

DIDIEREACEAE/PORTULACACEAE

CERARIA KAOKOENSIS, A NEW SPECIES FROM NAMIBIA, WITH NOTES ON GYNODIOECY IN THE GENUS

INTRODUCTION

Traditionally, Didiereaceae *s.str.* has been treated as a family endemic to Madagascar. Based on morphological similarities, a close affinity between Didiereaceae and the African portulacaceous genera *Ceraria* H.Pearson & Stephens and *Portulacaria* Jacq. has been suggested (Rauh & Schölch 1965). Molecular evidence indicates that *Ceraria* and *Portulacaria*, as well as the African genus *Calyptrotheca* Gilg, are more closely related to Didiereaceae than to other Portulacaceae (Hershkovitz & Zimmer 1997; Applequist & Wallace 2000, 2001). The circumscription of Didiereaceae was therefore enlarged to accommodate these three genera (Applequist & Wallace 2003). Didiereaceae *s.l.* is divided into three subfamilies, of which Portulacarioideae comprises *Ceraria* and *Portulacaria*.

Ceraria is endemic to the arid western parts of southern Africa. The infrageneric classification of the group is not satisfactory and what appear to be still undescribed taxa are encountered in the wild. Herbarium specimens of the group are generally incomplete, fragmentary and not very useful for comparative morphological studies. Depending on the authority, from four (Craven 1999; Germishuizen & Meyer 2003) to six (Rowley 2002) species are recognized at present. Two of the described species, *C. carrissoana* Exell & Mendonça and *C. longipedunculata* Merxm. & Podlech, are restricted to the Kaokoveld Centre of Endemism in northwestern Namibia and southwestern Angola (Van Wyk & Smith 2001), whereas the ranges of the other species are \pm centred on the Gariap Centre of Endemism in southwestern Namibia and northwestern South Africa (Van Wyk & Smith 2001; Curtis & Mannheimer 2005).

In this contribution, a new species of *Ceraria* from the Kaokoveld, Namibia, is described. Gynodioecy—a sexual state in which plants of the same species bear either functionally female or bisexual flowers—is also recorded in the genus for the first time. During a botanical expedition to the Otjhipa Mountains in northwestern Namibia, the author noticed a *Ceraria* that superficially resembles *C. fruticulosa* H.Pearson & Stephens from southern Namibia and the Northern Cape Province of South Africa. This taxon was subsequently found in several other localities in the northern Kaokoveld. It has apparently not been collected before, as no herbarium specimens of it could be found in either NBG, PRE, SAM or WIND.

Live material from the various known populations of the new species was studied in the field and from plants in cultivation. Morphological characters were all determined from mature leaves, fresh flowering material and from ripe fruit. Diagnostic features for all the above-mentioned species and *C. fruticulosa* were determined through examination of herbarium specimens and live plants in the Kaokoveld and southern Namibia (Rosh Pinah area), respectively. Additional information was found in Pearson & Stephens (1912), Exell & Mendonça (1938–1939), Merxmüller & Podlech (1961) and Podlech (1967).

***Ceraria kaokoensis* Swanepoel, sp. nov., *C. fruticulosam* H.Pearson & Stephens tangit ob arborem fruticosam et corticem brunneolam heterochromam, foliorum aliorum laminam oblanceolatam, flores singulares vel fasciculatos, roseos. Differt cortice fissurata longitudinaliter ramis ramulisque, alba incremento recente et viridi flavo-virenteve novo incremento, prunia carente; novo incremento oblecto pilis brevibus, conicis, papilliformibus; foliis petiolatis vel subsessilibus; lamina saepe lineari-oblanceolata vel lineari, angustata, 3–4 plo longiore quam latiore, tenuiore simili longitudine, bevis, conicis, papilliformibus pilis, viridi, prunia carente; florente profuse, ovario et ovulo parvulis.**

TYPE.—Namibia, 1712 (Posto Velho): Otjhipa Mountains, 4 km ESE of Otjinhungwa, 760 m, (–AD), 17-01-2005. *Swanepoel* 224 (WIND, holo.!, PRE, iso.!).

