AMARYLLIDACAE: AMARYLLIDEAE

A NEW SPECIES OF AMARYLLIS FROM THE RICHTERSVELD, SOUTH AFRICA

INTRODUCTION

With a taxonomic history of just over 350 years, the monotypic genus Amaryllis L. is considered to be one of South Africa's most important and widely grown ornamental taxa (Ferrari 1633; Dyer 1955). Amaryllis belladonna L. is currently cultivated in many countries throughout the world. In the wild, however, the species is well documented as endemic to the Cape Floristic Region, where it is restricted to the Western Cape (Bond & Goldblatt 1984). The recent discovery of a large population of Amaryllis plants in the Richtersveld, a particularly arid region of the Succulent Karoo Biome in the remote northwestern Cape, consequently engendered a great deal of surprise and focused attention on the need for a taxonomic reassessment of the genus.

Leafing bulbs of the Richtersveld population were first collected at Paradyskloof by Prof. N. du Plessis and Prof. G. Delpierre in 1978, by Mr E.J. van Jaarsveld in 1993, and by the first author in 1996. The cultivated collections maintained in the Kirstenbosch National Botanic Garden nursery, however, have thus far failed to flower. Flowers were first recorded in the wild by Mr J. Domroch, a Richtersveld Park ranger, who presented the second author with a single pressed flower in April 1996. This collection was added to one year later when the second author, while completing a floristic survey of the Richtersveld National Park, found the population at Paradyskloof flowering en masse. From the beautiful pink flowers the plants were tentatively identified as an Amaryllis, and this was later confirmed by the appearance of the fruits. A systematic study of the population

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thereafter revealed several morphological features that separate the geographically disjunt Richtersveld plants from *A. belladonna*. The plants are thus newly described as *A. paradisicola*, an epithet which commemorates the species' place of origin.

The discovery of this new species marks the first record of a wild *Amaryllis* outside the Cape Floristic Region and adds an extra, exceptionally ornamental representative to the 363 taxa already known as unique to the Gariep Centre of endemism (Nordenstam 1969; Hilton-Taylor 1996).

Amaryllis paradisicola Snijman, sp. nov., A. belladonnae L. affinis sed foliis latioribus, $70-130 \times 350-500$ mm; pilis brevibus patentibus in superficiebus ambabus foliorum saltem ubi juvenibus; floribus roseis concoloris; staminibus interioribus manifeste longioribus quam exterioribus; stigmate profunde trifido ramis gracilibus patentibus maturitate usque ad 1.5-2.5 mm longis. Figurae 11 & 12.

TYPE.—Northern Cape, 2817 (Vioolsdrif): Richtersveld National Park, Paradyskloof, on rocky slopes, (-AC), 11-4-1997, *Snijman 1576* (NBG, holo.; K, KMG, PRE).

Deciduous bulbous herbs, up to 800 mm tall when flowering and fruiting. *Bulbs* solitary or sometimes clustered, large, ovoidal, $\pm 100 \times 140$ mm, without a narrow 193

neck, sometimes more than half exposed above ground; tunics numerous, cream-coloured, papery, producing extensible threads when torn. Leaves 6-9, hysteranthous, distichous, suberect when emerging, spreading and apparently rosulate when mature; blade ligulate when young to lingulate when mature, up to $70-130 \times$ 350-500 mm, somewhat channelled, more or less thintextured, bright green, covered with short patent hairs on both surfaces at least while developing, producing copious brown sap when cut and numerous extensible threads when torn; abaxial surface with a prominent midrib; margins sometimes slightly thickened, reddened and undulate, at least when young. Inflorescence upright; scape solid, stout, succulent, 20-40 × 480-800 mm, somewhat compressed, slightly ancipitous, glaucous-green, reddish brown proximally, smooth, withering after seed dispersal; spathe valves 2, papery and reflexed at anthesis, $20-25 \times 50-55$ mm; bracteoles numerous, flattened, up to 2 × 50 mm. Flowers 10-21, trumpet-shaped, with funnel 30-40 mm long, 15-20 mm wide at throat, 70-80 mm wide at rim, in an evenly spreading, umbel-like cluster, uniformly pink, without contrasting colours in veins or throat, turning darker pink with age, scented; pedicels evenly spreading, firm, $3-5 \times 30-70$ mm at anthesis, elongating to 250 mm in fruit, mostly subterete but slightly triangular in cross section below developing fruit. Tepals free, broadly lanceolate, $12-20 \times 65-80$ mm, slightly recurved apically. Stamens declinate, shorter than tepals, biseriate; filaments stout, pale pink, basally fused and adnate to perigone for \pm 7 mm; outer whorl

