 2001, *Smook 11318* (WIND); ± 40 km N of Rosh Pinah, (–DA), 29 Sept. 1983, *Goldblatt 7018* (MO); Huib Hoch Plateau, between Zebrafontein and Witputs, (–DB), 29 Jun. 1989, *Oliver 9161* (NBG); Namuskluft, (–DD), *Mittendorf 43* (PRE, WIND); 12 Sept. 1973, *Giess 12900* (PRE). 2816 (Oranjemund): Luderitz Dist., gravel plain west of rooi duine, (–BA), 1 Oct. 1996, *Mannheimer & Mannheimer 449* (WIND); Schakel Mtn in sand, (–BA), 1 Aug. 1977, *Muller 775* (WIND).

NORTHERN CAPE.—2816 (Oranjemund): 37 km north of Lekkersing, red sand, (–DB), 10 Oct., 1991, *Germishuizen 5595* (PRE). 2817 (Vioolsdrif): Richtersveld, Rosyntjieberg, dry riverbed, (–AC), 30 Aug. 1977, *Oliver, Tölken & Venter 267* (PRE); 15 km south of Vioolsdrif, (–DC), 7 Aug. 1976, *Giess 14535* (PRE, WIND). 2821 (Upington): Sandveld, Upington, (–AC), 8 Aug. 1961, *Mostert 1415* (PRE). 2917 (Springbok): Richtersveld, road to Eksteenfontein, (–CD), 24 Aug. 1992, *Goldblatt & Manning 9312* (MO); 48 km W of Steinkopf, stony slope, (–BA), 25 Sept. 1974, *Goldblatt 2778* (MO). 2918 (Gamoe): Aggenys, Farm Nooisabes, (–AB), 11 Aug. 2000, *Desmet & Opel 2995* (NBG); Goegab Nature Reserve, (–CA), 10 Oct. 1999, *Zietsman 3869* (PRE). 2919 (Pofadder): 6 km from Pofadder to Springbok, (–AB), 21 Sept. 1975, *Boucher 2886* (NBG). 2921 (Kenhardt): golf course, (–AC), 28 Aug. 1977, *De Vos 2395* (NBG). 3019 (Loeriesfontein): 103 km from Brandvlei to Loeriesfontein, (–DC), Oct. 1975 (fr.), *Arnold 905* (PRE). 3023 (Britstown): Britstown, rock cracks, (–DA), Sept. 1961, *Mauve 4133* (PRE). 3119 (Calvinia): Boklandskloof, Lokenburg, (–CA), 11 Oct. 1958, *Acocks 19736* (PRE); Agterplaas, west of Calvinia, (–BC), 1 Sept. 1990, *Oliver 9615* (NBG).

NORTH-WEST.—2822 (Glen Lyon): Hay Dist., Langberg, (–DD), Jul. 1920, *Hunter 18* (PRE); Hay Dist., Farm Doring Aar, red sand, (–DD), 7 Aug. 1936, *Acocks 571* (PRE).

WESTERN CAPE.—3118 (Vanhynsdorp): top of Gifberg, (–DB), 25 Sept. 1975, *De Vos 2389* (NBG). 3119 (Calvinia): near Nieuwoudtville, Glen Lyon, rocky hills, (–AC), *Goldblatt & Porter 12216* (MO, NBG). 3218 (Clanwilliam): 12 km N of Clanwilliam on old road to Bulshoek, (–BB), 15 Sept. 2002, *Goldblatt & Porter 12210* (MO); Clanwilliam, 350 ft [106 m], (–BB), 5 Aug. 1896, *Schlechter 964* (PRE). 3219 (Wuppertal): Bidouw Valley, (–AA), 23 Sept. 1952, *Middlemost 1746* (NBG); Farm Jakkalsfontein, 25 km toward Middelpas from Calvinia–Ceres road, (–BD), 31 Aug. 1982, *Snijman 616* (PRE); Tanqua National Park, Maansedam, 10 Sept. 2007, *Goldblatt & Porter 12977* (MO, NBG, PRE). 3220 (Sutherland): ± 2 km N of Matjiesfontein, Farm Buelhouer, (–BA), 14 Sept. 2004, *Snijman 1925* (NBG). 3319 (Worcester): flats east of Prince Alfred's Hamlet, (–AD). 10 Oct. 1974, *Oliver 5062* (MO, NBG, PRE); Doorn River, 12 miles [19 km] N of Villiersdorp, (–CC), 25 Oct. 1962, *De Villiers s.n.* (NBG). 3320 (Montagu): Tweedside, (–AB), 26 Sept. 1951, *Barker 7463* (NBG). 3419 (Caledon): burned stony slopes on western outskirts of Caledon, (–AB), 29 Sept. 2110, *Goldblatt & Nanni 11939* (MO). 3420 (Bredasdorp): 25 km W of Swellendam, slopes of Bromberg, (–AA), 17 Sept. 1978, *Goldblatt 4882* (MO).

#### 15. *Ferraria flava* Goldblatt & J.C.Manning, sp. nov.

?*F. divaricata* subsp. *aurea* M.P. de Vos: 359 (1979). Type: South Africa, [Western Cape], ± 9 miles [± 13.5 km] north of Lambert's Bay, Farm Langdam, 28 Sept. 1973, *Van Breda sub M.P. de Vos 2297* (STE, holo.!, PRE, iso., two sheets!).

Plantae ± acaulescentes ad 120 mm altae foliis exclusis, foliis 5–7 ensiformibus ad 300 × 12–20 mm subrectis glaucis ± succulentis, rhipidiis 2-floris, spathis viridibus marginibus transparentibus spatha interna usitate 40–55 mm longa externa vaginanti vel supra divergenti apice incurvata, floribus flavis limbis tepalorum caer-

uleo-viridibus maculatis marginibus crispis pallidioribus, tepalis exterioribus ± 30 × 10 mm, interioribus ± 12 × 5 mm, unguibus ± 15 mm longis, columna filamentorum 11–12 mm longa, antheris ± 3.5 mm longis lobis divaricatis, ramis styli ± 3 mm longis, lobis ramorum prominenter fimbriatis.

TYPE.—Western Cape, 3118 (Vanhynsdorp): sandveld west of Koekenaap, Farm Kommandokraal, (–AD), 10 Sept. 2008, *Goldblatt & Porter 13105* (NBG, holo.; K, MO, PRE, iso.).

Plants ± acaulescent, up to 120 mm high excluding leaves. *Stem* with (2–)4 or 5 primary branches produced from below or shortly above ground level, each with several branches, these crowded basally and congested, together bearing up to 50 rhipidia. *Leaves* suberect, 5–7, sword-shaped, up to 300 mm long, lower 3–5 much exceeding spathes and flowers, mostly 12–20 mm wide, glaucous, ± succulent, without visible main vein. *Rhipidia* 2-flowered, numerous, crowded on short, ± horizontal or ascending branches; spathes green, margins transparent, inner mostly 40–55 mm long, outer ±  $\frac{2}{3}$  as long as inner, usually entirely sheathing or diverging above, apex curving inward. *Flowers* on pedicels up to 10 mm long, lasting one day, clear yellow, tepal limbs with minute blue-green spots in lower  $\frac{1}{3}$ , margins slightly paler in colour, claws translucent white inside, forming a floral cup 14–15 mm deep, 8–9 mm wide at rim, tepal limbs spreading, crisped, usually sweet vanilla-smelling, nectaries at tepal bases, pale green; outer tepals ± 30 × 10 mm, inner tepal limbs ± 12 × 5 mm, claws of both whorls ± 15 mm long. *Stamens* with filaments united in a column 11–12 mm long, free and arching outward in upper ± 1 mm; anthers pale yellow with dark purple-brown on the lines of dehiscence, ± 3.5 mm long before anthesis, ± 1.5 mm long after dehiscence, horizontal, thecae joined only at apices, widely diverging; pollen pale yellow. *Ovary* fusiform, 20–25 mm long, with a sterile beak, ± 10 mm long, style branches ± 3 mm long, dividing into diverging, prominently fringed arms, ± 5 mm long; stigmas on small lobes below tips of style arms and arching over anthers. *Capsules* and *seeds* unknown. *Flowering time*: early Sept.–late Oct. Figure 14, Plate 1J.

