



Lithops gracilidelineata subsp. *mopane* (Aizoaceae): a new subspecies from Mopane-*Pachypodium* shrubland in northwestern Namibia

S. A. Hatt^{1,2}, O. M. Grace^{1,3}, N. S. Ndilenga^{2,4}, S. Loots⁵ & G. Maggs-Kölling^{2,6}

Summary. During a comprehensive survey and conservation assessment of populations of *Lithops gracilidelineata* (Aizoaceae), a population at the northern limit of its distribution was identified as profoundly morphologically and ecologically distinct. Following a taxonomic revision of the infraspecific limits of *Lithops gracilidelineata*, a new subspecies is described from Mopane-*Pachypodium* shrubland in northwestern Namibia. *Lithops gracilidelineata* subsp. *mopane* S.Hatt can be distinguished by its completely smooth leaf surface relief (vs distinctly rugose), that is very pale, whitish-grey, occasionally with a very pale, pinkish-yellowish tint (vs pale pinkish-beige to very pale, greyish-beige in subsp. *gracilidelineata*; or pinkish or reddish-brown, rarely more beige or yellowish in subsp. *brandbergensis*) and being almost exclusively 1-headed (vs often 2 – 3 headed). It differs from all other *Lithops* species by growing in Mopane shrubland of *Colophospermum mopane*, with interspersed *Pachypodium lealii*, amongst quartz pebbles and gravel. Descriptions, photographic illustrations and preliminary conservation assessments are provided for all accepted subspecies of *Lithops gracilidelineata*. An infraspecific key is also given, completing a revised classification of this threatened and horticulturally important succulent species.

Key Words. Africa, Brandberg, Central Namib, Namib Desert, succulent

Introduction

Lithops N.E.Br. (Aizoaceae) is a genus of dwarf succulent plants endemic to southern Africa. They are commonly referred to as ‘flowering stones’ or ‘stone plants’ due to their remarkable resemblance to the rocks and pebbles amongst which they grow (Cole & Cole 2005). Their unusual morphology and appearance mean they camouflage convincingly with their surroundings, allowing them to remain concealed from herbivores (Loots & Nybom 2017). *Lithops* have significant aesthetic appeal and commercial value in the horticultural trade. This has attracted an international network of passionate collectors and amateur botanists, many of whom have published detailed books on the subject (e.g., Cole & Cole 2005; Earlé & Round 2010; Jainta 2017) and pioneered research on the genus.

Many species of *Lithops*, and other similar succulent plants in the Aizoaceae, such as *Conophytum* N.E.Br., are under significant threat from illegal collecting of live plants and seeds (Loots 2005; Loots & Nybom 2017). Reports of large numbers of succulent plants seized at the border are increasingly common (National Report 2023) and collecting has decimated wild populations (Margulies *et al.* 2023). Due to their inconspicuous size

and appearance, *Lithops* are likely to be overlooked in development projects and environmental impact assessments (EIAs). *Lithops* often occur in very small, geographically isolated populations, making them particularly vulnerable to disturbance (Loots & Nybom 2017).

Lithops gracilidelineata Dinter was described in 1928, following a collection made by Ernst Rusch a year earlier near Uis and Nainais (Dinter 1928). Its range spreads northwards, from ~40 km east of Walvis Bay to ~25 km southeast of Fransfontein, wrapping around the distribution of *Lithops ruschiorum* (Dinter & Schwantes) N.E.Br. to the west. The species was divided into two subspecies by Hendrik de Boer in 1963, who described a new subspecies from the Brandberg Mountain (de Boer 1963b). A variety of subsp. *gracilidelineata* was also published the same year (de Boer 1963a). The classification has not changed since then, with the exception of Jainta (2019) suggesting that all infraspecific taxa are disregarded.

The population known as ‘C373’ (Cole & Cole 2005), located ~25 km southeast of Fransfontein, was visited during a series of population surveys of *Lithops gracilidelineata* across its entire known range undertaken by the first and second authors in Oct. – Dec. 2023. This population was found to be morphologically, ecologically

Accepted for publication 31 March 2025.

¹ Royal Botanic Gardens, Kew, Richmond, TW9 3AE, UK. e-mail: s.hatt@kew.org

² Gobabeb - Namib Research Institute, Gobabeb, Namibia

³ Royal Botanic Garden Edinburgh, Edinburgh, UK

⁴ Department of Botany and Zoology, Stellenbosch University, Stellenbosch Campus, South Africa

⁵ Ministry of Environment, Forestry and Tourism, National Botanical Research Institute, Windhoek, Namibia

⁶ Unit for Environmental Sciences and Management, North-West University, Potchefstroom Campus, South Africa

and geographically distinct to all other populations observed. Here we present a revised infraspecific classification of *Lithops gracilidelineata*, with the description of a new subspecies: subsp. *mopane*. Photographs are provided for each subspecies (Fig. 1) together with a distribution map of known populations (Map 1). Given the significant threat faced by this species from poaching, exact co-ordinates are deliberately not provided for any specimens referenced.

Materials and Methods

This study used a combination of literature research, fieldwork and consultation of herbarium specimens. Fieldwork by SAH and NSN took place in Oct. – Dec. 2023, as part of a series of population surveys of *Lithops gracilidelineata* across its entire known range, to gather data for an IUCN (2012) Red List assessment. Extensive fieldwork and surveys of *L. gracilidelineata* and other *Lithops* species have also been undertaken by EM, GMK and SL over the last 20 years.

