

***Zanthoxylum kaokoense* (Rutaceae: Zanthoxyloideae), a new species from Angola and Namibia**

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Abstract

Zanthoxylum kaokoense, previously mistaken for *Z. ovatifoliolatum*, is formally described here as a new species. It is a range-restricted species, only known from the Kaokoveld Centre of Endemism, located in southwestern Angola and northwestern Namibia. The species typically grows on arid hillsides, in valleys, and along ephemeral rivers and drainage lines. Diagnostic characters for *Z. kaokoense* include its growth as a shrub or small tree, the presence of curved prickles on the branches, petioles, leaf rachises, and some leaflets, as well as fine pubescence (puberulous) on young branches, petioles, rachises, and inflorescence axes. The leaflets are discolorous and contain both marginal and scattered secretory cavities. The inflorescences are either paniculate or racemose-paniculate, and the female flowers have gynoeceia with one or two carpels. Morphologically and genetically, *Z. kaokoense* is most similar to *Z. chalybeum*, which is likely its closest relative. The taxonomic status of *Z. ovatifoliolatum* is still unresolved and will require further fieldwork and comparative analysis, particularly with *Z. chalybeum*, as the two species may be conspecific. According to IUCN Red List criteria, *Z. kaokoense* is provisionally assessed as Least Concern (LC) in terms of conservation status.

Key words: endemism, flora, Kaokoveld, Kaokoveld Centre of Endemism, Kunene Region, Namibe Province, Rutaceae, Serra Tchamalindi, *Zanthoxylum chalybeum*, *Zanthoxylum ovatifoliolatum*, taxonomy

Introduction

Currently, ca. 235 described species of *Zanthoxylum* Linnaeus (1753: 270) are recognised worldwide (Christenhusz *et al.* 2017, POWO 2025). Of these, one species is recorded for Namibia, five each for Angola and South Africa, and six for the *Flora of southern Africa* region (which includes South Africa, Namibia, Botswana, Eswatini, and Lesotho) (Germishuizen & Meyer 2003, Figueiredo & Smith 2008). In the present contribution, a new species of *Zanthoxylum* is described. Based on available distribution records, this new entity appears to be confined to the Kaokoveld Centre of Endemism, a biogeographical region rich in range-restricted plant species in northwestern Namibia and adjacent southwestern Angola (Van Wyk & Smith 2001).

In April 2021, during a botanical expedition to Serra Tchamalindi [Tchamalindi Mountain] in Angola's Namibe Province—conducted as part of the SCIONA Project (<http://sciona.nust.na/>)—one of us (VDC) collected a specimen (*De Cauwer TCH1-28*) from a small tree of the genus *Zanthoxylum* on the upper plateau at an elevation of 1659 m (Becker *et al.* 2021, De Cauwer *et al.* 2023). Several gatherings of the taxon were subsequently found in Herbs PRE, PRU, and WIND, all labelled as *Zanthoxylum ovatifoliolatum* (Engl.) N.Finkelstein in Retief & Finkelstein (1979: 637), or its basionym, *Fagara ovatifoliolata* Engler (1896: 150), a species described from material also collected in Angola.

However, a critical assessment of all available material in these herbaria revealed that none of them fully matched the type material or the protologue of *Z. ovatifoliolatum*. Based on this assessment, it was concluded that these specimens represent a previously undescribed species.

Phylogenetic analysis (Appelhans *et al.* 2018, Reichelt *et al.* 2021) of the specimen *Swanepoel SWA3/76*—previously identified as *Z. ovatifoliolatum*, but representing the new species—indicates that its closest known relative is *Z. chalybeum* Engler (1895: 227). Based on both genetic evidence and the new species' greater morphological similarity to *Z. chalybeum* than to *Z. ovatifoliolatum*, the species diagnosis includes comparisons with *Z. chalybeum*, including its variety *Z. chalybeum* var. *molle* Kokwaro (1978: 796), as well as with *Z. ovatifoliolatum*.