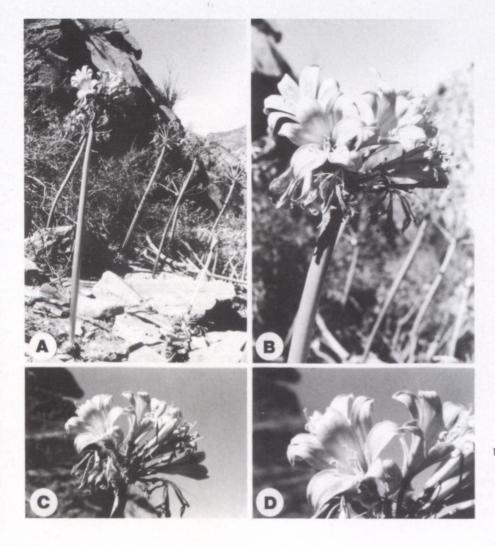


FIGURE 11.—Amaryllis paradisicola: A, flowering plants in habitat; B, C, scape and flower head; D, flower head showing lateral view of exserted trifid stigma.



FIGURE 12.—Amaryllis paradisicola: A, mature fruiting head; B, bulb in habitat during fruiting showing scape, young leaves and basal bulblet; C, plants in habitat showing mature hysteranthous leaves.

 \pm 35 mm long; inner whorl \pm 50 mm long, basally adnate to perigone for up to \pm 5 mm beyond tube; anthers versatile, dorsifixed, curved, 7–9 mm long, yellow; pollen yellow. *Ovary* green, trilocular, 5 mm across; ovules 4–6 per locule, axile; style declinate, \pm 65 mm long, longer than stamens, shorter than tepals, pale pink; stigma trifid with spreading, slender branches up to 1.5–2.5 mm long. *Capsule* loculicidal, subglobose, 20–30 mm across, leathery. *Seeds* fleshy, more or less ovoid, 12–17 mm across, glossy, whitish to pink; embryo green.

Flowering, fruiting and vegetative phenology

The bulbs bloom in early April and the flowering period of the population lasts approximately ten days. When *A. paradisicola* was collected in 1997, several hundred bulbs had flowered after rain fell in March that year but only two bulbs flowered at the same site during a prolonged dry autumn the following year. Flowering is thus profuse after good autumn rain but poor when precipitation in autumn is low. Despite the profusion of flowers in 1997, only a small number set seed and many infructescences had been damaged, possibly by baboons. The seeds take approximately one month to be released and germinate after another three to four weeks. Although the young leaves sometimes emerge at flowering time, the foliage is mostly absent until the start of the winter rainfall season. The leaves grow rapidly in May and persist until they dry off with the onset of the summer drought, usually at the end of September.

Diagnostic features

Amaryllis paradisicola differs from A. belladonna in having broad, tongue-shaped leaves, 70-130 × 350-500 mm, covered with short, patent hairs on both surfaces, at least during their development. Although the hairs become increasingly sparsely spaced as the leaf blades enlarge, they remain evident under a hand lens in most plants and are only rarely absent at maturity. Studies in the field and of the herbarium material at NBG and BOL indicated that populations of A. belladonna in the southern Cape, the Agulhas Plain and the Cape Peninsula have widely spreading, narrow leaves, $13-26 \times 270-680$ mm. whereas the western populations from Saldanha and the Cederberg have somewhat upright, slightly broader leaves, 36-73 × 300-675 mm, that arise from an elongated basal sheath, 110-300 mm long. The leaves of A. belladonna are therefore perceptibly longer and narrower than those of A. paradisicola while the leaf surfaces are consistently glabrous, even when young.

