



A new species of *Hymenodictyon* (Rubiaceae, Cinchonoideae) from Namibia

WESSEL SWANEPOEL^{1,3*} & ERNST J. VAN JAARSVELD^{2,4}

¹*H.G.W.J. Schweickerdt Herbarium, Department of Plant and Soil Sciences, University of Pretoria, Pretoria, 0002 South Africa. Postal address: P.O. Box 21168, Windhoek, Namibia.*

²*Babylonstoren Farm, Simondium, 7670 South Africa. Affiliate researcher and senior lecturer, University of the Western Cape, P. Bag X17, Bellville, 7535, South Africa.*

³ wessel@kaokosafari.com; <https://orcid.org/0000-0002-0181-3543>

⁴ ernst@babylonstoren.com; <https://orcid.org/0000-0003-0143-8090>

*Author for correspondence.

Abstract

Hymenodictyon kaokoensis, here described as a new species, has a restricted range and is only known from the mountains along the Kunene River in the Kaokoveld Centre of Endemism, northwestern Namibia. It is represented by shrubs or small trees growing in rocky places, on mountain slopes and river valleys. Diagnostic characters for *H. kaokoensis* include the thickset semi-succulent older stems, echinate (scabrid when dry) leaves that turn stramineous before falling, simple racemose, erect inflorescences, and ellipsoid fruits with round or elongated prominent lenticels. A comparison of some of the more prominent morphological features to differentiate between *H. kaokoensis* and its possible nearest relatives, *H. floribundum* and *H. parvifolium*, are provided. Based on IUCN Red List categories and criteria, a conservation assessment of Vulnerable (VU D1 & D2) is recommended for the new species.

Keywords: endemism, flora, Hymenodictyoneae, Kaokoveld Centre of Endemism, Kunene Region, taxonomy

Introduction

The tribe Hymenodictyoneae Razafimandimbison & Bremer (2001: 535) contains two genera, *Hymenodictyon* Wallich (1824: 148) and *Paracorynanthe* Capuron (in Capuron & Leroy 1978: 160). At present two species of *Hymenodictyon*, are reported in the *Flora of southern Africa* region (South Africa, Namibia, Botswana, Eswatini and Lesotho). *Hymenodictyon parvifolium* Oliver (1885: 1488) is recorded from northeastern South Africa (Germishuizen & Meyer 2003) and *H. floribundum* (Hochstetter & Steudel 1842: 234) Robinson (1910: 404) from Namibia (Klaassen & Kwembeya 2013) (but see “Notes” under “Taxonomic treatment” further on). *Hymenodictyon*, is a paleotropical genus with 22 species (generally medium-sized to emergent trees including three epiphytes), with local biocultural importance. The generic name, according to Jackson (1990), is derived from two Greek words, *hymena*, “membrane”, and *dictyon*, “net”, referring to the membranous wings which girdles the seeds. Within the tribe Hymenodictyoneae, *Hymenodictyon* is easily recognized by the thick, non-plated (i.e. more or less smooth) bark, and the ellipsoid, capsular fruit (Razafimandimbison & Bremer 2006).

In this contribution, a new species of *Hymenodictyon* endemic to the Kaokoveld Centre of Endemism, a biogeographical region rich in range-restricted plants and animals in north-western Namibia and adjacent southwestern Angola (Van Wyk & Smith 2001) is described. During a botanical expedition to the remote Baynes Mountains in 2005, the authors encountered an unfamiliar small thickset tree in the Slangpoort Gorge, provisionally identified as a member of the genus *Hymenodictyon*, with elliptic, ovate or oblong-obovate leaves and immature fruit. Subsequently the same taxon, but also without flowers, was collected on the nearby Omavanda Mountain (two sites, central and northern Omavanda) and in the Zebra Mountains. During a visit to the Zebra Mountains by one of us (WS) in November 2017, the plants were found in flower and fruit, enabling fertile material to be collected and the plants to be identified as an undescribed species of *Hymenodictyon*, due to the elongate inflorescences, conspicuous disks, ellipsoid lenticellate fruits and corolla lobes lacking appendages. In November 2019 more flowering material of the species was collected by the authors in the Baynes Mountains. The new species seems to be closely related to *H. floribundum* and *H.*

parvifolium due to similarities in leaf, inflorescence and fruit morphology. A study of the *Hymenodictyon* holdings in PRE and WIND revealed no earlier collections of the new species.

Material and methods

Morphological descriptions and ecological information presented here are based on field observations and material collected following extensive field work in Namibia. This was supplemented by study of relevant literature and herbarium collections. The following herbaria were consulted for possible collections of the new species: PRE, PRU and WIND (Thiers 2019). The distribution map was compiled from specimen data using ArcView 3.1 software. Conservation assessment follows IUCN (2012) recommendations.

Taxonomic treatment

Hymenodictyon kaokoensis W. Swanepoel & E.J. van Jaarsveld, *sp. nov.* (Figs. 1–3)

Type:—NAMIBIA. Kunene Region: Zebra Mountains, 5.5 km SSE of Ombuku, in kloof next to ephemeral stream, 17°18'53"S, 13°20'21"E, 1034 m, 4 November 2017, *W. Swanepoel 371* (holotype WIND!; isotype PRU!).

