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DOI:
https://doi.org/10.11646/phytotaxa.579.2.5

Phytotaxa 579 (2): 117–124
https://www.mapress.com/pt/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

https://doi.org/10.11646/phytotaxa.579.2.5

Ceropegia stylesii (Apocynaceae-Asclepiadoideae)—a novel species with rotate flowers from Ngome, South Africa

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Abstract

A novel species of *Ceropegia* sect. *Bowkerianae* (Apocynaceae: Asclepiadoideae-Ceropegieae-Stapeliinae), *C. stylesii*, is described from Ngome in northern KwaZulu-Natal, South Africa. This new species is vegetatively similar to *C. gerrardii*. The rotate non-trapping flowers of *C. stylesii* superficially appear to be miniature versions of a dark-flowered form of *C. gerrardii*, with which it is sympatric. *Ceropegia stylesii* is exceptionally rare with fewer than 10 individuals observed at two localities; its habitat is under anthropogenic threat. *Ceropegia stylesii* is considered as Critically Endangered (CR) according to IUCN criteria.

Keywords: *Bowkerianae*, *Brachystelma gerrardii*, Ceropegieae, critically endangered, endemism, KwaZulu-Natal, mistbelt grassland, Stapeliinae

Introduction

The subtribe Stapeliinae (Apocynaceae-Asclepiadoideae-Ceropegieae) is the largest subtribe in Apocynaceae and roughly includes 725 species. The traditional generic concept for this subtribe recognized 33 genera. i.e., *Ceropegia* Linnaeus (1753: 211) well-known for its charismatic tubular kettle-trap flowers (>230 species) (Masinde 2012), *Brachystelma* Brown (1822: t. 2343) without pollinator-trapping flowers (>140 species) (Masinde 2007), and 31 genera collectively known as the stapeliads, a clade of always stem-succulent plants (>355 species) (Meve & Liede 2004). While the stapeliads are a monophyletic group nested in *Ceropegia*, phylogenetic analyses have revealed that *Brachystelma* species are not a natural group but have apparently evolved multiple times within *Ceropegia*, and in both the Asian and the African lineage (Meve & Liede-Schumann 2007, Surveswaran *et al.* 2009, Bruyns *et al.* 2015). Initially, despite its paraphyly being understood, *Ceropegia* was still considered "taxonomically sound" (Meve & Liede-Schumann 2007) in order to appreciate the distinctiveness in flower morphology from other members of the subtribe, i.e., functionally highly specialized kettle-trap flowers. *Brachystelma* species were also taxonomically separated from other members in Stapeliinae by lacking tubular kettle-trap flowers typical of *Ceropegia* s.str., or not being stem-succulent as characteristic for stapeliads.

With increasingly higher resolution of molecular phylogenetic analyses in Stapeliinae, the incompatibility of DNA sequence similarities with the traditional taxonomic concept continued to create controversy. Eventually nomenclatural changes within the Stapeliinae were instigated. It was proposed to transfer all *Brachystelma* species and all of the 31 stapeliad genera to a giant monophyletic *Ceropegia* with >720 spp. in 30 sections (Bruyns *et al.* 2017). The result of dramatically enlarging *Ceropegia* for the sake of monophyly are more than 400 new name combinations; without doubt this creates much confusion. A pragmatic solution was soon suggested by Endress *et al.* (2019) who in their treatment of Apocynaceae accept the sinking of *Brachystelma* into *Ceropegia* but retain the monophyletic stapeliads separate. Embracing a single case of paraphyly to the clearly monophyletic stapeliads obviously causes less nomenclatural instability. This compromise, which considers both taxonomic and phylogenetic facts for the establishment of an expanded concept for *Ceropegia*, appears to be well-accepted and preferred (e.g., Goyder *et al.* 2020, Hyde *et al.* 2022); some authors even still sustain the traditional concept (e.g., Surveswaran *et al.* 2021).