Leaf surface pubescence in the form of soft hairs is rare in the family. Softly pubescent leaves is a derived character state in Amaryllideae and is so far known only in *Hessea* Herb. and *Strumaria* Jacq. (subtribe Amaryl-

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lidinae) but must now be considered for Amaryllis, the basal genus in subtribe Amaryllidinae (Snijman & Linder 1996). Similar leaf surface pubescence also occurs sporadically in *Haemanthus* L. and *Gethyllis* L. (tribe Haemantheae sensu Dahlgren et al. 1985) and Pancratium L. (tribe Pancratieae).

Amaryllis paradisicola is furthermore distinguished by several floral characters, of which flower colour and stigma shape are most diagnostic. The 10-21-flowered A. paradisicola is slightly more floriferous than A. belladonna, which has 6-12 or occasionally 21 flowers per inflorescence; and the tepals, although darkening with age, are uniformly pink, without the cream to lemon-yellow perigone throat of A. belladonna. The inner stamens relative to the outer stamens vary from 10 mm longer to almost equally long in A. belladonna, whereas the inner stamens of the new species exceed the outer stamens by 15 mm or more. Lastly, the mature stigma of A. paradisicola is distinctly trifid with slender, spreading branches that reach up to 1.5-2.5 mm long when mature, unlike the broader (up to 2 mm across), minutely trifid stigma of A. belladonna. Although not as strongly scented, the flowers of both species smell somewhat like those of Narcissus.

Distribution, habitat and phytogeography

Amaryllis paradisicola is endemic to the Richtersveld National Park, an arid, mountainous region in the Northern Cape. Here the species is known from a single large population in Paradyskloof, a narrow gorge overlooking a perennial pool along a tributary of the Abiekwa River between Hottentotsparadys and Paradysberg. The bulbs grow on south and east-facing, quartzitic cliffs, on narrow rock ledges and partially vegetated screes that are shaded for much of the day. If the locality is not patrolled, the population may be endangered by unscrupulous bulb collectors and by the large numbers of goats that gather to drink in Paradyskloof.

The discovery of *A. paradisicola* extends the distribution of the genus *Amaryllis* approximately 450 km beyond the Olifants River Valley mountains in the Western Cape, where the most northerly populations of *A. belladonna* are thus far known (Figure 13).

Other endemics of the Gariep Centre that occur at Paradyskloof include three geophytes: Cyrtanthus herrei (Leighton) R.A.Dyer, Bulbine pendens G.Will. & Baijnath, and an as yet unnamed Spiloxene species; also the Paradise Toad, Bufo robinsonii Branch & Braack (1995).

The highly disjunct distribution pattern in Amaryllis is repeated in several other geophytic genera. Cyrtanthus herrei is confined to the Gariep Centre whereas C. carneus (Reid & Dyer 1984) is found only in the southwestern Cape; furthermore Moraea garipensis and M. namaquamontana are narrowly restricted in the Gariep Centre and M. ramosissima occurs only in the Cape (Goldblatt 1986). Since the species in all three genera are putative sister taxa, they probably represent vicariants of previously widespread ancestral taxa. Methods are not yet available to determine the age of these species. Speciation may date from the advent of

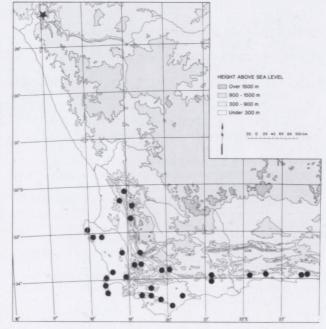


FIGURE 13.—Known distributions of *Amaryllis paradisicola*, ★; and *A. belladonna*, ●, based on collections at BOL, PRE and NBG.