Diagnosis:—Shrub or rarely a small tree, 2–5 m tall, related to *Hymenodictyon floribundum* and *H. parvifolium*, but at once distinguished from both by its thickset habit especially the semisucculent basal portion of the stem. Differing from *H. floribundum* by the lamina being subcoriaceous, softly echinate, scabrid when dry, turning stramineous before falling (*vs.* coriaceous, glabrous adaxially, puberulous to densely pubescent or tomentose abaxially, turning scarlet or crimson before falling), petiole usually 3–17 mm long (*vs.* 4–70 mm long), primary bracts absent or elliptic, sessile (*vs.* always present, elliptic to lanceolate, long-petiolate), fruit usually 15–34 mm long, with spherical or elongate, prominent lenticels, (*vs.* 8–15 mm long, spherical, non-elevated lenticels); from *H. parvifolium* by being a thickset shrub or small tree, 2–5 m tall (*vs.* small tree or shrub, sometimes scandent, 1.2–10 m tall), lamina 40–155 × 25–80 mm (*vs.* 10–90 × 4–59 mm), softly echinate, scabrid when dry (*vs.* glabrous to scabrous), petiole 3–17 mm long (*vs.* 0.3–5.5 mm long), inflorescences simple, racemose, erect (*vs.* trichotomous racemose, pendulous), and 8–12 ovules per locule (*vs.* 2–3).

Thickset shrub or small tree, 2–5 m tall, winter-deciduous, the lower portion of the stems semi-succulent, the subterranean portion often articulated at the nodes (particularly conspicuous in young plants). *Bark* grey to coppery grey with a dull sheen, smooth, sometimes transversely wrinkled, rarely corky and deeply fissured to form square segments. *Branchlets* lenticellate, younger branchlets brown, new growth green, echinate. *Stipules* narrowly to broadly lanceolate, or ligulate, 2.5–12.0 × 2.4–4.8 mm, ovate at base, acute at apex, apex often bifid or deeply bifid, echinate, margin often with one or more colleters, deciduous. *Leaves* deciduous, simple, opposite and decussate; petioles 3–17 mm long, yellow-green sometimes with a maroon tinge, echinate; blades ovate, elliptic, narrowly obovate or oblong-obovate, 40–155 × 25–80 mm, conduplicate, occasionally flat, sometimes recurved towards apex, subcoriaceous, somewhat shiny adaxially, pale green to green, paler below, (young leaves sometimes maroon-tinged), drying pale yellow to light brown, echinate; domatia absent; apex acuminate, acute or obtuse, base cuneate to attenuate, decurrent; margins entire or undulate; midrib conspicuous ad- and abaxially, prominent abaxially, secondary veins 4 to 8 on each side of midrib; tertiary venation reticulate, conspicuous and prominent abaxially, echinate. *Inflorescences* both terminal and axillary, inserted at distal nodes, 35–65 mm long, erect, solitary, simple racemose, cylindrical or conical-cylindrical, compact, often subtended by one or two pairs of short bracts, sessile, green, echinate, 7–10 mm long, elliptic and trifid or lanceolate; peduncle robust, 5–10 mm long, ca. 3.5 mm diam., echinate; rachis echinate, with numerous 2–6-flowered cymules in axils of echinate lanceolate bracts, 10–14 × 2–3 mm. *Flowers* 4- or 5-merous, 8–11 mm long, including pedicel (and excluding style), subtended by a linear-lanceolate bracteole, ca. 5–7 mm long. Pedicels 0.5–1.0 mm long, echinate. *Hypanthium* flattened ellipsoid, ca. 1.5 mm long, echinate. *Calyx* lobes linear, reaching base of cupular part of corolla, green, echinate, 1.5–2.5 mm long, with a pedicellate colleter at lobe sinuses, 0.3–1.0 mm long, lobe margins often with one or more colleters. *Corolla* tube narrowly infundibular up to midpoint, abruptly opening into ovate cup, 6–8 mm long, purple-brown, green-brown at anthesis, sparsely echinate outside;

lobes ovate, ca. 0.9×0.9 mm, sparsely echinate, ciliate. *Filaments* caniculate, ca. 1 mm long; anthers oblong, ca. 2.2 mm long. *Style* terete, ca. 10 mm long, well exerted; style branches ovoid or oblongoid, ca. 1 mm long, functioning as pollen presenter. Ovary 2-locular; ovules 8–12 per locule. *Fruit* narrowly elliptic, 15–34 mm long, grey-brown to red-brown, with spherical or elongate, prominent lenticels; pedicels 3–17 mm long, lenticellate. *Seeds* elliptic, 6–20 \times 4–8 mm (wing included), broadly winged, deeply to not bifid at base, margins entire or with few irregular dentate teeth especially towards apex, reddish brown with a paler or darker nucleus; testa strongly reticulate; nucleus elliptic or narrowly ovate, 4.1–6.2 \times 2.5–3.4 mm, strongly compressed.

Phenology:—Specimens with flowers were collected in November and December. Specimens with fruits were collected in May.

