Two new species of Aizoaceae (Ruschieae, Ruschoideae) from the Cape, South Africa.

Cornelia Klak[1]*, Pavel Hanáček[2], Peter V. Bruyns[1]

[1]Bolus Herbarium, Department of Biological Sciences, University of Cape Town, 7701, Rondebosch, South Africa; e-mail cornelia.klak@uct.ac.za

*Author for correspondence

[2] Department of Plant Biology, Mendel University in Brno, Zemědělská 1, 613 00 Brno, Czech Republic

Abstract: *Smicrostigma warmwaterbergense* is described from the summit of the Warmwaterberg on the Little Karoo of the Western Cape. It resembles *S. viride* in its habit and leaves but differs in that the flowers open during the day and close at night and the reproductive parts are fully visible when the flowers are open. The new species highlights the close links of *Smicrostigma* to *Octopoma* and *Zeuktophyllum*, which are also centered on the Little Karoo and share the leaves with a smooth surface, solitary, (sub-) sessile flowers and many-locular fruits.

Namaquanthus cephalophylloides is described from patches of quartz-gravel north of Kleinzee in Namaqualand in the Northern Cape. This new species shares with *N. vanheerdei* the thick, finger-shaped leaves and distinctly echinate seeds but differs from it by its dwarf habit, its gray leaves and downward-pointing fruit, which drop off once mature.

Keywords: Cape Floristic Region, Little Karoo, Namaqualand, *Namaquanthus*, *Smicrostigma*, taxonomy

INTRODUCTION

Recent fieldwork in Namaqualand and the Little Karoo, South Africa, led to the discovery of two new species of the large and diverse tribe Ruschieae (Ruschioideae, Aizoaceae). These two new species form parts of a larger study, which also includes molecular data, on the relationships of *Ruschia* Schwantes to the remaining species in the Ruschieae (Klak et al. in prep.). Morphologically it is clear that the collection from the Warmwaterberg in the Little Karoo belongs to *Smicrostigma* and the one from the coastal plain in Namaqualand is a species of *Namaquanthus*.

Only one species is recognized in *Smicrostigma* N.E.Br. (Hartmann 2017). This had been described already by Haworth (1795) as *Mesembryanthemum viride* and then moved to *Erepsia* (Bolus 1927). Brown (1930) erected a new genus, *Smicrostigma*, for this single species, which Rowley (1978) later transferred to *Ruschia*, as *Ruschia viridis* (Haw.) G.D. Rowley. In later accounts *Smicrostigma* was re-instated (Hartmann 2001). A further species, *Mesembryanthemum integrum* L.Bolus (Bolus 1922, Fig. 1), which later became *Ruschia integra* (L. Bolus) Schwantes (Schwantes 1926)), is considered to be conspecific with *Smicrostigma viride* (Hartmann 2017).

Smicrostigma was placed by Schwantes (1971) in the Erepsiinae, which was characterized by the presence of a hypanthium, inwardly curved stamens and flowers which remain open for several

Fig. 1. *Smicrostigma viride* (= *Mesembryanthemum integrum*), Concordia Valley, Montagu District, *BH 17175* (BOL). Artist: M.M. Page.

Fig. 2. *Namaquanthus vanheerdei, Klak 493* (BOL). (**A-D**): **A.** Large colony of *N. vanheerdei* on a rocky slope in northern Namaqualand. **B.** Dense cushion forming habit, with dark green leaves. **C.** Solitary magenta flowers showing the different stages of flowering: during the first days after opening the inner petals hide the center (left), in older flowers (right) the center is visible. Note: pollen is yellow in some plants. **D.** Close-up of a young flower showing the inner petals curved over the center.

days after anthesis. Liede (1989) later showed that *Smicrostigma* does not possess a true hypanthium and that, in addition, the stamens have an essentially erect orientation in the flower. The fact that the flowers do not close each evening but remain open day and night was recognized as a phenomenon that evolved repeatedly in unrelated lineages within the Ruschieae (Liede 1989). Mainly on account of features of the fruits, Hartmann (1988) allied *Smicrostigma* to members of the *Lampranthus* group, including *Zeuktophyllum*. Analyses of molecular data (Klak et al. 2013) indicated that *Smicrostigma* is most closely related to *Zeuktophyllum* (2 spp.) and *Octopoma s.str.* (3 spp.). Powell et al. (2016) later showed conclusively that *Octopoma s. str.* includes only the three species whose distributions are centered on the Little Karoo, while the other species of *Octopoma,* concentrated in Namaqualand, belong to *Schlechteranthus* subg. *Microphyllus* R.F. Powell (Powell et al. 2017).