*Distribution and habitat*: endemic to the sandveld of coastal Western Cape and Namaqualand, *Ferraria flava* extends from the sandy flat country north of Lambert's Bay and Klaver to the Groen River and Komaggas (Figure 12). Plants grow in deep, moderately fine sand among sandveld species such as *Willdenowia* (Restionaceae) and the small, tree-like, willowy *Wiborgia obcordata* (Fabaceae), and occur most often on the slopes of low, stabilized and vegetated dunes. It shares this habitat at some sites with the rare *F. ornata* which blooms in May and June and has ripe capsules when *F. flava* comes into flower in September. Its pollination biology is unknown. The flowers last one day, with the tepals unfolding at ± 9:00 and collapsing at ± 16:00. They produce small quantities of watery nectar 6–8 % sucrose equivalents, a feature of *F. divaricata* and its immediate allies (Goldblatt *et al.* 2009). No potential pollinating visitors have been observed.



FIGURE 14.—*Ferraria flava*, Goldblatt & Porter 13105. A, flowering plant; B, flower, side view; C, inner tepal; D, outer tepal; E, staminal column and style; F, anther, undeheisced (above), dehiscent (below). Scale bar: A, B, 10 mm; C, D, 8 mm; E, F, 1.6 mm. Artist: J.C. Manning.

**Diagnosis and relationships:** *Ferraria flava* is recognized by the yellow, sweetly scented flowers and typically acaulescent habit with well-grown plants bearing 3 or 4 main branches arising below the ground and bearing numerous rhipidia set closely together. Combined with the acaulescent habit are the several broad, firm, almost, rigid leathery leaves up to  $300 \times 20$  mm. The leaves recall those of *F. divaricata*, which has aerial stems and larger, usually predominantly brown flowers (but sometimes dull yellow) with a wider floral cup. The flowers of *F. flava* recall those of *F. macrochlamys* and its immediate allies in the narrow floral cup but they are somewhat

larger, with tepals  $\pm 30 \times 10$  mm and claws  $\pm 15$  mm long, and last a single day, unlike those of the *F. macrochlamys* group, which have somewhat smaller tepals with shorter claws, 10–14 mm long, and last two days. We noted that at one site near Koekenaap, *F. divaricata*, with tall stems and brown flowers (Goldblatt & Porter 13188 NBG), occurs together with *F. flava*, but blooms later in the season, coming into flower there in October.

We provisionally include *Ferraria divaricata* var. *aurea* in synonymy here. The type, from near Lambert's Bay, has short, aerial stems but other collections cited by De Vos (1979) under this name are more or less stemless

and do belong here. Flower colour and shape of the type collection with aerial stems are consistent with *F. flava*. We have not been able to locate plants at the type locality and wonder whether subsp. *aurea* is simply a short-stemmed variant of *F. flava*. Living plants from the type locality need to be examined to determine the true identity of subsp. *aurea*.

#### Representative specimens

NORTHERN CAPE.—2917 (Springbok): Komaggas, (–DC), 6 Oct. 1934, *Herre s.n.* (BOL). 3017 (Hondeklipbaai): Farm Hardevlei, NW of Kotzesrus on road to Groenrivier, sandy flats, bright yellow with greenish dots in V-shaped pattern, sweetly scented, (–DC), 29 Sept. 1987, *Reid 1292* (BOL, MO, PRE).

WESTERN CAPE.—3117 (Lepelfontein): sandy flats and dunes west of Lepelfontein, ± 160 m, (–BB), 10 Sept. 2009 (sterile), *Goldblatt & Porter 13309* (NBG); Brand-se-Baai, sandy slopes inland of coast, (–DD), 15 Sept. 2008, *Goldblatt & Porter 13122* (MO, NBG). 3118 (Vanrhynsdorp): sand dunes 3–4 miles [4.5–6.0 km] north of Klaver station, (–DA), 27 Oct. 1944, *Leipoldt 4166* (BOL).

#### Series Uncinatae

16. *Ferraria uncinata* Sweet in The British flower garden: t. 161 (1826a); De Vos: 365 (1979), excluding subsp. *macrochlamys*. Type: South Africa, without precise locality, illustration in Sweet l.c. (1826a), originally collected by *W. Synnot* (no preserved specimen known).

*F. framesii* L.Bolus: 123 (1931). Type: South Africa, [Western Cape], ± 6 miles [± 9 km] south of Clanwilliam, 22 Oct. 1931, *Ross Frames s.n.* BOL19928 (BOL, holo.!, SAM, iso.!).

Plants 90–200(–300) mm high. *Stem* either ± subterranean and then few-branched at base, or stem produced above ground and branched from upper nodes. *Leaves* lanceolate, mostly 8–12 mm wide, sheaths usually concealing stem, usually without visible main vein, prominently multi-veined, flat or slightly twisted, apex often hooked, margins thickened, hyaline, smooth, usually crisped and undulate at least proximally. *Rhipidia* 2-flowered; spathes green, usually with hooked tips, inner mostly 40–60 mm long, outer 26–40 mm long (±  $\frac{1}{2}$  to  $\frac{2}{3}$  as long as inner), usually entirely sheathing. *Flowers* on pedicels 12–20 mm long, lasting two days, usually pale to dark blue-violet, or light brown with blue speckling, margins crisped, dull yellow-green to khaki, with a narrow cup, 8–12 mm deep, ± 7 mm wide at rim, often unscented, faintly foetid-smelling, or scented of lemon and cinnamon, nectaries minute, at base of tepals; outer tepals 28–35 × 7–10 mm, limb at least 1.5 times as long as claw, and up to 3 times as long, often long-attenuate and coiled, claws 8–12 mm long; inner tepals 28–30 mm long, limbs reflexed, claws slender, 7–12 mm long. *Filaments* united in a column 7–11 mm long, free in upper ± 1.5 mm; anthers ± 3 mm long, thecae divergent, shrinking to ±  $\frac{1}{2}$  their length after dehiscence. *Ovary* fusiform, 15–28 mm long, with beak 8–12 mm long; style branches ± 1.5 mm long, dividing into diverging, prominently fringed arms, ± 1.5 mm long; stigmas terminal on small lobes below tips of style arms and arching over anthers. *Capsules* 12–15 mm long, excluding beak. *Seeds* angular, 5- or 6-sided, 3–4 mm long, dark brown, facet surfaces slightly wrinkled. *Flowering time*: late Aug.–Oct. Plate 1A.

*Distribution and biology*: *Ferraria uncinata* extends from the slopes of the Gifberg near Klaver southward,

through the Olifants River Valley and Piketberg to Malmesbury and Mamre, some 65 km north of Cape Town (Figure 15). Plants are most often found in sandstone outcrops and relatively dry sites, but also sometimes in open ground in coarse, granite-derived gravel or on sandstone slopes in deep sand.

*Diagnosis and relationships*: as circumscribed here, *Ferraria uncinata* includes plants with a narrow floral cup 8–12 mm deep, tepals either deep blue to violet edged with dull yellow-green or in the north of its range, buff to dull yellow with violet speckles with yellow-brown margins. The leaves have thickened margins with at least the edges of the lower leaves crisped and undulate. The margin surface itself is smooth. The hooked tips of the leaves and spathes, the character for which the species was named (*uncinatus* is Latin for hooked), is frequent, though not constant, not only in *F. uncinata* but in several other species of the genus.