The capsules split during autumn and winter (May–August), when the winged seed are dispersed by wind.

Distribution, habitat and ecology:—At present *Hymenodictyon kaokoensis* W. Swanepoel & E.J. van Jaarsveld is only known from four localities, in the mountainous region south of the Kunene River, northwestern Namibia (Fig. 4), where it is localized and rare with less than 25 plants recorded. The species may, however, eventually prove to be more widespread, also extending into southern Angola, as what appears to be suitable habitat is not limited to the specific localities where it was found. *Hymenodictyon kaokoensis* grows on rocky mountain and valley slopes in *Colophospermum-Commiphora* woodland at elevations of 990–1590 m, at 120–170 km from the Atlantic Ocean. Average annual rainfall in the area is 200–300 mm (Mendelsohn *et al.* 2002).

The plants were noticed on northern aspects, amongst boulders, on scree slopes and at the type locality in a kloof next to an ephemeral stream. The associated vegetation is clearly semi-arid savannah and although sometimes growing amongst boulders where fires are not likely to reach, is subject to occasional fire after a period of good rainfall.

At the Zebra Mountains (type location) plants were recorded growing on igneous anorthosite of the Kunene Complex (Miller & Schalk 1980, Mendelsohn *et al.* 2002) which give rise to basic clay soils, whilst at the two sites along the lower and medium slopes of Omavanda and the upper reaches of Slangpoort, plants were found on quartzitic sandstone which gives rise to sandy and slightly acidic soils.

The plants are often confined to boulder screens on dry, hot, exposed slopes and the thickset semi-succulent stems most probably enable the plants to survive the dry winters and periods of drought and especially in sites where other non-succulent shrubs and trees struggle to cope. The basal shoots are clearly succulent, often articulated (Fig. 1 C) and when taken as cuttings, they root quite readily in a sandy medium.

Conservation status:—*Hymenodictyon kaokoensis* is rare and localised with only four subpopulations known from uninhabited to sparingly inhabited parts of the Kunene Region of Namibia. The species does not seem to be utilised by humans or browsed by domestic animals. It should be considered as Vulnerable (VU D1 & D2) due to the small population size of less than 25 individual plants known from only four localities (IUCN 2012).

Etymology:—The specific epithet refers to the Kaokoveld in northwestern Namibia, a region forming part of the Kaokoveld Centre of Endemism (Van Wyk & Smith 2001). This biogeographically well-defined region extends into southwestern Angola.

Notes:—*Hymenodictyon kaokoensis* differs from *H. floribundum* and *H. parvifolium* in habit, leaf, indumentum, inflorescences, flower, and fruit characters. Apart from the differences in habit and morphological characters, the distribution of the three taxa differs with *Hymenodictyon kaokoensis* being confined to the Kaokoveld Centre of Endemism in Namibia and *H. parvifolium* to northeastern South Africa and eastern tropical Africa, whilst *H. floribundum* has a wide periguinean distribution in tropical Africa. Some of the more prominent morphological features to differentiate amongst *H. kaokoensis*, *H. floribundum* and *H. parvifolium* are supplied in Table 1. Diagnostic features for *H. kaokoensis* were determined through examination of fresh material and for *H. floribundum* and *H. parvifolium* from herbarium material and the literature (Coates Palgrave 2002; Verdcourt 2003; Razafimandimbison & Bremer 2006). Note that the indumentum on all parts of *H. kaokoensis* is softly echinate but laterally flattened and scabrid in herbarium material.

Hymenodictyon floribundum is recorded for Namibia in the *Tree Atlas of Namibia* (Curtis & Mannheimer 2005) (specimen *Hoffmann LH944* from the mountains to the south of the Kunene River cited in support). Klaassen and Kwembeya (2013) and Mannheimer and Curtis (2009, 2018) also mention it as occurring in Namibia. However, during the present study no herbarium collections of the cited collection could be found in either WIND or PRE. The photographs of *H. floribundum* in Mannheimer and Curtis (2009, 2018) were taken in the Lowveld Botanical Garden, Nelspruit (Mbombela) (A.E. [B.] van Wyk, pers. comm.). These claimed records almost certainly refer to the new species, since the latter is the only *Hymenodictyon* encountered by the authors following intensive field work in the area.