One of the most striking features of *Smicrostigma* is the manner in which the bases of the leaves are fused into a gradually-narrowing sheath around the branch (Fig. 1). Here the free parts of the leaves are shorter than the fused parts that form this sheath and each leaf ends in a sharp tip. Very similarly shaped leaves are also typical of *Ruschia* subg. *Ruschia*, but in subg. *Ruschia* the capsules are 5-locular and have closing-bodies, whereas they are multi-locular (> 7 locules) and lack closing-bodies in *Smicrostigma*.

In both *Octopoma s. str.* and especially in *Zeuktophyllum* the plants have a more compact habit than in *Smicrostigma*, and the leaves are highly succulent but do not extend downwards along the branch to form a sheath. Their flowers are also solitary and ± sessile, as in *Smicrostigma*, but they are always white to cream (never magenta or pink as in *Smicrostigma*), they open and close repeatedly over several days and their reproductive parts are clearly visible. The capsules of *Octopoma* can be separated from those of the other two genera by their closing-bodies. In contrast, both *Zeuktophyllum* and *Smicrostigma* lack closing-bodies. Their capsules have between 8 and 10 locules (slightly lower in *Octopoma*, Table 1).

Leaves with a smooth, xeromorphic surface, solitary, (sub-) sessile flowers and many-locular fruits is a combination of characters that is unique to the clade consisting of *Smicrostigma*, *Zeuktophyllum* and *Octopoma* s.str. (Klak et al. 2013). The major characters distinguishing the three genera show considerable overlap between the genera (Table 1). This suggests that the generic boundaries need to be re-assessed. The high similarity of the habit as well as the leaves between *Smicrostigma viride* (Fig. 1) and the new species, suggest that this new species belongs to *Smicrostigma*.

The single species of *Namaquanthus* L. Bolus, *N. vanheerdei* L.Bolus, is only known from a single local-

Table 1. Major morphological characters used to distinguish *Octopoma, Zeuktophyllum* and *Smicrostigma*. The number of species in each genus is given in brackets.

	Octopoma (3)	*Zeuktophyllum* (2)	*Smicrostigma* (1)	*Smicrostigma sp. nov.*
Leaves	Not fused into a sheath	Not fused into a sheath	Basally fused into a long sheath clasping the stem	Basally fused into a long sheath clasping the stem
Flower color	Cream to white	Cream to white	Pink, rarely cream to white	magenta
Opening of flowers	diurnal	diurnal	remaining open day and night	diurnal
Stamens	visible	visible	partly concealed	visible
Stigmas	visible	visible	concealed	visible
Locule number	6-8	8-10	7-10	9-13
Closing bodies	present	absent	absent	absent