Gynodioecious, semisucculent, densely branched, shrub-like tree, 0.3–2.0 \times 0.3–2.0 m. *Trunk* branching repeatedly just above ground level into many stems, rarely up to 0.2 m high, up to 0.5 m wide when wedged between rocks. *Bark* smooth, longitudinally fissured, often peeling in small flake-like pieces, dark brown, reddish brown or greyish brown, new growth green to yellowish green, bark on more recent growth creamy white, with short, brittle, conical hairs, becoming glabrous with age. *Branches and branchlets* with small, raised, cushion-like nodes, opposite and decussate at intervals of 2–13 mm; new branchlets often growing from cushions, glabrous; younger growth with short, conical, papilla-like hairs, some hairs bifid at apex; ultimate branchlets 1–2 mm diam.; when dried, irregularly winged or grooved in places when viewed under magnification, younger growth usually \pm square in *t/s*. *Leaves* deciduous, single or clustered, opposite and decussate on new growth, green or yellow-green; lamina fleshy, flat or falcate towards abaxial side, oblanceolate, linear-oblanceolate or linear, (0.8–)3.0–12.0(–14.5) \times (0.4–)1.2–3.0(–3.8) \times (0.3–)0.6–1.1(–1.3) mm, ratio of length versus width 3–4:1, in *t/s* narrowly elliptic, crescent-shaped, reniform or oblong, adaxial side flat, convex or concave, abaxial side convex or flat, apex obtuse, acute or emarginate, often minutely apiculate, base cuneate or cuneate and abruptly rounded onto petiole, with short, conical, papilla-like hairs; margin entire; midrib or veining not visible; petiolate or subsessile, petiole up to 1 mm long, in *t/s* \pm circular, 0.1–0.5 \times 0.1–0.3 mm long, glabrous or with very short, conical, papilla-like hairs. *Inflorescence*: flowers borne on cushion-like nodes in clusters of 2–14 or solitary, usually flowers profusely. *Flowers* bisexual or female, pedicellate, glabrous, appearing before or with leaves; bracts \pm ovate, flat to cucullate, up to 0.6 mm long, glabrous; pedicel very slender, 0.1–0.2 mm diam., green or reddish green, inserted on a short, peduncle-like structure, up to 0.3 mm long, involucreted by bracts; receptacle conical, green or reddish green, fleshy. *Calyx* of 2 sepals, short, broad, membranous, contiguous or distant, bract-like, persistent, hemispherical or triangular, white with pinkish tinge or pink, apical part often drying soon to conspicuous reddish brown colour. *Corolla*:



FIGURE 10.—*Ceraria kaokoensis* in its natural habitat, 1.2 m tall.

petals 5, persistent, oblanceolate, linear-oblanceolate or elliptic, often cucullate, especially towards apex, pinkish white, pink or pinkish red. *Ovary* flask-shaped, in *t/s* slightly flattened, triquetrous or rarely elliptic, pinkish white, pink or cherry red; style none; stigmas 3, yellowish white or white; ovule oblong-ellipsoid, up to 0.3×0.1 mm long. *Bisexual flowers* 1.8–2.8 mm long; pedicel 1.9–3.6 mm long; receptacle $0.3\text{--}0.4 \times 0.5\text{--}0.6$ mm; sepals $\pm 0.4 \times 0.6$ mm; petals $1.9\text{--}2.4 \times 0.4\text{--}0.8$ mm; stamens 5; anthers conspicuously pinkish red, 0.3–0.5 mm long; filaments 1.3–2.3 mm long, subterete, pinkish white or pink; pollen orange-yellow or cherry-red; pistil 0.9–1.5 mm long; ovary $0.9\text{--}1.3 \times 0.3\text{--}0.4 \times 0.2$ mm; stigmas \pm linear, pustulate above, short, up to 0.1 mm long, rarely patulous and triangular. *Female flowers* 1.1–2.0 mm long; pedicel 1.2–2.0 mm long; receptacle 0.3×0.6 mm; sepals $\pm 0.3 \times 0.6$ mm; petals $\pm 1.4 \times 0.5$ mm; stamens 5, rudimentary; anthers not developed; pistil 1.2–1.5 mm long; ovary $1.0\text{--}1.3 \times 0.3\text{--}0.4 \times 0.3$ mm; stigmas linear or triangular, pustulate above, spreading, relatively long when linear, up to 0.4 mm long. *Fruit* asymmetrically elliptic or hemispherical, $3.3\text{--}4.4 \times 1.4\text{--}1.8 \times 0.9\text{--}1.1$ mm, apiculate, almost flat, very narrowly triquetrous in *t/s*, soft, pink, soon drying to brown, pod-like, one-seeded, indehiscent; pedicel extremely thin, brittle; probably wind-dispersed. *Flowering time*: November to March. *Pollination*: various species of flies, blowflies and bees, including mopane bees, were observed visiting the flowers. Figures 10–12.