Methods

Morphological descriptions and ecological information presented here are based primarily on field observations and material collected following extensive field work in Angola and Namibia. Diagnostic features for the new species were determined through examination of fresh material and supplemented by the study of the protologues and available herbarium collections. The herbaria of the National Botanical Research Institute in Namibia (WIND), the South African National Biodiversity Institute, Pretoria (PRE), the University of Pretoria (PRU), and the Instituto Superior de Ciências de Educação da Huíla, Angola (LUBA), were consulted for possible collections of the new species (herbarium codes follow Thiers 2025).

For *Zanthoxylum chalybeum* and *Z. ovatifoliolatum* diagnostic features were determined from specimens in the herbaria of the British Museum of Natural History (BM), the Instituto de Investigação Científica Tropical (LISC), the University of Coimbra (COI), PRE, and WIND, the protologues, other literature, and images downloaded from JSTOR Global Plants (<https://plants.jstor.org/>) and the Global Biodiversity Information Facility (GBIF; <http://www.gbif.org>). A 6.5–45.0× magnification stereo microscope was used for studying morphological features. Descriptive terminology follows Beentje (2016) and Hewson (2019).

Locality information for specimens cited also provides the quarter degree grid squares following the degree reference system of Edwards & Leistner (1971). The distribution map was compiled from specimen data using ArcView 3.1 software. A preliminary conservation assessment was conducted using the standard procedures based on IUCN guidelines (IUCN 2012, IUCN Standards and Petitions Committee 2024), and the online GeoCAT tool (Bachman *et al.* 2011).

Taxonomic treatment

Zanthoxylum kaokoense Swanepoel, De Cauwer & A.E.van Wyk, *sp. nov.* (Figs 1–3)

Diagnosis:—A woody shrub or tree up to 8 m tall, morphologically and genetically most similar to *Zanthoxylum chalybeum* and previously mistaken for *Z. ovatifoliolatum*, both from which it differs in having branches puberulous, leaflets glabrous or with widely spaced tortuous trichomes and/or indumentum sparsely puberulous on veining, inflorescence axes puberulous (*vs.* branches glabrous, leaflets glabrous [*Zanthoxylum chalybeum* var. *chalybeum*] or tomentose [*Zanthoxylum chalybeum* var. *molle*], inflorescence axes glabrous); gynoecium 1- or 2-carpellate (*vs.* only 1-carpellate). It furthermore differs from *Z. ovatifoliolatum* in the curved prickles (*vs.* nearly straight), leaflets (1)3–5-jugate (*vs.* 2- or 3-jugate), leaflet apices acute or obtuse (*vs.* acuminate), leaflet size on a given leaf either uniform, slightly increasing or decreasing towards the tip, or with the terminal pair notably shorter than the others (*vs.* a consistent increase in size towards the tip), and calyx lobes deltoid (*vs.* suborbicular).

Type:—NAMIBIA. Kunene Region: 1813 (Opuwo), Otjomatempa Pass, ca. 8 km south of Otjomatempa on road C43, (–DD), 1207 m a.s.l., 12 January 2025, *Swanepoel 656* (holotype WIND!; isotypes PRE!, PRU!).

Fagara ovatifoliolata auct. non Engler (1896): Schreiber (1968: 2).

Zanthoxylum ovatifoliolatum auct. non Engler (1896): Coates Palgrave (2002: 409, in key); Curtis & Mannheimer (2005: 257); Mannheimer & Curtis (2018: 196).

Illustrations:—Curtis & Mannheimer (2005: 257, as *Zanthoxylum ovatifoliolatum*, line drawing of shoot with leaves and fruit); Mannheimer & Curtis (2018: 195, as *Zanthoxylum ovatifoliolatum*, photographs of habit, prickles, stem, and leaves).