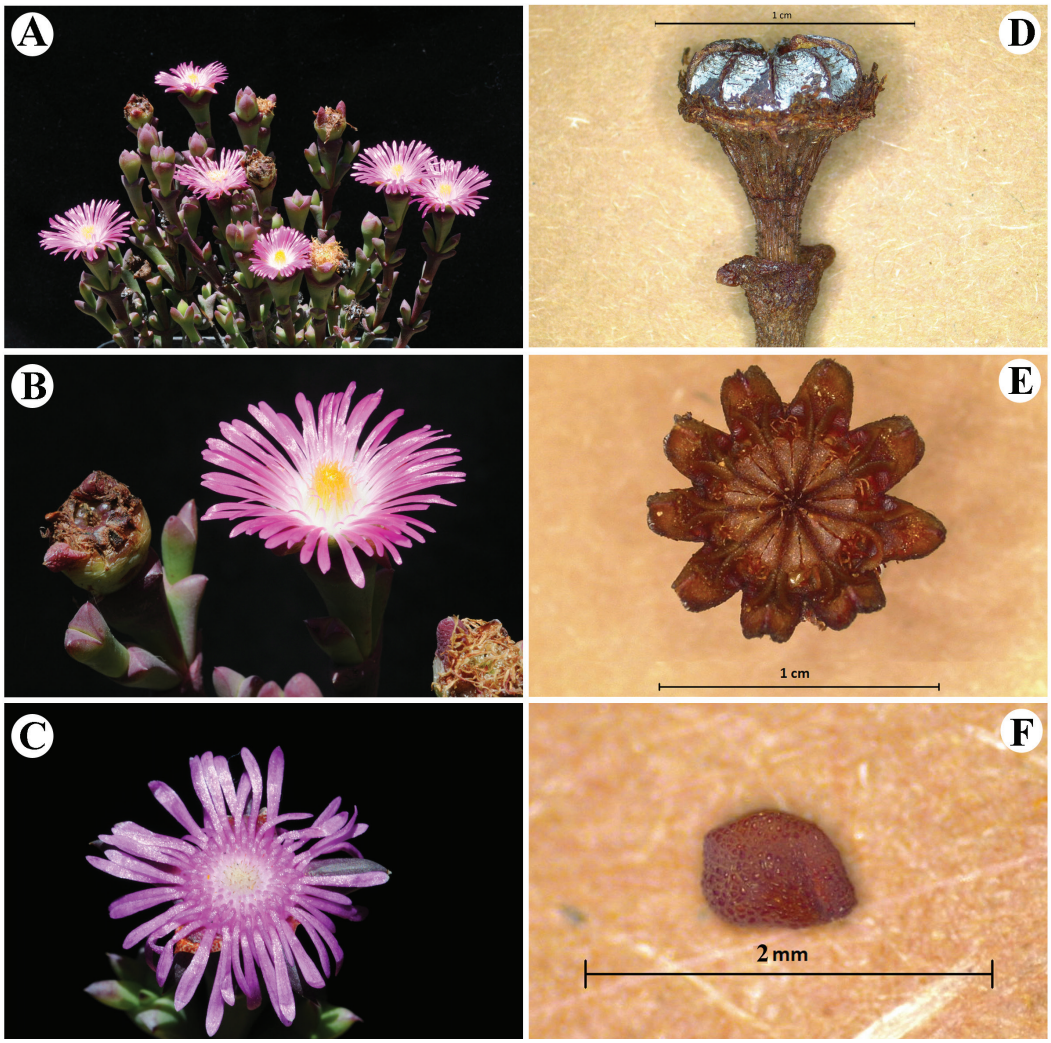

Fig. 3. *Smicrostigma warmwaterbergense*, *Bruyns 14033* (BOL) (**A, B, D-F**): **A.** Flowering branch, December 2021, South Africa. **B.** Close-up of flower with stamens visible. **D.** Side view of closed capsule. **E.** Top view onto open capsule. **F.** Seed. *Smicrostigma viride*: **C.** Close-up of flower showing the stamens and stigmas concealed by the staminodes, *Klak 3035* (BOL).

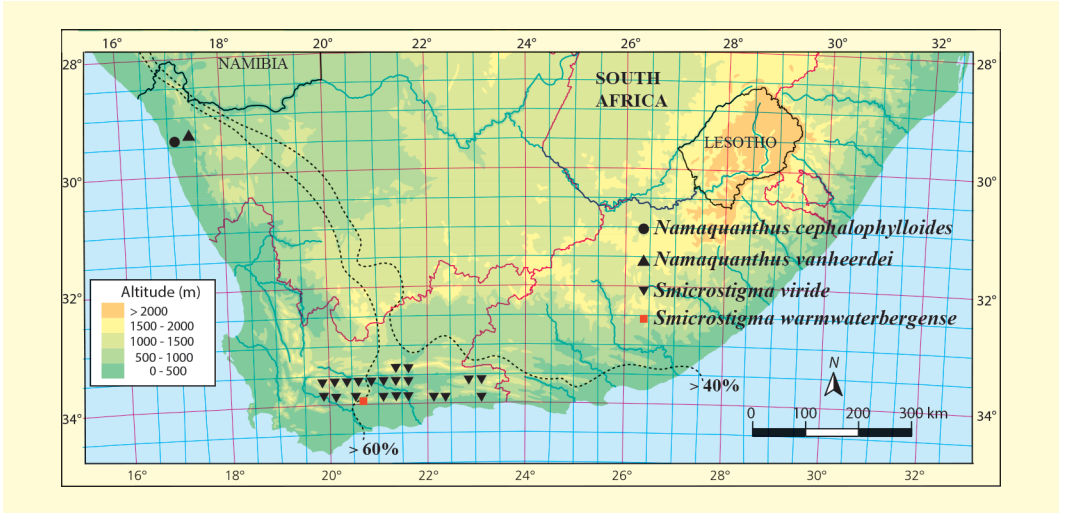

Fig. 4. Distribution of *Namaquanthus cephalophylloides* (circle), *N. vanheerdei* (triangle), *Smicrostigma viride* (inverted triangle), *S. warmwaterbergense* (square).

ity in the coastal plain of Namaqualand, where it forms large colonies (Fig. 2A) of relatively large plants on stony N-facing slopes. The plants form sturdy, densely branched, succulent shrublets, with thick, finger-shaped leaves and large magenta flowers. Their many-locular fruits lack closing-bodies. This monotypic genus occupies an isolated position within the *Conophytum*-clade (Klak et al. 2013), together with *Cheiridopsis* and several monotypic genera, including *Enarganthe* N.E.Br., *Jensenobotrya* Herre and *Ruschianthus* L.Bolus. Most members of the *Conophytum*-clade are 'stemless' dwarfs, except for *Enarganthe*, *Jensenobotrya* and *Namaquanthus* which may form shrubs to 45 cm tall. Although the relationships between these genera are not well resolved, they form a geographically coherent grouping that mainly occurs between the southern part of the Namib Desert and northern Namaqualand.