Diagnostic characters and affinities: *Ceraria kaokoensis* is very attractive when in flower and as such would be a valuable addition to succulent gardens. During the flowering season it is easily recognized, even from a distance, due to the profuse pink flowers. *C. kaokoensis* is probably most closely related to *C. fruticulosa*, from which it differs mainly in bark, leaf and inflorescence characters, as well as geographical distribution. *C. kaokoensis* can also be confused with the sympatric *C. longipedunculata*, a species with which it shares a much-branched habit and narrow, superficially similar leaves. However, the leaf lamina is \pm cylindrical in *C. longipedunculata*, but distinctly flattened in *C. kaokoensis*. Vegetatively *C. longipedunculata* is most similar to *C. namaquensis* (Sond.) H. Pearson & Stephens, a species from southern Namibia and adjacent parts of South

Africa (Namaqualand). Some of the more prominent morphological characters to differentiate between *C. kaokoensis* and *C. fruticulosa* are summarized in Table 2.

Etymology: the specific epithet refers to the Kaokoveld of northwestern Namibia. The distribution of *Ceraria kaokoensis* falls within the previous politically demarcated Kaokoland, now part of the Kunene Region.

Distribution and habitat: *Ceraria kaokoensis* is presently known from a few isolated localities, all within



FIGURE 11.—Bark of *Ceraria kaokoensis*.

the Kaokoveld Centre of Endemism in northwestern Namibia (Figure 13). More specific localities include the Otjihipa and Hartmann Mountains to the east and west of the Marienfluss respectively; the rocky area to the south of the Engo River Valley and the mountainous area to the west and north-northwest of Sesfontein. It is localized and common to rare in these areas. The species almost certainly occurs in the adjacent mountainous parts of southwestern Angola as well, especially the Serra Cafema range, and may prove to be more widespread on the mountains of the Kaokoveld Centre of Endemism, most of which remains botanically poorly explored (Van Wyk & Smith 2001). It is found 40–110 km from the coast at altitudes of 700–1 100 m, where the mean annual rainfall is 50–150 mm (Mendelsohn *et al.* 2002). It appears to be habitat specific as it was only found in rocky places on mountain slopes, plateaus

and on rocky outcrops. It is limited to the granites and gneisses of the Epupa Metamorphic Complex and to mica schist of the Damara Supergroup (Miller & Schalk 1980; Mendelsohn *et al.* 2002). At all the presently known locations, *C. kaokoensis* was found to be sympatric with *C. longipedunculata* and in some instances also with *C. carrissoana*.

Other specimens examined

NAMIBIA.—1712 (Posto Velho): Hartmann Valley Mtns, highest peak (–AC), *Swanepoel* 225 (WIND), 6 km NW of Ombivango, (–AD), *Swanepoel* 226 (WIND), Hartmann Valley, peak of 1 039 m high mountain, (–CA), *Swanepoel* 265 (WIND), 4 km SW of Ombivango (–CB), *Swanepoel* 227 (WIND); 10 km south of Engo River Valley, near Skeleton Coast Park boundary, (–CC), *Swanepoel* 233 (WIND). 1813 (Opuwo): 10 km SE of Ozombari, (–DC), *Swanepoel* 228 (WIND). 1913 (Sesfontein): Ganamub River, 10 km N of junction with Hoanib River, (–AB), *Swanepoel* 260 (WIND), 10 km NNW of Sesfontein, (–BA), *Swanepoel* 229, 231, 232 (WIND).

