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 portulaceous genera Ceraria H.Pearson & Stephens and Portulacaria Ia. 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 & Zimmerman 1997; Appelquist & Wallace 2000, 2001). The circumscription of Didiereaceae was therefore enlarged to accommodate these three genera (Appelquist & 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. cassissiana Exell & Mendonça and C. longipedunculata Merxm. & Podlech, are restricted to the Kaokoveld Centre of Endemism in southwestern Namibia and southwestern Angola (Van Wyk & Smith 2001), whereas the ranges of the other taxa are ± centred on the Gariep Centre of Endemism in southwestern Namibia and southwestern South Africa (Van Wyk & Smith 2001; Curtis & Mannheimer 2005).

In this contribution, a new species of Ceraria from the Kaokoveld, Namibia, is described. Gynodioecious, semisucculent, densely branched, shrub-like tree, 0.3–2.0 × 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, papilliform 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 ± 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) ± (4.0–)1.2–3.0 × (3.8) ± (3.0–)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, papilliform hairs; margin entire; midrib or veinings not visible; petiole or subpetiole, petiole up to 1 mm long, in t/s ± circular, 0.1–0.5 × 0.1–0.3 mm long, glabrous or with very short, conical, papilliform 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 ± 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:
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 x 0.1 mm long. Bisexual flowers 1.8–2.8 mm long; pedicel 1.9–3.6 mm long; receptacle 0.3–0.4 x 0.5–0.6 mm; sepals ± 0.4 x 0.6 mm; petals 1.9–2.4 x 0.4–0.8 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 0.9–1.3 x 0.3–0.4 x 0.2 mm; stigmas ± 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 x 0.6 mm; sepals ± 0.3 x 0.6 mm; petals ± 1.4 x 0.5 mm; stamens 5, rudimentary; anthers not developed; pistil 1.2–1.5 mm long; ovary 1.0–1.3 x 0.3–0.4 x 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, 3.3–4.4 x 1.4–1.8 x 0.9–1.1 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 ± 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
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 Marienhof river 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 700–1000 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 Etupu Metamorphic Complex and to mica schist of the Damara Super group (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 Omvibango, (–AD), Swanepoel 226 (WIND), Hartmann Peak, peak of 1 039 m high mountain, (–CA), Swanepoel 265 (WIND), 4 km SW of Omvibango (–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