De Vos (1959) included the yellow-flowered central Namaqualand species, *Ferraria macrochlamys* in *F. uncinata* as subsp. *macrochlamys*, but we regard this plant as a separate species (Goldblatt & Manning 2004). It differs not only in the pale yellow flower colour but the leaf margins in those populations with thickened margins resemble those of *F. uncinata* only superficially. In *F. macrochlamys* subsp. *macrochlamys* the marginal thickenings are usually densely ciliate and irregularly serrulate or crenulate, as well as sometimes being slightly crisped. The tepal limbs of *F. uncinata* are at least 1.5 times as long as the claws and up to three times as long in the northern populations, the tepal apices of which are unusually extended. In *F. macrochlamys* the tepal limbs are slightly shorter to ± 1.5 times as long as the claws and are less prominently attenuate.

The type illustration, of a plant with the tepal limbs speckled with dark blue dots on a light brown background, suggests that it was collected between Clanwilliam and Bulshoek in the Olifants River Valley. Elsewhere across its range, *Ferraria uncinata* has blue-violet tepal limbs with somewhat obscure, darker blue spot-

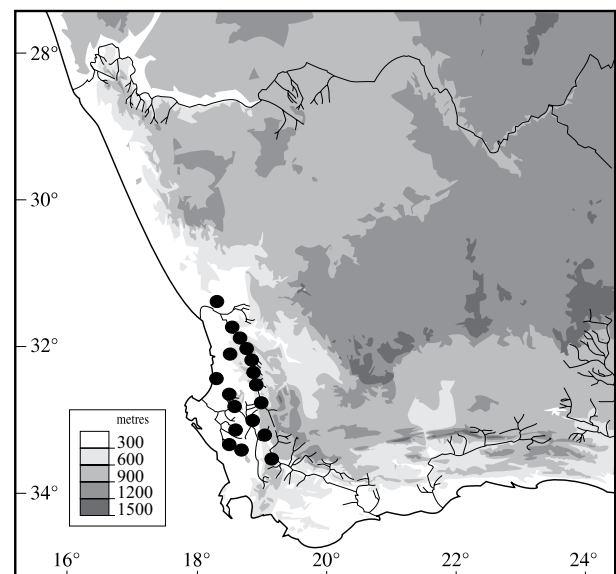


FIGURE 15.—Known distribution of *Ferraria uncinata*.



ting. The northern populations of *F. uncinata* differ not only in colouring, but in the proportions of the flower. Elsewhere, the floral cup is  $\pm 11$ – $12$  mm deep and the tepal limbs are  $16$ – $18$  mm long. In the northern populations, however, the floral cup is  $8$ – $9$  mm deep and the tepal limbs are  $25$ – $28$  mm long, the extended length due largely to the long, trailing, attenuate tip.

#### Representative specimens

WESTERN CAPE.—3218 (Clanwilliam): Olifants River Valley, stony slopes at turn-off to Nardouw, (–BB), 26 Aug. 1957, *Lewis 5213* (NBG), 15 Sept. 2002, *Goldblatt & Porter 12213* (MO, NBG, PRE); Clanwilliam, 5 Aug. 1896, *Schlechter 8413* (K, MO, PRE, S); Olifants River Valley, Farm Klawervlei, N-facing slopes at bridge over Olifants River, (–BD), 2 Sept. 1994, *Goldblatt & Manning 9959* (MO); hills N of Aurora near Redelinghuis, (–DA), 14 Sept. 2001, *Goldblatt & Porter 11882* (MO, NBG). 3219 (Wuppertal): Brandewyn River, (–AA), 26 Aug. 1950, *Barker 6572* (NBG); Cedarberg, Algeria Forest Station, (–AC), 10 Sept. 1997, *Van Rooyen et al. 729* (NBG). 3318 (Cape Town): Malmesbury, western edge of town in new development, (–BC), 1 Oct. 1998, *Goldblatt & Manning 11034* (MO); near Groenekloof (Mamre), (–AD), Nov. (fr.), *Ecklon 305* (K, MO, S). 3319 (Worcester): Mostertshoek, Romans River, (–AC), Sept. 1976, *De Vos 2338* (NBG).

**17. *Ferraria macrochlamys* (Baker) Goldblatt & J.C.Manning** in *Novon* 14: 293 (2004). *Lapeirousia macrochlamys* Baker: 338 (1876). *F. uncinata* subsp. *macrochlamys* (Baker) M.P.de Vos: 369 (1979). Type: South Africa, without precise locality or date, as Herb. Forsyth (K, holo.).

Plants mostly  $70$ – $100$  mm high forming low tufts. *Stem* few- to several-branched (rarely simple), branches crowded close to base; branches and spathes all  $\pm$  same length. *Leaves* narrowly sword-shaped to linear, mostly  $(2.0\text{--})4.5$ – $7.0$  mm wide,  $\pm$  straight, or all curving to same side, or serpentine (loosely wavy in concertina fashion), tips oblique or hooked, sometimes densely papillate-ciliate; margins heavily thickened then sometimes velvety, often irregularly serrulate or crenate, sometimes slightly crisped. *Rhipidia* 2-flowered; inner spathes  $37$ – $62$  mm long, abaxial margins sometimes crisped, outer  $24$ – $50$  mm long, usually entirely sheathing, or free distally, often hooked at apex. *Flowers* on pedicels  $10$ – $23$  mm long, lasting two days, pale watery yellow with slightly darker yellow to light brown margins, outer tepal limbs often minutely speckled grey-blue at base, with a narrow cup,  $9$ – $13$  mm deep,  $5$ – $7$  mm wide at rim, with a faint, green apple or slightly sour odour; outer tepals  $26$ – $32$  mm long, limbs spreading to slightly reflexed, inner tepals  $26$ – $28$  mm long, limbs often ultimately  $\pm$  reflexed, claws of both whorls  $10$ – $14$  mm long. *Stamens* with filaments united in a column  $10$ – $12$  mm long, free and diverging in upper  $\pm 1$  mm; anthers  $2.2$ – $3.0$  mm long, thecae divergent; pollen orange. *Ovary* fusiform,  $15$ – $20$  mm long with beak  $7$ – $15$  mm long; style branches  $1.0$ – $1.5$  mm long, dividing into diverging, prominently fringed arms,  $1.0$ – $1.5$  mm long; stigmas on small lobes below tips of style arms and arching over anthers. *Capsules*  $15$ – $20$  mm long excluding beak. *Seeds* angular, mostly 5- or 6-sided,  $\pm 2.7$ – $3.0$  mm diam., dark brown, facets slightly wrinkled. *Flowering time*: late Aug. to end of Sept., rarely to mid-Oct. Figures 16–19.

*Distribution and biology*: an exclusively Namaqualand species, the range of *Ferraria macrochlamys*

extends from Steinkopf in the north to the southern foothills of the Kamiesberg near Bitterfontein in the south and west toward the coast (Figure 17). Plants grow on a variety of soils, subsp. *macrochlamys* and subsp. *kamiesbergensis* in gritty to loamy granite-derived soils, sometimes in granite outcrops, in vegetation dominated by succulent-leaved shrubs and subsp. *serpentina* mostly in quartzitic sand, usually among rocks. As in other members of series *Uncinatae*, the flowers last two days and often have a slightly unpleasant, sour odour, but sometimes they appear to have no scent at all. Pollination biology is known only for subsp. *kamiesbergensis*, the flowers of which are pollinated by the masarine wasp (Vespidae: Masarinae) *Ceramius* (Gess 1997, reported as *F. divaricata*, now *F. variabilis*). So similar are the flowers of all three subspecies that we infer the same pollination strategy for the other two subspecies.