Key to species

- 1a Leaves relatively large; lamina broad, flattened, elliptic, obovate, broadly oblanceolate or suborbicular, 10–37 × 10–31 mm. Sparsely branched shrubs or small trees. Otjihipa and Baynes Mountains, Kaokoveld, Namibia; also in southwestern Angola. *C. carrissoana*
- 1b Leaves relatively small; lamina narrow to broad, up to 15 × 9 mm, ± circular in *t/s* or flattened. Much-branched shrubs or small trees. Kaokoveld (northwestern Namibia) or Gariiep Centres of Endemism (southern Namibia and adjacent parts of Northern Cape, South Africa):
- 2a Leaf lamina cylindrical (± circular in *t/s*), narrowly cuneate, conspicuously succulent. Inflorescences racemose or subpaniculate; flowers red, pink, pinkish white or white. Shrubs or small trees up to 5 m tall. Bark on stems dark- to pale-coloured: blackish brown, dark brown, reddish brown, cream-coloured or greyish white, smooth but peeling horizontally in tough, papery strips or pieces. Widespread in northern half of Kaokoveld Centre of Endemism, Namibia and in southwestern Angola. *C. longipedunculata*
- 2b Leaf lamina flattened (narrowly elliptic in *t/s*), slightly succulent. Flowers solitary or in clusters, pink. Shrubs or shrub-like trees up to 2 m tall. Bark on stems dark-coloured. Kaokoveld and Gariiep Centres of Endemism:
- 3a Bark on branches/branchlets longitudinally fissured, younger growth with short, conical, papilla-like hairs. Leaves with lamina narrow, ratio of length versus width 3–4:1, linear, linear-oblanceolate or oblanceolate, with short, conical, papilla-like hairs. Flowers produced in profusion, usually borne in dense clusters on cushion-like nodes along stems. Shrub-like trees up to 2 m tall. Locally in northern half of Kaokoveld Centre of Endemism, Namibia; probably also in southwestern Angola. *C. kaokoensis*
- 3b Bark on branches/branchlets smooth, glabrous. Leaves with lamina narrow to broad, ratio of length versus width 1–3:1, oblanceolate, obovate, oblong-obovate or obcordate, glabrous. Flowers few, sparsely scattered along stems. Shrubs up to 1.5 m tall. Mainly Gariiep Centre of Endemism, southern Namibia and Northern Cape (South Africa) *C. fruticulosa*

TAXONOMIC SIGNIFICANCE OF GYNODIOECY IN *CERARIA*

The genus *Ceraria* was described by Pearson & Stephens (1912) and distinguished from *Portulacaria* in being dioecious, whereas the latter is hermaphroditic (flowers bisexual). Subsequently this sexual distinction has been widely employed in identification keys to differentiate between the two genera (Dyer 1975; Carolin 1993; Jordaan 2000; Egli 2002). Dyer (1975), Carolin

(1993), Rowley (2002) and others noted that flowers in *Ceraria* may be rarely bisexual. However, functionally unisexual flowers in *Ceraria* bear rudiments of the reciprocal organs, hence flowers may easily be mistaken for being either structurally or functionally bisexual.