FIGURE 1. *Zanthoxylum kaokoense*; habit, leaves and inflorescences. **A.** Spreading multi-stemmed shrub, ca. 1.4 m high; growing in soil derived from dolomite near Otjomatempa, Namibia. **B.** Shoots with leaves and female inflorescences. Photographs by W. Swanepoel. Voucher: *Swanepoel 656*.

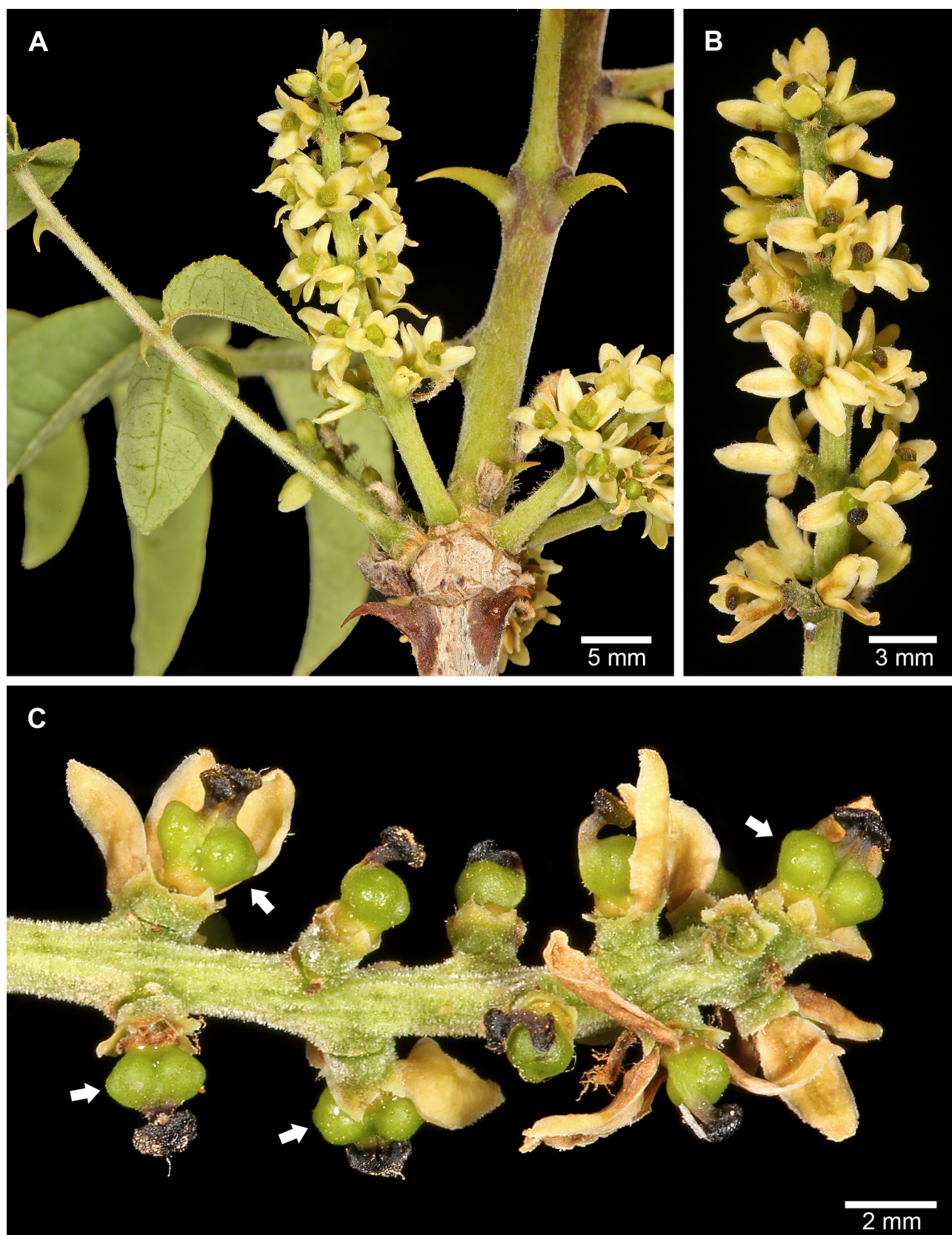


FIGURE 2. *Zanthoxylum kaokoense*; morphology of flowering shoots, inflorescences, and flowers. **A.** Flowering shoot with female inflorescences positioned below the leaves at the base of new growth. Note the slightly to distinctly curved prickles on the stem and leaves, as well as the fine puberulous indumentum on the leaf rachis, inflorescences axes, and young stem. **B.** Female flowers arranged in a short raceme. **C.** Portion of a mature female inflorescence with most petals already shed. Visible features include the gynoeceia, which are either bicarpellate (indicated by arrows) or unicarpellate, the yellowish cushion-shaped disc visible below some gynoeceia, deltoid calyx lobes, and the stigmas, which have turned a blackish colour. Photographs by W. Swanepoel. Voucher: *Swanepoel 656*.