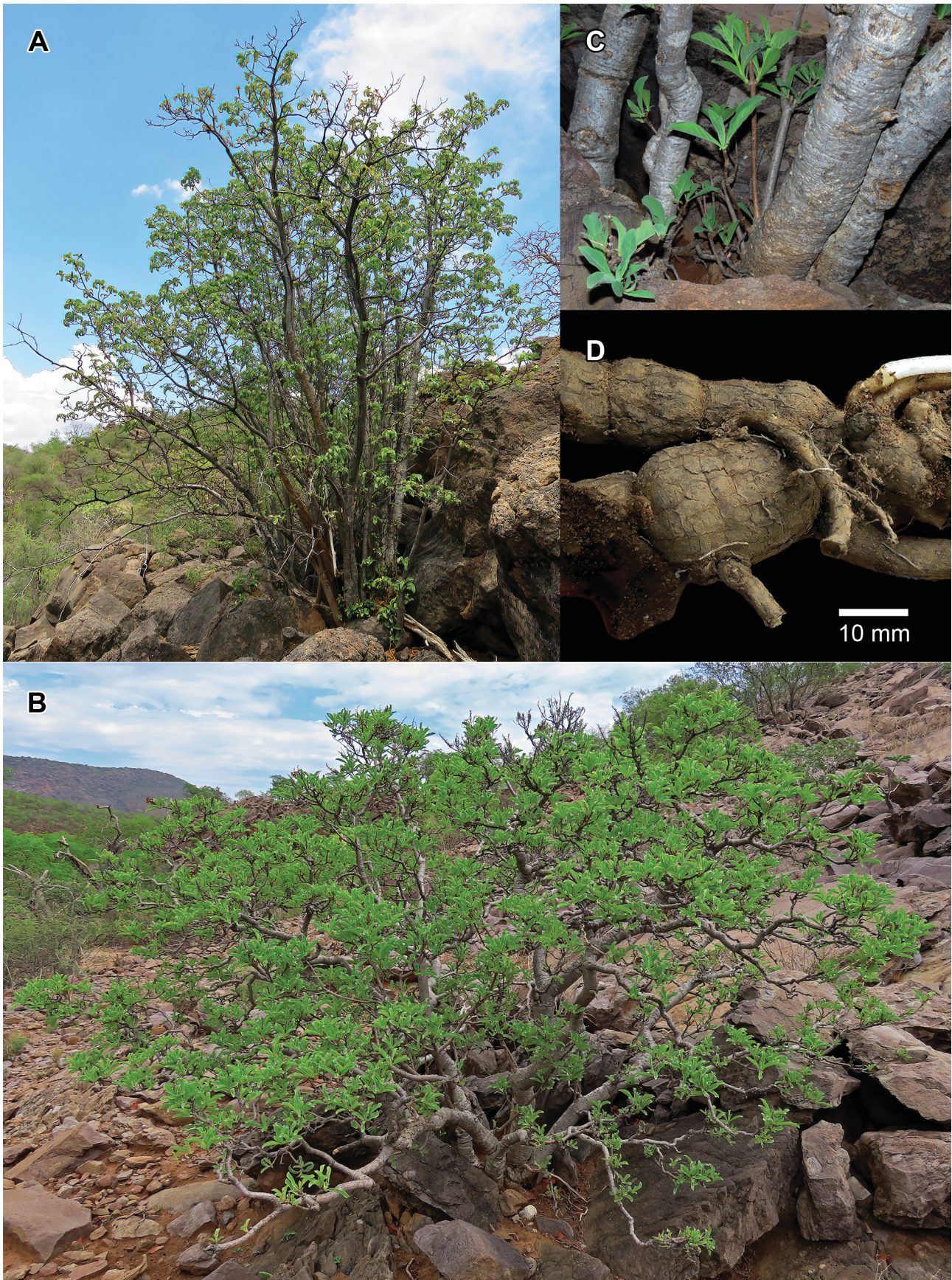


FIGURE 1. *Hymenodictyon kaokoensis*. Plants in natural habitat amongst rocks: **A**, In the Zebra Mountains (type locality, about 4.0 m tall); **B**, In the Baynes Mountains, about 2.5 m tall; stems bark and leaves; **C**, Basal older cylindrical articulated succulent stems and shoots with leaves; **D**, Subterranean portion of a sucker shoot; note articulation at the nodes. (A–C, photographs by W. Swanepoel; D, photograph by E.J. van Jaarsveld).