As in other members of the genus, flowers of *Ceraria kaokoensis* appear structurally bisexual, although the stamens are smaller with indehiscent anthers in female flow-

TABLE 2.—Prominent differences between *Ceraria kaokoensis* and *C. fruticulosa*

Character	<i>C. kaokoensis</i>	<i>C. fruticulosa</i>
Bark texture		
on branches/branchlets	longitudinally fissured	smooth
on recent growth	creamy white	different shades of brown
on new growth	green or yellowish green, with short, conical, papilla-like hairs	reddish green or yellowish green with pale bloom, glabrous
on dried branches/branchlets	winged or grooved in places (not prominently)	prominently winged or grooved
Branchlets	in dry material, ± square in <i>t/s</i>	in dry material, not ± square in <i>t/s</i>
Leaves		
attachment	petiolate or sessile	sessile
lamina shape	oblanceolate, linear-oblanceolate or linear; ratio of length versus width 3–4:1	oblanceolate, obovate, oblong-obovate or obcordate; ratio of length versus width 1–3:1
lamina size	0.8–14.5 × 0.4–3.8 × 0.3–1.3 mm	3.1–15.0 × 1.5–9.0 × 0.9–2.8 mm
colour	green or yellowish green	pale green, yellowish green or glaucous
indumentum	short, conical, papilla-like hair	glabrous, often with white bloom
Flowers		
inflorescence	clusters of 2–14; usually flowers profusely	clusters of 2–6; flowers few and scattered
ovary size	± 1.1 × 0.4 × 0.3 mm	± 1.5 × 0.8 × 0.5 mm
ovule size	± 0.3 × 0.1 mm	± 0.6 × 0.4 mm
Distribution	Kaokoveld Centre of Endemism, northwestern Namibia	southern Namibia and Northern Cape Province, South Africa

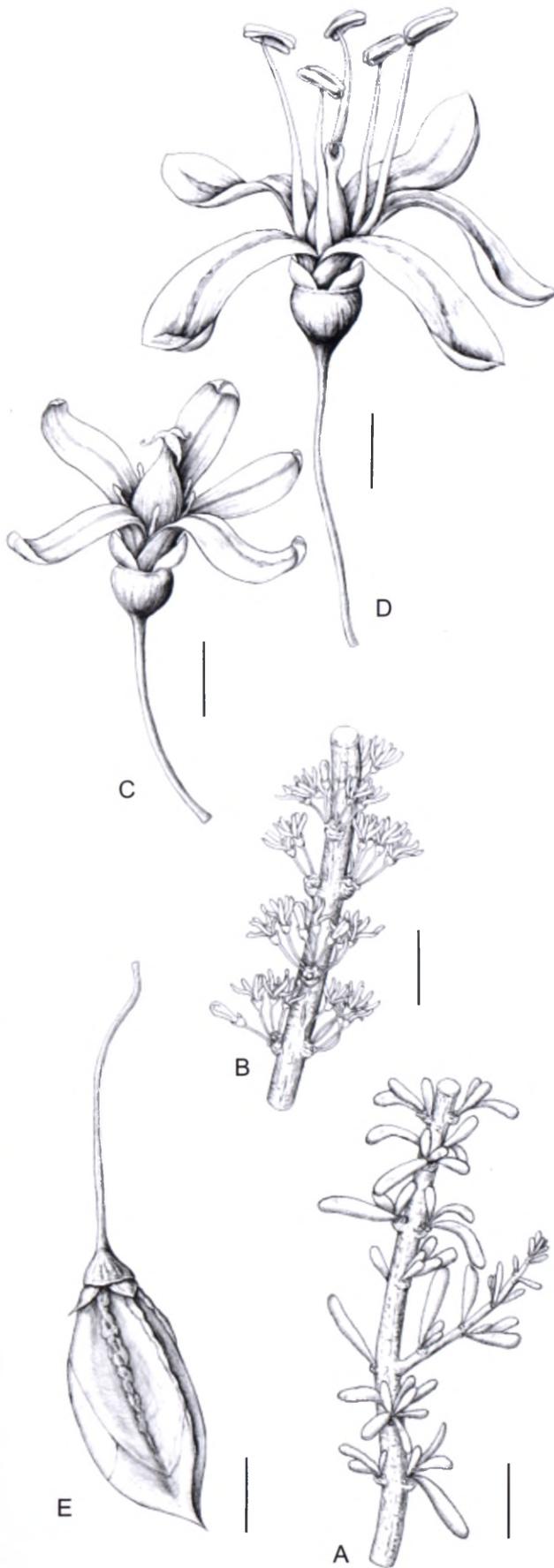


FIGURE 12.—*Ceraria kaokoensis*. A, branch with leaves; B, flowering branch; C, female flower; D, bisexual flower; E, fruit. C & E, Swanepoel 226; D, Swanepoel 227. Scale bars: A, 10 mm; B, 3 mm; C, D, 0.5 mm; E, 1 mm. Artist: Julia Kreiss.