<table>
<thead>
<tr>
<th>Character</th>
<th>C. kaokoensis</th>
<th>C. fruticulosa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bark texture</td>
<td>longitudinally fissured</td>
<td>smooth</td>
</tr>
<tr>
<td>on branches/branchlets</td>
<td>white</td>
<td>different shades of brown</td>
</tr>
<tr>
<td>on recent growth</td>
<td>green or yellowish green, with short, conical, papilla-like hair</td>
<td>reddish green or yellowish green with pale bloom, glabrous</td>
</tr>
<tr>
<td>on new growth</td>
<td>winged or grooved in places (not prominently)</td>
<td>prominently winged or grooved</td>
</tr>
<tr>
<td>on dried branches/branchlets</td>
<td>in dry material, ± square in t/s</td>
<td>in dry material, ± square in t/s</td>
</tr>
<tr>
<td>Branchlets</td>
<td>petiolate or subsessile</td>
<td>sessile</td>
</tr>
<tr>
<td>Leaves</td>
<td>oblong-oblancoolate or oblancoolate, or linear, ratio of length versus width 3–4:1</td>
<td>oblong-oblancoolate, oblong-ebablate or oblong-eobvate; ratio of length versus width 1–3:1</td>
</tr>
<tr>
<td>attachment</td>
<td>0.8–14.5 × 0.4–3.8 × 0.3–1.3 mm</td>
<td>3.1–15.0 × 1.5–9.0 × 0.9–2.8 mm</td>
</tr>
<tr>
<td>lamina shape</td>
<td>green or yellowish green</td>
<td>pale green, yellowish green or glaucous</td>
</tr>
<tr>
<td>lamina size</td>
<td>short, conical, papilla-like hair</td>
<td>glabrous, often with white bloom</td>
</tr>
<tr>
<td>colour</td>
<td>clusters of 2–14; usually flowers profusely 1.1 × 0.4–0.3 mm</td>
<td>clusters of 2–6; flowers few and scattered</td>
</tr>
<tr>
<td>indumentum</td>
<td>± 0.3 × 0.1 mm</td>
<td>± 1.5 × 0.8 × 0.5 mm</td>
</tr>
<tr>
<td>Flowers</td>
<td>Kaokoveld Centre of Endemism, southwestern Namibia</td>
<td>southern Namibia and Northern Cape Province, South Africa</td>
</tr>
<tr>
<td>ovule size</td>
<td>± 0.6 × 0.4 mm</td>
<td>± 0.6 × 0.4 mm</td>
</tr>
<tr>
<td>ovary size</td>
<td>2.15 × 0.8 × 0.5 mm</td>
<td>2.15 × 0.8 × 0.5 mm</td>
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<tr>
<td>Florescence</td>
<td>3.1–15.0 × 1.5–9.0 × 0.9–2.8 mm</td>
<td>pale green, yellowish green or glaucous</td>
</tr>
<tr>
<td>leaf size</td>
<td>0.8–14.5 × 0.4–3.8 × 0.3–1.3 mm</td>
<td>3.1–15.0 × 1.5–9.0 × 0.9–2.8 mm</td>
</tr>
<tr>
<td>leaf shape</td>
<td>longipedunculata</td>
<td>sessile</td>
</tr>
<tr>
<td>leaf texture</td>
<td>smooth</td>
<td>different shades of brown</td>
</tr>
<tr>
<td>leaf arrangement</td>
<td>oblong-ovate or obcordate, glabrous</td>
<td>reddish green or yellowish green with pale bloom, glabrous</td>
</tr>
<tr>
<td>leaf size</td>
<td>clusters of 2–14; usually flowers profusely</td>
<td>clusters of 2–6; flowers few and scattered</td>
</tr>
<tr>
<td>leaf shape</td>
<td>± 1.5 × 0.8 × 0.5 mm</td>
<td>± 0.6 × 0.4 mm</td>
</tr>
<tr>
<td>leaf texture</td>
<td>0.6 × 0.4 mm</td>
<td>2.15 × 0.8 × 0.5 mm</td>
</tr>
<tr>
<td>leaf arrangement</td>
<td>sessile</td>
<td>sessile</td>
</tr>
<tr>
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<tr>
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<td>sessile</td>
<td>sessile</td>
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</tr>
<tr>
<td>leaf arrangement</td>
<td>sessile</td>
<td>sessile</td>
</tr>
</tbody>
</table>

TAXONOMIC SIGNIFICANCE OF GYNO DioECY 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; Eggli 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
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 gyno-
dioecious. Plants of the new species are either function-
ally 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 dio-
cey are rarely absolute (Policansky 1982). The possibil-
ity 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-assess-
ment 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 moni-
toring 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 mem-
ber of Ceraria is of considerable phylogenetic signifi-
cance. Current knowledge would indicate that all other
Portulacaceae are hermaphroditic, with the exception of
Talinella Baill., a Madagascan genus (12 species) of ±
woody shrubs with lax and slender branches. Most spe-
cies of Talinella are dioecious, with either the stamens
or the gynoecium vestigial. Indications are that some of
the species may at least be morphologically gynodioe-
associated Talinella with Portulacaria and Ceraria, sub-
sequent molecular studies have clearly shown that it is
most closely related to Talinum Adans. (Hershkovitz &
Zimmer 1997; Applequist & 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.* (Applequist & 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 *Calyptriotheca*. It also provides support for the suggested placement of *Ceraria* in an expanded Didiereaceae.

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**REFERENCES**


**CRASSLACEAE**

**BRYOPHYLLUM PROLIFERUM NATURALIZED IN KWAZULU-NATAL, SOUTH AFRICA**

The most efficient method of multiplication by succulents is via adventitious plantlet proliferation. A number of alien succulents that use this method of propagation has become naturalized or weedy in South Africa. Well-known examples include *Agave sisalana* Perrine (Smith & Mössmer 1996) and *Opuntia ficus-indica* L. (Obermeyer 1976). Abnormal (adventitious) development is reflected in the panicle of *A. sisalana* becoming bulbiferous after flowering, and shooting and rooting of the detached fruits occurring in *O. ficus-indica*. Amongst the few Crassulaceae that have been recorded naturalized in southern tropical Africa, the genus *Bryophyllum* Salisb. features prominently (Fernandes 1983). However, in the *Flora of southern Africa* region, *Bryophyllum delagoense* (Eckl. & Zeyh.) Schinz is the only member of this family to have been recorded as such (Toelken 1985; Dreyer &