*Diagnosis and relationships*: De Vos (1979) treated *Ferraria macrochlamys* as a subspecies of the dark blue-flowered *F. uncinata*, a plant of the western half of Western Cape. She considered that the two shared identically specialized leaves with heavily thickened and crisped margins and derived flowers with a narrow floral cup and that they differed only in flower colour, either violet-blue with dull greenish yellow margins in subsp. *uncinata* or pale yellow with yellow to brown margins in subsp. *macrochlamys*. The leaf morphology in the two taxa is, however, not identical: whereas *Ferraria uncinata* has leaf margins crisped and sometimes undulate with the thickened edges smooth, *F. macrochlamys* has more often straight leaf margins but the marginal thickenings, when present, are usually irregularly serrate to crenate, or sometimes crisped, and are also sometimes densely velvety. Only occasionally do the lower leaf blades have undulate or crisped margins. Their flowers differ in size as well as colour. The tepal limbs of *F. uncinata* exceed the claws by at least 1.5 times and are usually at least twice and sometimes up to three times as long, and  $(18\text{--})28$ – $35$  mm long (with claws  $8$ – $12$  mm long), whereas the tepals limbs of *F. macrochlamys* are  $15$ – $20$  mm long and at most half again as long as the claws,  $10$ – $18$  mm long, and are less strongly attenuate. While *F. macrochlamys* is clearly allied to *F. uncinata*, it seems to us most closely related to *F. brevifolia*, a local endemic of southern Namaqualand. This species has virtually identical flowers to those of *F. macrochlamys* but the broad leaf blades are shorter than the sheaths.

We recognize three subspecies in *Ferraria macrochlamys*, based on differences in leaf morphology and sometimes in habitat. Only subsp. *macrochlamys* has leaves with thickened and crisped to undulate margins and sometimes papillate-ciliate leaf blades. The  $\pm$  falcate leaves of subsp. *kamiesbergensis* are all recurved in the same direction and have smooth, unthickened margins. In subsp. *serpentina* the leaf margins are also unthickened but the blades are serpentine, thus loosely wavy in concertina fashion.

*History*: *Ferraria macrochlamys* was initially described as *Lapeirousia macrochlamys* by J.G. Baker (1876). It remained so poorly understood that in 1931 H.M.L. Bolus, who collected plants at Bowesdorp in central Namaqualand in 1929, described it anew as *F. crispulata*. Goldblatt (1972), in his revision of southern



African *Lapeirousia*, noted that the type of *L. macrochlamys* was a species of *Ferraria* akin to *F. crispulata*, but it remained to M.P. de Vos in her revision (De Vos 1979) to transfer the species to the genus. The species was based on a specimen in the Kew Herbarium, ostensibly collected by W. Forsyth. It is now understood that the specimen was part of a collection purchased in 1835 by George Bentham of the Royal Botanic Gardens, Kew, from the estate of William Forsyth, son of W.F. Forsyth (1737–1804). Forsyth, a distinguished Scottish horticulturist, was one of the founders of the (Royal) Horticultural Society of London and was also associated with the Chelsea Physic Garden (1771–1784). The brief comment about Forsyth by Gunn & Codd (1981) in their history of plant collecting in southern Africa, is thus inaccurate with regard to Forsyth (Nelson 2006). It seems reasonable to suggest that at least some specimens of the Forsyth herbarium were gathered by the Scottish botanist, James Niven, who collected plants at the Cape for British patrons and later the Empress Josephine of France. Niven visited Namaqualand in 1799 and travelled to the Kamiesberg through country where *F. macrochlamys* grows. Another possibility is that *F. macrochlamys* was first collected by William Paterson, who travelled through Namaqualand collecting plant and animal specimens in 1778 and 1779. Paterson was for a time associated with W.F. Forsyth.

#### Key to subspecies

- 1a Leaf margins thickened, hyaline, and sometimes shortly velvety, at least lower leaves with serrulate to crenulate margins; leaf blades  $\pm$  straight or laxly undulate; outer spathes sheathing for most of their length and no more than  $\frac{2}{3}$  as long as inner ..... 17a. subsp. *macrochlamys*
- 1b Leaf margins hardly, if at all, thickened, and smooth:
  - 2a Leaf blades in upper  $\frac{1}{2}$  inclined to curving to same side; outer spathes not sheathing in distal half and  $\pm$  as long as inner; outer tepals 25–35 mm long; filament column  $\pm$  12.5 mm long ..... 17b. subsp. *kamiesbergensis*
  - 2b Leaf blades in upper  $\frac{1}{2}$  serpentine, thus loosely folded back on themselves in concertina fashion; outer spathes sheathing for most of their length and  $\pm \frac{2}{3}$  as long as inner; outer tepals 25–30 mm long; filament column 10–11 mm long ..... 17c. subsp. *serpentina*

#### 17a. subsp. *macrochlamys*

*Ferraria crispulata* L.Bolus: 260 (1931). Type: South Africa, [Northern Cape], near Bowesdorp, 27 Aug. 1929, *L. Bolus s.n. BOL19162* (BOL, holo.; BM, K!, iso.).

Plants with leaves often densely papillate-ciliate; margins heavily thickened, thickenings smooth or densely ciliate, often irregularly serrulate or crenate, sometimes slightly crisped. *Rhipidial spathes*: inner 45–62 mm long, abaxial margins sometimes crisped, outer 30–50 mm long, usually entirely sheathing, or tips free. *Flowers* with narrow cup 11–13 mm deep,  $\pm$  7 mm wide at rim, with faint, green-apple or slightly sour odour; outer tepals 28–32 mm long, limbs spreading to slightly reflexed, inner tepals 26–28 mm long, claws of both whorls (11–)12–14 mm long. *Stamens* with filaments united in column  $\pm$  12 mm long, free and diverging in upper  $\pm$  1 mm; anther thecae  $\pm$  3 mm long before dehiscence. *Ovary* 23–28 mm long with beak 15–18 mm long. *Flowering time*: late Aug.–late Sept. Figure 16.

*Distribution and habitat*: restricted to central Namaqualand, subsp. *macrochlamys* extends from Steinkopf in the



FIGURE 16.—*Ferraria macrochlamys* subsp. *macrochlamys*, Goldblatt, Manning & Porter 13406 (NBG). Scale bar: 10 mm. Artist: J.C. Manning.

north to Garies in the south and inland to the northern Kamiesberg (Figure 17). Plants grow in gritty to loamy granite-derived soils.

*Diagnosis*: most distinctive of the three subspecies, subsp. *macrochlamys* stands out in its spreading leaves with thickened margins that are crenate or crisped and sometimes velvety. The flowers often serve to distinguish it from subsp. *serpentina* in their slightly larger size, but that difference is not consistent, hence unreliable. Subsp. *macrochlamys* is always acaulescent, whereas subsp. *serpentina*, in years of ample rainfall, develops an aerial stem rendering it quite different in general appearance.

#### Representative specimens

NORTHERN CAPE.—2917 (Springbok): 48 km west of Steinkopf, stony slope, (–BA), 25 Sept. 1974, Goldblatt 2778 (PRE); 1 mile [1.6 km] west of Springbok, (–DB), 9 Sept. 1950, Barker 6701 (NBG); Mesklip, (–DD), Lewis 1035 (SAM). 3017 (Hondeklipbaai): road to Soebatsfontein,  $\pm$  1 km from N7, (–BB), 17 Sept. 2002, Goldblatt & Porter 12229 (MO); 1 km south of Kamieskroon, (–BB), 29 Sept. 1981, Hugo 2889 (PRE); top of Garies hill along road to Hondeklipbaai, (–BD), 2 Sept. 2000, Goldblatt & Nänni 11454 (MO, NBG), 4 Sept. 1945, Compton 17179 (NBG). 3018 (Kamiesberg): Kamiesberg, slopes north of Leliefontein, burned previous summer, (–AC), 17 Sept. 2002, Goldblatt & Porter 12228 (MO).