We give detailed descriptions for the two new species. We also show and discuss the distributions of both species of *Smicrostigma* and *Namaquanthus.*

MATERIALS AND METHODS

Morphological data were obtained through examination of fresh as well as pressed material in the herbaria at BOL and NBG (abbreviations from Thiers 2020+). Data on the distribution of the species was gathered from herbarium material and the records are listed according to the quarter-degree system of Edwards and Leistner (1971).

TAXONOMY

1. *Smicrostigma warmwaterbergense* Klak **sp. nov.** (Fig. 3)

This new species resembles *Smicrostigma viride* in its habit and the shape of its leaves but differs in that its flowers open and close repeatedly over several days and expose the reproductive parts fully when open (remaining open with reproductive parts hidden in *S. viride*). It differs further in having. 9–13 locules in its capsules (7–10 locules in *S. viride*).

Type: SOUTH AFRICA. Western Cape, **Montagu (3320)**: Summit of southern side of Warmwaterberg, towards boundary of 'Cocktail', Sanbona (--DC), ± 1000 m, 9 Dec. 2021, *Bruyns 14033* (holotype BOL!, isotype NBG).

Erect perennial, densely branched shrubs 15–20 × 15–20 cm, branching from the base, branches slightly succulent, becoming woody with age, 3–5 mm diam., smooth, young internodes pale brown, 10–13 × 1.5–2 mm. ***Leaves*** opposite, spreading, united at the base and sheathing the branch for 10–13 mm, sheath without a line and becoming woody with age, smooth, free parts 4–5 mm long, trigonous, adaxially flat, inconspicuously keeled, 2–3 mm broad and thick, apiculate. ***Flowers*** solitary, sessile, bracteoles not different from the leaves, 25–30 mm diam.; sepals 5, subequal, succulent; petaloid staminodes brilliant magenta, 2- to3-seriate, inner petals shorter and emarginate, outer ones lanceolate, 13 × 1.2 mm, filamentous staminodes in 3–4 rows, white, outer ones pale pink, collected into a cone around the stamens, 5.5–6 × 0.3 mm; stamens numerous, filaments white, without papillae, 2–4 mm long, inner ones shortest, anthers yellow; stigmas 9–13, slender, ± 2.5 mm long, top of ovary slightly raised in center; nectary forming green, crenulated ring. ***Capsule*** 9- to 13-locular, covering membranes completely covering locules, 8–9 mm diam., top low, bowl-shaped, base of capsule funnel-shaped, rims low, expanding keels basally parallel and apically spreading, tapering into awns instead of valve wings, closing-bodies absent, no additional closing-device below the covering membranes. ***Seeds*** brown, ca. 0.7 mm long, testa cells cushion shaped.

DISTRIBUTION AND ECOLOGY

Smicrostigma warmwaterbergense is apparently rare and it is only known from the type locality from near Montagu on the southern side of the Warmwaterberg (Fig. 4), within the Sanbona Wildlife Reserve. It appears to be restricted to the plateau, at around 1000 m. The species is associated with sandstone soils within *fynbos*, where it grows in flat rocky areas, among other short shrubby, open vegetation. A population of an estimated 80 to 100 plants was found in flower in an area which had burnt seven years before. The vegetation is classified as Rainshadow Valley Karoo, SKv8 Western Little Karoo (Mucina et al. 2006). *Smicrostigma warmwaterbergense* flowers in December.

The distribution of *S. warmwaterbergense* overlaps with *S. viride*, which has been recorded between Montagu and Uniondale (Fig. 4). However, in the area where the two species co-occur, *S. viride* is restricted to lower altitudes on different soils. *Smicrostigma viride* is typically found in *renosterveld*, in shaly often stony or gravelly and loamy soils, either in flats or on gentle slopes. Elsewhere, it has been observed in rocky spots within *fynbos*.

DISTINGUISHING FEATURES AND RELATIONSHIPS

Smicrostigma warmwaterbergense has a similar habit to *Smicrostigma viride*. The fruits of *S. warmwaterbergense* only differ in the higher number of locules (Table 1). The major differences lie in their flowers: In *S. viride* the flowers remain open after anthesis and until they fade, whereas they are open and close each day for several days in *S. warmwaterbergense*. In addition, in *S. viride* the staminodes are recurved at the tips and partly conceal the stamens. For this reason, Louisa Bolus had transferred this species to *Erepsia*, which differs by the possession of a true hypanthium. In contrast, in *S. warmwaterbergense* the filamentous staminodes are collected first into a cone around the stamens and then later spread as the flower matures.

ETYMOLOGY

The epithet refers to the Warmwaterberg, a mountain-range in the Little Karoo, where the species was discovered.

CONSERVATION STATUS

While botanical surveys in future are likely to uncover additional populations of this species, it nevertheless appears to be rare. Given the isolated nature of the known population, we recommend that it is considered Vulnerable and placed on the Red Data List of South African plants.