Accepted by Michele Rodda: 23 Dec. 2022; published: 17 Jan. 2023

Although the inclusion of *Brachystelma* in *Ceropegia* seems justified based on molecular evidence, both concepts of a larger *Ceropegia* disguise the intriguing differences in flower morphology and functionality, i.e., trap-flower vs. non-trap flower, which were thus far well reflected in the traditional generic concept. The pattern of recurrent evolutionary shifts between highly functional tubular kettle-trap flowers and open-rotate non-trap flowers is fascinating and should not be concealed by an enlarged concept. This is particularly so, considering that the evolution, loss and re-emergence of trap flowers in Stapeliinae, as well as the diversification of both flower types, has been driven by Diptera as the sole, albeit taxonomically and functionally extremely diverse pollinator group (Ollerton *et al.* 2019). However, the underlying evolutionary processes are far from being understood.

The novel species here described as *Ceropegia stylesii* does not have kettle-trap flowers nor a tubular corolla and would prior to the expansion of *Ceropegia* be included in *Brachystelma. Ceropegia stylesii* is placed in section *Bowkerianae* (Huber 1957: 33) Bruyns in Bruyns *et al.* (2017: 432) where it is morphologically closest to *C. gerrardii* (Harvey 1863: t.196) Bruyns in Bruyns *et al.* (2017: 432). At both known localities, *C. stylesii* and *C. gerrardii* co-occur and cannot be distinguished when not in flower. However, when flowering *C. stylesii* is clearly distinct. It has flowers about three times smaller than *C. gerrardii* and densely pilose corolla lobe tips which are ascending instead of horizontal to reflexed as in *C. gerrardii*. The staminal corona lobes are appressed to the stamen and style-head in *C. stylesii*, whereas in *C. gerrardii* they are erect and protrude from the flower centre alongside each other.

After the recent discovery and description of *Ceropegia heidukiae* D. Styles & Meve (2021: 21) in the same grassland habitat, *C. stylesii* is another exceptional member of Stapeliinae from Ngome, and may be endemic to this area.

Taxonomic treatment

Ceropegia stylesii Heiduk, ***sp. nov.*** (Figs. 1 and 2)

Type:—SOUTH AFRICA. KwaZulu-Natal province, Ngome, 975 m, 04 February 2021, *D.G.A. Styles & A. Heiduk 5870* (holotype: NU0092554!).

Diagnosis:—*Ceropegia stylesii* is vegetatively very similar to *C. gerrardii*. The flowers, however, apart from being considerably smaller (diameter ca. 6 mm vs. >20 mm in *C. gerrardii*), are distinct from *C. gerrardii* with ascending corolla lobe tips (vs. radially spreading to reflexed in *C. gerrardii*) which are densely pilose to tomentose (vs. puberulent in *C. gerrardii*). The staminal corona lobes of *C. stylesii* are adpressed to the stamen and the style-head with their tips covering the style-head (vs. erect, exceeding the style-head and protruding as a bundle from the flower centre in C. *gerrardii*).

Description:—*Plants* perennial, erect herbs. *Rootstock* composed of fleshy, fusiform roots. *Stems* annual, green, rigid, hirsute to hispid, single or two from rootstock, 250–400 mm tall, 25–35 mm in diameter, internodes 13–24 mm, often branched at some internodes starting from second internode. *Leaves* porrect to spreading, shortly petiolate; *petiole* channelled above, hirsute, 1.2–1.8 mm; *lamina* ovate, 17–30 × 11–20 mm, with 3–5 lateral nerves, base cordate, apex acute to obtuse, green, scabrid to hirsute above and below, *margin* entire, undulate, hirsute to hispid. *Inflorescence* axillary, at upper internodes, uniflorous, semi-pendulous; *bracts* narrowly triangular, 3.2–3.6 × 0.5 mm, densely hirsute to hispid; *pedicel* hirsute to hispid, green, sometimes reddish-brown speckled, slender, curved, 14–16 × 0.5 mm. *Sepals* narrowly lanceolate, acute, radially spreading and protruding from underneath the flower base, hirsute with densely pilose margins, 5.5–6.2 × 1.5 mm, slightly reflexed, green with sparse reddish-brown speckles. *Flowers* superficially resembling miniature versions of *C. gerrardii* flowers, with faint sweet scent. *Corolla* rotate, non-tubular, ca. 6.0 mm in length and diameter. *Corolla lobe bases* glabrous, waxy in appearance, creamish-white inside, greenish-white and dark purple speckled outside, basally fused and forming an annulus surrounding the base of the gynostegial column, then free but forming an inflated, apically slightly constricted basket-like structure around the gynostegium, margins fringed with unicellular, clavate, vibratile, ca. 1.0 mm long purple trichomes. *Corolla lobe tips* free, porrect, 3.7–5.0 mm long, radially spreading from basket-like corolla base, replicate, folded back longitudinally forming a raised median ridge, concave below, underside light purple or greenish and purple speckled, scatteredly puberulent, upper surface convex, deeply dark purple to almost black, velvety in appearance, densely pilose to villose, margins with longer stiffer trichomes 0.5 mm in length. *Gynostegium* shortly stipitate. *Gynostegial corona* of staminal and interstaminal parts, 2.5–3.0 mm in diam., ca. 3.5 mm in height, forming a nectar cup underneath each guide rail; *interstaminal corona lobes* erect, 0.7 × 0.6 mm, each divided into two short lobules, greenish-purple at base, dark purple at tips, with white ca. 0.2 mm long trichomes; *staminal corona lobes* adpressed to stamen and style-head, covering the latter with tips