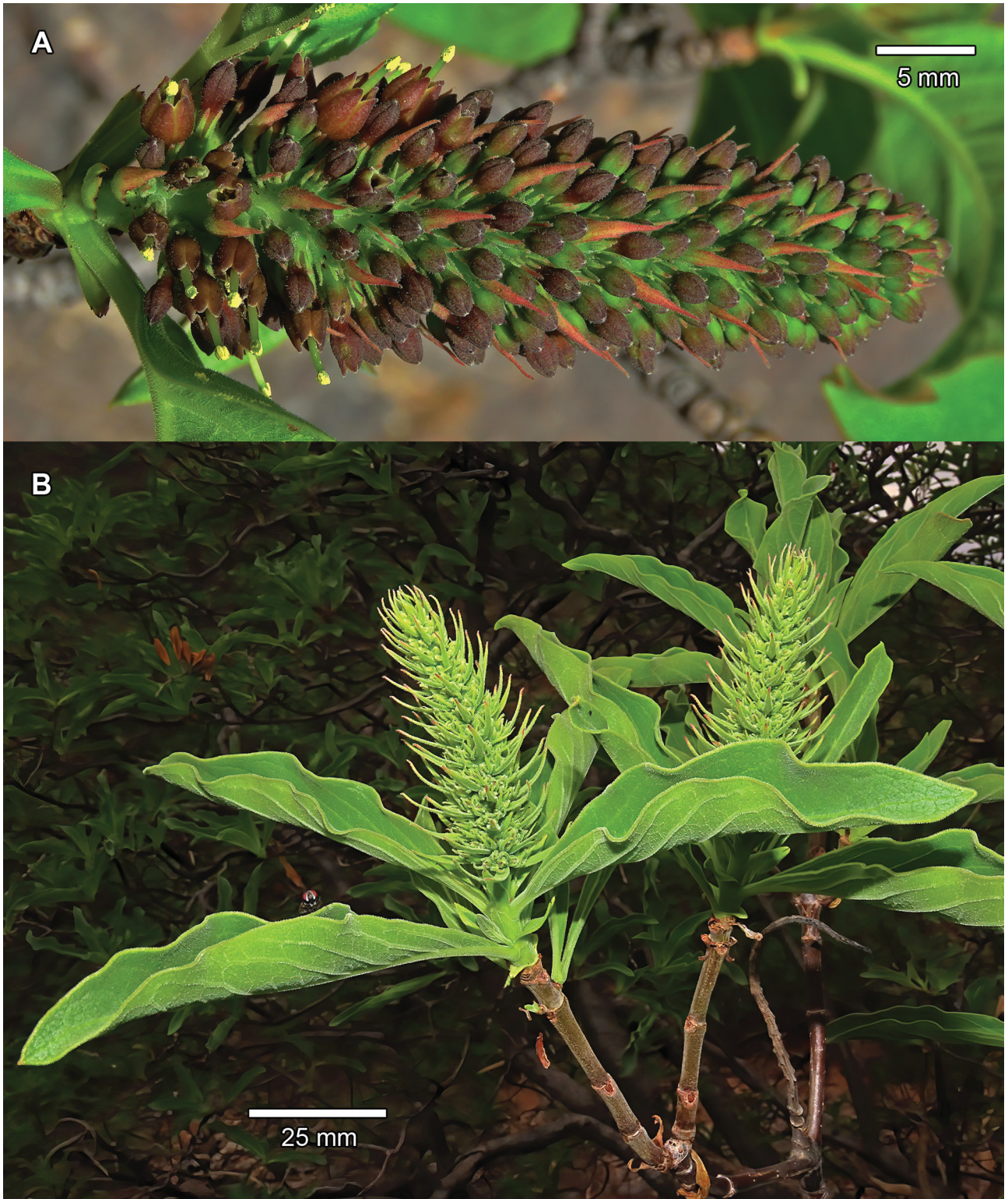


FIGURE 2. *Hymenodictyon kaokoensis*. **A**, Inflorescence with lower flowers fully developed; **B**, Leaves and young inflorescences. (Photographs by W. Swanepoel).



FIGURE 3. *Hymenodictyon kaokoensis*. **A**, Close up view of inflorescence showing fully developed flowers and secondary bracts; note stigmas covered in yellow pollen and functioning as pollen presenters; **B**, Fruits (A, photograph by W. Swanepoel; B, photograph by E.J. van Jaarsveld).