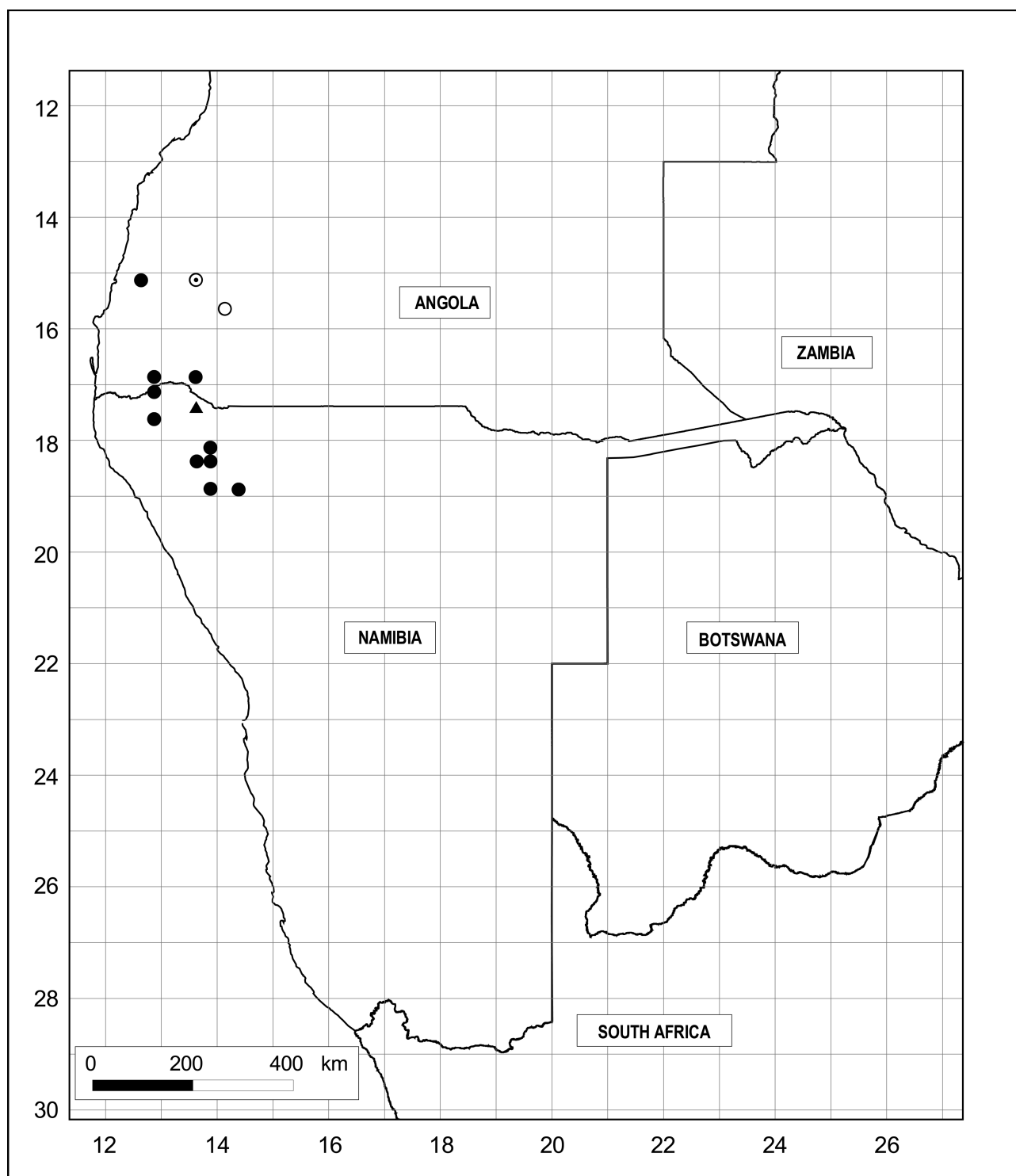


FIGURE 3. Known distribution of *Zanthoxylum kaokoense* (herbarium specimens: black dots; sight record: black triangle) and *Z. ovatifoliolatum* (open circles; the one with the small central dot indicates the type locality of the species). Based on herbarium specimens in Herbs COI, K, LISC, LUBA, PRE, PRU, and WIND.

Dioecious shrub or tree up to 8 m tall; single or multi-stemmed from below or just above ground level, stems up to 120 mm in diam., aculeate, prickles recurved, up to 12 mm long, black, dark brown or grey, puberulous initially, glabrescent, terminal buds protected by deltoid scales, indumentum puberulous to villous, light brown, bark irregularly longitudinally ridged, grey, dark grey or grey-brown, black-dotted on older branches, ridges often paler coloured, puberulous, often with few longer tortuous simple trichomes in addition, glabrescent. *Leaves* alternate and spirally on new shoots, whorled on brachyblasts, up to 180 mm long; petiole flattened adaxially towards base, 15–45 mm long; rachis 20–95 mm long, leaflets opposite to subopposite, sessile or subsessile, (1)3–5-jugate, leaflets papyraceous, all

pairs on a specific leaf of similar length or slightly increasing towards distal end or vice versa, or distal pair markedly shorter than others; lamina narrowly ovate, ovate-elliptic or elliptic, 7–70 × 4–35 mm, apex acute or obtuse, base obtuse-acute, obtuse, rounded or that of terminal one sometimes cuneate, sub-conducuplicate, sometimes asymmetrical and/or oblique, margins crenulate or crenulate-serrulate, with single orbicular secretory cavity (pellucid gland) in all sinuses, sparsely (<5/cm²) to densely (up to >50/cm²) scattered throughout rest of lamina, discolorous, green adaxially, paler abaxially, glabrous or with widely spaced tortuous trichomes including on margins, sometimes sparsely puberulous on veining, crushed leaves aromatic, aroma citrus-like, midrib