overlapping (or rarely connivent), 1.5 × 0.5 mm, tips slightly asymmetrically bilobed, whitish-purple with dark purple spots, glabrous. *Pollinarium: pollinia* ovoid, ca. 310 × 230 µm, yellow, insertion crest ca. 150 × 50 µm; *caudicles* ca. 50 µm long; *corpusculum* oblong, 215 × 75 µm, brown. *Follicles* paired, narrowly fusiform, ca. 70 × 5.0 mm, glabrous. *Seeds* ovate, brown with lighter brown margin, coma white.

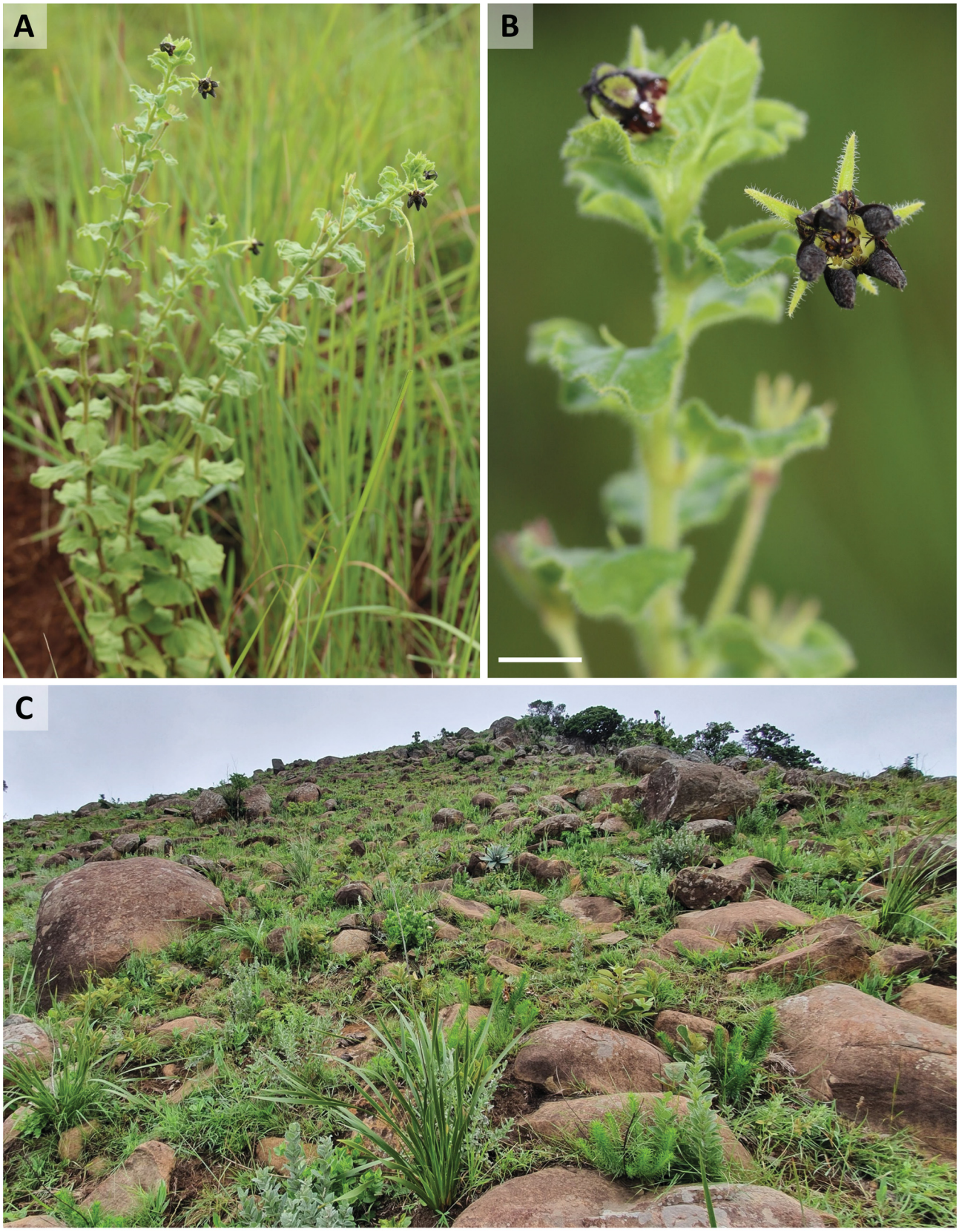

FIGURE 1. *Ceropegia stylesii* from Ngome, KwaZulu-Natal, South Africa. **A,** Habit of a plant in habitat. **B,** Stem with flower and bud. **C,** Habitat on a steep and rocky slope at the type locality. Scale bar in B: 0.5 mm. Photographs: David Styles.