Key to the species of *Smicrostigma*

1. Flowers remaining open day and night, stigmas and stamens at least partly concealed, capsule with 7–10 locules..... ***S. viride***

1. Flowers opening each day for several days, stigmas and stamens visible in center, capsule with 9–13 locules ..... ***S. warmwaterbergense***

Additional specimens examined: *Smicrostigma viride*: —SOUTH AFRICA. Western Cape Province, **Worcester (3319)**: Concordia Valley (--DB), Feb 1922, *Cook sub NBG1694/22* (BOL); Robertson, north of Koningrivier Dam [Klipbergdam] (--DD), 300 m, 23 May 1997, *P. Bruyns 7151* (BOL); **Montagu (3320)**: Ouberg Pass (--CA), 14 Apr 1962, *H. Meyer sub SUG14738* (BOL); steep south facing slope south of Slagkloof se Berg (--CB), 600 m, 25 May 2002, *P. Bruyns 9000* (BOL); 20 miles from Montagu along the old Ladismith road (--CB), 23 Sep 1935, *E. Esterhuysen sub BOL 40895* (BOL); Bonnievale (--CC), Dec 1929, *E. Ryder sub BOL 40892* (BOL); near Bonnievale on the way to McGregor (--CC), 4 May 1973, *H. Glen 627* (BOL); Ashton (--CC), Nov 1921, *F. Rogers sub BOL 17175* (BOL); Near Montagu Baths (--CC), 243 m, Dec 1892, *H. Bolus sub BOL 6714* (BOL); *H. Bolus sub Guthrie 2772* (NBG); Ashton (--CC), Nov 1921, *F. Rogers sub BOL 17175* (BOL); Dobbelaars Kloof (--DA), 152 m, 1 May 1940, *E. Esterhuysen sub BOL 31160* (BOL); Farm Plankkraal, along northern aspect of Touwsberg (--DB), 600-700 m, 30 May 1999, *P. Bruyns 7841* (BOL); Barrydale - Montagu road, at turn-off to Soutkloof (--DC), 1 Oct 2004, *C. Klak 1139* (BOL); **Ladismith (3321)**: 8 km east of Ladismith (--AD), 700 m, 28 Dec 2020, *C. Klak 2822* (BOL); Farm Opsoek, near Amalienstein (--BC), 506 m, 27 Dec 2020, *C. Klak 2817* (BOL); Little Karroo, Farm Witkoppie (--CA), 28 Mar 1997, *C. Klak 180* (BOL); Farm Rietbakkiesfontein, near northern slopes of Rooiberg (--CB), 500 m, 29 May 1999, *P. Bruyns 7833* (BOL); Between Garcia's Pass and Muis Kraal (--CC), 518 m, Oct 1904, *H. Bolus sub BOL 11289* (BOL); About 8 km on Vanwyksdorp road from Riversdale to Calitzdorp (--CD), 360 m, 26 Sep 2006, *P.M. Burgoyne 10689* (NBG); Rooiberg Pass (--DA), 19 Aug 1973, *W. Wisura 2746* (BOL, NBG); 6 Jan 1985, *P.A. Bean 1556* (BOL); Roodeberg, between Calitzdorp and Van Wyksdorp (--DA), 4 Jul 1948, *J.P.H. Acocks 14616* (BOL); Van Wyksdorp, Farm Uitspan (--DC), 200 m, 27 May 2002, *P. Bruyns 9044* (BOL); **Oudtshoorn (3322)**: North foot of Outeniquas, between Robinson Pass and Oudtshoorn, Moeras River Valley (--CC), 6 Dec 1951, *E. Esterhuysen 19606* (BOL); 10 Apr 1984, *P.A. Bean, J.H.J. Vlok & M. Viviers 1429*