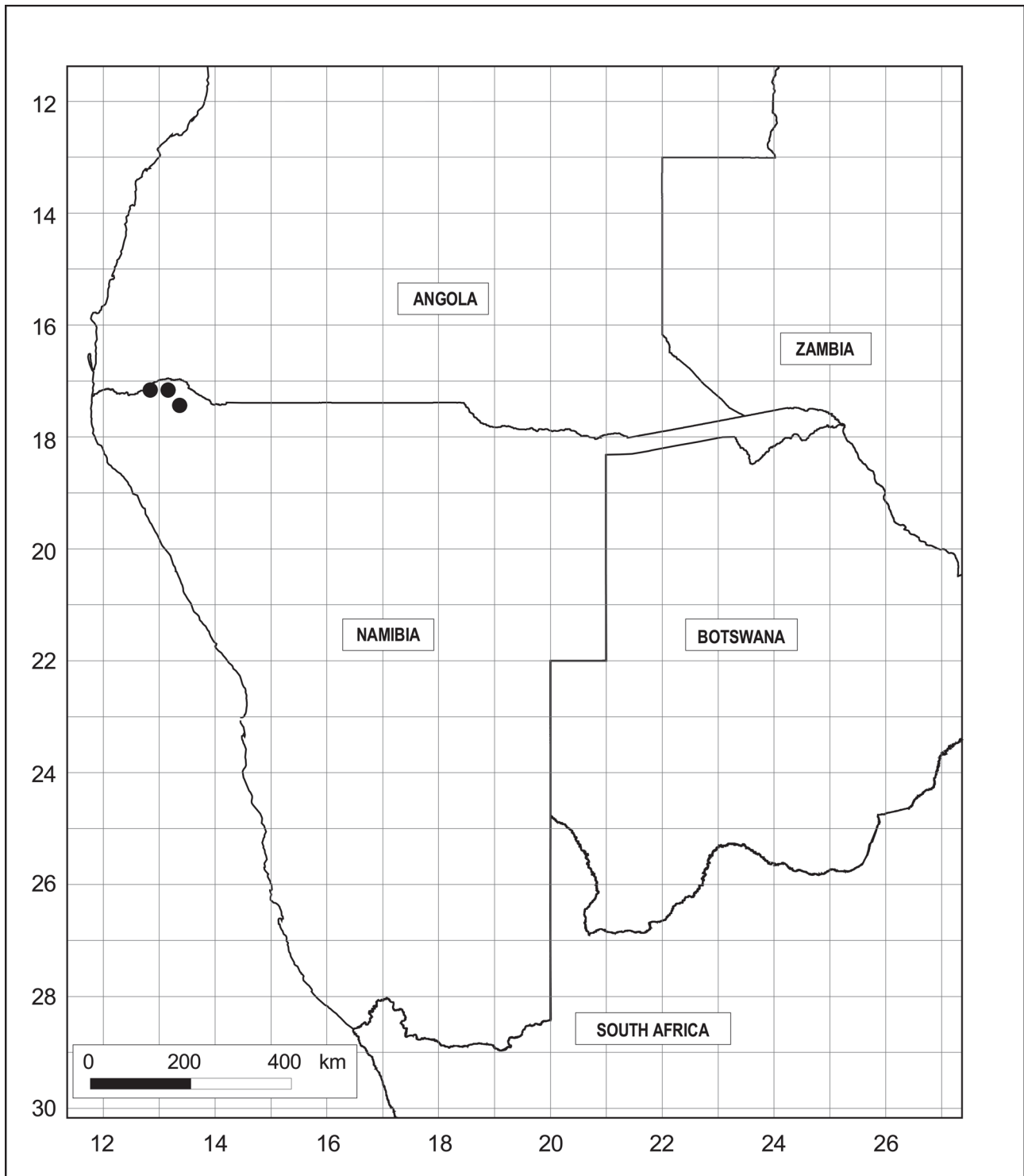


FIGURE 4. Known distribution of *Hymenodictyon kaokoensis*.

Figueiredo (2008) mentions *Hymenodictyon* sp. A, related to *H. pachyantha* Krause (1920: 26). This taxon differs from the new species in the quite distinct, long, fusiform fruits (*vs.* fruits narrowly elliptic and not particularly long [15–34 mm]) and the grassland habitat (*vs.* rocky mountain and valley slopes in woodland).

Additional collections (paratypes):— NAMIBIA. Kunene Region: Baynes Mountains, upper Slangkloof, on low slope above river, 17°14'27"S, 12°52'46"E, 1105 m, 12 November 2019, *W. Swanepoel & E.J. van Jaarsveld* 373 (WIND!); Omavanda Mountain, northern section on slope amongst boulders, 17°08'58"S, 13°00'22"E, 1590 m, 14 May 2018, *W. Swanepoel & E. J. van Jaarsveld* 372 (WIND!); Zebra Mountains, 5.5 km SSE of Ombuku, in kloof next to ephemeral stream, 17°18'53"S, 13°20'21"E, 1034 m, 27 May 2012, *W. Swanepoel & E.J. van Jaarsveld* 370 (WIND!).

TABLE 1. Prominent morphological differences amongst *Hymenodictyon kaokoensis*, *H. floribundum* and *H. parvifolium*.

	<i>H. kaokoensis</i>	<i>H. floribundum</i>	<i>H. parvifolium</i>
Habit	Thicket shrub or small tree, 2–5 m tall	Shrub to medium-sized tree, 1.5–9 m tall	Shrub or small tree, sometimes scandent, 1.2–10 m tall
Bark	Grey to coppery grey with a dull sheen, smooth, sometimes transversely wrinkled, rarely corky and deeply fissured to form square segments	Grey-black, usually rough, flaking, reticulate	Light grey or tinged purple-grey, smooth or rarely rough
Leaf blades	Elliptic, ovate, narrowly obovate or oblong-obovate, 4–15.5 × 2.5–8 cm, subcoriaceous, turning stramineous before falling	Elliptic to obovate, 5–18 × 2–12 cm, coriaceous, turning scarlet or crimson before falling	Elliptic to lanceolate or oblanceolate or ovate, 1–9 × 0.4–5.9 cm, subcoriaceous, turning yellow before falling
Leaf blades indumentum	Echinate (soft) on both sides, scabrid when dry	Glabrous adaxially, puberulous to densely pubescent or tomentose abaxially	Glabrous to scabrous
Venation	Secondary veins 4–8 on each side of midrib; tertiary venation reticulate, conspicuous and prominent abaxially, echinate	Secondary veins 6–9 on each side of midrib, tinged yellow-red, conspicuous, glabrous above, puberulous to pubescent beneath; tertiary venation inconspicuous and glabrous adaxially, puberulous pubescent and reticulate abaxially	Secondary veins 2–5 on each side of midrib, tinged yellow, inconspicuous adaxially, conspicuous abaxially, glabrous to scabrous; tertiary venation inconspicuous
Petiole length (mm)	3–17	4–70	0.3–5.5
Inflorescences	Terminal and axillary at uppermost leaf-pair, simple racemose, erect, 3.5–6.5 cm long	Terminal, simple racemose, erect, 6–26 cm long	Terminal, trichotomous racemose, pendulous, 1–8 cm long
Primary bracts	One or two pairs at distal portion of peduncle; sessile, elliptic and deeply trifid or lanceolate, short, 7–10 mm long, echinate; often absent	A pair at distal portion of peduncle; long-petiolate, narrowly elliptic to lanceolate, 35–100 × 11–32 mm, puberulous to pubescent	Absent
Flowers	4- or 5-merous	5-merous	5- or 6-merous
Pedicel length (mm)	0.5–1.0	0.3–2.0	0.5–1.5
Calyx lobes	Linear, reaching base of cupular part of corolla, green, echinate, 1.5–2.5 mm long	Narrowly ovate to linear, 0.25–1.0 mm long, green, glabrous to puberulous, ciliate	Linear or lanceolate, 0.5–2.5 mm long, puberulous to pubescent, sometimes ciliate
Corolla	6–8 mm long, purple-brown in bud, green-brown at anthesis, sparsely echinate outside	3.5–7 mm long, red to yellow-red-tinged or green-yellow-tinged, glabrous to puberulous outside	2.5–5.0 mm long, white to light green or light yellow, sometimes tinged red in bud, sometimes turning black, glabrous to puberulous outside