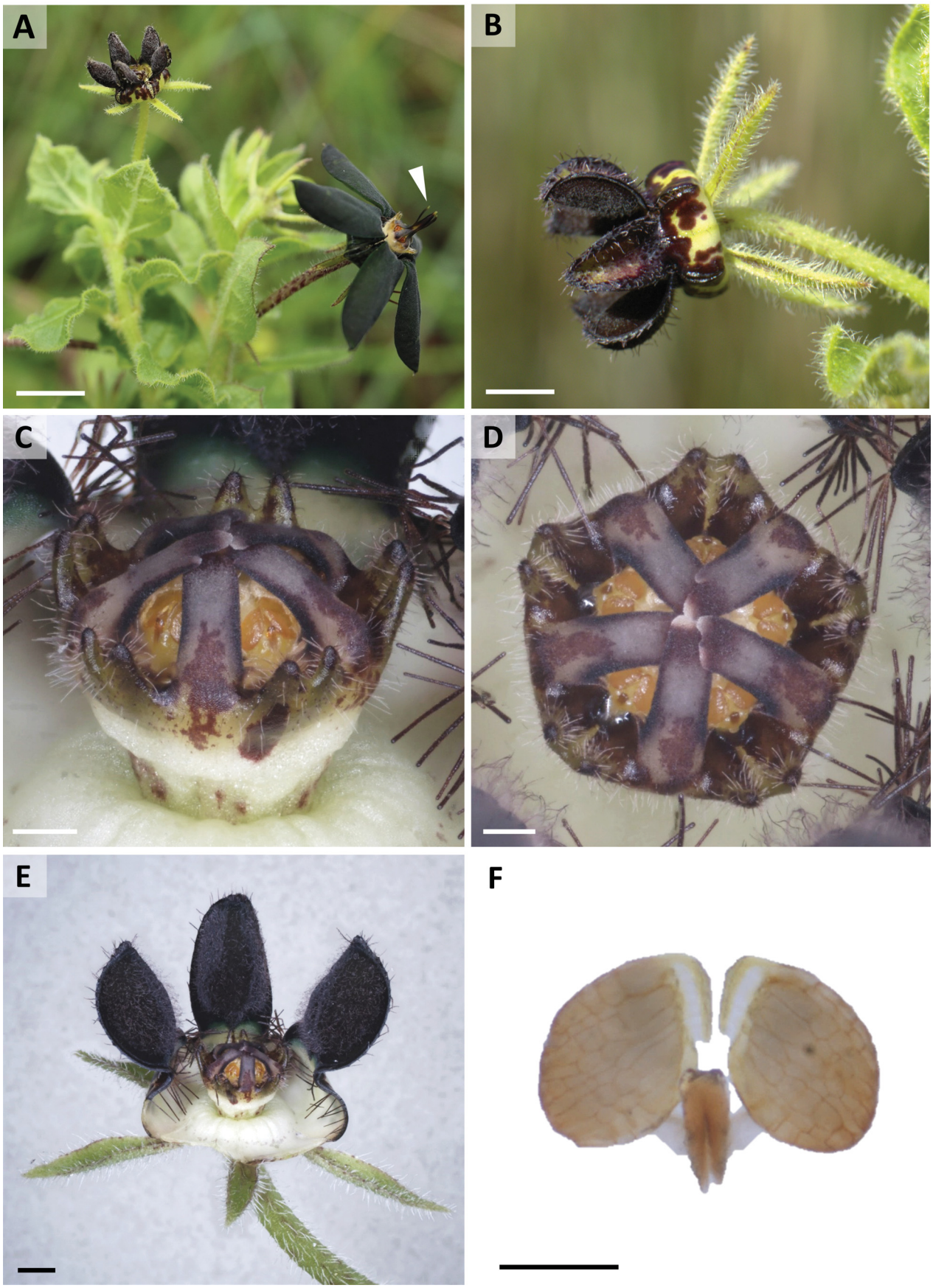

FIGURE 2. Morphological details of *Ceropegia stylesii* flowers. **A,** Flower of *C. stylesii* in comparison to a *C. gerrardii* flower (right). Note the staminal corona lobes protruding much from the *C. gerrardii* flower (white arrow). **B,** Side view of a *C. stylesii* flower *in situ*. **C,** Gynostegium and corona. **D,** Gynostegium and corona in top view. **E,** Longitudinal section through a flower. **F,** Pollinarium. Scale bars: 5 mm (A), 2 mm (B), 1 mm (E), 0.5 mm (C, D), 0.2 mm (F). Photographs: David Styles (A, B) and Annemarie Heiduk (C–F).

Additional specimens examined

Ceropegia stylesii:—SOUTH AFRICA. KwaZulu-Natal province, Ngome, 1130 m, 07 February 2021, in Northern Zululand Mistbelt Grassland on moderate to steep, mainly north-facing hillsides *D.G.A. Styles & A. Heiduk 5891* (NU0092553!); 930 m, 24 February 2020 (cultivated in Pietermaritzburg, internodes more elongated than in habitat, flowering material harvested in late January 2021), *D.G.A. Styles & A. Heiduk 5868* (NU0092551!, NU0092552!, flowers in ethanol: NU0092555!).