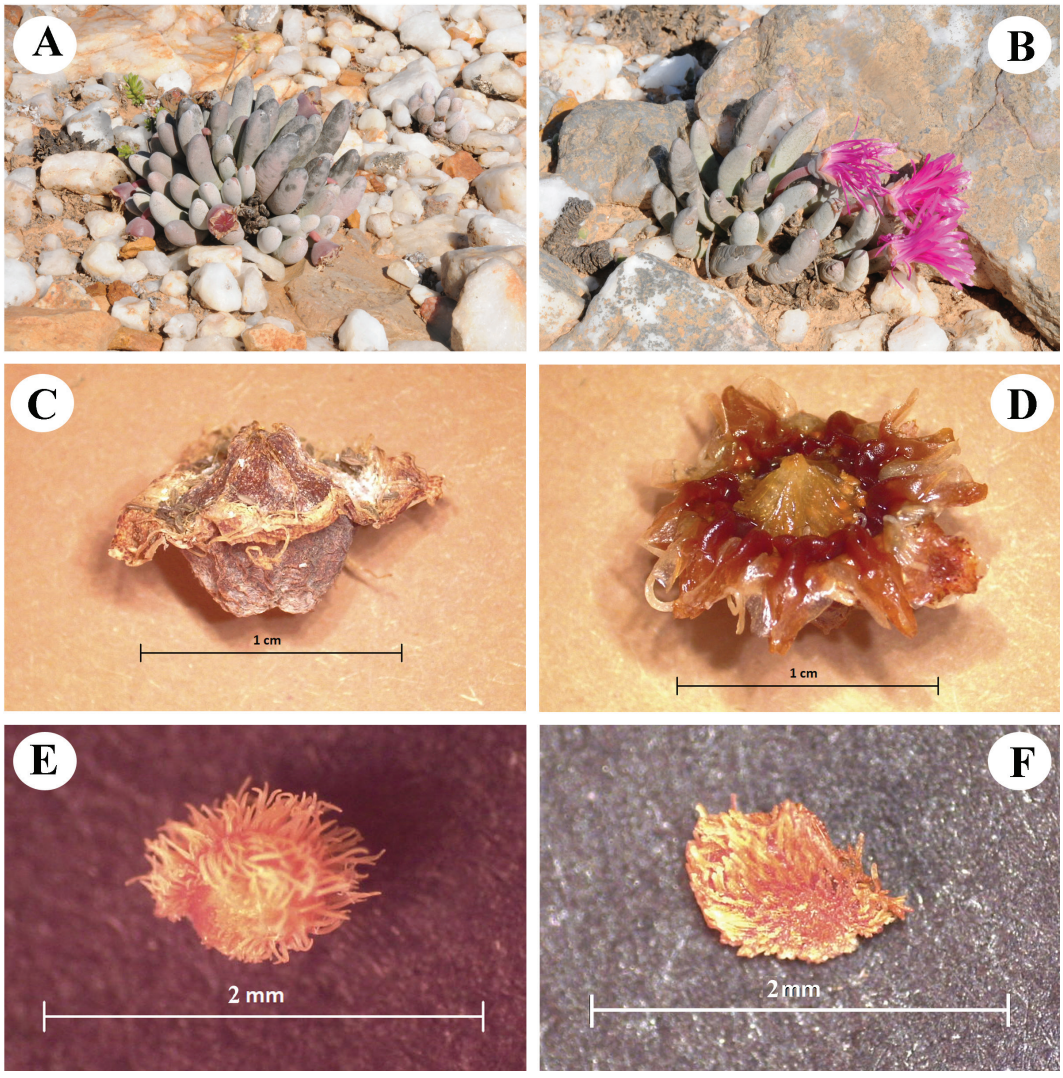

Fig. 5. *Namaquanthus cephalophylloides*, *Klak 2917* (BOL) (**A -E**): **A.** Clump- forming plants among quartz-gravel. Maturing fruits are pointing downwards. **B.** Solitary magenta flowers on long pedicels. **C.** Side view of closed capsule. The fruit is no longer attached to the pedicel. The lower part of fruit is indented in the area where the pedicel is attached. **D.** Top view of open capsule. **E.** Seed distinctly echinate. *Namaquanthus vanheerdei*, *Klak 493* (BOL): **F.** Seed.

(BOL; NBG); Jonkersberg, Paardepoort, Doring River Valley (--CD), 1 Dec 1980, *P.A. Bean 377a* (BOL); 4.4 km west of Laudina on road to Dysselsdorp from Uniondale (--DB), 10 Sep 1985, *P.A. Bean 1579* (BOL); De Rust, Farm Buffelsdrif (--DB), 660 m, 20 Jan 2008, *C. Klak 1633* (BOL); **Willowmore (3323)**: 1 km S of Uniondale (--CA), 24 Aug 1998, *R.J. Chinnock 9201* (NBG); Uniondale (--CA), 8 Nov 1949, *E. Esterhuysen 16434* (BOL); 2 km south of Uniondale above road to Avontuur (--CA), 24 Jun 1998, *H. Kurzweil 1898A* (NBG); Keurbooms River, Long Kloof (--CC), 609 m, Jan 1923, *H. Fourcade 2508* (BOL);

2. *Namaquanthus cephalophylloides* Klak **sp. nov.** (Fig. 5)

Type: South Africa, Northern Cape, Kwaganap River, between Port Nolloth and Grootmis (2917 AC), 19 Jul. 2021, 150 m, *Klak 2917* (BOL, holo.).

Differs from *N. vanheerdei* by its much smaller stature (to 10 cm tall as opposed to 30 cm tall in *N. vanheerdei*). In addition, the stalks of maturing fruit bend downwards and the fruit finally detach from the plant along a preformed incision, whereas the fruit remain erect and attached to the fruit-stalk in *N. vanheerdei*.