.....continued on the next page

TABLE 1. (Continued)

	<i>H. kaokoensis</i>	<i>H. floribundum</i>	<i>H. parvifolium</i>
Filaments length (mm)	ca. 1	1–1.5	0.3–1
Anthers length (mm)	ca. 2.2	1.8–2	1–2.5
Hypanthium	Ellipsoid, laterally flattened, echinate	Obovoid, pubescent	Obovoid, puberulous to densely pubescent
Ovules per locule	8–12	5–16	2 or 3
Style length (mm)	ca. 10	8–10	ca. 14
Shape of style branches	Ovoid or oblongoid	Clavate to globose	Clavate to globose or ellipsoid
Fruits	Narrow ellipsoid, 15–34 mm long, grey-brown to red-brown, lenticels spherical or elongate, prominent; pedicels 3–17 mm long	Ellipsoid, 8–15 mm long, lenticels spherical, non-elevated; pedicels 6–9 mm long	Ellipsoid, 10–40 mm long, lenticels elongate, prominent or not; pedicels up to 10 mm long
Seeds	Elliptic, 6–20 × 4–8 mm (wings included), broadly winged, deeply to not bifid at base; nucleus elliptic or narrowly ovate, 4.1–6.2 × 2.5–3.4 mm	Narrowly elliptic, 7–10 × 2.5–4 mm, (wings included), broadly winged only at both ends, deeply bifid at base; nucleus narrowly elliptic, 2–2.5 × 1–1.5 mm	Broadly elliptic, 8–20 × 5–13 mm (wings included), bifid at base; nucleus broadly elliptic or broadly ovate, ca. 4.5 × 3.6 mm
Distribution	Kaokoveld Centre of Endemism, NW Namibia	Tropical Africa (including Angola)	Eastern South Africa and eastern Tropical Africa

Following the description of *Hymenodictyon kaokoensis*, six species are recognized in Africa. Of these, four species are confined to tropical Africa. These are *H. biafranum* Hiern (1877: 42), *H. epiphyticum* Razafimandimbison & Bremer (2006: 362), *H. floribundum* and *H. pachyantha*. *Hymenodictyon parvifolium* occurs in both tropical and southern Africa and *H. kaokoensis* is found only in southern Africa.

Key to the African species of *Hymenodictyon*

- 1a. Inflorescences unbranched2
- 1b. Inflorescences branched4
- 2a. Woody epiphytes; ovules and seeds 30–40 per locule *H. epiphyticum*
- 2b. Terrestrial shrubs3
- 3a. Inflorescences > 220 mm long; ovules and seeds 5–16 per locule; seeds 7–10 × 2.5–4 mm (wings included), broadly winged only at both ends *H. floribundum*
- 3b. Inflorescences 35–65 mm long; ovules and seeds 8–12 per locule; seeds 6–20 × 4–8 mm (wings included), broadly winged *H. kaokoensis*
- 4a. Inflorescences subtended by long-petiolate leafy bracts; ovules and seeds 25–40 per locule; filaments 3–4 mm long *H. biafranum*
- 4b. Inflorescences lacking long-petiolate bracts; number of ovules and seeds < 10 per locule; filaments up to 1 mm long5
- 5a. Leaf blades 8–31 × 5–11 cm; inflorescences elongate, 10–32 cm long; calyx lobes 4.5–7 mm long, recurved and longer than the mature corollas; corollas napiform, densely pubescent outside; ovaries elongate *H. pachyantha*
- 5b. Leaf blades 1–9 × 0.4–5.9 cm; inflorescences globose, 1–8 cm long; calyx lobes 0.5–2.5 mm long, straight and shorter than the mature corollas; corollas narrowly tubular and abruptly widening at mouth, glabrous outside; ovaries obovoid *H. parvifolium*

Acknowledgements

We would like to thank Prof. Abraham E. van Wyk, University of Pretoria, for advice and support and Dr Hester Steyn, SANBI, for preparing the distribution map. The curator and staff of the National Herbarium of Namibia (WIND) and the National Herbarium of South Africa (PRE) are thanked for their assistance during visits to the herbarium. We are grateful to two anonymous reviewers for suggesting improvements to the manuscript. We are especially grateful to Hannelie Swanepoel, Pikkie Hoffman, Werner Voigt, Reghardt Joubert, Cornell Beukes and Freddie Versfeld for assistance and support during field trips.

