



# Expanding our knowledge of the coffee family in continental Africa: a synopsis of the genus *Pyrostria* (Rubiaceae)

Kennedy W. Matheka<sup>1</sup> , David Goyder<sup>2</sup> & Iain Darbyshire<sup>2</sup>

**Summary.** A summary of the species of *Pyrostria* from continental Africa is presented, including full descriptions of three new species, *P. makovui*, *P. namacubiensis* and *P. rovumensis* from the coastal forests of the Tanzania-Mozambique border region, and one new subspecies, *P. lobulata* subsp. *bridsoniae* from Zambia. *Pyrostria makovui* is the first species with plurilocular (3-lobed) fruits and the second hermaphrodite species for the study area, characters that are otherwise found mainly in taxa of *Pyrostria* from Madagascar and surrounding islands. Five of the 16 species treated in this synopsis remain undescribed because they are known only from incomplete material. A key to the species of *Pyrostria* occurring in continental Africa is presented and notes on the distribution, habitat and relevant taxonomic considerations are provided, along with an assessment of the conservation status (extinction risk) for each species. The *Coastal Forests of Eastern Africa* Biodiversity Hotspot is found to be a centre of diversity for *Pyrostria*, with the Rovuma Centre of Plant Endemism in Mozambique and Tanzania being particularly rich in endemic species.

**Key Words.** Conservation, IUCN Red List, new species, Rovuma Centre of Endemism, taxonomy, Vanguerieae.

## Introduction

*Pyrostria* Comm. ex Juss. (Jussieu 1789: 206) is classified in the tribe Vanguerieae in subfamily Ixoroideae s.l. of the coffee family, Rubiaceae (Bremer *et al.* 1999). The tribe consists of more than 600 species in 27 genera (Razafimandimbison *et al.* 2009; Alejandro *et al.* 2013). It is easily delimited from other related tribes of Rubiaceae by having a specialised secondary pollen presenter, sometimes referred to as a stigmatic knob, at the tip of the style. Furthermore, Vanguerieae is the only tribe of Ixoroideae to have valvate corolla lobes, the inflorescences strictly axillary and the locules always uniovulate (Verdcourt 1987; Bridson 1991).

The genus *Pyrostria* is estimated to comprise  $\pm$  70 species (POWO 2021, continuously updated; Arriola *et al.* 2016). Although this is a substantial increase from the 45 species cited by Bridson (1991, 1998) and Schatz (2001), and a significant increase on the 58 accepted species listed on the Plant List (2013), the figure may yet increase if the many specimens held at a range of herbaria, most notably collections from Madagascar, are fully investigated to species level. Similarly, the genus appears to be underestimated in continental Africa, with nearly half of the known or postulated species not formally described (Verdcourt 1983; Bridson 1991, 1998). This may be a consequence of the dioecious nature of some taxa of the tribe Vanguerieae (Lantz & Bremer 2004), including many *Pyrostria*, since fertile male and female plants must be collected for complete circumscription of taxa when this is the case. The highly restricted, known ranges of some species further

contribute to our incomplete knowledge of *Pyrostria* in Africa, as several taxa are described from only single or few collections. However, recent botanical expeditions across parts of its continental African range have led to new collections of some of these taxa, providing new knowledge on the diversity of African *Pyrostria* beyond the most recent treatments of the genus by Verdcourt (1983) and Bridson (1987, 1991, 1998).

*Pyrostria* is predominantly Afro-Madagascan in its distribution, with Madagascar home to more than half of the known species (Madagascar Catalogue 2022). In continental Africa, the genus occurs principally in eastern tropical and subtropical regions, from the Horn of Africa to KwaZulu-Natal, with fewer species and more scattered occurrences in West and Central Africa (Bridson 1991; Davis *et al.* 2009). Elsewhere, it is also found in Socotra (*P. socotrana* (Radcl.-Sm.) Bridson); Arabia (*P. phyllanthoidea* (Baill.) Bridson); India, Andaman & Nicobar Is. (*P. lalji* M.C.Naik, Arriola & Bheem.) and tropical Southeast Asia (the *Pyrostria* group IB of Bridson 1987, e.g. *Pyrostria brunnescens* (Craib) Utteridge & A.P.Davis).

The genus ordinarily comprises small shrubs to medium-sized trees, without spines, except *Pyrostria hystrix* (Bremek.) Bridson, whose reduced branches can be spinose. *Pyrostria* is diagnosed by the combination of obscure tertiary leaf venation; pedunculate, umbellate inflorescences, each with an apical pair of persistent, internally pubescent bracts which usually fully encapsulate the inflorescence in bud (cardinal character); functionally dioecious unisexual or hermaphrodite flowers; a densely hairy corolla throat; 2-locular or plurilocular

Accepted for publication 3 January 2023.

<sup>1</sup> East African Herbarium, Botany Department, National Museums of Kenya, Museum Hill Road, P.O. Box, Nairobi 40658 – 00100, Kenya

<sup>2</sup> Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AE, UK. e-mail: i.darbyshire@kew.org

ovaries; and the style attached to the base of the pollen presenter (Bridson 1987; Razafimandimbison *et al.* 2009). Species occur in a variety of habitats, ranging from montane to coastal dry forests, where most are concentrated; around littoral zones; and a few distinct species occupy savanna and dry bushland (Bridson 1987).

Although little is documented about the uses of *Pyrostria*, some species are noted to be beneficial to the communities where they occur. For instance, fruits of *P. bibracteata* (Baker) Cavaco and *P. phyllanthoidea* are edible, with the hardwood of the former also used for construction, firewood, poles, charcoal and tool handles and, in addition, the trees provide shade, and forage for bees (Beentje 1994; Lovett *et al.* 2006).

### Taxonomic history and phylogenetic relationships

The genus *Pyrostria* was described by A. L. de Jussieu in 1789, based on a P. Commerson-collected specimen from Mauritius, this plant was subsequently described as *P. commersonii* J.F.Gmel. (Gmelin 1791). Four further species from the Mascarenes were later published by de Candolle (1830), and other researchers gradually described more, before a revision was eventually conducted by Verdcourt (1983). Over time, several species now placed in *Pyrostria* were included in other genera by various authors. For example, Baillon (1879a, 1880) treated *Psydrax angustifolius* A.Rich. ex DC., *P. major* A.Rich. ex DC. and *P. medius* A.Rich. ex DC. as species in *Canthium* Lam. section *Psydracium* Baill., despite these species having the paired bracts diagnostic for *Pyrostria*. Elsewhere, the genus *Dinocanthium* Bremek. was proposed by Bremekamp (1933) to include *D. hystrix* Bremek. from South Africa before the later addition of two other species (*D. affine* Robyns and *D. bequaertii* Robyns) by Robyns (1943).

Arènes (1960) described *Pseudopeponidium* Homolle ex Arènes and included six Malagasy species. Although its diagnostic characters were not clearly articulated, he noted the presence of plurilocular ovaries and paired bracts, which coincided with those of *Pyrostria*. Cavaco added more new species to this genus between 1966 and 1971 and also observed, among other characters, the presence of paired bracts in the inflorescence (Cavaco 1966, 1969, 1971a). Capuron (1969), on the other hand, did not differentiate between *Canthium*, *Pyrostria*, *Peponidium* (Baill.) Arènes and *Pseudopeponidium* and instead included the last three genera within a broadly circumscribed *Canthium*, without discussing reasons for doing so.

As a part of her reclassification of the tribe Vanguerieae, Bridson (1987) recircumscribed *Pyrostria*, using the presence of paired bracts as the key diagnostic character and subsuming *Dinocanthium* and *Pseudopeponidium*. In that work, Bridson also suggested that several other segregate genera may belong within *Pyrostria*, but did not formally synonymise them, including the Malagasy and

Mascarene genera *Leroyia* Cavaco, *Neoleroia* Cavaco and *Scyphochlamys* Balf.f. Schatz (2001) later included *Leroyia* (as *Leroia*) and *Neoleroia* within his concept of *Pyrostria*.