prominently raised on both sides, 3–9 principal lateral vein pairs prominent adaxially; petioles, rachises and midribs puberulous, often with few longer tortuous simple trichomes in addition, aculeate (on midribs abaxially only, sometimes lacking), prickles up to 4 mm long, curved, green, reddish brown, brown or black. *Inflorescences* (female plants—male plants not seen) at the base of new branches below leaves or terminally on brachyblasts, whorled, paniculate or racemose-paniculate, peduncle 3–14 mm long, rachis straight, 7–45 mm long, puberulous often with few longer tortuous simple trichomes in addition, bracts narrowly triangular, up to 1.5 × 0.4 mm, cobwebby, trichomes pale brown. *Flowers* 4- or 5-merous on pedicel ca. 0.6 mm long. *Calyx* shallowly cupular, tube ca. 1 mm long, lobes deltoid, ca. 0.5 × 0.5 mm, sparsely ciliate, glandular abaxially, persistent on the fruit. *Petals* imbricate, narrowly ovate or oblong-elliptic, ca. clawed, apices acute or obtuse, sometimes incurved, ca. 3.2 × 1.2–1.6 mm, cream-yellow, darker in centre, margins pellucid with widely spaced papillae or papillae absent. *Staminodes* vestigial, reduced to the aborted anthers, inserted at the base of a disc. *Disc* cushion-shaped, pale yellow, ca. 0.3 mm high. *Gynoecium* borne on the disc, 1- or 2-carpellate, ca. 1.8 mm long, glabrous; 2-carpellate ovary (“ovariole”) proximally connate and stylodia usually joined in a common style or at least with joined stigmas, bilobed, 2-locular; 1-carpellate ovaries subglobose, ca. 0.8 mm long, prominently ridged, 1 locular; each locule 2-ovulate (1 aborts); style terete, oblique, incurved, ca. 0.4 mm long, grooved; stigma discoid, 0.6–0.8 mm diam., yellowish green, turning black with age. *Fruit* a subglobose or globose follicle (carpels separating in fruit), dehiscent, ca. 8 mm diam., subsessile, glandular-foveolate or glandular-verrucose, reddish brown; seed subglobose, 4–6 mm diam., black, smooth, shiny.