Species descriptions for taxa were compiled from Sprechman (1970), Hammer (1999), Cole & Cole (2005), Hartmann (2017), Jainta (2017), Earlé & Young (2020), species protologues, and measurements of plants observed *in situ* by the authors. The following herbaria were consulted for specimens of *Lithops*, either by in-person visits, information requests to curators or via online databases: A, BOL, G, GBB, K, L, NBG, P, PRE, US, WIND (herbarium acronyms follow Thiers 2025). The distribution map was generated using ArcGIS Pro 2.8 (ESRI 2024, <https://www.esri.com/en-us/home>) based on precise locality data. We have withheld specific locality data to help protect the plants from illegal harvesting. Information regarding conservation status has been collected for each subspecies and will be made available as formal IUCN (2012) Red List assessments published on the IUCN Red List of Threatened Species (<https://www.iucnredlist.org>).

Taxonomic Treatment

Lithops gracilidelineata Dinter (1928: 18); Schwantes (1957: 203); Cole (1973: 50); Cole (1987: 14); Cole (1988: 216); Hammer (1999: 64); Cole & Cole (2005:

144); Jainta (2017: 370); Jainta (2019: 13). Neotype, designated here (see Notes below): Namib Naukluft Park, near Husab Mine [precise locality withheld], 7 Nov. 2012, Loots SL 299 (WIND).

Lithops streyi Schwantes (1951: 74 – 75). Type: Abb. 2:

Lithops streyi Schwant. spec. nov. 2/3 nat. Grösse.

Bild: Jacobsen. (lectotype, photograph of cultivated material in the protologue, pp. 75, designated here).

Lithops gracilidelineata subsp. *gracilidelineata* var. *waldroniae* de Boer (1963a: 20).

Lithops pseudotruncatella var. *gracilidelineata* (Dinter) B.Fearn (1970: 92).

Lithops pseudotruncatella var. *gracilidelineata* forma *waldroniae* (de Boer) B.Fearn (1970: 92).

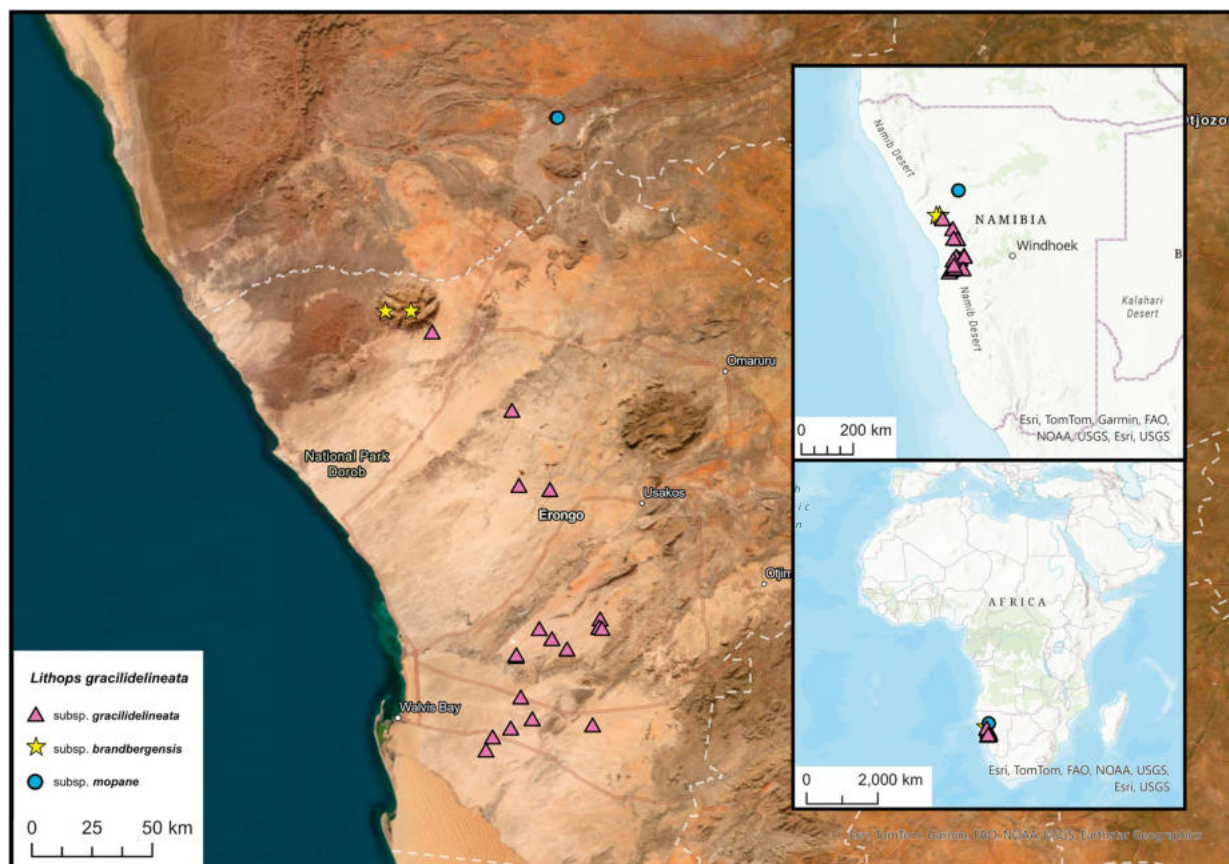
Dwarf succulent, 1 – 2 (– 5)-headed. *Leaves* truncate, usually somewhat convex-topped, occasionally flat; fissure shallow, 2 – 7 mm; lobes conjunct; leaf surface (face) pale beige to yellowish to reddish to very pale greyish-white, 15 – 36 (– 50) × 15 – 25 (– 38) mm, flush, round to elliptic, lobes mostly equal, opaque to mostly opaque; fenestrations (windows) absent or not clearly distinguishable; leaf surface relief a branching system of interconnected channels rendering the surface distinctly rugose, rarely smooth; the channels forming a mostly unbroken network, sometimes with irregularly branched lines tapering off into the marginal area; leaf surface markings (rubrications) obscure to strongly defined, usually a number of fine dots, dashes or short lines set in the channels, usually indistinguishable from the channels if rugose. *Flower* solitary, 10 – 35 (– 45) mm in diameter, occasionally with almond-like scent; calyx lobes 6 – 7, pale reddish-pink to greenish, almost as long as petaloid staminodes, rarely longer, lanceolate to oblanceolate, somewhat concave towards apex; petaloid staminodes 40 – 60, in 2 – 3 rows, bright yellow with paler base, narrowly lanceolate to linear; filamentous staminodes many, apically yellow with paler base, gathered around stamens, somewhat constricted around the base; stigmas 6 – 7, yellowish-green. *Capsule* 6 – 7 (– 12)-merous, boat-shaped to rotund, top flat to slightly convex or peaked; face round to broadly elliptic, 6 – 9 (– 11.5) mm across. *Seeds* light yellow-brown, 0.60 – 0.80 mm, smooth to rugose; globes flattened, or rounded with prominent eminence.