Molecular studies by Bremer *et al.* (1995) reported Vanguerieae as a well-supported monophyletic tribe, but the first attempt to construct a more detailed phylogeny for the tribe members was carried out by Lantz *et al.* (2002) using molecular data from the ITS (Internal Transcribed Spacer) region of the nuclear rDNA. Their study established *Keetia* E.Phillips, *Lagynias* E.Mey. ex Robyns, *Multidentia* Gilli and *Pyrostria* as a monophyletic group, while both *Canthium* and *Rytigynia* Blume were found to be polyphyletic at the generic level. However, a follow-up study by Lantz & Bremer (2004), which included more taxa than Lantz *et al.*'s study, established a dioecious clade within Vanguerieae for the first time. This clade comprised species of *Canthium* subgenus *Bullockia* Bridson, *Pyrostria* (including *Dinocanthium*), *Leroyia*, *Neoleroia*, *Peponidium*, *Pseudopeponidium*, *Scyphochlamys* and the ebracteate Pacific genus *Cyclophyllum* Hook.f. They suggested that the taxa in this dioecious clade could be included within *Pyrostria*, although some of their relationships within the clade were largely unresolved. A further molecular study by Razafimandimbison *et al.* (2009) sought to, *inter alia*, recircumscribe taxa within the dioecious group in Vanguerieae. Their results were largely consistent with Bridson's (1987) generic combinations, as well as reaffirming the dioecious group sensu Lantz & Bremer (2004). Their study established four clades in the dioecious group, and that generic limits required recircumscription. They contemplated i) subsuming all the genera of the group under *Pyrostria* (as previously suggested by Lantz & Bremer 2004); ii) retaining *Cyclophyllum* at genus level and placing all other genera into *Pyrostria*; and, finally, iii) recognising the four clades within the group as separate genera. The latter option was eventually adopted to preserve the monophyletic and morphologically distinct genera, thereby reducing the number of nomenclatural changes needed. These genera are *Bullockia* (Bridson) Razafim., Lantz & B.Bremer (elevated to generic rank from *Canthium* subgenus *Bullockia*), *Cyclophyllum*, *Peponidium* and *Pyrostria*. Razafimandimbison *et al.* included a formal synonymisation of *Scyphochlamys*, along with taxa previously synonymised by Bridson (1987). More recent work, by Wong *et al.* (2018), formally treated Group IV of Bridson (1987) as a new genus, *Dibridsonia* K.M.Wong, bringing the current number of recognised genera in the dioecious clade to five (see Table 1), for differences between them, refer to Bridson (1987: Table 1). It is noteworthy that only two of these genera, *Pyrostria* and *Bullockia*, occur in continental Africa.

Based on this latest circumscription, *Pyrostria* is easily diagnosable from all other genera of the dioecious

group by its persistent paired bracts which are connate basally, often acuminate, and sometimes large in comparison to the inflorescence in bud. *Peponidium*, on the other hand, which is often confused with *Pyrostria*, can be distinguished by the small, deciduous, cupular bracts located at the base of the inflorescence peduncles which do not enclose the young inflorescences (Razafimandimbison *et al.* 2009). This, readily observable, principal diagnostic character for *Pyrostria* has been used as the basis in recent taxonomic works for the transfer of more species from allied genera within Vanguerieae to *Pyrostria*, as well as for the description of new species from new collections; see, for example, Lantz *et al.* (2007), Razafimandimbison *et al.* (2007), Utteridge & Davis (2009), Alejandro *et al.* (2013, 2014), Arriola *et al.* (2015, 2016) and Kainulainen & Razafimandimbison (2016).

### Objectives

The objective of this study is to present a revised synopsis of the genus *Pyrostria* in continental Africa, by 1) establishing the current status of members of the genus; 2) formally describing new species where sufficient herbarium material has accumulated in the 35 years since Bridson's revision; 3) providing a key to identify the recognised taxa; 4) mapping the currently known distributions of the newly described taxa; and 5) assessing the conservation status (extinction risk) of these taxa. With regard to conservation status, only five continental African species of *Pyrostria* have, to date, been assessed and published on the IUCN Red List of Threatened Species (IUCN 2022b).

### Materials and Methods

Morphological examination of nearly 330 herbarium specimens, mainly held at K, was undertaken, with additional material studied at BM and EA. Images were examined from LISC and BNRH and resulting

from searches of virtual herbaria such as BR, C, P, PRE and WAG (herbarium abbreviations follow Thiers 2020, continuously updated). Type specimens not examined directly were viewed via JSTOR Global Plants (<https://plants.jstor.org/>). Specimens seen are marked “!”, specimen images seen are marked “\*”.

A morphological species concept was used sensu Stuessy (2009). Dry floral and fruit samples were softened by boiling, for easier dissection, and key identification characters were observed under a Leica S9i camera microscope connected to an Iiyama monitor (23.8”). Measurements of small features ( $\leq 1$  cm) were made using a microscope eyepiece graticule and a ruler was used for larger features. The descriptions were compiled with reference to existing literature including the *Flora of Tropical East Africa* (Verdcourt & Bridson 1991) and *Flora Zambesiaca* (Bridson 1998), which contain most of the species in the study area. Terminology follows the *Key Plant Glossary* (Beentje 2016). In this study, we only provide full descriptions for new taxa, those of existing taxa can be found in the Flora treatments and protologues, apart from *Pyrostria bispathacea* (Mildbr.) Bridson, which is only known from the type specimen from Cameroon. Typification and designation of names for new taxa were guided by the *International Code of Nomenclature for Algae, Fungi and Plants* (Turland *et al.* 2018) and the reference guide for botanical Latin (Stearn 2004).

The species are arranged in an approximation of their taxonomic relationships, based on morphological similarities. The position of the newly described *Pyrostria rovumensis* I.Darbysh. & Matheka is highly tentative, given that this species is rather atypical of the genus (see note accompanying the description). It is placed after *P. bibracteata* in the sequence, as this is the species with which *P. rovumensis* is most likely to be confused.

Species distribution maps were prepared using Arc-Map version 10.1 (Esri, Redlands, USA). Coordinates

**Table 1.** Currently accepted genera in the dioecious clade of Vanguerieae and their distribution, with their equivalent taxa in the study of this clade and key references for taxonomic changes post Bridson (1987).

Currently Accepted Genus	Equivalent taxon/taxa in Bridson (1987)	Key references for taxonomic changes (synonymy or new combinations)	Geographical distribution
<i>Pyrostria</i>	Group I [A & B] <i>Pyrostria</i> s.l. (including <i>Leroyia</i> and <i>Neoleroia</i> ) Group II <i>Scyphoclamys</i>	Razafimandimbison <i>et al.</i> (2007)	tropical and southern Africa; Arabia; Madagascar and Mascarenes; SE Asia
<i>Cyclophyllum</i>	Group III <i>Cyclophyllum</i>	Smith & Darwin (1988)	Australia, New Guinea, Pacific Islands
<i>Dibridsonia</i>	Group IV	Wong <i>et al.</i> (2018)	Thailand, Malaysia, Indonesia, Philippines
<i>Peponidium</i>	Group V	Razafimandimbison <i>et al.</i> (2007); Davis & Razafimandimbison (2010); Kainulainen & Razafimandimbison (2016)	Madagascar, Comoros, Seychelles
<i>Bullockia</i>	<i>Canthium</i> subgen. <i>Bullockia</i>	Razafimandimbison <i>et al.</i> (2007)	Ethiopia and Somalia to eastern South Africa

were obtained directly from specimen data labels where indicated, or alternatively by use of gazetteers of collecting localities or by searching for the localities using Google Earth Pro (2022).

Species conservation assessments were made, assisted by the IUCN Species Information Services tool, using the IUCN (2012, 2022a) categories, criteria and guidelines. The Kew geospatial conservation assessment tool, GeoCAT (Bachman *et al.* 2011), was used to analyse species location data, providing estimates of the extent of occurrence (EOO) and area of occupancy (AOO), using a 2 × 2 km cell size, following the IUCN (2022a) guidelines.

## Results and Discussion

Our study delimits 16 species and four subspecies of *Pyrostria* in continental Africa, of which three species and one subspecies are newly described. They include the first mainland African species with fully formed multilocular (3-lobed) fruits, a character often found on *Pyrostria* taxa from Madagascar and surrounding islands. They also include only the second hermaphrodite species to be documented for this area: *P. makovvui* Matheka & I. Darbysh., hitherto hermaphrodite flowers were known only from *P. bibracteata*. Specimens of the newly described species chiefly result from recent fieldwork programmes in the dry forests of Cabo Delgado Province, northern Mozambique.