Phenology:—Flowers and fruit have been recorded from March to June.

Distribution and habitat:—In Angola, *Zanthoxylum kaokoense* is currently known only from three localities (near Caraculo, the Tchamalindi Mountain and the Viluvioaengua Mountain), but is more widespread in northwestern Namibia, from the mountainous area bordering the Kunene River southwards to near Sesfontein (Fig. 3). *Zanthoxylum kaokoense* occurs on arid hillsides, plains and along drainage lines and ephemeral riverbeds at elevations of 500–1700 m a.s.l., 50–200 km inland from the Atlantic Ocean. The region receives approximately 100–350 mm of annual rainfall, mostly during the summer months (Atlas of Namibia Team 2022, Mendelsohn & Huntley 2023).

Conservation status:—*Zanthoxylum kaokoense* has been recorded at 18 localities where it is uncommon to rare. The extent of occurrence (EOO) has been calculated as 29716 km² and the area of occupancy (AOO) as 76 km², based on a cell width of 2 km, as recommended by the IUCN Standards and Petitions Committee (2024). Although *Zanthoxylum kaokoense* has a limited geographical range (AOO <2000 km²) and a continuing decline is projected due to its habitat being under pressure from prolonged droughts, it is known from more than five locations. It therefore does not qualify for the Vulnerable (VU) category and is here provisionally assessed as Least Concern (LC) (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, Craven 2009). This biogeographically well-defined region extends into southwestern Angola. *Zanthoxylum kaokoense* is endemic to the Kaokoveld Centre.

Common names and uses:—English vernacular names in use for *Zanthoxylum kaokoense* are “Ovambo knobwood” and “Kaoko knobwood”, and Afrikaans names are *ovamboknophout* and *ovamboperdepram* (Van Wyk *et al.* 2011). The first mentioned English and Afrikaans names are the ones recommended by the Dendrological Society of South Africa (Von Dürckheim *et al.* 2014). In Namibia preference is given to *nokoma*, the Khoekhoegowab (Nama) name for the species. In Otjiherero (Herero), the language spoken by the majority of people within the species’ sparsely populated range, local names include *ohandua*, *ohandwa*, *omuhandu*, and *omuhandwa* (Van Wyk *et al.* 2011).

The species is well known among local communities for its biocultural significance. According to Mannheimer and Curtis (2018), the roots are commonly traded through barter, and the dried, powdered fruit is used as a cosmetic. Additionally, an infusion made from the fruit is used to treat various ailments in both humans and animals, particularly for stomach-related complaints (Von Koenen 1996, Mannheimer & Curtis 2018).