Key to the infraspecific classification of *Lithops gracilidelineata*

1. Leaf surface (face) pinkish or reddish-brown, rarely more beige or yellowish; leaf surface markings (rubrications) strongly defined, blood-red; growing amongst granitic rock; only known from the Brandberg Mt....
..... 2. subsp. **brandbergensis**
1. Leaf surface (face) pale pinkish-beige to very pale greyish-beige or greyish-white; leaf surface markings (rubrications) present to obscure, but not strongly defined; growing amongst quartz or marble; not restricted to the Brandberg Mt..... 2



Fig. 1. The three subspecies of *Lithops gracilidelineata* and their respective habitats. Subsp. *gracilidelineata*. **A** flowering individual; **B** water-deprived individual; **C** multi-headed individual, mostly concealed by windblown sand; **D** typical marble ridge habitat. Subsp. *brandbergensis*. **E** turgid individual; **F** post-fruiting individual; **G** individual concealed amongst granite pebbles of similar colour; **H** typical granite boulder habitat on the Brandberg Mountain. Subsp. *mopane*. **J** turgid, post-fruiting individual; **K** individual with desiccated old leaves still attached; **L** two individuals camouflaged amongst quartz pebbles; **M** the quartz pebble Mopane-*Pachypodium* habitat of the only known population. PHOTOS: **A** GILLIAN MAGGS-KÖLLING; **B – D, H – M** SEBASTIAN HATT; **E, G** ERNST VAN JAARSVELD; **F** MHAIRI MCFARLANE.



Map 1. Distribution map of the subspecies of *Lithops gracilidelineata*. To protect sensitive locality information, observation points have been spatially randomised within a 15 km radius of their true locations.

2. Leaf surface relief almost completely smooth, without channels or islands; very pale whitish-grey, occasionally with very pale pinkish-yellowish tint; most often 1-headed; only known from Mopane shrubland near Fransfontein/Khorixas..... **3. subsp. mopane**
2. Leaf surface relief distinctly rugose, with clearly defined channels and islands; pale pinkish-beige to very pale greyish-beige; usually 1 – 2 (– 5) headed; not known from Mopane shrubland... **1. subsp. gracilidelineata**

1. *Lithops gracilidelineata* Dinter (1928: 18) subsp. gracilidelineata; Schwantes (1957: 203); Cole (1973: 50); Cole (1987: 14); Cole (1988: 216); Hammer (1999: 64); Cole & Cole (2005: 144). Type as for species.

Dwarf succulent, 1 – 4 (– 10)-headed. *Leaves* truncate, usually somewhat convex-topped, occasionally flat; fissure shallow, 2 – 7 mm; lobes conjunct; leaf surface (face) fairly uniform, pale pinkish-beige to very pale whitish-greyish-beige, 15 – 35 (– 50) × 15 – 25 (– 38) mm, flush, round to elliptic, lobes mostly equal, opaque, usually distinctly rugose; fenestrations (windows) absent or not clearly distinguishable; leaf surface relief a branching system of interconnected channels rendering the surface distinctly rugose, the channels form a mostly unbroken network, sometimes with irregularly branched

lines tapering off into the marginal area, translucent greyish-green to brown; leaf surface markings (rubrications) obscure, usually a number of fine dots, dashes or short lines set in the channels, usually indistinguishable from the channels. *Flower* solitary, 10 – 35 (– 45) mm in diameter, occasionally with almond-like scent; calyx lobes 6 – 7, pale reddish-pink to greenish, almost as long as petaloid staminodes, rarely longer, lanceolate to oblanceolate, somewhat concave towards apex; petaloid staminodes 40 – 60, in 2 – 3 rows, bright yellow with paler base, narrowly lanceolate to linear; filamentous staminodes many, apically yellow with paler base, gathered around stamens, somewhat constricted around the base; stigmas 6 – 7, yellowish-green. *Capsule* 6 – 7 (– 12)-merous, boat-shaped to rotund; top part flat to slightly convex or peaked, face round to broadly elliptic,

6–9 (–11.5) mm across. *Seeds* light yellow-brown, 0.60–0.80 mm, smooth to wavy-rugose, globes rounded with prominent eminence. (Fig. 1A–C).