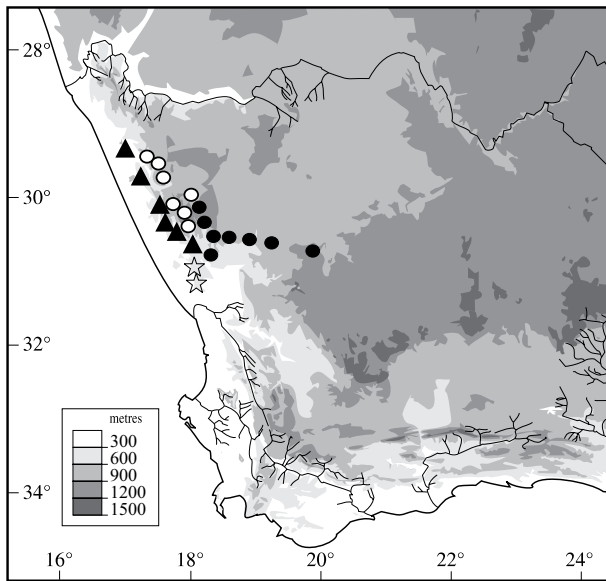


FIGURE 17.—Known distribution of *Ferraria macrochlamys* subsp. *macrochlamys*, ○; subsp. *kamiesbergensis*, ●; subsp. *serpentina*, ▲; and *F. brevifolia*, ☆.

17b. subsp. **kamiesbergensis** (M.P.de Vos) Goldblatt & J.C.Manning, comb. et stat. nov., *Ferraria kamiesbergensis* M.P.de Vos: 362 (1979). Type: South Africa, [Northern Cape], Kamiesberg, Rondefontein, 1 Sept. 1976, Oliver 5970 (NBG, lecto.!, designated by Goldblatt & Manning, 2004: 292).

Plants forming low tufts, rarely unbranched. *Leaves* firm, suberect-curved to falcate-incurved, mostly 70–100 × 3–6 mm, all weakly to strongly curving to same side; margins plane, barely or not at all thickened. *Rhipidial spathes*: inner 50–65 mm long, outer 50–57 mm long, sheathing in lower half, arching outward distally. *Flowers* with tepal claws forming narrow cup mostly 12–14 mm deep, ± 7 mm wide at rim, limbs laxly spreading; outer tepals 25–35 mm long, 8–10 mm at widest, limbs 13–20 mm long, slightly exceeding claws, inner tepals 25–30 mm long, claws of both whorls 12–14 mm long. *Stamens* with filaments united in a column 10.5–12.5 mm long, free and diverging in upper 1 mm; anther thecae ± 3 mm long, shorter after anthesis. *Ovary* 18–22 mm long with tubular beak ± 12 mm long; style branches ± 1 mm long, dividing into diverging, prominently fringed arms, ± 2 mm long. *Flowering time*: Sept.–early Oct. Figure 18, Plate 1B.

*Distribution and biology*: subsp. *kamiesbergensis* is centred in the southern highlands where it extends from Rooiberg in the Kamiesberg to Bitterfontein but isolated populations occur to the east toward Loeriesfontein and the hills northwest of Calvinia in the western Karoo (Figure 17). In the Kamiesberg, plants grow in coarse, gritty soil derived from decomposed granite or in cracks in granite pavement. Soils favoured by *F. kamiesbergensis* in the western Karoo are not recorded and we have not seen the species there ourselves. The flowers last two days and, in the one population we examined for nectar, produced modest quantities of dilute nectar, mean 10.6 % sucrose equivalents. The one record of pollination in subsp. *kamiesbergensis*, by Gess (1997, originally reported as *F. divaricata*) is by the masarine wasp,

*Ceramius* (Eumenidae). We have seen no potential pollinators on the other subspecies.

*Diagnosis and relationships*: subsp. *kamiesbergensis* is distinctive only in its vegetative morphology. The leaves are firm and leathery to almost succulent and the blades are often dark green and in the upper half all curve to the same side and the margins are plane, smooth and not at all, or only barely, thickened. Otherwise plants have the tufted habit of subsp. *macrochlamys* and flowers virtually identical to that subspecies. The ranges of subsp. *kamiesbergensis* and subsp. *macrochlamys* do not overlap: populations of the latter are mostly from the highlands west and north of the Kamiesberg and in the Kamiesberg itself are only known from Leliefontein and nearby, which is north of the range of subsp. *kamiesbergensis*.



FIGURE 18.—*Ferraria macrochlamys* subsp. *kamiesbergensis*, Goldblatt & Porter 13176. Scale bar: 10 mm. Artist: J.C. Manning.

Typification of this taxon has proved problematic (Goldblatt & Manning 2004) as the illustration in the protologue (De Vos 1979) is not this species but, at least in leaf, resembles the widespread and common *Ferraria variabilis*. Of the three plants on the type sheet only one, now the lectotype, resembles subsp. *kamiesbergensis*. When seen alive, the flowers of the true *F. kamiesbergensis* and *F. variabilis* are quite different but in specimens with poorly pressed flowers, they are remarkably similar. Because of lingering confusion over the identity and circumscription of *F. kamiesbergensis* (now subsp. *kamiesbergensis*) we list all specimens of the subspecies that we have seen below, including our own recent collections.

#### Representative specimens

NORTHERN CAPE.—3018 (Kamiesberg): Farm Karas, Die Kom, (–CA), Oct. 1940, *Leipoldt 3563* (BOL); Wilgehout Ravine, (–CA), Sept. 1911, *Pearson 6812* (K); Farm Rondefontein, south of Karas, in fallow field on SE-trending slope, (–CA), 17 Sept. 2002, *Goldblatt & Porter 12223* (MO, NBG); NE slopes of Rooiberg, (–CA), 17 Sept. 1987, *Davidse 33353* (MO); southern Kamiesberg, between Farms Doringkraal and Gembokkloof, (–CA), 25 Sept. 2008, *Goldblatt & Porter 13176* (MO, NBG). 3019 (Loeriesfontein): between Kliprand and Loeriesfontein, Farm Onderste Camdini, (–CD), 11 Sept. 1976, *Thompson 2882* (NBG). 3119 (Calvinia): near Hantams River, 30 miles (± 45 km) NW of Calvinia on Loeriesfontein road, (–BB), 26 Sept. 1952, *Lewis 2534* (SAM); 32 miles (± 48 km) from Calvinia to Loeriesfontein, (–BB), 27 Sept. 1952, *Johnson 603* (NBG).

WESTERN CAPE.—3018 (Kamiesberg): ± 10 km north of Bitterfontein, sandy slope, (–CC), 2 Sept. 2002, *Goldblatt & Porter 12146* (MO).

17c. subsp. ***serpentina*** Goldblatt & J.C.Manning, subsp. nov.

*Ferrariae macrochlamydi* subsp. *macrochlamydi* similis sed foliis linearibus usitate 3–4 mm latis laminis undulatis marginibus non incrassatis, spathis interioribus 37–45 mm longis, exterioribus 24–38 mm longis, floribus cupulo florali 9–11 mm profundo munitis, limbis tepalorum exteriorum 16–18 mm longis interiorum ± 16 mm longis, ovario 15–28 mm longo.

TYPE.—Northern Cape, NE of Kotzesrus on road to Garies, 16 Sept. 2001, *Goldblatt & Porter 11900* (NBG, holo.; K, MO, PRE, iso.).

Plants like subsp. *macrochlamys* with branches crowded close to base or branching above ground, thus forming rounded plants. *Leaves* in a loose fan, linear, (2–)3–4 mm wide, without a central vein, blades serpentine (loosely wavy in concertina fashion, sometimes appearing coiled when pressed); margins plane, not thickened. *Rhipidial spathes*: inner 37–45 mm long, outer 24–38 mm long, sheathing in lower two thirds. *Flowers* on pedicels 10–15 mm long, with tepal claws forming a narrow cup, 9–11 mm deep, ± 5 mm wide at rim; outer tepal limbs 16–18 mm long, tips attenuate and twisted, inner tepal limbs ± 16 mm long, slightly reflexed, claws of both whorls 10–12 mm long. *Stamens* with united filaments in a column 10–11 mm long, free in upper 1 mm; anther thecae ± 2.2 mm long. *Ovary* 15–28 mm long, with a beak 7–18 mm long; style branches diverging, with style arms ± 1 mm long. *Flowering time*: late Aug. and Sept., rarely to mid-Oct. Figure 19.