References

- Capuron, R. & Leroy, J.F. (1978) *Paracorynanthe*, genre nouveau de Rubiacées-Cinchonées malgache. *Adansonia* 18: 159–166.
- Coates Palgrave, M. (2002) *Keith Coates Palgrave Trees of Southern Africa*, 3rd ed. Struik, Cape Town, 1212 pp.
- Curtis, B.A. & Mannheimer, C.A. (2005) *Tree Atlas of Namibia*. National Botanical Research Institute, Ministry of Agriculture, Water and Forestry, Windhoek, 674 pp.
- Figueiredo, E. (2008) The Rubiaceae of Angola. *Botanical Journal of the Linnean Society* 156: 537–638.
<https://doi.org/10.1111/j.1095-8339.2007.00750.x>
- Germishuizen, G. & Meyer, N.L. (Eds.) (2003) Plants of southern Africa: an annotated checklist. *In: Strelitzia* 14. National Botanical institute, Pretoria, 1231 pp.
- Hiern, W.P. (1877) *Hymenodictyon biafranum*. *In: Oliver, D. (Ed.) Flora of Tropical Africa*, vol. 3. Spottiswoode, London, pp. 42–43.
- Hochstetter, C.F.F. & Steudel, E.F. von (1842) Flora No.15. *In: Hoppe, D.H. & Fürnrohr, A.E. (Eds.) Flora oder allgemeine botanische zeitung*, vol. 25. Königlicher bayerische botanischen Gesellschaft zu Regensburg, Regensburg, pp. 225–240.
- IUCN (2012) *IUCN red list categories and criteria: Version 3.1*. Second edition. Gland, Switzerland, and Cambridge U.K., iv + 32 pp.
- Jackson, W.P.U. (1990) *Origins and meanings of names of South African plant genera*. University of Cape Town, Rondebosch, Cape Town, 189 pp.
- Klaassen, E. & Kwembeya, E. (2013) A checklist of Namibian indigenous and naturalised plants. *In: Occasional Contributions*. No. 5. National Botanical Research Institute, Windhoek, 591 pp.
- Krause, K. (1920) Rubiaceae africanae. V. (IX). *Botanische Jahrbücher für Systematik* 57: 26–27.
- Mannheimer, C.A. & Curtis, B.A. (Eds.) (2009) *Le Roux and Müller's Field Guide to the Trees & Shrubs of Namibia*. Macmillan Education Namibia, Windhoek, 526 pp.
- Mannheimer, C.A. & Curtis, B.A. (Eds.) (2018) *Le Roux and Müller's Field Guide to the Trees & Shrubs of Namibia*, 2nd ed. Namibia Publishing House, Windhoek, 546 pp.
- Miller, R. McG. & Schalk, K.E.L. (1980) *Geological map of South West Africa/Namibia* (1: 1000000). Geological Survey of the Republic of South Africa and South West Africa/Namibia, Windhoek, 4 sheets.
- Mendelsohn, J., Jarvis, A., Roberts, C. & Robertson, T. (2002) *Atlas of Namibia*. Philip, Cape Town, 200 pp.
- Oliver, D. (1885) Plate 1488. *In: Hooker, J.D. (Ed.) Hooker's Icones Plantarum; or figures, with brief descriptive characters and remarks of new or rare plants* 15: 69.
- Razafimandimbison, S.G. & Bremer, B. (2001) Tribal delimitation of Naucleaeae (Cinchonoideae, Rubiaceae): inference from molecular and morphological data. *Systematics and Geography of Plants* 71: 515–538.
<https://doi.org/10.2307/3668697>
- Razafimandimbison, S.G. & Bremer, B. (2006) Taxonomic revision of the tribe Hymenodictyeae (Rubiaceae, Cinchonoideae). *Botanical Journal of the Linnean Society* 152: 331–386.
<https://doi.org/10.1111/j.1095-8339.2006.00567.x>
- Robinson, B.L. (1910) Spermatophytes, new or reclassified, chiefly Rubiaceae and Gentianaceae. *Proceedings of the American Academy of Arts and Sciences* 45: 404–412
<https://doi.org/10.2307/20022574>
- Van Wyk, A.E. & Smith, G.F. (2001) *Regions of floristic endemism in southern Africa: a review with emphasis on succulents*. Umdaus Press, Hatfield, Pretoria, 199 pp.
- Verdcourt, B. (2003) Rubiaceae. *In: Pope, G.V. (Ed.) Flora Zambesiaca*, vol. 5, part 3. Royal Botanic Gardens, Kew, pp. 423–427.
- Wallich, N. (1824) Descriptions of plants more recently discovered by Nathaniel Wallich. *In: Carey, W. & Wallich, N. (Eds.) Flora Indica; or descriptions of Indian plants, by the late William Roxburgh* 2. Serampore, pp. 1–588.