DISTRIBUTION AND HABITAT. The Central Namib Desert spans several vegetation zones (Juergens *et al.* 2013), from about 40 km N of Uis southward to the Tumas River area and Hamilton Range (Map 1). The western range limit of this species is the Khan River until about 50 km SW of Usakos, lying east of the distribution of *Lithops ruschiorum*. Approximately 20 populations have been identified around the Swakop River and Husab region, usually along low, marble/calc-silicate/quartzite ridges. Fewer populations have been identified N of Usakos, but scattered populations have been located from Usakos north-westward to the surrounds of the Brandberg Mountain. Populations are distributed unevenly across the range, with marble/calc-silicate/quartzite ridges and outcrops serving as islands in an otherwise inhospitable matrix of barren gravel plains or unsuitable rock types. Typically found growing in crevices of light-coloured marble, quartzite and calc-silicate rock, often partially concealed by windblown quartzite gravel and coarse sand; often on low ridges (Fig. 1D); elev. 300–c. 900 m. Flowering after rainfall, typically February to May.

SPECIMENS EXAMINED. NAMIBIA. ERONGO: Namib Naukluft Park, near Husab Mine [precise locality withheld], 28 June 2010, *Loots* SL 274 (WIND [image only]); Namib Naukluft Park, near Husab Mine [precise locality withheld], 11 June 2011, *Loots* SL 281 (WIND); Namib Naukluft Park, near Langer Heinrich Mine [precise locality withheld], 14 June 2011, *Loots* SL 282 (WIND); Namib Naukluft Park, near Husab Mine [precise locality withheld], 6 Nov. 2012, *Loots* SL 298 (WIND); Namib Naukluft Park, near Husab Mine [precise locality withheld], 7 Nov. 2012, *Loots* SL 299 (WIND); Namib Naukluft Park, near Tumas Mine [precise locality withheld], 29 April 2021, *Burke* 21013 (WIND [WIND00102944]!); Namib Naukluft Park, near Hamilton Range [precise locality withheld], 2 Nov. 2023, *Hatt* 45 (WIND!).

CONSERVATION STATUS. In the *Red Data Book of Namibian Plants*, *Loots* (2005) assessed the extinction risk of this subspecies as Least Concern (LC). However, this species is range restricted, AOO = 92 km², EOO = 18,585 km² and occurs in 5–8 locations. The population has declined by 10–20% since 2008 due to habitat loss and illegal collecting. Climate change is projected to reduce habitat by up to 61% by 2070, leading to an inferred population decline of 60–70%, with an overall reduction of 70–90% suspected over three generations (2008–2068). An IUCN (2012) Red List assessment for *Lithops gracilidelineata* is currently in preparation, and preliminary results suggest a classification of Critically

endangered [CR A4cd] for the species as a whole. This suggests a significant escalation in risk of extinction since 2005.

ETYMOLOGY. After the finely-drawn lines on the leaf surface (Latin: *gracili-* ‘slender’, *delineata* ‘marked, lined, drawn’).

NOTES. The first recorded collection of this species was by Ernst Rusch in August 1927, near Uis and Nainais (Dinter 1928). This specimen was used by Kurt Dinter to formally describe the species in 1928 as *Lithops gracilidelineata*: a small species of light yellow-grey to milky-tea colour, with a mostly flat leaf surface divided into c. 30 or more islands, defined by slender, dark brown lines (Dinter 1928). This species has been retained since then, but has been subdivided into subspecies and varieties. The type collection has not been located at GBB, K, NBG, PRE or WIND and is thus considered lost. As such, we neotypify the species here. We select a specimen collected by Sonja Loots in 2012, as the identity has been verified and a physical specimen is deposited in the National Herbarium of Namibia (WIND).

Several authors (Hammer 1999; Cole & Cole 2005; Jainta 2017) have noted the similarity of this species to *Lithops pseudotruncatella* (A.Berger) N.E.Br., *L. ruschiorum* and *L. werneri* Schwantes & H.Jacobsen, and suggested these four taxa may form a closely related species group. Although the distribution of *L. gracilidelineata* and *L. ruschiorum* appears to be fairly well-defined, there have been a few reports of sites where the two species occur near-sympatrically (Cole & Cole 2005; Jainta 2017).

Lithops gracilidelineata var. *waldroniae* was described by Hendrik de Boer in 1963 from a specimen provided to him by Mrs Molly Waldron, who collected it c. 50 km E of Walvis Bay (de Boer 1963a), likely on the Hamilton Range or at Vogelfederberg. Emil Jensen likely collected a specimen of it earlier, around 1957, from a locality ‘south of Walvis Bay, from the spur of the mountain of the Gungochoab’. He sent this specimen to Schwantes, who apparently did not consider it distinct from other *L. gracilidelineata* he had seen.

Some authors (Cole & Cole 2005; Jainta 2017) have expressed doubt at the status of this variety, with Desmond Cole describing it as ‘rather tenuous’. Indeed, Jainta (2017) and the authors (pers. obs.) report a gradient of rugosity/reticulation from south to north, with var. *waldroniae* more prevalent in the south. According to the proposed guidance on *Lithops* taxonomic rank allocation, by Cole & Cole (2005), we opt to relinquish its status as a variety due to it being poorly distinguished by only minor characters (somewhat smaller flower, larger seeds, and a generally more reticulately-lined leaf surface, but with the characters presenting on a gradient with var. *gracilidelineata*). A study of population genetics is required to better understand such population-level variation in this species.

2. *Lithops gracilidelineata* subsp. *brandbergensis* (de Boer) D.T. Cole (1988: 217); Hammer (1999: 64); Cole & Cole (2005: 144). Neotype, designated by Cole & Cole (2001: 120): Namibia, Brandberg Mountain, 14 May 1986, Cole 383 (PRE).

Lithops pseudotruncatella var. *brandbergensis* de Boer (1963b: 53).