Ceropegia gerrardii:—SOUTH AFRICA. KwaZulu-Natal province, Ngome, ca. 1120 m, 04 February 2021, flowers dark brown to nearly black with velvety appearance, in Northern Zululand Mistbelt Grassland on moderate to steep, mainly north-facing hillsides *D.G.A. Styles & A. Heiduk 5871* (NU0092546!, NU0092547!, NU0092548!, NU0092549!, NU0092550!).

Distribution and ecology:—*Ceropegia stylesii* is only known from Ngome in northern KwaZulu-Natal, South Africa, where it occurs in Northern Zululand Mistbelt grassland at an altitude between 820–1300 m a.s.l., in close proximity to Paulpietersburg Moist Grassland (Mucina *et al.* 2006). A small number of plants were found at two localities with ~14 km distance of each other.

The type locality (Fig. 1C) comprises a hilltop capped by a dolerite sill which transitions to hillslopes comprised of sandstones and siltstones of the Vryheid Formation (Karoo Supergroup). At the second locality, *C. stylesii* occurs on hillslopes which comprise dolerite-derived soils and outcropping. National vegetation mapping in the vicinity of the localities appears to rely heavily on differentiating grassland types according to certain altitudinal thresholds, however, in areas of transition there do not appear to be marked floristic differences (D. Styles, pers. comm.).