Dwarf, clump forming more or less stemless perennial succulent, with only basal part very woody, < 10 × 15 cm. ***Leaves*** opposite, ascending, ± free to their bases, finger-shaped, with upper side only slightly flattened, 45–60 × 8–13 mm, tips obtuse. ***Flowers*** solitary, 45–50 mm diam., pedicels erect to slightly bent, bending further down as fruit matures, to 45 mm long, bracts succulent and positioned near the base of plant and thus hidden between the leaves; sepals 4, subequal, succulent, flat and broad, ± 8.5 × 8.2 mm, 2 slightly narrower to 5 mm broad and with membranous margins; petaloid staminodes brilliant magenta, paler towards the center, 2- to 3-seriate, ± same length, 22–24 × 2.8 mm, lanceolate to obtuse, filamentous staminodes absent; stamens numerous, filaments 3.5–5.2 mm long, inner ones shortest, white, papillate at base, in 3–4 rows, pollen white; stigmas 8–9, short, feathery, 2.5 mm long, yellowish, top of ovary slightly raised in the center; nectary forming green, crenulated ring. ***Capsule*** 8- to 9-locular, detaching from pedicel once mature, 10 mm diam., top raised to 3 mm, with low rims, lower part 7 mm deep, rounded to bell-shaped, basally indented where pedicel attached, covering membranes thin and flexible, raised in the center, without additional closing-devices below, completely covering the locules, without closing-bodies, valve wings broad, ± rectangular. ***Seeds*** ochre, to 1.1 mm long, echinate with slender papillae.

DISTRIBUTION AND ECOLOGY

The species is only known from the Kwaganap River south-east of Port Nolloth, in the arid winter-rainfall region of northern Namaqualand (Fig. 4). Here it occurs on shallow loamy soils overlaying gneiss with quartz-gravel on the surface. The species occurs at an altitude of around 150 m. It flowers between May and July. The similarly restricted *N. vanheerdei* is only known from north- and west-facing quartzitic slopes around 30 km east of Port Nolloth (Fig. 4).

DISTINGUISHING FEATURES AND RELATIONSHIPS

N. vanheerdei forms shrubs to 30 cm high and to 50 cm diameter, whereas *N. cephalophylloides* is a clump-forming dwarf shrub that does not exceed 15 cm broad. Both species of *Namaquanthus* have thick, finger-shaped leaves that are more or less free to their bases. However, in the new species the leaves are gray, almost white from a thick covering of wax, whereas *N. vanheerdei* has dark green leaves, which are typically partially blackened by a fungus or a lichen in their habitat (Fig. 2B). Furthermore, both species possess large brilliantly colored, magenta, solitary flowers. However, the pedicels are erect and only reach 10 mm long in *N. vanheerdei* (Fig. 2), whereas they are to 45 mm long and curved in *N. cephalophylloides* (Fig. 5B). Unusual for *N. vanheerdei* is that the inner petals unfold only after several days, hiding the center of the flower in the beginning (Fig. 2C, D). Such slow opening of the flowers was not observed for *N. cephalophylloides*. Bolus (1954) reported the anthers and pollen to be deep purple for *N. vanheerdei*. However, our own observations revealed that some plants can also have yellow pollen (Fig. 2C), whereas the pollen is white in *N. cephalophylloides*. Noteworthy are the echinate seeds (Fig. 5E, F), which are common to both species. Unusual in *N. cephalophylloides* are the downward pointing fruits (Fig. 5A), which become detached once they are mature. This contrasts with most of the species in the Ruschioideae, where the fruits are retained on the plant for 1–2 years or longer. In *Cephalophyllum*, the tops of the fruits always point upwards and possess closing-bodies. Although papillate seeds are also found in *Astridia*, the fruits of *Astridia* have closing-bodies, which are absent in *Namaquanthus*. A possible close relative is the monotypic *Enarganthe*, which differs in its trigonous to club-shaped leaves and the pear-shaped, elongated, almost smooth seeds.

ETYMOLOGY

The epithet refers to the superficial resemblance of the new species to members of *Cephalophyllum*.

CONSERVATION STATUS

We consider this species to be rare, because of its specific habitat requirements. These are large patches of quartz-gravel close to the sea. A similar habitat at Grootmis near Kleinzee, did not contain this species. This contrasts with *Drosanthemopsis kwaganapensis* Klak, which is found at the type locality of *N. cephalophylloides* and also at Grootmis (Klak et al. 2018). Given the isolated nature and the high habitat-specificity of the known population, we recommend that it is considered Vulnerable and placed on the Red Data List of South African plants.