Dwarf succulent, mostly 1-headed, rarely 2. *Leaves* truncate, usually somewhat convex-topped, occasionally flat; fissure shallow, 4 – 8 mm; lobes conjunct; leaf surface (face) usually pinkish or reddish-brown, rarely more beige or yellowish, c. 20 – 36 (– 48) × c. 20 – 28 (– 36) mm, flush, round to elliptic, lobes mostly equal, mostly opaque, rugose, margins not clearly distinguishable, irregularly indented, often lighter in colour than face; fenestrations (windows) mostly absent; leaf surface relief a branching system of interconnected channels forming islands that render the surface distinctly rugose; leaf surface markings (rubrications) strongly defined, blood red or brownish to purplish-red, a network of fairly regular bold lines, sometimes with intermediate branches, usually bifurcating digitately into the margins, the network occasionally reduced to a number of dots, dashes or short lines. *Flowers* solitary, 25 – 30 (– 35) mm in diameter, occasionally with almond-like scent; calyx lobes 6 (– 7), pale reddish-pink to greenish, almost as long as petaloid staminodes, rarely longer, lanceolate to oblanceolate, somewhat concave towards apex; petaloid staminodes 40 – 60, in 2 – 3 rows, bright yellow with paler base, narrowly lanceolate to linear; filamentous staminodes many, apically yellow with paler base, gathered around stamens, somewhat constricted around the base; stigmas 6 – 7, yellowish-green. *Capsule* 6 (– 7)-merous, boat-shaped to rotund; top part convex to peaked, face broadly elliptic, 7.5 – 9 mm across. *Seeds* light yellow-brown, (0.74 –) 0.76 – 0.82 mm, rugose, globes flattened. (Fig. 1E – G).

DISTRIBUTION AND HABITAT. Known only from a few isolated populations on the Brandberg Mountain in the Erongo Region, Namibia (Map 1). Two populations are known from near the peak of the Brandberg, at c. 2300 m, and a few other populations have been noted on the lower slopes to the east and west. Given that this species is easily missed and much of the Brandberg has not been searched for *Lithops*, it may be more widely distributed across the Brandberg than currently appreciated. One or two populations have been identified surrounding the Brandberg, e.g. J239 (Jainta 2017), which may represent an intermediate form between subsp. *brandbergensis* and subsp. *gracilidelineata*, the plants usually amongst brown granitic gravel (Fig. 1H); elev. 800 – 2350 m.

SPECIMENS EXAMINED. The type specimen is the only known report of an herbarium collection, although this specimen has not been seen by the authors.

CONSERVATION STATUS. In the *Red Data Book of Namibian Plants*, Loots (2005) assessed the extinction risk of this subspecies as Near Threatened (NT). This subspecies has a restricted range and is facing threats from illegal harvesting and trampling, with some evidence of population decline. An IUCN (2012) Red List assessment for *Lithops gracilidelineata* subsp. *brandbergensis* is currently in preparation, with preliminary results suggesting a classification of Endangered [EN].

ETYMOLOGY. Named after the Brandberg mountain, to which this subspecies is endemic.

NOTES. This subspecies was first collected by Jalmar Rudner in 1955 in the high valleys of the Brandberg (Wiss 1956; Lempp 1956; Nordenstam 1974). Gustav Schwantes initially considered it a population of *Lithops dendritica* Nel (de Boer 1963b), until it was published as *Lithops pseudotruncatella* var. *brandbergensis* by Hendrik de Boer in 1963 (de Boer 1963b). Although de Boer noted it could be considered a variety of *L. gracilidelineata*, and even commented on the similarity on the pattern of the leaf surface relief, he assigned it to *L. pseudotruncatella* based on how strongly defined the leaf surface markings (rubrications) were. He closed the protologue by suggesting that it may represent an intermediate form between the two species. In his diagnosis, he wrote that it differed from the type by ‘its uniformly yellow-brown leaf faces, strongly defined dendritic lines surrounded by a hazy, grayish-blue margin or dots’ (de Boer 1963b, pp. 53, author’s translation).

Desmond Cole speculated that this subspecies likely belonged to *Lithops gracilidelineata* (Cole 1973), but only confirmed this rearrangement after having seen the plant in situ many years later (Cole 1986, 1988). This decision was based in part on the similarity of its seed structure to this species, and not to *L. pseudotruncatella* (Earlé & Round 2010). Considerate of the proposed guidance on *Lithops* taxonomic rank allocation by Cole & Cole (2005), we retain its status as a subspecies, due to its unique ecological context (granitic rock on the Brandberg Mountain) and morphological distinction afforded by its distinctive reddish-brown colour and strongly defined reddish rubrications. Individuals collected in the overlapping zone between the ranges of subsp. *brandbergensis* and subsp. *gracilidelineata* which appear intermediate in form, e.g. J239 (Jainta 2017), do not invalidate the classification proposed here: such occasional intermediate forms are expected between subspecies with overlapping distributions, but are otherwise discrete entities.

The type collection by Rudner has not been located. Therefore, Cole & Cole (2001) designated their collection as a neotype, deposited at PRE, although this specimen has not been seen by the authors.

3. *Lithops gracilidelineata* subsp. *mopane* S.Hatt subsp. nov. Type: Namibia, Kunene Region, near Khorixas [precise locality withheld], 15 Nov. 2023, *Hatt* 48 (holotype WIND).