## Distributions and phylogeographical linkages of *Pyrostria* in continental Africa

Of the 16 species of *Pyrostria* accepted here, nearly half (seven) occur in the Coastal Forests of the East Africa biodiversity hotspot (CEPF 2022) and, of these, five are restricted to the Rovuma Centre of Plant Endemism (CoE) in the coastal lowlands of southern Tanzania and northern Mozambique (Burrows & Timberlake 2011; Darbyshire *et al.* 2019a, 2020). They include all three of the species newly described here. It is becoming increasingly evident that the coastal dry forests and thickets of the Rovuma CoE are very rich in highly range-restricted endemics (Timberlake *et al.* 2011; Darbyshire *et al.* 2020). However, large portions of these habitats have already been lost and many remaining, intact forests and thickets in this coastal zone are poorly protected and imminently threatened from expansion of human activities (Timberlake *et al.* 2011; Darbyshire *et al.* 2020). In Mozambique, two critical areas of coastal dry forest are located along the lower Rovuma river escarpment and in the vicinity of the coastal village of Quiterajo. Together, these two sites hold all or most of the known ranges of the three new species of *Pyrostria* documented here, as well as numerous other rare and range-restricted species. These two areas have been designated as Important Plant Areas (IPAs), as part of the national network of 57

IPAs identified in Mozambique (Darbyshire *et al.* 2023), to highlight their biodiversity importance and help target conservation efforts appropriately.

Elsewhere, the forests of the ancient Eastern Arc Mountain chain in Kenya and Tanzania, which are linked biogeographically to the Coastal Forests of the East Africa hotspot, famed for its high endemism (Burgess *et al.* 2007), have two endemic species of *Pyrostria*. *P. uzungwaensis* Bridson from the Udzungwa Mountains and the incompletely known *P. sp. D* from the West Usambara Mountains. A further undescribed species, *P. sp. A*, extends into the Eastern Arc in the Taita Hills of Kenya, but also occurs in adjacent lowland hill forests away from the Eastern Arc. Elsewhere, only one other truly montane species, *P. chapmanii* Bridson, is known from the inselbergs of southern Malawi and northern Mozambique, an area recently proposed as a (sub)centre of plant endemism, the Mulanje-Namuli-Ribáuè centre, due to its high numbers of unique plant species (Darbyshire *et al.* 2019a).

Other major phytochoria of Africa support few species of *Pyrostria*. The *Acacia-Commiphora* woodlands of the Somalia-Masai regional centre of endemism (White 1983) have only one, *P. phyllanthoidea*. That species also extends into the Zambesian regional centre, which otherwise has only *P. lobulata* Bridson. Finally, the Guinea-Congolian forests of West and Central Africa support only two species, the widespread but rather scarce *P. affinis* (Robyns) Bridson and the highly localised *P. bispathacea*, which is known only from the type locality close to Yaoundé in Cameroon. The remnant forests around Yaoundé, including those situated on small inselbergs, are noted for a number of other rare and localised taxa, such as *Morinda mefou* Cheek and *Talbotiella breteleri* (Aubrév.) Mackinder & Wieringa (Cheek *et al.* 2011; Onana & Cheek 2011).

Detailed botanical surveys of the Mozambican coastal forests between 2003 and 2009 resulted in the discovery of many plant species new to science, including over 15 species of Rubiaceae, while a further 68 species were documented as new records for the country (Timberlake *et al.* 2011; Darbyshire *et al.* 2020, 2021). These studies highlight not only the high species richness and species turnover of these forests, with many highly range-restricted taxa, but also the fact that this area is understudied for its biodiversity, thus making it a priority for botanists and conservationists. Their views have been echoed by Burrows *et al.* (2018), who emphasise the botanical importance of the Namacubi forest at Quiterajo as the only known home to the recently described species *Memecylon aenigmaticum* R.D. Stone and *Warneckea albiflora* R.D. Stone & N.P. Tenza, (Melastomataceae) as well as the presence of a range of other national or regional endemic species. Indeed, such is the importance of this forest that Burrows *et al.* (2018) dedicated their voluminous book to this irreplaceable site.

## Taxonomic Treatment

**Pyrostria** *Comm. ex Juss.* (Jussieu 1789: 206). Type species: *P. commersonii* J.F.Gmel.

*Scyphochlamys* Balf.f. (Balfour 1877: 14). Type species: *S. revoluta* Balf.f. (= *Pyrostria revoluta* (Balf.f.) Razafim., Lantz & B.Bremer).

*Canthium* Lam. section *Psydracium* Baill. (Baillon 1879a: 199). Type species: *Pyrostria major* (A.Rich. ex DC.) Kainul. & Razafim. (syn. *Psydrax majus* A.Rich. ex DC., *Canthium major* (A.Rich. ex DC.) Drake).

*Dinocanthium* Bremek. (Bremekamp 1933: 259). Type species: *D. hystrix* Bremek. (= *Pyrostria hystrix* (Bremek.) Bridson).

*Pseudopeponidium* Homolle ex Arènes (1960: 19). Type species: *P. neriifolium* Homolle ex Arènes (= *Pyrostria neriifolia* (Homolle ex Arènes) Razafim., Lantz & B.Bremer).

*Leroyia* Cavaco (1970: 335). Type species: *L. mada-gascariensis* Cavaco (= *Pyrostria antsiranensis* Razafim., Lantz & B.Bremer).

*Neoleroia* Cavaco (1971b: 122). Type species: *N. verdcourtii* Cavaco (= *Pyrostria verdcourtii* (Cavaco) Razafim., Lantz & B.Bremer).

*Small shrubs to medium-sized trees. Leaves* usually petiolate, sometimes sessile or subsessile; lamina drying dull green, blackish-brown or slate-grey, normally subcoriaceous but sometimes coriaceous or chartaceous, usually glabrous, rarely pubescent; tertiary venation obscure except occasionally; domatia present, mostly as glabrous to ciliate pockets in the axils of the lateral leaf veins and the midrib beneath, or sometimes absent; stipules connate, usually triangular, tapering towards apex, persistent or caducous on older branches, enclosing silky hairs and colleters. *Inflorescences* opposite (paired) axillary pedunculate umbels, infrequently both peduncle and pedicels reduced;

flowers 4- or 5-merous, unisexual or hermaphrodite; female inflorescence with fewer flowers (often solitary) than the male inflorescence in dioecious species; bracts paired, persistent, connate and usually fully enveloping the inflorescence in bud, silky hairs and colleters present internally. *Hypanthium* ± ovate in female and hermaphrodite flowers, much reduced in male flowers. *Calyx* tube very reduced, usually only forming a narrow rim, with equal to unequal short lobes or sometimes cup-like. *Corolla* often dried dark, lobes shorter or longer than tube, usually reflexed when mature to expose a dense mass of white hairs in the throat, lobes involute (valvate, thickened at margins and with contact zone), mostly tapering or apiculate at apex, interior surface minutely grainy, lumpy or scaly. *Stamens* alternating with corolla lobes, filaments essentially absent or very short, attached dorsally close to anther base; anthers ovate, oblong-ovate or slightly obovate, tapered or apiculate at apex; usually erect or seldom reflexed; connective blackish dorsally, except for the pale edges. *Style* very slender; with a solid apical pollen presenter (stigmatic knob) not or very slightly recessed at base; 2- or several-lobed in conformity with the number of locules; ovary with 2 – 10 locules, one ovule per locule. *Fruit* fleshy, flattened laterally when 2-seeded, broader above, often with many smaller lobes when fresh, or variously shaped when multi-seeded. *Pyrenes* thinly woody, obovoid to ellipsoid or nearly so, crested apically, somewhat depressed at the point of attachment from where it splits open.

**DISTRIBUTION.** Tropical Africa, from Guinea to Somalia and south to Angola and northern and eastern South Africa; in Madagascar and the Mascarenes; in southern Arabia; in India, the Andaman and Nicobar Islands; and in southeast Asia, from Thailand and Vietnam to the Philippines and Borneo.