At both the type locality and the second site, *Hyparrhenia hirta* Stapf (1919: 315) and *Cymbopogon caesius* (Nees ex Hooker & Arnott 1838: 244) Stapf (1906: 341) are dominant grasses. Both localities have been extensively transformed by silviculture with grassland occurring between or below commercial tree plantations. While the grassland contains many herbaceous species, this shows signs of overgrazing and over-burning, including localized erosion at the type locality.

Species of conservation concern (Raimondo *et al.* 2009) occurring in small numbers at the type locality include *Aloe kniphofioides* Baker (1890: t. 1939) (Near Threatened), *Ceropegia gerrardii* (Endangered, dark-flowered form), *Dierama erectum* Hilliard (1988: 80) (Endangered), *Dracosciadium italae* Hilliard & B.L.Burtt (1986: 223) (Vulnerable) and *Gerbera aurantiaca* C.H. Schultz Bipontinus (1844: 781) (Endangered, yellow-flowered form). *Ceropegia heidukiae*, assessed by Styles & Meve (2021) as Critically Endangered, is also present. At the second locality, *C. gerrardii* (dark-flowered form) (Endangered), *Dierama erectum* and *Gerbera aurantiaca* (yellow-flowered form) also occur in similarly small numbers.

Phenology:—*Ceropegia stylesii* was discovered in February and was seen in flower throughout this month. One plant with an early stage developing follicle was seen in late February. All above-ground parts die back entirely during the winter, from about May, but the rootstock remains intact and dormant underground. New stems start to shoot from the fleshy storage roots in about late November.

Eponymy:—*Ceropegia stylesii* is named for David Gordon Alexander Styles (Bulawayo, Zimbabwe, 7 January 1968–), botanical explorer and collector, who has contributed many valuable herbarium records including a number of novelties from South Africa's KwaZulu-Natal and Eastern Cape provinces. He discovered this species together with the author, while exploring grasslands in the area of Ngome.

Conservation status:—The Biodiversity Act (Act 10 of 2004, DEA 2011) identifies a number of ecosystems as threatened and in need of protection. Amongst these is the Ngome Mistbelt Grassland and Forest Ecosystem, which is mapped as 24 000 ha in extent and assessed as Endangered and stated to contain at least nine threatened or endemic animal or plant species (DEA 2011), although this is likely a great underestimate. Northern Zululand Mistbelt Grassland, a core vegetation type within the ecosystem, is also assessed as Endangered and poorly protected (Skowno *et al.* 2019). At the type locality, no more than six individuals of *Ceropegia stylesii* were found on a scattered basis within an area of about 0.1 km^2. At the second locality, only three plants were found with around 2 m distance from each other. The grassland at the type locality experiences grazing, appears to be very frequently burned and shows lower species richness than some other grassland in the Ngome area, together with localized erosion. At the second locality, the grassland appears to be more intact but is confined between plantations, and is certainly grazed by cattle. This, combined with the threat status afforded to the Ngome Mistbelt Grassland and Forest Ecosystem and Northern Zululand Mistbelt Grassland, and the small numbers and extremely localized occurrence of *Ceropegia stylesii* result in it being assessed as Critically Endangered (CR) under the criteria B1(a)(b), C2(a)(i) and D (IUCN Standards and Petitions Subcommittee 2022).

Discussion

Ngome in north-western KwaZulu-Natal is an insufficiently recognized area of endemism in need of further botanical exploration and collection (Scott-Shaw 1999). *Ceropegia ngomensis* (R.A.Dyer 1977: 255) Bruyns in Bruyns *et al.* (2017: 434), *Dierama erectum*, *Helichrysum ingomense* Hilliard (1982: 255) and *Schizochilus gerrardii* (Reichenbach 1867: 116) Bolus (1889: 205) are all species currently only known from the Ngome area. Much of the plant endemism in this area is associated with two vegetation types, Ithala Quartzite Sourveld and Northern Zululand Mistbelt Grassland (Mucina *et al.* 2006). *Ceropegia stylesii*, the novel species described here, occurs in Northern Zululand Mistbelt Grassland at Ngome as does the recently discovered and morphologically exceptional *C. heidukiae*, reaffirming the botanical and conservation importance of this vegetation type. With *C. stylesii*, Ngome gains another outstanding member of the subtribe Stapeliinae.