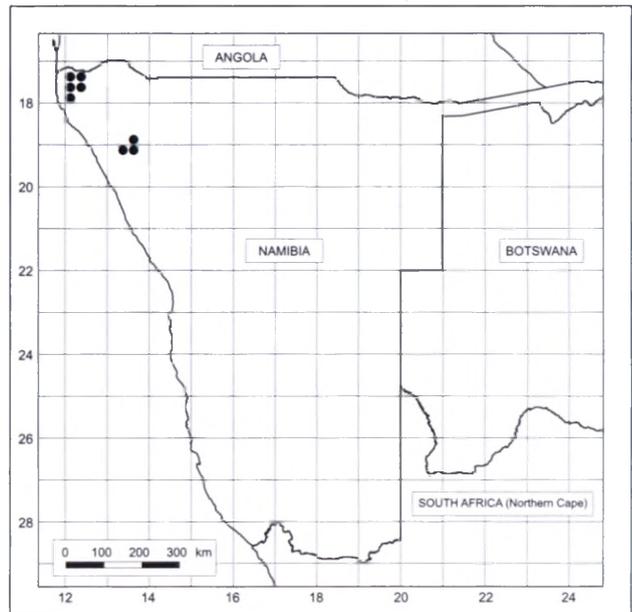


FIGURE 13.—Known distribution of *Ceraria kaokoensis*.

ers and the pistil is smaller in male flowers. However, in *C. kaokoensis* both types of flowers were seen to develop fruit with seed and the species is best described as gynodioecious. Plants of the new species are either functionally female or hermaphroditic and this is supported by observations on plants grown in the author's garden in Windhoek. However, in angiosperms, all forms of dioecy are rarely absolute (Policansky 1982). The possibility that at times some structurally bisexual flowers in *C. kaokoensis* may still be functionally male cannot be excluded.

Following the confirmation of gynodioecy in at least some plants of *Ceraria kaokoensis*, a critical re-assessment of the sexual state in other species traditionally referred to *Ceraria* is required as more members may be predominantly gynodioecious, and not dioecious (or rarely hermaphroditic) as have hitherto been reported. More field work, preferably involving long-term monitoring of specific plants, is required to fully elucidate patterns of sexual expression in the group. Moreover, observations on the sexual state of *Portulacaria armiana* Van Jaarsv. is required to confirm its current generic placement; it may well be better classified as a *Ceraria* (E.J. van Jaarsveld pers. comm.).

The presence of gynodioecy in at least one member of *Ceraria* is of considerable phylogenetic significance. Current knowledge would indicate that all other *Portulacaceae* are hermaphroditic, with the exception of *Talinella* Baill., a Madagascan genus (12 species) of \pm woody shrubs with lax and slender branches. Most species of *Talinella* are dioecious, with either the stamens or the gynoecium vestigial. Indications are that some of the species may at least be morphologically gynodioecious (Appelquist 2005). Although Hershkovitz (1993) associated *Talinella* with *Portulacaria* and *Ceraria*, subsequent molecular studies have clearly shown that it is most closely related to *Talinum* Adans. (Hershkovitz & Zimmer 1997; Appelquist & Wallace 2001). Gynodioecy has, however, also been reported in the monotypic *Decaryia* Choux, one of the more basal lineages of the

otherwise dioecious Didiereaceae *s.str.* (Appelquist & Wallace 2000; Schatz 2001). The presence of gynodioecy in *Decaryia* might be a plesiomorphy, an interpretation supported by its presence in the even more distantly related genus *Ceraria*. This argument presupposes reversion to hermaphrodite flowers in *Calyptrotheca*. It also provides support for the suggested placement of *Ceraria* in an expanded Didiereaceae.

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