## Key to *Pyrostria* species in continental Africa

- 1 Leaves small, 0.5 – 3.5 (– 4.5) cm long, if reaching 4.5 cm long then linear-oblong, secondary veins usually not apparent but sometimes present; shrubs; lateral branches reduced, spur- or spine-like ..... 2  
 Leaves usually more than 3 cm long, if less than 4.5 cm then not linear-oblong, secondary veins usually visible; shrubs or (small) trees, lateral branches rarely reduced or, if so, then leaves crowded near tips of branches ...  
 ..... 4
- 2 Leaves oblong-elliptic to linear-oblong; lateral branches not at right angles to main branch ..... **13. *P. phyllanthoidea***  
 Leaves narrowly obovate to elliptic; lateral branches ± at right angles to main branch ..... 3
- 3 Branches often with spine-like short-shoots; leaves with inconspicuous lateral venation; domatia absent; bracts very reduced (± 1 mm long); pedicels up to 1 mm long; corolla-tube ± 1.5 mm long ..... **16. *P. hystrix***  
 Branches reduced but short-shoots not spiny; leaves with three main pairs of lateral veins visible; domatia present as pubescent cavities; bracts larger, up to 4 × 3.5 mm, often with lateral lobe(s); pedicels 1.5 – 2.5 mm long; corolla-tube up to 3.1 mm long ..... **15. *P. namacubiensis***
- 4 Leaves ± 3.1 × 1 cm, clustered at branch tips, brownish upon drying, three pairs of lateral veins present, apex obtuse; domatia present; branches thinly covered with greyish bark which peels off to expose a reddish-brown

- inner layer; peduncle and pedicel very reduced in young inflorescence; deciduous treelet of coastal dunes ..... **14. P. sp. E**
- Leaves larger, well dispersed along branches or rarely clustered at branch tips, drying brown, black-brown or dark green, lateral veins three or more, apex obtuse to rounded, acute or acuminate; domatia present or absent; bark greyish or brownish, rarely peeling; peduncle and pedicel various ..... **5**
- 5 Leaves with tertiary veins raised above and below; leaf apex long-acuminate, with an apiculum at the tip; young stems laterally compressed and hairy on sulcate sides ..... **8. P. sp. C**
- Leaves with tertiary veins obscure or  $\pm$  apparent on or beneath the surface, not raised, apex acute, obtuse or acuminate, apiculate or not; young stems usually glabrous but sometimes puberulous on opposing compressed sides..... **6**
- 6 Leaves short- to long-acuminate at apex..... **7**
- Leaves obtuse to rounded or acute to bluntly acuminate at apex ..... **10**
- 7 Leaves papery, drying blackish-brown; tertiary veins visible but not prominent; stipules linear from a triangular base; pedicels  $\pm$  1 cm long ..... **9. P. sp. D**
- Leaves (sub)coriaceous or rigidly chartaceous, drying blackish or dark green, tertiary veins obscure or rarely visible; stipules triangular, triangular-ovate or rarely linear-lobed; pedicels < 1 cm ..... **8**
- 8 Young stems pubescent on compressed sides; leaves, tertiary veins visible but not prominent; peduncles pubescent near base of bracts ..... **10. P. uzungwaensis**
- Young stems glabrous or rarely pubescent; leaves, tertiary veins obscure or faintly visible; peduncles glabrous ..... **9**
- 9 Stipules narrowly triangular or tapering towards apex; pedicels  $\pm$  7 mm long; corolla-tube up to 4 mm long, lobes 3 – 3.5 mm long; anthers deflexed ..... **11. P. bispathacea**
- Stipules triangular with a narrowed, keeled lobe; pedicels up to 4 mm long; corolla-tube 4 – 10 mm long, lobes less than 2.5 mm long; anthers erect ..... **12. P. affinis**
- 10 Leaves usually acute at apex or infrequently obtuse, blades greyish-green upon drying ..... **11**
- Leaves often obtuse to acute or rarely bluntly acuminate, blades usually drying blackish-brown or green-brown ....  
..... **12**
- 11 Lateral branches shortened, nodes close together, leaves somewhat clustered towards ends of branches; peduncle and pedicels distinct; fruit 2-lobed ..... **6. P. sp. B**
- Lateral branches with well-spaced nodes and leaves; peduncle and pedicels much reduced to give a sessile appearance to inflorescence; fruit  $\geq$  3-lobed ..... **7. P. makovui**
- 12 Leaves oblong-elliptic to slightly obovate, apex rounded or obtuse; domatia conspicuous as tufts of hairs; inflorescences mostly borne at leafless nodes; fruit tapered or rounded at base ..... **5. P. chapmanii**
- Leaves typically broadly elliptic or narrowly to broadly obovate, acute, obtuse, rounded or somewhat acuminate at apex; domatia inconspicuous or present as tufts of hairs; inflorescences borne at leafy axils, fruit not distinctly tapered at base ..... **13**
- 13 Stipules usually with a linear lobe above a triangular base, 4 – 14 mm long ..... **14**
- Stipules triangular or triangular-ovate, 5 – 10 mm long ..... **15**
- 14 Paired bracts conspicuous, 2 – 7 mm long, acuminate; leaves elliptic to oblong-elliptic, apex usually acute but can be obtuse, upper surface flat; young stems subterete to only slightly angular, not striated; flowers 4-merous, corolla-tube 2 – 3 mm long, lobes 2 – 2.5 mm long ..... **1. P. bibracteata**
- Paired bracts inconspicuous, 1 – 1.2 mm long, not acuminate; leaves typically obovate with apex rounded or obtuse (often damaged), upper surface with shallow corrugated appearance from lateral veins raised within shallow furrows; young stems square and striated; flowers 5-merous, corolla-tube 0.6 – 0.7 mm long, lobes  $\pm$  1.5 mm long ..... **2. P. rovumensis**
- 15 Leaves, lateral veins usually 6 (– 5); pedicels shortly hairy; pollen presenter  $\pm$  spherical ..... **3. P. lobulata**
- Leaves, lateral veins mostly 3 – 4 (– 5); pedicels usually glabrous; pollen presenter broadly ellipsoid ..... **4. P. sp. A**

**1. *Pyrostria bibracteata*** (Baker) Cavaco (1968: 1015); Bridson (1987: 625; 1991: 887; 1998: 341); Beentje (1994: 540); Burrows (2018: 931). Type: Seychelles, fl., 1841, *Perville* 82 (holotype K! [K000412467]).

*Protonia bibracteata* Baker (1877: 146).

*Canthium bibracteatum* (Baker) Hiern (1877: 145); Bullock (1932: 375); Brenan (1949: 487); Dale & Greenway (1961: 427); Fosberg & Renvoize (1980: 150).

**DISTRIBUTION.** Kenya, Tanzania, Mozambique, Zimbabwe, Madagascar and the Seychelles (including Aldabra; see note).

**SPECIMENS EXAMINED. KENYA.** Kwale, fl., 1929, *Graham* 1653 (EA, 3 sheets!, K!); Kilifi – Malindi road, sterile, 6 Sept. 1936, *Swynnerton* 96 (K!); Kilifi, fr., June 1936, *Moggridge* 94 (EA!, K!); Sokoke Forest, in bud, Sept. 1936, *Moggridge* 184 (EA!, K!); Kilifi, in bud, 30 Sept.