Notes:—*Zanthoxylum kaokoense* is morphologically and genetically most similar to *Z. chalybeum*. However, in herbarium collections, the new species has so far been misidentified as *Zanthoxylum ovatifoliolatum* (Fig. 4). Hence these three species were compared in the diagnosis above. Some of the morphological features to distinguish between *Z. kaokoense*, *Z. chalybeum*, and *Z. ovatifoliolatum* are also provided in Table 1.



FIGURE 4. A specimen of Welwitsch 4561 (in Herb BM, BM000923681), part of the type gathering on which both the names *Zanthoxylum ovatifoliolatum*, and its synonym *Z. citriodorum*, are based. Hitherto the name *Z. ovatifoliolatum* has been misapplied to *Z. kaokoense*. Photograph reproduced with kind permission from the Trustees, Natural History Museum, London.

TABLE 1. Prominent morphological differences between *Zanthoxylum kaokoense*, *Z. chalybeum*, and *Z. ovatifoliolatum*.

Character	<i>Z. kaokoense</i>	<i>Z. chalybeum</i>	<i>Z. ovatifoliolatum</i>
Indumentum			
Branches	Puberulous; glabrescent	Glabrous	Glabrous
Leaflets	Glabrous or with few tortuous trichomes or sparsely puberulous on veining	Glabrous (var. <i>chalybeum</i>) Tomentose (var. <i>molle</i>)	Glabrous
Inflorescences (axes)	Puberulous	Glabrous	Glabrous
Prickles	Curved	Curved	Nearly straight
Leaflets (number of)	(1)3–5-jugate	1(2)–5-jugate	2–4-jugate
Leaflets (size)	All pairs on a specific leaf of similar length or slightly increasing towards distal end or vice versa, or distal pair markedly shorter than others	Leaflets on a specific leaf markedly increasing in length towards distal pair	Consistent increase in size towards distal end
Leaflets (principal lateral veins)	3–9 pairs	6–9 pairs	4–6 pairs
Leaflets (apices)	Acute or obtuse	Acute or obtuse	Acuminate
Flowers (female; gynoecium)	1- or 2-carpellate	1-carpellate	Probably 1-carpellate (only fruiting material known)
Fruit (size) (mm)	4–6	5–8	4–6
Distribution	Angola: southern part of Namibe and Cunene provinces. Namibia: northern part of Kunene Region. Known range confined to the Kaokoveld Centre of Endemism	East Africa from Ethiopia and Somalia southwards to Zimbabwe	Angola: southwestern part of Huila Province

In existing phylogenetic studies of *Zanthoxylum* (Appelhans *et al.* 2018, Reichelt *et al.* 2021), material from the gathering *Swanepoel SWA3/76* (housed at US), was used for sequencing under the name *Z. ovatifoliolatum*. However, this specimen is actually *Z. kaokoense* and originates from the same population in Namibia as its type specimen. As a result, *Z. ovatifoliolatum* was not sequenced, nor were any of the other Angolan species of *Zanthoxylum*.

The type gathering of *Z. ovatifoliolatum* (*Welwitsch 4561*, specimens housed at Herbs BM, COI, G, LISC, and K; see Fig. 4) comes from Morro de Lopol(1)o—a hill near the modern-day town of Huila in Angola—which lies well outside the Kaokoveld Centre (Figueiredo & Smith 2020; E. Figueiredo, pers. comm.). This locality (Fig. 3) is situated on the Huila Plateau, approximately 100 km east of Caraculo and 240 km north-northeast of Tchamalindi Mountain and Serra Viluoviaengua, the only known sites for *Z. kaokoense* in Angola.

Given our view that *Z. ovatifoliolatum* is not conspecific with *Z. kaokoense*, and considering that the name *Z. ovatifoliolatum* has largely been applied to what we now describe as *Z. kaokoense*, questions naturally arise regarding its true taxonomic status.