<http://www.ipni.org/urn:lsid:ipni.org:names:77361738-1>

Dwarf succulent, almost exclusively 1-headed. *Leaves* truncate, usually somewhat convex-topped, occasionally flat; fissure shallow, 2–4 mm, lobes conjunct; leaf surface (face) very pale whitish-grey, occasionally with very pale pinkish-yellowish tint, c. 15–35 (–45) × c. 15–25 (–35) mm, flush, round to elliptic, lobes mostly equal, opaque, consistently almost completely smooth; fenestrations (windows) absent or not clearly distinguishable; leaf surface smooth, rarely with delicate rubrications interspersed with slight humps; leaf surface markings (rubrications) a network of very delicate dashes or dots across the leaf surface, these markings usually so interrupted that distinct islands are not possible to define, deep reddish but often so thin and delicate that they appear translucent. *Flower* not seen in habitat. *Capsule* 6 (–7)-merous, boat-shaped to rotund; top part flat to slightly convex or peaked, face round to broadly elliptic; c. 8 (–11) mm across. *Seeds* not seen. (Fig. 1J–L).

RECOGNITION. Similar to *Lithops gracilidelineata* subsp. *gracilidelineata*, but differs in having a completely smooth leaf surface relief (vs distinctly rugose in subsp. *gracilidelineata*), that is very pale whitish-grey, occasionally with a very pale pinkish-yellowish tint (vs pale pinkish-beige to very pale greyish-beige in subsp. *gracilidelineata*; or pinkish or reddish-brown, rarely more beige or yellowish in subsp. *brandbergensis*) and being almost exclusively 1-headed (vs often 2–3-headed). Differs from all other *Lithops* species in growing amongst Mopane shrubland.

DISTRIBUTION AND HABITAT. Confirmed from a single, small population growing in a field of quartz, c. 25 km SE of Fransfontein [precise locality withheld] (Map 1). A separate population has been cited ‘near Fransfontein, 100 km W of Outjo’ (Jacobsen 1955; Schwantes 1957), but this was not verified at the time by any photograph or specimen evidence, and has not been recorded since. This population may be extinct, inaccurate, or in need of rediscovery. Found amongst quartz pebbles and gravel, amongst a moderately dense shrubland of *Colophospermum mopane* (J.Kirk ex Benth.) J.Léonard with interspersed *Pachypodium lealii* Welw. (Fig. 1M); elev. 1120–1140 m.

SPECIMENS EXAMINED. NAMIBIA. Kunene Region, near Khorixas [precise locality withheld], 15 Nov. 2023, *Hatt* 48 (holotype WIND).

CONSERVATION STATUS. This subspecies has a very restricted range and population size and is only known from an area of active farmland. Consequently, the risk

of extinction is likely very high. An IUCN (2012) Red List assessment for *Lithops gracilidelineata* subsp. *mopane* is currently in preparation, with preliminary results suggesting a classification of Critically Endangered [CR].

ETYMOLOGY. Named after Mopane (*Colophospermum mopane* (J.Kirk ex Benth.) J.Léonard). This subspecies has only been found amongst Mopane shrubland, a unique habitat for *Lithops*.

NOTES. While conducting a series of population surveys of *Lithops gracilidelineata* across its entire range to gather data for an IUCN (2012) Red List assessment, the authors visited the population of *Lithops* found ‘25 km SE of Fransfontein’, a locality also known as ‘C373’ in Cole & Cole’s (2005) widely referenced list of *Lithops* localities. Having surveyed and examined *Lithops gracilidelineata* at a great number of populations and localities across the entirety of its known geographic range, it was immediately clear that the *Lithops* at C373 were distinct from other *L. gracilidelineata* taxa.

Leaf surface relief and colour of individuals at C373 distinguish them as unique from all other members of the species. For example, the leaf surfaces of all other *Lithops gracilidelineata* encountered in their natural habitat are distinctly rugose, regardless of recent rainfall, whereas the leaf surfaces of plants at C373 are consistently and almost completely smooth, lacking any channels or islands. Leaf surface markings (rubrications) are present, but usually so interrupted that distinct islands are not possible to define. Individuals at C373 are consistently light-grey to white, which is distinct from subsp. *gracilidelineata* (pale pinkish-beige to very pale greyish-beige) and subsp. *brandbergensis* (pinkish or reddish-brown, rarely more beige or yellowish). Their colour camouflages perfectly with the surrounding quartz pebbles, making them extremely challenging to detect. The plants we found were consistently 1-headed, which differed from all other populations of *L. gracilidelineata*, where individuals with two or more heads were predominant.

The *Lithops* at C373 are approximately 100 km NE of the nearest known population of *L. gracilidelineata*. This is considerably more geographically isolated than any other population in the species. Here, they grow amongst quartz pebbles and gravel in Mopane shrubland, amongst *Pachypodium lealii*; a habitat not observed for any other *Lithops*. Typical habitats for *L. gracilidelineata* are low marble ridges or outcrops, or quartz gravel in barren, arid areas of the Namib Desert (subsp. *gracilidelineata*), or granitic rock high on the Brandberg mountain (subsp. *brandbergensis*). The substrate at C373, soil strewn with quartz pebble and gravel, is also distinct from the typical substrate of *L. gracilidelineata* — windblown quartzite gravel and coarse sand amongst marble rock. Furthermore, almost all the known localities of *L. gracilidelineata* are in areas with <100 (–150) mm annual rainfall, while

C373 lies in an area with c. 150 – 250 mm annual rainfall (Atlas of Namibia 2022). The considerably higher rainfall, distinct substrate and surrounding shrubland of Mopane and *Pachypodium* make the ecology of this population unique amongst *Lithops gracilidelineata*.

Cole & Cole (2005), who completed the latest and mostly widely accepted taxonomic monograph of *Lithops*, provide the following criteria suggestion for subspecific rank designation: ‘(a) Have the same general characteristics as the species and (b) are closely related to one another, but (c) are clearly distinguishable from one another (i.e. with minimal or no overlap) by certain subsidiary or sub-specifically peculiar features which characterise them, and (d) are geographically discrete or have only minimal overlap in range’. Under these criteria, for the reasons outlined above, the authors believe that the population at C373 should be regarded as a distinct subspecies of *L. gracilidelineata*. In contrast to the suggestion of Jainta (2019), the authors favour recognising with sub-specific rank the evident morphologically, ecologically and therefore, presumably, genetically distinct lineages within the species. Consequently, a name must be selected and designated for this new taxon.