1937, *Moggridge* 494 (EA!); Kasigau, fl., Sept. – Oct. 1938, *Bally* 9403 (K!); Milimani, Boni Forest, fr., 31 Dec. 1946, *Adamson* in *Bally* B.5826 (K!); 2 km W of Sokoke, 200 m S of the road to Ganze, fr., 17 July 1951, *Kuyper* 5 (EA!); 5 miles E of Kinango, in bud, 9 Sept. 1958, *Moomaw* 831 (EA!); Kwale Distr., Shimba Forest near Kwale, fl., 14 March 1968, *Magogo & Glover* 294 (EA!, K!); Kwale Distr., Kwale Forest area on the road to the Wireless Station, fl., 23 March 1968, *Magogo & Glover* 412 (EA!, K!); Kilifi Distr., forest 1 mile S of Jilore, fl., 11 Sept. 1969, *Perdue & Kibuwa* 10022 (EA!, K!); Lamu Distr., 2 km N of Hindi, fl., 25 Aug. 1973, *Gillett* 20346 (EA!, K!); Lamu Distr., Boni Forest, Basuba near Mangai, 10 miles W of Mangai, fr., 7 Aug. 1975, *Katz* 75/12 (EA!); Kwale Distr., Tiwi, c. 1 km inland from Tiwi Beach just S of 'Bowa', fl., 17 Nov. 1978, *Kuchar* 10134 (EA!); Kwale Distr., Tiwi – Kiwala road 1 mile S of junction Mombasa road, fl., 18 Nov. 1978, *Brenan et al.* 14550 (EA!, K!); Kilifi, Mnarani Club, in bud, 11 July 1979, *Kuchar* 11838 (EA!); Lamu Distr., 1.5 km N of Hindi, fl., 7 March 1980, *Kuchar* 12848 (EA!); Kajiado, Emali Hill, fr., 20 Dec. 1986, *Luke & Robertson* 109 (K!); Kilifi Distr., Kaya Ribe, fr., 10 July 1987, *Robertson & Luke* 4823 (EA!); Mangepa Hill, fr., 18 July 1987, *Luke & Robertson* 622 (EA!); Tana River Distr., Kanwe Mayi Forest patches, fr., 7 Aug. 1988, *Robertson & Luke* 5384 (EA!, K!); Lamu Distr., Witu Forest, in bud, 16 Nov. 1988, *Robertson & Luke* 5523 (EA!, K!); Lamu Distr., 15.6 km Hindi to Kiunga, fl., 23 Nov. 1988, *Luke & Robertson* 1449 (EA!, K!); Lamu Distr., Lunghi Forest Reserve (proposed), fl., 24 Nov. 1988, *Luke & Robertson* 1470 (EA!); Lamu Distr., Boni Forest Reserve (proposed), 24 km W of Basuba, in bud, 1 Dec. 1988, *Luke & Robertson* 1523 (EA!); Kwale Distr., Dzombo Hill, fr., 13 Feb. 1989, *Robertson et al.* MDE 387 (EA!); Shimba Hills, sterile, 1992, *Mutangah et al.* 534 (EA!); Kwale Distr., Shimba Hill National Park, in bud, 4 June 1998, *De Block et al.* 384 (EA!); Kwale, Shimba Hills, 5 km from Sable Bandas towards Sheldrick falls, fr., 3 July 2006, *Muasya* NMK 700 (EA!, K!); Lamu Distr., Nairobi Ranch, fr., 18 July 2006, *Festo & Luke* 2523 (EA!, K!). **TANZANIA.** Zanzibar, fl., without date, *Kirk* s.n. (K, 2 sheets!); town of Zanzibar, fl., without date, *Kirk* s.n. (BM!, K!); no loc. [probably Zanzibar], without date, fl., *Vaughan* 930 (EA!); Amboni, fr., June 1893, *Holst* 2713 (HBG, K!); Dfuani, (?) Mafia Island, fr., 25 March 1912, *Braun* 3652 (EA!, K!); Usaramo, Soga – Baha, fl., 14 Dec. 1915, *Peter* 55845 (K!); Tanga, Amboni to Gombero, fr., 19 March 1918, *Peter* 56118 (K!); Tanga, Amboni to Sigi, fr., 21 June 1918, *Peter* 56142 (K!); Usaramo, km 20.5 – 21.5 längs der Bahnstrecke, fl., 23 Oct. 1925, *Peter* 31294 (K!); Usaramo, Pugu längs der Bahnstrecke, fl., 23 Oct. 1925, *Peter* 31294a (K!); Usaramo, bei Msua, fl., 2 Nov. 1925, *Peter* 31711 (K!); Usaramo, SW von Msua, fl., 3 Nov. 1925, *Peter* 31760 (K!); Tanga, Dorf Langoni, fr., 22 April 1926, *Peter* 39881 (K!); Zanzibar, Kiungani, fr., 2 Feb. 1929, *Greenway* 1309 (EA!, K!); Zanzibar, Kurekwe-Kilimani Kzall, fl., 3 Dec. 1930, *Greenway* 2643 (EA!, K!); Zanzibar, fr., 1931, *Vaughan* 1040 (EA!, K!); *ibid.*, fl., 1931, *Vaughan* 1453 (EA!, K!); *ibid.*, fl., 1931, *Vaughan* 1536 (EA!, K!); Lindi Distr., Mlinguru, fl., 18 Dec. 1934, *Schlieben* 5742 B (K!); Makuyuni Distr., West Usambaras, fr., June 1935, *Koritschner* 1107 (K!); Tanga Distr., Pongwe, fl., 31 Jan. 1937, *Greenway* 4847 (K!); Kisarawe, in bud, 31 July 1937, *Greenway* 4976 (EA!, K!); Mafia Island, Mwakuni, fl., 2 Oct. 1937, *Greenway* 5374 (BM!, EA!, K!); Kisarawe Distr., Kisiju, Koresese Forest Reserve, fl., Sept. 1953, *Semsei* 1382 (EA!, K!); Tanga – Pangani road, Machui, fl., 11 Feb. 1955, *Faulkner* 1556 (K!); Morogoro Distr., about 26 km E of Morogoro, fl., 26 Nov. 1955, *Milne-Redhead & Taylor* 7385 (EA!, K!); Tanga Prov., Pangani, Mongo, Mkwaja, fr., 25 March 1956, *Tanner* 2675 (K!); Tanga Prov., Pangani, Kokoni, Mseko, Mwera, fr., 12 July 1956, *Tanner* 3042 (K!); Tanga Prov., Pangani, Mwembeni, Madanga, fr., 28 Oct. 1956, *Tanner* 3316 (K!); Morogoro, near Kingolwira Station, fl., 23 Nov. 1956, *Welch* 343 (EA!, K!); Tanga Prov., Pangani, Mvumoni, Madanga, fr., 20 March 1957, *Tanner* 3444 (K!); Zanzibar, Massazwe, fl., 4 May 1959, *Faulkner* 2248 (K!); *ibid.*, fl., 15 Nov. 1959, *Faulkner* 2398 (EA!, K!); Zanzibar, Massazwe, fr., 19 Jan. 1960, *Faulkner* 2462 (K!); Zanzibar, Mara hubi, fl., 14 Nov. 1963, *Faulkner* 3304 (K!); *ibid.*, fl., 28 Oct. 1964, *Faulkner* 3441 (K!); Kisarawe Distr., Banda Forest Reserve, fr., Jan. 1965, *Procter* 2850 (EA!, K!); near cement factory 12 miles N of Dar es Salaam, fr., Jan. 1965, *Procter* 2878 (EA!, K!); Kisarawe Distr., Kazimzumbwi Forest Reserve, fr., Feb. 1965, *Procter* 2897 (EA!, K!); Kisarawe Distr., Msolwa, fr., May 1965, *Procter* 3014 (EA!, K!); Bagamoyo Distr., Kiona Plateau, fr., 4 March 1966, *Mgaza* 843 (EA!, K!); Tanga Distr., Mwango near Sawa, fl., 19 March 1968, *Faulkner* 4083 (K!); Bagamoyo, Dar es Salaam, Kerege, imm. fr., 27 March 1968, *Robertson* TRU 613, (EA!); *ibid.*, imm. fr., 28 March 1968, *Robertson* TRU 619 (EA!, K!); 15 miles S of Dar es Salaam, fr., 20 April 1968, *Harris* 1626 (K!, EA!); Korogwe Distr., Kabuku Forest, fl., 6 Nov. 1968, *Faulkner* 4166 (K!); University College Dar es Salaam, fl., 6 Nov. 1968, *Harris & Gardiner* BJH 2541 (EA!); Rufiji-Utete Distr., Ikwiriri, Ngumbuluni Forest Reserve, fr., 20 Dec. 1968, *Ngoundai* 200 (EA!, K!); Utete Distr., Kibiti, Ngulakula Forest Reserve, fr., 20 Dec. 1968, *Shabani* 281 (EA!, K!); Banda Forest Reserve, Kisarawe, fl., 13 Nov. 1969, *Shabani* 484 (EA!, K!); Banda Forest Reserve near Mfyoza, fl., 14 Nov. 1969, *Ruffo* 333 (EA!, K!); Pande Forest Reserve, fl., 22 Nov. 1969, *Harris* 3608 (EA!, K!); Korogwe Distr., Segoma, fr., 23 March 1970, *Faulkner* 4341 (K!); Selous, Tundu Hills, fl., 4 Oct. 1970, *Rodgers* 1153 (EA!); Lushoto Distr., Mlungui near Manolo area, fr., 26 May 1972, *Ngonyani* 82 (K!); 5 km S on Kisha road, fl., 16 Oct.