summer aridity and winter rainfall conditions in the Pliocene (Tankard & Rogers 1978) or from the great climatic fluctuations of the Pleistocene (Deacon 1983; Tyson 1986). In particular, preliminary palynological data from spring deposits at Eksteenfontein in the Richtersveld showed a marked change from predominantly Chenopodiaceae-Amaranthaceae and different Asteraceae pollen in the Late Pleistocene (before 10 700 BP) to assemblages totally dominated by pollen of the succulent Aizoaceae-Mesembryanthemaceae type in the early Holocene, 10 700-8 450 years BP (Scott et al. 1995). A tentative interpretation of this data is that it reflects change from cooler to warmer conditions (Scott et al. 1997). If this is correct, the mountains from the Richtersveld to the Cape may have provided suitable habitats for a widespread ancestral taxon in Amaryllis at least during the Late Pleistocene. However, when the available moisture reached its present level in the early Holocene, populations in the Cape Region were probably ecologically isolated from those in the Gariep Centre and thus diverged. We hypothesise that A. belladonna radiated widely in the southwestern Cape, where it became adapted to frequent disturbance by fire, whereas A. paradisicola became narrowly restricted to relatively cool, moist montane habitats in the otherwise arid Richtersveld, where it evolved xerophilous, pubescent leaves.

NORTHERN CAPE.—2817 (Vioolsdrif): Richtersveld National Park, Paradyskloof, (-AC), Snijman 1550 (NBG), Snijman 1576 (K, KMG, NBG, PRE), Snijman 1578 (K, KMG, NBG, PRE), Williamson 5904 (NBG).

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REFERENCES

- BOND, P. & GOLDBLATT, P. 1984. Plants of the Cape Flora. Journal of South African Botany Suppl. Vol. 13: 1-455.
- BRANCH, W.R. & BRAACK, H.H. 1995. A new toad from paradise. Madoqua 19: 15-23.
- DAHLGREN, R.M.T., CLIFFORD, H.T. & YEO, P.F. 1985. The families of the monocotyledons. Springer-Verlag, Berlin.
- DEACON, H.J. 1983. Another look at the Pleistocene climates of South Africa. South African Journal of Science 79: 325–328.
- DYER, R.A. 1955. Amaryllis belladonna. The Flowering Plants of Africa 30: t. 1200.
- FERRARI, G. 1633. De florum cultura libri IV: t. 121, Rome.
- GOLDBLATT, P. 1986. The moraeas of southern Africa. Annals of Kirstenbosch Botanic Garden 14: 1-224.
- HILTON-TAYLOR, C. 1996. Patterns and characteristics of the flora of the Succulent Karoo Biome, southern Africa. In L.J.G. van der Maesen, X.M. van der Burgt & J.M. van Medenbach de Rooy, The biodiversity of African plants. Proceedings XIVth AETFAT Congress, August 1994, Wageningen, Netherlands: 58-72. Kluwer Academic Publishers, Dordrecht.
- NORDENSTAM, B. 1969. Phytogeography of the genus Euryops (Compositae). A contribution to the phytogeography of southern Africa. Opera Botanica 23: 1–77.
- REID, C. & DYER, R.A. 1984. A review of the southern African species of Cyrtanthus. American Plant Life Society, La Jolla, California.

- SCOTT, L., ANDERSON, H.M. & ANDERSON, J.M. 1997. Vegetation history. In R.M. Cowling, D.M. Richardson & S.M. Pierce, Vegetation of southern Africa: 62–84. Cambridge University Press, Cambridge.
- SCOTT, L., STEENKAMP, M. & BEAUMONT, P.B. 1995. Palaeoenvironments in South Africa at the Pleistocene-Holocene transition. *Quaternary Science Reviews* 14: 937–947.
- SNIJMAN, D.A. & LINDER, H.P. 1996. Phylogenetic relationships, seeds characters, and dispersal system evolution in Amaryllideae (Amaryllidaceae). Annals of the Missouri Botanical Garden 83: 362-386.
- TANKARD, A.J. & ROGERS, J. 1978. Late Cenozoic palaeo-environments on the west coast of southern Africa. *Journal of Bio*geography 5: 319–337.
- TYSON, P.D. 1986. Climatic change and variability in southern Africa. Oxford University Press, Cape Town.

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