The novel species described here would traditionally be placed in *Brachystelma*. However, after the sinking of *Brachystelma* into *Ceropegia*, it falls within a group of species with and without kettle-trap flowers, recognized as *Ceropegia* section *Bowkerianae* (Bruyns *et al.* 2017). The type species of this section is *C. bowkeri* Harvey (1859: 254), a species of *Ceropegia* s.str. with distinct kettle-trap flowers. The majority of species placed in *Bowkerianae* are former members of *Brachystelma*, such as *C. cana* (R.A.Dyer 1977: 254) Bruyns in Bruyns *et al.* (2017: 432), *C. franksiae* (N.E.Brown 1912: t. 588) Bruyns in Bruyns *et al.* (2017: 432), *C. gerrardii, C. macropetala* (Schlechter 1895: 51) Bruyns in Bruyns *et al.* (2017: 432), *C. neocompta* Bruyns in Bruyns *et al.* (2017: 432), *C. ramosissima* (Schlechter 1895: 50) Bruyns in Bruyns *et al.* (2017: 432), *C. sandersoniana* (Oliver 1883: t. 1449) Bruyns in Bruyns *et al.* (2017: 432), and *C. schizoglossoides* (Schlechter 1894a: 357) Bruyns in Bruyns *et al.* (2017: 432). None of these species has the corolla fused to form a tubular kettle-trap. In phylogenetic analyses, these non-trap flowering species, except for *C. neocompta* (formerly *Brachystelma comptum* Brown (1908: 854)), form a group separate from those species with trap flowers in *Bowkerianae*, i.e., *C. bowkeri, C. scabriflora* Brown (1908: 810), *C. tomentosa* Schlechter (1894b: 33), *C. rudatisii* Schlechter (1907: 94) and *C. heidukiae* (Bruyns *et al.* 2017, own analyses). The exceptional grouping of *C. neocompta* in the sub-clade of species with trap flowers in *Bowkerianae* is intriguing considering that the corolla structure of this species has obvious affinity with that of *C. gerrardii* (Dyer 1983) and *C. stylesii* imputing a close relationship with both these species. The molecular data presented by Bruyns *et al.* (2017) suggest that the particular "*C. gerrardii*-type" corolla structure (i.e., a basket-shaped corolla lobe base, vibratile trichomes on the margins of the corolla lobe bases, and spreading, replicate corolla lobe tips) has apparently evolved twice within the section *Bowkerianae.*

The first plant of *Ceropegia stylesii* (Fig. 1A) was seen at a locality where sympatric with the dark-flowered form of *C. gerrardii*. When not in flower, *C. stylesii* and *C. gerrardii* cannot be readily distinguished; early buds are also alike. At a first glance, the flowers of *C. stylesii* (Figs. 1B, 2A,B), though being considerably smaller, superficially resemble flowers of the dark-flowered form of *C. gerrardii* (Fig. 2A). However, the corolla lobes are always ascending in *C. stylesii* while in *C. gerrardii* they are commonly reflexed when flowers are fully opened. The gynostegial structure of *C. stylesii* differs considerably from that of *C. gerrardii* in the staminal corona lobes being short and appressed to the style-head (Figs. 2C,D) while they are erect and markedly exceed the mouth of the corolla as a bundle in *C. gerrardii* (white arrow-head in Fig. 2A). These differences in gynostegial morphology are unlikely to facilitate hybridization, an assumption supported by the absence of intermediate forms. Moreover, small flies of the family Ceratopogonidae were observed on *C. stylesii* flowers, while *C. gerrardii* flowers are visited by larger flies of the families Milichiidae and Chloropidae (Heiduk *et al.* in prep.). This suggests that species integrity is maintained through differences in pollinating flies.

Acknowledgments

Ulrich Meve and Sigrid Liede-Schumann (University of Bayreuth) are thanked for their continuous support and expert advice. Benny Bytebier, curator of the Bews Herbarium (NU), and Christina Curry, collection manager at NU, are both thanked for assistance in taking care of the collections.

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