1973, *Rodgers* 1661 (EA!); Kisarawe Distr., Ruvu Forest Project, Madabala Forest Reserve, fr., 5 Jan. 1977, *Magogo* 756 (K!); Handeni Distr., Kwa Mkono, fr., 27 Feb. 1980, *Archbold* 2772 (K!); *ibid.*, fr., 28 April 1981, *Archbold* 2813 (K!); Mwera Estate, Kilimanguido, Pangani, in bud, 21 May 1982, *Hawthorne* 732 (K!); Mwera Estate, Langoni Forest, sterile, 8 July 1982, *Hawthorne* 1406 (K!); Handeni Distr., Kwa Mkono, fr., 7 July 1983, *Archbold* 2995 (K!); Pemba Is., Ngezi Forest, imm. fr., Dec. 1983, *Rodgers et al.* 2763 (EA!, K!); Pemba, fr., 27 Jan. 1984, *Groenendijk et al.* 815 (K!); Handeni Distr., Kwa Mkono, fr., 5 March 1986, *Archbold* 3101 (K!); Kinondoni Distr., University of Dar es Salaam, Botany Dept. reserved forest, fr., 28 May 1986, *Kisena et al.* 281 (K!); Bagamoyo Distr., Zaraninge Forest, Kiono Plateau, fr., 16 March 1990, *Frontier Tanzania Programme* 1086 (K!); Handeni Distr., Kwamkono, fl., 10 Nov. 1990, *Archbold* 3337 (K!); Kisarawe Distr., Kinyanyiko (Pugu Forest Reserve), fr., 15 Nov. 1990, *Ruffo & Mmari* 3173 (K!); Kinondoni Distr., University of Dar es Salaam, fl., 20 Nov. 1990, *Ruffo & Mmari* 3191 (K!); Kisaware Distr., Kazimzumbwi Forest, fr., Jan. 1991, *Frontier Tanzania Programme* 1693 (K!); *ibid.*, fr., Jan. 1991, *Frontier Tanzania Programme* 1697 (K!); *ibid.*, fr., Feb. 1991, *Frontier Tanzania Programme* 1842 (K!); Kiserawe Distr., Ruvu South Forest, 30 km SW of Dar es Salaam, fr., 12 Feb. – 14 March 1991, *Frontier Tanzania Programme* 2123 (K!); Lindi Distr., 12 km on Mnazimoja – Mtwara road, fr., 2 March 1991, *Bidgood et al.* 1755 (EA!, K!); Rufiji Distr., Matumbi Hills, Kiwengoma Forest Reserve, near WWF office, fl., 15 Nov. 1999, *Kibwe* 562 (K!); Zaraninge Forest Reserve, near WWF office, Gongo village, fl., 29 Nov. 1999, *Abeid* 795 (K!).

**MOZAMBIQUE.** Sul do Save, Inhachengo, fr., 26 Feb. 1955, *Exell & Mendonça* 615 (BM!, LISC\*); Zambézia, Pebane, praia de Pebane, junto ao Farol, fr., 12 Jan. 1968, *Torre & Correia* 17095 (LISC\*); Antonio Enes [Angoche], Aube, ao km 6, estrada para Beila, fr., 22 Jan. 1968, *Torre & Correia* 17304 (LISC\*); Manica e Sofala, Serra Macuta, in bud, 2 June 1971, *Müller & Gordon* 1776 (K!); Beira Distr., Gorongosa National Park, Cheringoma Plateau, 4 km along Urema road from its junction with Inhaminga – Beira main road, fr., Jan. 1972, *Tinley* 2336 (K!); *ibid.*, fl./fr., Sept. 1972, *Tinley* 2726 (K!); Gorongosa National Park, Cheringoma Plateau, Mussambidzi catchment, in bud, May 1973, *Tinley* 2820 (K!); Nampula, Mossuril, Serra de Mesa, fr., 19 Feb. 1984, *Köning et al.* 9734 (K!); *ibid.*, fr., 19 Feb. 1984, *Köning et al.* 9748 (K!); Cabo Delgado, Pemba, a 15 km de Pemba, caminho para Montepuez, fr., 27 Jan. 1984, *Groenendijk et al.* 815 (K!); Nangade – Palma, pt. 535, sterile, 15 Dec. 2003, *Luke et al.* 10167 (EA!); Zambezia Prov., Gilie Reserve, fl., 17 Oct. 2005, *Schmidt* 4003 (BNRH\*); Cabo Delgado, Quiterajo, track N of the airstrip leading to the Messalo R., fr., 26 Nov. 2008, *Burrows & Burrows* 10784 (K!); Cabo Delgado,

Quiterajo, Mirepa, imm. fr., 29 Nov. 2008, *Matimele* 04 (K!); Cabo Delgado, Nhica Camp to Pundanhar, pt. 445, fr., 17 Nov. 2009, *Luke & Luke* 13837 (EA!, K!); *ibid.*, fl., 17 Nov. 2009, *Luke & Luke* 13838 (EA!, K!); Cabo Delgado, Quiterajo, close to margin of Namacubi Forest above Messalo R. floodplain, fl., 23 Nov. 2009, *Crawford* FC 698 (K!); Cabo Delgado, Quiterajo, northern part of Namacubi Forest above Messalo River floodplain, on road to Moenhe R., fr., 23 Nov. 2009, *Crawford* FC 706 (K!).

**ZIMBABWE.** Melsetter [Chimanimani] Distr., Hayfield B, near Chisengu R., fl., 25 Aug. 1977, *Müller* 3433 (K!).

**HABITAT.** Wooded grassland, *Brachystegia* (miombo) woodland, thickets and forest margins, at elevations of 0 – 870 m.

**CONSERVATION STATUS.** This species is distributed widely over four countries in mainland Africa and is known to occur in protected areas such as Arabuko Sokoke Forest and Shimba Hills in Kenya and Gorongosa National Park in Mozambique; among others. The EOO is calculated at slightly more than 1.2 million km<sup>2</sup> in mainland Africa, however, it also occurs outside the study region on three Indian Ocean islands, hence the total EOO is in excess of 3.2 million km<sup>2</sup>. The species also appears to tolerate some disturbance, sometimes being recorded from secondary habitats. Therefore, it is assessed here as Least Concern [LC].

**NOTES.** Friedmann (1994), under the name *Canthium bibracteatum*, noted that unisexual as well as hermaphrodite flowers occur in this species in the Seychelles. As the type specimen is from the Seychelles, it is possible, therefore, that this name is not applicable to continental African populations currently called *P. bibracteata*, but more detailed study is needed for confirmation. Bridson (1987) also notes that the material from Aldabra is somewhat different from other material of this species in being smaller, particularly with regard to fruit size, but suggested that any recognition of further taxa within the *P. bibracteata* complex is best left until a full revision of *Pyrostria* on Madagascar is carried out. Fig. 1.

**2. *Pyrostria rovomensis* I. Darbysh. & Matheka sp. nov.** Type: Mozambique, Cabo Delgado Prov., Palma Distr., Pundanhar, fl., 10 Nov. 2009, *Matimele* 149 (holotype K! [K000787497]; isotypes EA! LMA).

<https://www.ipni.org/urn:lsid:ipni.org:names:77329668-1>.

*Pyrostria* sp. nov. sensu Darbyshire *et al.* (2020: 443).

*Small tree* to 2 – 10 (– 15) m high, sometimes shrubby; young branches glabrous, pale greyish- or sandy-brown, ± square and with two opposite furrows, longitudinally striated; mature stems with