*Distribution and biology*: restricted to central southern Namaqualand, subsp. *serpentina* occurs on the low, sandy or stony hills inland of the coast between Killians Pass and Kotzesrus (Figure 17). Plants grow in gritty soils, either on stony slopes or in deep, red, quartzitic sand. Like the other subspecies of *Ferraria macrochlamys*, the flowers of subsp. *serpentina* produce modest quantities of unusually dilute nectar, mean 8.1 % sucrose equivalents (Goldblatt *et al.* 2009). Pollination is unknown.

*Diagnosis and relationships*: evidently first collected by the American botanist, A.L. Grant in 1929 in 'Namaqualand' and shortly thereafter by R.H. Compton near Wallekraal in 1935, these specimens were misunderstood by De Vos (1979), who identified them as *F. divaricata* subsp. *divaricata* (now *F. variabilis*). Later collections made in 2001 and 2002 east of Kotzesrus, some 70 km south-southeast of Wallekraal, but in a similar sandy habitat, made it clear that the flowers of these plants closely resemble those of what are now *F. macrochlamys* subsp. *macrochlamys* and subsp. *kamiesbergensis*, differing if at all only in their slightly smaller size. Thus they have a pale yellow perianth and narrow, comparatively deep floral cup. Most striking are the leaves, the narrow blades of which are undulate in loose concertina fashion and have unthickened, plane margins. The leaf contrasts starkly with the straight leaves of typical *F. macrochlamys*, which have strongly thickened, crisped or crenate margins, and in addition in some populations, shortly velvety. The flowers of subsp. *serpentina* have a floral cup, 9–11 mm deep, ± 5 mm wide at the rim, outer tepals 25–30 mm long, and filaments 10–11 mm long, thus slightly smaller than in most populations of typical *F. macrochlamys*, which have a cup, 11–13 mm deep, 6–7 mm wide at the rim, outer tepals 28–32 mm long, and filaments ± 12 mm long. The inner spathes are 37–45 mm long, compared to 45–62 mm in subsp. *macrochlamys*, and the flowers have pedicels 10–15 mm long (versus 20–23 mm in subsp. *macrochlamys*), reflecting the shorter spathes. A particularly narrow-leaved form of subsp. *serpentina* has been recorded in the Komaggas area west of Springbok by Rupert Koopman, the blades ± 2 mm wide and when dry, showing the outline of a raised central vein.

#### Representative specimens

NORTHERN CAPE.—2917 (Springbok): near Kommagas, sandy field, (–CD), 10 Sept. 2007, *Koopman s.n.* (NBG). 3017 (Hondeklipbaai): Wallekraal, (–BC), 30 Aug. 1935, *Compton 5405* (BOL, NBG); Farm Horees 441, on road between Killian's Pass and Wallekraal, (–BC), 8 Oct. 2003, *Le Roux 5124* (NBG); road to Groen River Mouth, near Farm Nariep, (–DC), 16 Sept. 2008, *Goldblatt & Porter 13131* (MO, NBG); ± 6 km NE of Kotzesrus on road to Garies, 573 ft [175 m], (–DD), 28 Aug. 2001, *Goldblatt & Porter 11782* (MO), 2 Sept. 2002, *Goldblatt & Porter 12141* (MO, NBG, PRE); ± 10 km NE of Kotzesrus, (–DD), 3 Sept. 2001, *Goldblatt & Porter 11820* (MO).

WESTERN CAPE.—3018 (Kamiesberg): Bitterfontein–Garies, at border of Northern Cape, stony slopes facing Swartdoorn River, (–CC), 24 Sept. 2008, *Goldblatt & Porter 13167* (MO, NBG, PRE).

18. ***Ferraria brevifolia*** G.J.Lewis in *Annals of the South African Museum* 40: 119 (1954); De Vos: 369 (1979). Type: South Africa, [Western Cape], 2 miles [3 km] south of Nuwerus, Sept. 1945, *Lewis 1374* (SAM, holo.!).



FIGURE 19.—*Ferraria macrochlamys* subsp. *serpentina*, Goldblatt & Porter 13131. A, flowering plant; B, staminal column and style; C, capsules. Scale bar: A, C, 10 mm; B, 2.5 mm. Artist: J.C. Manning.

Plants 70–120(–180) mm high, usually  $\pm$  acaulescent. *Stem* with 2–4 short branches borne close to ground, all  $\pm$  equal in length. *Leaves* overlapping to form a tight fan, sheaths completely enclosing stem and much exceeding blades, blades oblong, mostly  $7\text{--}15 \times 5\text{--}7$  (–10) mm, obtuse or acute with tips often hooked; margins thickened especially abaxially, thickenings often crenate to slightly crisped. *Rhipidia* 2-flowered; inner spathe mostly 45–55 mm long, outer 35–38 mm long, sheathing in lower  $2/3$ , arching outward distally. *Flowers* on pedicels 15–23 mm long, lasting two days, pale to watery yellow with darker yellow to brown or orange margins, nectaries small, at base of tepals, claws forming a narrow cup,  $\pm 12$  mm deep,  $\pm 7$  mm wide at rim, faintly sweet-scented; outer tepals  $32\text{--}40 \times \pm 9$  mm, attenuate, tips slightly coiled, claws slender, 10–13 mm long, inner tepals 30–37 mm long. *Stamens* with filaments united in a column  $\pm 10$  mm long, free in upper  $\pm 1$  mm; anther thecae divergent, initially  $\pm 2.5$  mm long,  $\pm 1.5$  mm long after dehiscence; pollen orange. *Ovary* fusiform, (15–)18–25 mm long, with a beak 8–12 mm long; style branches  $\pm 1.5$  mm long, dividing into diverging, prominently fringed arms,  $\pm 1.5$  mm long; stigmas on small lobes below tips of style arms and arching over anthers.

*Capsules* ovoid, 15–25 mm long. *Seeds* angular, irregularly 5- or 6-sided,  $\pm 3$  mm diam., brown, shiny. *Flowering time*: Aug.–Sept.

*Distribution and biology*: with a recorded range covering a linear distance of about 40 km (Figure 17), *Ferraria brevifolia* has one of the narrowest distributions of any member of the genus. Records are mostly from the immediate vicinity of Nuwerus, but plants have also been collected near Bitterfontein to the north—its most northern station is just 10 km north of the town. Plants occur on shrub-covered slopes of gritty, granite-derived ground. The flowers last two days and secrete small quantities of nectar of the low concentration,  $\pm 6.4\%$  sucrose equivalents, typical of the *F. uncinata* alliance. There are no reports of pollination in the species.

*Diagnosis and relationships*: distinctive in *Ferraria*, the leaves of *F. brevifolia* form a tight, 2-ranked fan and have elongate sheaths 40–80 mm long, much exceeding the short, ovate, obtuse blades, 7–15 mm long. The blades, usually less than half as long as the sheaths, have relatively thick margins and oblique, acute or apiculate, hooked tips. The pale yellow flowers, in contrast, are virtually identical to those of *F. macrochlamys* and have

a narrow floral cup,  $\pm 12$  mm deep, and tepal limbs, 22–28 mm long, with crisped, light brown or rarely reddish brown margins. The flowers produce a faint, slightly sweet scent. They can be distinguished from those of its apparent nearest relative, *F. macrochlamys*, if at all, by their somewhat longer outer tepals with long, tapering loosely coiled tips. Although only formally described in 1954, an early collection of the species, and possibly the first, *Schlechter 11031*, made in 1897, bears the annotation '*F. namaquensis* Schltr.' in Schlechter's hand.