A search conducted near the type locality by one of us (WS) in February 2023 failed to locate any *Zanthoxylum* specimens. Beyond the type gathering of *Z. ovatifoliolatum*—and its later synonym *Z. citriodorum* Welw. ex Hiern (1896:114)—represented by *Welwitsch 4561* (Fig. 4), we have encountered only one additional collection that resembles the type: *Azancot de Menezes 580*, housed in Herb K (K004663896; accessed via GBIF). This specimen originates from Tchimbolelo near Chimbemba in Angola, also within Huila Province and approximately 100 km southeast of the type locality (Fig. 3).

These findings suggest that within Angola, *Z. ovatifoliolatum* is likely restricted to Huila Province. The species' inland distribution and apparent association with relatively high-rainfall savannah raise two possibilities: it may either represent a distinct, Angolan endemic species, or it could be an outlier population of *Z. chalybeum*, a species recorded further east in Zambia and Zimbabwe (and extending further north in Africa) and with which it shares morphological similarities (Table 1). If the latter scenario proves correct, the name *Z. ovatifoliolatum*—validly published in 1896—would become a synonym of *Z. chalybeum*, which was published slightly earlier in 1895.

However, it is too early to make a definitive taxonomic decision. Further detailed comparisons and targeted fieldwork in Angola are essential before the true status of *Z. ovatifoliolatum* can be confidently resolved.

Additional specimens examined (paratypes):—ANGOLA, Namibe Province:—Moçamedes: Dois Irmãos, Caraculo, 1512BA, 9 May 1962, *Santos 1040* (LISC!); Serra Tchamalindi, eastern part of range, 1612DD, 1659 m, 26

April 2021, *De Cauwer TCH1-28* (LUBA!); Serra Viluvioaengua, ca. 35 km south-southeast of Oncocua in drainage line, 1613DC, 883 m, 17 June 2025, *Swanepoel 664* (LUBA!, PRU!)

NAMIBIA, Kunene Region:—Baynes Mountains, 1712BB, 3 April 2003, *Burke 03077* (WIND!); 57 km west of Okangwati on track to Otjitanda, 1712DB, 1400 m, 3 June 2006, *Kolberg & Tholkes 1984* (WIND!); 3.5 miles north of Ohopoho, 1813BB, 29 March 1957, *De Winter & Leistner 5254* (PRE!, WIND!); 4 km nördlich Ohopoho, 1813BB, 8 April 1973, *Giess & Van der Walt 12642* (PRE!, WIND!); 5 km noord van Okarosave, 1813BB, 23 June 1977, *Viljoen 409* (WIND!); Road from Opuwo to Sesfontein, 1813BB, 10 April 2000, *Curtis CUR410* (WIND!); 18 km west of Kaoko Otavi on track to Orupembe, 1813BC, 1000 m, 11 June 2001, *Kolberg, Loots & Moses HK1150* (WIND!); Quarry [Quartz?] outcrop ± 100 m south of camp site, 1813BC, 1203 m, 30 March 2002, *Curtis, Aronson & Le Floc'h CUR1640* (WIND!); Orumana, 1813BD, 30 January 1968, *Grobbelaar 45* (WIND!); 18°52'30" south and 13°52'30" east, 1813DD, 20 February 1999, *Tagg & Neuhaus JT5* (WIND!); 12 km south of Otjomatamba, 1813DD, 1160 m, 4 January 2004, *Swanepoel SWA3/76* (WIND!); 18°52'6" south and 14°22'4" east, 1814CD, 4 April 2000, *Curtis CUR346* (WIND!); Kaokoveld. Ondore, late 1957, *Abner 64* (PRE!, WIND!); Kaokoveld. Near Ohopoho, 20 May 1961, *Gibson 80* (WIND!); Joubert-Berge südlich Ohopoho, 6 June 1963, *Giess & Leippert 7376* (WIND!); Kaokoveld. In deep gorge on road between Sesfontein and Kaoko Otavi, January 1968, *Tinley 1669* (WIND!); Kaokoveld. Oruandje, 6 January 1973, *Owen-Smith 149* (WIND!).

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