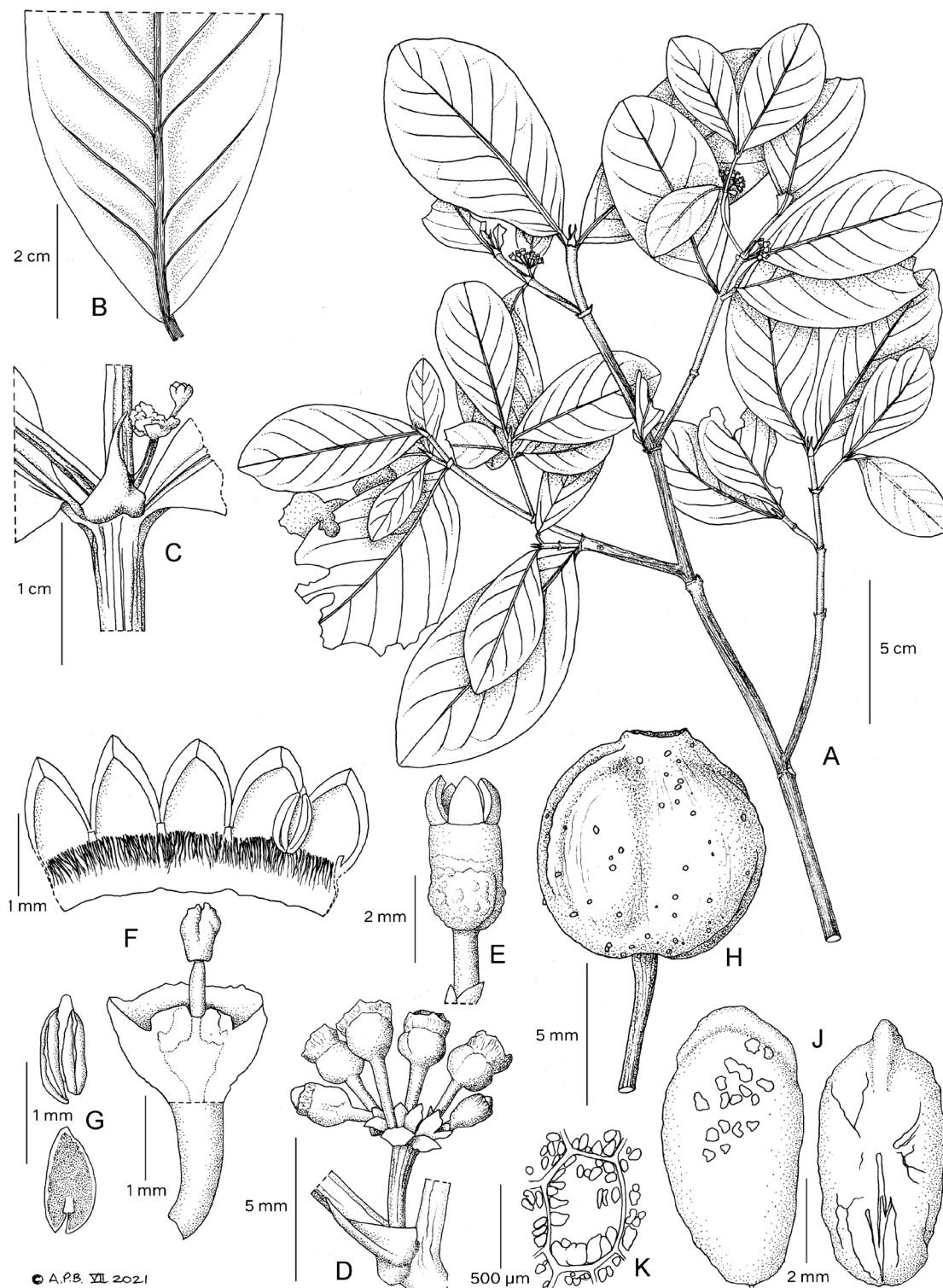


**Fig. 1.** *Pyrostria bibracteata* in the field. **A** flowering branch, Base Titanium proposed mining site, Kwale, Kenya (collected as a sight record, Luke SR 303); **B** fruiting branch, Quiterajo, Mozambique (collected as Burrows & Burrows 10784). PHOTOS: Q. LUKE & J. E. BURROWS.

rough grey to brown bark with reticulate fissuring. *Leaves* narrowly obovate or elliptic, coriaceous, drying brown or pinkish-brown above, green or green-brown beneath,  $5.5 - c. 10 \times 2.7 - 5.3$  cm, base cuneate to obtuse, apex rounded or obtuse but very often eaten or malformed; 5–8 main pairs of lateral veins, these and midrib somewhat prominent beneath, also prominent above but within furrows, the leaves therefore appearing shallowly corrugated when mature; midrib broad and with a central furrow above; tertiary veins obscure; *domatia* absent or inconspicuous; petiole absent or obscure, to 2.5 mm long. *Stipules* triangular-connate at base with a linear lobe centrally,  $4 - 9.5 \times 2.5 - 4.2$  mm, glabrous within; soon caducous. *Inflorescences* axillary umbels; peduncles 0.7–4.5 mm long, sometimes largely enclosed within stipules, pedicels 1.7–3 mm long in flower, extending to 4.5 mm long in fruit, glabrous; bracts minute, broadly triangular, 1–1.2 mm long, secondary bracts present, similar to primary bracts but smaller and shorter; flowers apparently functionally unisexual, c. 10–16 per umbel, 5-merous. *Calyx* cupular, 0.4–0.6 mm long, lobes barely developed and uneven, glabrous. *Corolla* colour unknown, minute, tube 0.6–0.7 mm long, with white deflexed hairs internally; lobes oblong-ovate, broadest at base,  $\pm 1.5 \times 0.8$  mm, margins involute, glabrous. *Anthers* subsessile, attached between corolla lobes, 0.9–1.1 mm long, slightly curved, apiculate at apex, connective red and covering most of exterior of anther. *Pistil* of functionally male flowers with style,  $\pm 0.6$  mm long; *pollen presenter*  $\pm$

0.7 mm long. *Fruit* green, drying brown, usually with 2 (rarely 3) well-developed pyrenes, hence 2-lobed, 7–8 mm long and wide in face view, somewhat compressed laterally, glabrous; *pyrenes* ellipsoid or slightly kidney-shaped,  $\pm 6.8 \times 3.5 \times 3.2$  mm, with a narrow apical crest, surface shallowly rugose. Fig. 2.

**RECOGNITION.** Most likely to be confused with *Pyrostria bibracteata* but differing in the inconspicuous paired bracts at the apex of the peduncle, 1–1.2 mm long, not acuminate (vs bracts conspicuous, 2–7 mm long, acuminate); leaves typically obovate with a rounded or obtuse apex which is often damaged (vs elliptic to oblong-elliptic, apex usually acute but can be obtuse); leaves having a shallow, corrugated appearance due to the raised lateral veins within shallow furrows (vs leaf surfaces flat, not appearing corrugated); leaf midrib broad with a central furrow on the adaxial surface (vs narrower, without conspicuous central furrow); petioles short to 2.5 mm long, or absent (vs petioles 2–7 mm long); young stems more markedly square and striated (vs subterete to only slightly angular, not striated); flowers 5-merous and smaller, tube 0.6–0.7 mm long and lobes  $\pm 1.5$  mm long (vs flowers 4-merous, corolla-tube 2–3 mm long, lobes 2–2.5 mm long); and pyrenes larger,  $\pm 6.8$  mm long (vs 5.5–6 mm long). It differs from other continental African species of *Pyrostria* in the small and inconspicuous bracts 1–1.2 mm long (although those of *P. hystrix*, 1–2 mm long, are scarcely longer), in having secondary bracts and in having a ring of deflexed hairs in the corolla throat.



**Fig. 2.** *Pyrostria rovomensis*. **A** habit, flowering branches; **B** adaxial leaf surface, showing raised veins in shallow channels; **C** node showing stipule and young inflorescence; **D** inflorescence; **E** open flower; **F** dissected flower with corolla (above) parted from calyx and hypanthium (below); one stamen drawn in situ; **G** anther, inner face (upper) and outer face (lower); **H** fruit; **J** pyrene, face view with indication of pale areas (left), edge view with bundles of fibres (right); **K** detail of one loop of fibres and attached red scales on pyrene surface. **A, B, D & E** from *Matimele et al.* 149 (K); **C** from *Timberlake et al.* 5776 (K); **F & G** from *Luke & Luke* 13778 (K); **H – K** from *Timberlake et al.* 5610. DRAWN BY ANDREW BROWN.

**DISTRIBUTION.** Coastal Cabo Delgado Province of north-east Mozambique, see Map 1.

**SPECIMENS EXAMINED. MOZAMBIQUE.** Cabo Delgado Prov., N of Palma on Quionga road, sterile, 12 Oct. 2005, *Burrows & Burrows* 9206 (BNRH\*); Namacubi Forest (the Banana), W of Quiterajo, sterile, 25 Nov. 2008, *Burrows & Burrows* 10754 (BNRH\*); Palma Distr., 25 km NW of Palma, fr., 4 Dec. 2008, *Timberlake et al.* 5610 (K!, LMA); Palma Distr., Pundanhar, fl., 10 Nov. 2009, *Matimele* 149 (EA!, K!, LMA); Nhica do Rovuma Camp to Palma pt. 435, fl., 14 Nov. 2009, *Luke & Luke* 13778 (EA!, K, 3 sheets!, LMA, P); Nangade Distr., hunting concession above Rio Metambue, in bud, 15 Nov. 2009, *Timberlake et al.* 5776 (K!, LMA).