#### Representative specimens

WESTERN CAPE.—3018 (Kamiesberg):  $\pm 10$  km N of Bitterfontein, granite bank, (–CC), 2 Sept. 2000, *Goldblatt & Nänni 11450* (MO); hills at Bitterfontein, 1200 ft [365 m], (–CC), 2 Sept. 1897, *Schlechter 11031* (BOL, K, MO, PRE, S; B, BM, BR, Z, not seen). 3118 (Vanhynsdorp): Nuwerus, stony veld, (–AB), 7 Sept. 1945, *Barker 3734* (NBG), 6 Aug. 1972 (flowered at Vredendal), *Hall 4114* (NBG, PRE); 2 miles [3 km] south of Nuwerus, (–AB), 6 Sept. 1974, *De Vos 2326* (PRE).

#### EXCLUDED SPECIES

*Ferraria fimbriata* Burm. in *Nova acta physico-medico Academiae Caesareae Leopoldino-Carolinae germanicae naturae curiosorum* 2: 201 (1761). Type: South Africa, without precise locality, illustration in Burman, loc. cit.: t. 3, fig. 2 (1761).

The woodcut illustration is inadequate to determine this plant to species (see History). Our best guess is that this may represent *Ferraria divaricata* or alternatively *F. variabilis*.

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#### REFERENCES

ANDREWS, H. 1803. *Ferraria viridiflora*. *The botanist's repository* 4: t. 285. London.  
 BAKER, J.G. 1876. New Gladiolae. *Journal of Botany*, new ser. 5: 333–339.  
 BAKER, J.G. 1878. On the Liliaceae, Iridaceae, Hypoxidaceae, and Haemodorumaceae of Welwitsch's Angolan herbarium. *Transactions of the Linnean Society, London, Botany*, ser. 2, 1: 245–273.  
 BAKER, J.G. 1877 [as 1878]. Systema Iridearum. *Journal of the Linnean Society, Botany* 16: 61–180.  
 BAKER, J.G. 1892. *Handbook of the Iridae*. Bell, London.  
 BAKER, J.G. 1896. Iridaceae. In W.T. Thiselton-Dyer, *Flora capensis* 6: 7–71. Reeve, Ashford.

BAKER, J.G. 1898. Iridaceae. In W.T. Thiselton-Dyer, *Flora of tropical Africa* 7: 337–376. Reeve, London.  
 BAKER, J.G. 1901. Iridaceae. In H. Schinz, Beiträge zur Kenntniss der Afrikanischen Flora (Neue Folge). *Bulletin de l'Herbier Boissier*, sér. 2, 1: 853–868.  
 BARNES, P.E. 1930. Plants—new and noteworthy. *South African Gardening and Country Life* 20: 313, 314.  
 BOLUS, L. 1931. Novitates africanae. New Iridaceae. *Journal of Botany (London)* 69: 258–262.  
 BOLUS, L. 1932a. Plants—new and noteworthy. *South African Gardening and Country Life* 22: 57.  
 BOLUS, L. 1932b. Plants—new and noteworthy. *South African Gardening and Country Life* 22: 275–277.  
 BURMAN, J. 1761. Ferrariae character. *Nova acta physico-medico Academiae Caesareae Leopoldino-Carolinae germanicae naturae curiosorum* 2: 198–202.  
 CARTER, S. 1963. Synonymy in the Iridaceae. *Kew Bulletin* 17: 317.  
 COETZEE, J. 1993. African flora since the terminal Jurassic. In P. Goldblatt, *Biological relationships between Africa and South America*: 37–61. Yale University Press, New Haven.  
 DE VOS, M.P. 1977. Knolontwikkeling by sommige genera van die Iridaceae en die systematiese posisie. *Tydskrif vir Natuurwetenskap* 17: 9–19.  
 DE VOS, M.P. 1979. The African genus *Ferraria*. *Journal of South African Botany* 45: 295–375.  
 DIETRICH, A.G. 1832. *Species plantarum*, edn. 6, 2. Nauck, Berlin.  
 DINTER, K. 1920. Plantae novae Schäferianae. *Repertorium Novarum Species Regni Vegetabilium* 16: 335–344.  
 ECKLON, C.F. 1827. *Topographisches Verzeichniss der Pflanzensammlung von C.F. Ecklon*. Esslingen.  
 FAEGRI, K. & VAN DER PIJL, L. 1979. *The principles of pollination ecology*, edn 3. Pergamon Press, New York.  
 FERRARI, G.B. 1633. *Flora seu de floribus cultura*. Rome [1746 Amsterdam].  
 FOSTER, R.C. 1936. Notes on nomenclature in Iridaceae. *Contributions from the Gray Herbarium of Harvard University* 114: 37–50.  
 GEERINCK, D. 2005. Iridaceae. *Flore d'Afrique Centrale*. Jardin Botanique National de Belgique, Meise.  
 GESS, F.W. 1997. Contributions to a knowledge of *Ceramius* Latreille, *Celonites* Latreille, *Jugurtia* Saussure and *Masarina* Richards in South Africa (Hymenoptera: Vespidae: Masarinae). *Journal of Hymenopteran Research* 6: 36–74.  
 GOLDBLATT, P. 1971. Cytological and morphological studies in the southern African Iridaceae. *Journal of South African Botany* 37: 317–460.  
 GOLDBLATT, P. 1972. A revision of the genera *Lapeirousia* Pourret and *Anomatheca* Ker in the winter rainfall region of South Africa. *Contributions from the Bolus Herbarium* 4: 1–111.  
 GOLDBLATT, P. 1976. Evolution, cytology and subgeneric classification in *Moraea* (Iridaceae). *Annals of the Missouri Botanical Garden* 63: 1–23.  
 GOLDBLATT, P. 1986. The moraeas of southern Africa. *Annals of Kirstenbosch Botanical Gardens* 14: 1–224.  
 GOLDBLATT, P. 1990. Phylogeny and classification of Iridaceae. *Annals of the Missouri Botanical Garden* 77: 607–627.  
 GOLDBLATT, P. 1993. Iridaceae. *Flora zambesiaca* 12.4. Flora Zambesiaca Managing Committee, London.  
 GOLDBLATT, P. 1996. *Gladiolus in tropical Africa*. Timber Press, Portland, OR.  
 GOLDBLATT, P. 1998. Reduction of *Barnardiella*, *Galaxia*, *Gynandriris*, *Hexaglottis*, *Homeria* and *Roggeveldia* in *Moraea* (Iridaceae: Irideae). *Novon* 8: 371–377.  
 GOLDBLATT, P. & BERNHARDT, P. 1999. Pollination mechanics of *Moraea* species (Iridaceae) with a staminal column. *Annals of the Missouri Botanical Garden* 86: 47–56.  
 GOLDBLATT, P., BERNHARDT, P. & MANNING, J.C. 2009. Adaptive radiation of the putrid perianth; fly, wasp and bee pollination in the African genus *Ferraria* (Iridaceae). *Plant Systematics and Evolution* 278: 53–65.  
 GOLDBLATT, P., DAVIES, T.J., MANNING, J.C., POWELL, M.P., VAN DER BANK, M. & SAVOLAINEN, V. 2008. Iridaceae 'Out of Australasia'? Phylogeny, biogeography, and divergence time based on plastid DNA sequences. *Systematic Botany* 33: 495–508.  
 GOLDBLATT, P., DAVIES, T.J., MANNING, J.C., VAN DER BANK, M. & SAVOLAINEN, V. 2006. Phylogeny of Iridaceae subfamily Crocoideae based on combined multigene plastid DNA analysis. In J.T. Columbus, E.A. Friar, J.M. Porter, L.M. Prince & M.G. Simpson, *Monocots: comparative biology and evolu-*