Key to the species of *Namaquanthus*

1. Shrubs forming cushions to 30 cm high, leaves dark green, pedicels of fruit erect…..... ***N. vanheerdei***

2.′ Stemless compact clump-forming dwarf succulent < 10 cm tall, leaves gray from thick covering of wax, pedicel of fruit first erect and then pendulous with mature fruits pointing downwards..... .....***N. cephalophylloides***

Additional specimens examined: ***Namaquanthus vanheerdei*****:** —SOUTH AFRICA. Northern Cape, 30 km east of Port Nolloth, 2917 AD, on quartzitic slopes, 11 Jul 1998, *Klak 493* (BOL).

ACKNOWLEDGEMENTS

We would like to thank Liesl Vorster for assistance during field work in the Sanbona Wildlife Reserve, as well as the staff of Sanbona for their hospitality. The curator of NBG is thanked for permission to examine specimens. Our thanks go also to Northern Cape Nature Conservation and Cape Nature for collecting permits. Field work was funded in part by a block grant from the University of Cape Town. Two anonymous reviewers are thanked for constructive comments.

REFERENCES

Bolus, H.M.L. 1922. Novitates Africanae. *Annals of the Bolus Herbarium 3*: 134.

Bolus, H.M.L. 1927. *Erepsia viridis*. *Flowering Plants of South Africa* 7: t. 270.

Bolus, H.M.L. 1954. *Namaquanthus vanheerdei*. Notes on Mesembryanthemum [H.M.L. Bolus] 3: 257–258.

Brown, N.E. 1930. *Mesembryanthemum*. *Gardener's Chronicle* 87: 71–72.

Edwards, D. and O.A. Leistner. 1971. A degree reference system for citing biological records in southern Africa. *Mitteilungen der Botanischen Staatssammlung München* 10: 501–509.

Hartmann, H.E.K. 1988. Fruit types in Mesembryanthema. *Beiträge zur Biologie der Pflanzen* 63: 313–349.

Hartmann, H.E.K. 2001. *Illustrated handbook of succulent plants*, Aizoaceae F-Z. – Berlin [a. o.], Springer.

Hartmann, H.E.K. 2017. *Smicrostigma*. Ruschioideae. *In* Hartmann, H.E.K. (ed.) *Illustrated Handbook of Succulent Plants. Aizoaceae H–Z.* Vol. 2, 2nd edition, Springer Verlag Germany, Pp. 1173–1175.

Haworth, A.H. 1795. *Observations on the genus Mesembryanthemum…*, part 2. The author, London.

Klak, C., P.V. Bruyns and P. Hanáček. 2013. A phylogenetic hypothesis for the recently diversified Ruschieae (Aizoaceae) in southern Africa. *Molecular Phylogenetics and Evolution* 69: 1005–1020.

Klak, C., P. Hanáček and P.V. Bruyns. 2018. A recircumscription of *Jacobsenia* (Aizoaceae): Re-instating *Drosanthemopsis*, with two new quartz-endemics from Namaqualand, South Africa and sinking *Knersia*. *South African Journal of Botany* 116: 67–81.

Liede, S. 1990. Untersuchungen zum Merkmalsbestand und der Taxonomie zur "Erepsiinae" (Mesembryanthemaceae). *Beiträge zur Biologie der Pflanzen* 64: 391–479.

Mucina, L., N. Jürgens, A. Le Roux, M.C. Rutherford, et al. 2006. Succulent Karoo Biome. In L. Mucina and M.C. Rutherford (Eds.), *The vegetation of South Africa, Lesotho and Swaziland* (Strelitzia 19, pp. 221–299). South African National Biodiversity Institute, Pretoria.

Powell, R.F., J.S. Boatwright, C. Klak and A.R. Magee. 2016. Phylogenetic placement and generic re-circumscriptions of the multilocular genera *Arenifera, Octopoma* and *Schlechteranthus* (Ruschieae; Aizoaceae): evidence from anatomical, morphological and plastid DNA data. *Taxon* 65 (2): 249–261. DOI http://dx.doi.org/10.12705/652.3

Powell, R.F., C. Klak, J.S. Boatwright and A.R. Magee. 2017. A taxonomic revision of *Schlechteranthus* subgenus *Microphyllus* (Ruschieae; Aizoaceae). *Systematic Botany* 42(4): 943–963. DOI 10.1600/036364417X696429

Rowley, G.D. 1978. Reunion of some genera of Mesembryanthemaceae. *The National Cactus and Succulent Journal* 33: 6–9.

Schwantes, G. 1926. Zur Systematik der Mesembrianthemen. *Sukkulentenkunde* 2: 173–189.

Schwantes, G. 1971. (revised and completed by H. Straka and H.-D. Ihlenfeldt) The classification of the Mesembryanthemaceae. In H. Herre (Ed.), *The genera of the Mesembryanthemaceae* (pp. 3–6). Cape Town, Tafelberg.

Thiers, B. (2020+) Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. Retrieved from http://sweetgum.nybg.org/ih (accessed: 16 May 2022).