The C373 population has been widely known as *Lithops gracilidelineata* syn. *streyi*, after *Lithops streyi*, a name that was described by Schwantes in 1951 (Schwantes 1951), but which he sunk not long after (Jacobsen 1955). Indeed, Cole & Cole (2005) cite C373 as the type locality for *L. streyi*. Interestingly, there is no explicit reference to the C373 population in the protologue of *Lithops streyi*; Schwantes simply wrote (Schwantes 1951, pp. 75, author’s translation from German): ‘I received this extraordinarily distinctive species from Mr R.G.Strey in Windhoek, with the information: *quartz mountain in the Namib*. It is only a few years later in Hermann Jacobsen’s 1955 *Handbook of Succulent Plants* (Jacobsen 1955), of which Schwantes was a named contributor, that the name *L. streyi* was directly linked to the population ‘25 km SE of Fransfontein’. Here, a locality of *L. gracilidelineata*: ‘near Witklip, 65 miles southwest of Outjo’ is mentioned, which is referenced in the sentence that follows: ‘...the occurrence near Witklip... an isolated quartz mountain in the middle of an extended granite region, here representing Schwantes’ *L. streyi*. This locality description is equivalent to ‘25 km SE of Fransfontein’, and, therefore, likely refers to the same population of *Lithops*. Accordingly, the name *Lithops streyi* does indeed likely refer to the C373 population. Interestingly, Nel (1947) mentions Fransfontein as a locality for *L. gracilidelineata* in his account for the species, but does not provide further information or comments than that. This suggests that the Fransfontein population was known at least some years before Schwantes’ description of *L. streyi* in 1951.

However, there are inconsistencies with the type description of *Lithops streyi*, and the population observed at C373. The description is brief, but reads (Schwantes 1951, pp. 74, author’s translation from Latin): ‘Obconic bodies; 2–2.5 cm long; apex sub-flat; orbicular; fissure 4 mm high, pale grey-white, very rugose; wrinkles with branched tips. Flowers 2.5 cm wide, yellow, as in the genus.’ Schwantes specifically notes that the leaves are *valde rugosa* (very rugose). This description contradicts our observations of the plants being unusually smooth, which have been corroborated by other authors who visited, described and photographed the population (Cole & Cole 2005; Jainta 2019). Furthermore, the type description is accompanied by a photograph that depicts an individual of *Lithops gracilidelineata* with a distinctly rugose leaf surface relief, apparently taken in cultivation and not in its natural habitat. Schwantes did not see the plant in its habitat, having described it from a specimen provided by Mr R. G. Strey, who apparently collected the material himself. It is unknown whether this specimen was living or dead when it reached Schwantes. If Schwantes received a live specimen, it is unknown whether this was grown from seed, propagated from an uprooted individual, or taken directly from the wild population. As a result, the provenance of the specimen received by Schwantes cannot be confirmed and may therefore be dubious. Given there is no preserved type specimen known or cited, the photograph provided in the protologue must instead serve as the lectotype (Turland *et al.* 2018: Sec. 2, Art. 9.9), which the authors designate here. This lectotype, although apparently depicting an individual of *Lithops gracilidelineata*, is clearly different from subsp. *mopane*. Furthermore, the provenance of the individual appearing in the lectotype photograph is dubious.

According to the Code of Nomenclature, a name has no priority outside the rank at which it is published (Turland *et al.* 2018: Sec. 3, Art.11.2), allowing the authors to select a new name to describe this subspecies, thus avoiding any confusion surrounding the identity of *Lithops streyi*. The authors, therefore, name this population *Lithops gracilidelineata* subsp. *mopane*, after the unique, Mopane shrubland habitat of these plants.

Acknowledgements

We are very grateful to the owners of the farm on which the type specimen of subsp. *mopane* was collected, for kindly allowing us onto their land, helping us fix our broken tyre and especially to Michael for assisting in the search for the plants. We are very grateful to Eugene Marais at Gobabeb for his expert guidance on fieldwork planning and for sharing his extensive

knowledge of the area, to Roy Earlé at Alte Kalköfen for sharing valuable co-ordinate data that greatly aided fieldwork, and to Ernst van Jaarsveld and Mhairi McFarlane for kindly sharing photographs of *Lithops gracilidelineata* subsp. *brandbergensis* for use in Fig. 1. We would like to thank the: Mohamed bin Zayed Species Conservation Fund (Grant No.: 232531392), the British Cactus and Succulent Society (BCSS) Conservation Grant and the International Organisation for Succulent Plant Study (IOS) Research Fund, for generously awarding funds for the first author to visit Namibia in Oct. – Dec. 2023, to undertake fieldwork for this research. The National Commission on Research, Science and Technology in Namibia issued Research Authorisation (# 20230816) under Gobabeb's Registration Certificate (# RCIV00062018) for this work, upon endorsement of the Ministry of Environment, Forestry and Tourism.

Declarations

Funding Mohammed bin Zayed Species Conservation Fund, 232531392, Sebastian A. Hatt, British Cactus and Succulent Society, International Organisation of Succulent Plant Study.

Data Availability All relevant data is included in the text or cited specimen.