- tion, vol. 1: 399–411. Rancho Santa Ana Botanical Garden, Claremont, California.
- GOLDBLATT, P. & MANNING, J.C. 2002. Rediscovered after 200 years, *Moraea ovata* Thunberg is a rare *Ferraria* (Iridaceae: Iridoideae) from Namaqualand, South Africa. *Novon* 12,4: 460–464.
- GOLDBLATT, P. & MANNING, J.C. 2004. New species of *Ixia* (Crocoideae) and *Moraea* (Iridoideae), and taxonomic notes on some other African Iridaceae. *Novon* 14: 288–298.
- GOLDBLATT, P. & MANNING, J.C. 2005. Taxonomic notes on *Babiana* and *Ferraria* (Iridaceae) in arid western southern Africa. *Bothalia* 35: 71–74.
- GOLDBLATT, P. & MANNING, J.C. 2006. Radiation of pollination systems in the Iridaceae of sub-Saharan Africa. *Annals of Botany (London)* 97: 317–344.
- GOLDBLATT, P., MANNING, J.C. & BERNHARDT, P. 1998. Adaptive radiation of bee-pollinated *Gladiolus* species (Iridaceae) in southern Africa. *Annals of the Missouri Botanical Garden* 85: 492–517.
- GOLDBLATT, P., MANNING, J.C. & BERNHARDT, P. 1999. Evidence of bird pollination in Iridaceae of southern Africa. *Adansonia*, sér. 3, 21: 25–40.
- GOLDBLATT, P., MANNING, J.C. & BERNHARDT, P. 2001. Radiation of pollination systems in *Gladiolus* (Iridaceae: Crocoideae) in southern Africa. *Annals of the Missouri Botanical Garden* 88: 713–734.
- GOLDBLATT, P., SAVOLAINEN, V., PORTEOUS, O., SOSTARIC, I., POWELL, M.P., REEVES, G., MANNING, J.C., BARRACLOUGH, T.G. & CHASE, M.W. 2002. Radiation in the Cape flora and the phylogeny of peacock irises *Moraea* (Iridaceae) based on four plastid DNA regions. *Molecular Phylogenetics and Evolution* 25: 341–360.
- GOLDBLATT, P. & TAKEI, M. 1997. Chromosome cytology of Iridaceae, base numbers, patterns of variation and modes of karyotype change. *Annals of the Missouri Botanical Garden* 84: 285–304.
- GUNN, M. & CODD, L.E. 1981. *Botanical exploration of southern Africa*. Balkema, Cape Town.
- JACQUIN, N.J. VON. 1770. *Hortus botanicus vindobonensis*. Kalwoda, Vienna.
- JACQUIN, N.J. VON. 1790. *Collectanea botanica* 4. Wappler, Vienna.
- JACQUIN, N.J. VON. 1804. *Plantarum rariorum horti caesarei schoenbrunnensis* 4. Wappler, Vienna.
- JUSSIEU, A.L. 1789. *Genera plantarum*. Herissant, Paris.
- KER GAWLER, J. 1804. *Ferraria antherosa*. Green variegated ferraria. *Curtis's Botanical Magazine* 19: t. 751.
- KER GAWLER, J. 1827. *Genera iridearum*. De Mat, Brussels.
- LEWIS, J.G. 1954. Iridaceae—new species and miscellaneous notes. *Annals of the South African Museum* 40: 115–135.
- LINNAEUS, C. 1759. *Flora capensis*. Edman, Uppsala.
- LINNAEUS, C. 1763. *Species plantarum*, edn 2. Salvius, Stockholm.
- LODDIGES, C. 1828. *Ferraria atrata*. *The botanical cabinet* 14: t. 1356.
- MANNING, J.C. & GOLDBLATT, P. 1996. *West Coast*. South African Wild Flower Guide 7. Botanical Society of South Africa, Cape Town.
- MANNING, J.C., GOLDBLATT, P. & SNIJMAN, D. 2002. *The color encyclopedia of Cape bulbs*. Timber Press, Portland, OR.
- MANNHEIMER, C., MARAIS, A. & SCHUBERT, S. 2008. *Toxic plants of veterinary importance in Namibia*. Ministry of Agriculture, Water and Forestry, Windhoek.
- MATHEW, B. 1980. *The iris*. Batsford, London.
- MILLER, P. 1759a. *Figures of plants*, vol. 2. Miller, London.
- MILLER, P. 1759b. *The gardeners dictionary*, edn 7. Miller, London.
- MILLER, P. 1768. *The gardeners dictionary*, edn 8. Miller, London.
- MOLSEED, E. 1970. The genus *Tigridia* (Iridaceae) of Mexico and Central America. *University of California Publications in Botany* 54: 1–128.
- MOORE, H.E. 1974. *Ferraria crispa* (Iridaceae). *Baileya* 19: 110.
- MORISON, R. 1680. *Plantarum historiae universalis*. Oxford.
- NELSON, C.E. 2006. 'Forsyth (fl. 1835)' a phantom botanical collector at the Cape of Good Hope explained. *Bothalia* 36: 167, 168.
- RAND, R.F. 1898. Wayfaring notes in Rhodesia. *Journal of Botany (London)* 36: 141–145.
- RAVEN, P.H. & AXELROD, D. 1974. Angiosperm biogeography and past continental movements. *Annals of the Missouri Botanical Garden* 61: 539–673.
- REDOUTÉ, J.P. 1802. *Ferraria crispa*. *Les Liliacées* 1: t. 6. Paris.
- REEVES, G., CHASE, M.W., GOLDBLATT, P., RUDALL, P.J., FAY, M.F., COX, A.V., LEJEUNE, B. & SOUZA-CHIES, T. 2001. Molecular systematics of Iridaceae: evidence from four plastid DNA regions. *American Journal of Botany* 88: 2074–2087.
- RENDLE, A.B. 1899. Monocotyledons. In W.P. Hiern, *Catalogue of the African plants collected by Dr. Friedrich in 1853–61*, vol. 2. Trustees of the British Museum, London.
- RENDLE, A.B. 1905. Apetalae and monocotyledons. In A.B. Rendle, Mr. Eyles's Rhodesian plants: 52–54. *Journal of Botany (London)* 43: 44–54.
- RODIN, R.J. 1985. The ethnobotany of the Kwanyama Ovambo. *Mono-graphs in Systematic Botany from the Missouri Botanical Garden* 9.
- RUDBECK, O. 1701. *Reliquiae rudbeckianae*. Smith, London.
- SALISBURY, R.A. 1796. *Prodromus stirpium in horto ad Chapel Allerton vigentium*. London.
- SCHINZ, H. 1900. Iridaceae. In C. de Candolle, E. Koehne & H. Schinz, *Diagnoses plantarum Africanum novarum. Mémoires de l'Herbier Boissier* 10: 77.
- SCOTT ELLIOT, G. 1891. Notes on the fertilisation of South African and Madagascan flowering plants. *Annals of Botany* 5: 333–405.
- STRID, A. 1974. A taxonomic revision of *Bobartia* L. (Iridaceae). *Opera Botanica* 37: 1–45.
- SWEET, R. 1826a. *Ferraria uncinata*. *The British flower garden*: t. 161.
- SWEET, R. 1826b. *Ferraria obtusifolia*. *The British flower garden*: t. 148.
- SWEET, R. 1827. *Ferraria divaricata*. *The British flower garden*: t. 192.
- THUNBERG, C.P. 1787. *Dissertation de Moraea*. Uppsala.
- THUNBERG, C.P. 1800. *Prodromus plantarum capensium*. Edman, Uppsala.
- TILLIE, N., CHASE, M.W. & HALL, T. 2001. Molecular studies in the genus *Iris* L.: a preliminary study. *Annali di Botanica (Roma)*, nov. ser. 1, 2: 105–122.
- VOGEL, S. 1954. Blütenbiologische Typen als Elemente der Sippen-gliederung. *Botanische Studien* 1: 1–338.
- WILLDENOW, C.L. 1800. *Species plantarum*, edn 4, 3. Berlin.