Conflicts of Interest The authors declare no conflict of interest.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Atlas of Namibia Team (2022). *Atlas of Namibia*. Namibia Nature Foundation, Windhoek.
- de Boer, H. W. (1963a). *Lithops gracilidelineata* Dint. (*Lithops streyi* Schwant.). *Succulenta* 2: 19 – 21.
- ____ (1963b). *Lith. pseudotruncatella* var. *brandbergensis* var. nov. de Boer. *Succulenta* 4: 51 – 54.
- Cole, D. T. (1973). *Lithops: A Checklist and Index*. *Excelsa* 3: 37 – 71.
- ____ (1986). Atop the Brandberg — at last! *ALOE* 23: 81 – 85.
- ____ (1987). *Lithops* of SWA/Namibia. *Madoqua Memoir* 1.
- ____ (1988). *Lithops: flowering stones*. Acorn Books, Randburg.
- ____ & Cole, N. A. (2001). *Lithops*, pp. 114 – 134. In: H. E. K Hartmann (ed.), *Illustrated Handbook of Succulent Plants: Aizoaceae F-Z*. Springer, Berlin Heidelberg.
- ____ & ____ (2005). *Lithops: flowering stones*. New Ed., updated and partially rev. [s.l.]. Cactus & Co. Libri.
- Dinter, K. (1928). *Südwestafrikanische Lithopsarten*. R. Graessner, Perleberg.
- Earlé, R. A. & Round, J. E. (2010). *Lithops in habitat and cultivation*. The Lavenham Press, Lavenham, Suffolk.
- ____ & Young, A. J. (2020). The form, structure and size of *Lithops* N.E.Br. seeds and the taxonomic implications. *Bradleya* 38: 195 – 224. <https://doi.org/10.25223/brad.n38.2020.a20>.
- ESRI (2024). *ArcGIS Pro*. Environmental Systems Research Institute, Inc., Redlands, CA. <https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview>.
- Fearn, B. (1970). New combinations and an analytical key for the genus *Lithops*. *Cact. Succ. J. (Los Angeles)* 42: 89 – 93.
- Hammer, S. A. (1999). *Lithops: treasures of the veld; (observations on the genus Lithops N.E.Br.)*. British Cactus and Succulent Society, Ansty.
- Hartmann, H. E. K. (ed.) (2017). *Aizoaceae*. Springer, Berlin, Heidelberg. <https://doi.org/10.1007/978-3-662-49260-4>.
- IUCN (2012). *IUCN Red List Categories and Criteria*, Version 3.1. Second Edition. Species Survival Commission, International Union for Conservation of Nature, Gland and Cambridge.
- Jacobsen, H. (1955). *Handbuch der sukkulenten Pflanzen, Vol. III, Mesembryanthemaceae*. Gustav Fischer Verlag, Jena.
- Jainta, H. (2017). *Wild Lithops*. Klaus Hess Publisher, Göttingen Windhoek.
- ____ (2019). A new taxonomic approach for the genus *Lithops* N.E.Br. *Avonia* 37: 6 – 17.
- Juergens, N., Oldeland, J., Hachfeld, B., Erb, E. & Schultz, C. (2013). Ecology and spatial patterns of large-scale vegetation units within the central Namib Desert. *J. Arid Environm.* 93: 59 – 79. <https://doi.org/10.1016/j.jaridenv.2012.09.009>.
- Lempp, F. (1956). Eine Erkundung der Brandberge in Südwestafrika. *Kosmos* 52: 424 – 436.

- Loots, S. (2005). *Red data book of Namibian plants*. Southern African Botanical Diversity Network, Pretoria.
- ____ & Nybom, H. (2017). Towards better risk assessment for conservation of flowering stones: Plant density, spatial pattern and habitat preference of *Lithops pseudotruncatella* in Namibia. *S. African J. Bot.* 109: 112 – 115. <https://doi.org/10.1016/j.sajb.2016.12.023>.
- Margulies, J. D., Moorman, F. R., Goettsch, B., Axmacher, J. C. & Hinsley, A. (2023). Prevalence and perspectives of illegal trade in cacti and succulent plants in the collector community. *Conservation Biol.* 37: e14030. <https://doi.org/10.1111/cobi.14030>.
- National Report (2023). *Wildlife Protection and Law Enforcement in Namibia for the year 2023*. Windhoek, Namibia.
- Nel, G. C. (1947). *Lithops*. University Press, Stellenbosch.
- Nordenstam, B. (1974). The flora of the Brandberg. *Dinteria* 11: 3 – 67. https://hdl.handle.net/10520/AJA00123013_223
- Schwantes, G. (1951). Bemerkungen zu einigen Mesembryanthemaceen: *Lithops streyi* Schwant. spec. nov. *Sukkulantenkunde* 4: 74 – 75.
- ____ (1957). *Flowering Stones and Mid-Day Flowers*. Ernest Benn, London.
- Sprechman, D. L. (1970). *Lithops*. Fairleigh Dickinson Univ. Press, Cranbury, NJ.
- Thiers, B. (2025, continuously updated). *Index Herbariorum: a global directory of public herbaria and associated staff*. New York Botanical Garden's Virtual Herbarium. Available online from: <http://sweetgum.nybg.org/science/ih/>. [Accessed 27 May 2025].
- Turland, N. J., Wiersema, J. H., Barrie, F. R., Greuter, W., Hawksworth, D. L., Herendeen, P. S., Knapp, S., Kusber, W. H., Li, D. Z., Marhold, K., May, T. W., McNeill, J., Monro, A. M., Prado, J., Price, M. J. & Smith, G. F. (2018). International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. *Regnum Veg.* 159. Koeltz Botanical Books, Glashütten. <https://doi.org/10.12705/Code.2018>.
- Wiss, H.-J. (1956). Brandberg Expedition 1955 — Ein Bericht über die gesammelten und beobachteten Pflanzen. *South West African Scientific Society Journal* 12: 4 – 68.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.