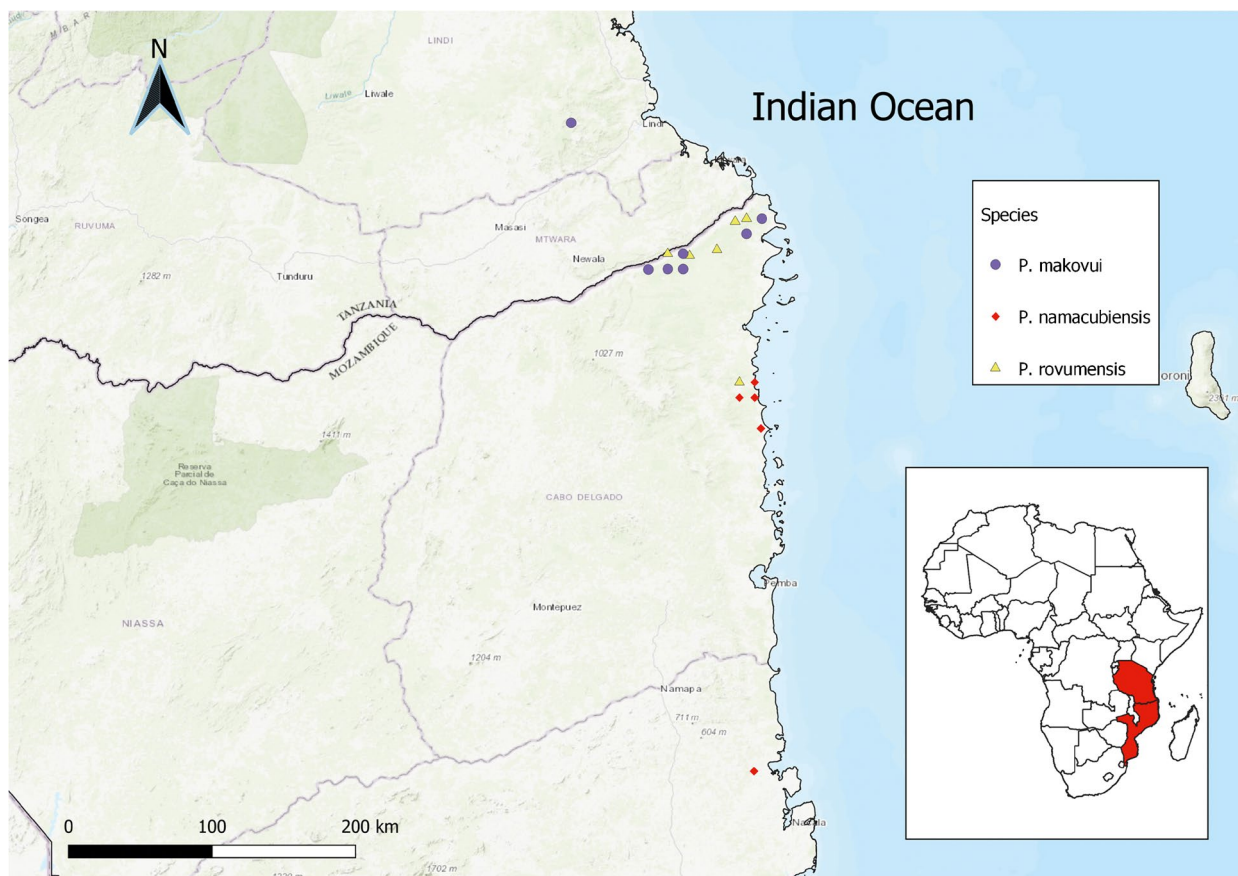
**HABITAT.** Recorded from dry coastal forest on sand, including areas dominated by *Guibourtia schliebenii* (Harms) J.Léonard with an understorey dominated by *Memecylon*, *Warneckea* and *Strychnos* spp. It has also been recorded in areas of mixed dry forest, thicket and miombo woodland. It occurs at elevations of 90 – 150 m.

**CONSERVATION STATUS.** This species has a very restricted range, with an EOO of 3,977 km<sup>2</sup> and an

AOO of 24 km<sup>2</sup>. It has been recorded as “occasional” (*Burrows & Burrows* 10754) to “rare” (*Timberlake et al.* 5776). None of its known subpopulations is within a protected area, and there are a range of threats to its dry forest and thicket habitats. Threats include clearance for agricultural land, aided by deliberate burning, which is particularly severe in the vicinity of Palma and along main transport routes (*Darbyshire et al.* 2020). With an ongoing decline in the extent and quality of habitat across its range, and with fewer than five locations known, this species is assessed as Endangered [EN B1ab(iii)+2ab(iii)].

**ETYMOLOGY.** The species epithet “rovumensis” is named for the Rovuma River, which forms the border between Tanzania and Mozambique in the coastal lowlands. This species has been recorded mainly from the escarpment on the south side of this river valley. This river also gives its name to the Rovuma Centre of Plant Endemism, a key phytogeographical region for *Pyrostria* diversity in continental Africa.

**NOTES.** *Pyrostria rovumensis* is compared in the Recognition section to *P. bibracteata*, since the two species are sympatric and superficially similar, vegetatively.



**Map 1.** Distribution of the three new species of *Pyrostria* based on herbarium collections: *P. makovui* (purple circles), *P. namacubiensis* (red diamonds) and *P. rovumensis* (yellow triangles).

However, this new species is unlikely to be confused with any of the other continental African species of *Pyrostria* in view of its minute, paired bracts that must only enclose the inflorescence in very young bud, differing from the conspicuous, usually acuminate paired bracts in other species of *Pyrostria*. The shallowly corrugated appearance of the mature leaves is also diagnostic.

The small, paired bracts and the small, functionally unisexual flowers with conspicuous deflexed hairs in the tube (Fig. 2F) are characters shared with the genus *Bullockia* (see Bridson 1987 [as *Canthium* sect. *Bullockia*]; Razafimandimbison *et al.* 2009), and *P. rovumensis* could easily be confused with that genus. However, on close inspection, some characters of *P. rovumensis* fit better with *Pyrostria*, most notably the dorsal faces of the anthers which are almost entirely covered by a dark connective (vs dark connective absent or only covering the central area of the dorsal face in *Bullockia*) and the pollen presenter which is solid and only shallowly concave at the attachment point of the style (vs pollen presenter hollow, at least towards the base, and with a notably recessed style in *Bullockia*). While molecular phylogenetic data could help to confirm the generic placement of *P. rovumensis*, on the available morphological evidence it is considered best placed in *Pyrostria* (D. Bridson, pers. comm.).

It is also worth comparing *Pyrostria rovumensis* with the Malagasy genus *Peponidium*, as that genus also has small, cupular, paired bracts. However, in *Peponidium* the bracts are deciduous, whereas in *Pyrostria*, including *P. rovumensis*, they are persistent. Further, in *Peponidium* the bracts are positioned at the base of the peduncle without enclosing the young flowers (Razafimandimbison *et al.* 2009), and, in the many species observed in this study, the inflorescences had very short peduncles or were sessile, such that they are fascicles of

pedicellate flowers and quite unlike those of *P. rovumensis*. In keeping with most members of the dioecious group of Vanguerieae (D. Bridson, pers. comm. 2022), the functionally female inflorescences in *Peponidium* are usually few-flowered, often with only one or two fruits developing per fascicle, whereas those of *P. rovumensis* have more numerous flowers and fruits. A full circumscription of *Peponidium* is, however, required to aid better comparison to *Pyrostria*, including *P. rovumensis*.

**3. *Pyrostria lobulata* Bridson (1987: 627, fig. 3; 1991: 887, fig. 158; 1998: 343, tab. 68; 2009: 530, fig. 218, 4).** Type: Rwanda, Kibungo Préfecture, chutes de l'Akagera, fl./fr., 24 Jan. 1980, Bridson 281 (holotype K! [K000412483, K000412484]; isotypes BR\* [BR0000008855213], C\* [C10001259], EA! [EA000001543], LG\* [LG0000090029691], LISC\* [LISC002647], UPS, WAG\* [WAG0003053]).

*Canthium bibracteatum* sensu Bridson & Troupin (1982: 546, fig. 182.2) & Bridson (1985: 148, fig. 42.2).

### 3a. *Pyrostria lobulata* Bridson subsp. *lobulata*.

**RECOGNITION.** This subspecies differs from the new subspecies described below based on the habit, it is a ± erect shrub or treelet and 3 – 8 m tall. On the leaves, which are elliptic and usually large, 2.5 – 13.5 × 1 – 6 cm, subcoriaceous, dull on the upper surface and with obscure tertiary venation. And on the anthers, which are broader for much of their length above, minutely notched to oblique at the base and measure ± 1.3 × 0.6 mm. Fig. 3.

**DISTRIBUTION.** D. R. Congo, Rwanda, Tanzania and Zambia.



**Fig. 3.** *Pyrostria lobulata*. **A & B** comparison of anther morphology; **A** subsp. *bridsoniae* (Merrett 1994, K); **B** subsp. *lobulata* (Fanshawe 8163, K); **C** ventral and dorsal faces of pyrene of subsp. *bridsoniae* (Osborne JO 1115, K).

**SPECIMENS EXAMINED. DEMOCRATIC REPUBLIC OF THE CONGO.** Kalemie, sterile, 29 Oct. 1974, *Matsui* 1189 (EA!); *ibid.*, sterile, 12 Jan. 1975, *Matsui* 1683 (EA!); Tanganyika (Shaba), sterile, 22 Jan. 1977, *Terashima* 20 (EA!); Kumama, in bud, 17 Nov. 1977, *Malaisse* 9365 (K!). **RWANDA.** Rusumo, près des chutes de l'Akagera, fl., 26 Aug. 1976, *Troupin* 15859 (K!); Kibungo Préfecture, chutes de l'Akagera, fr., 24 Feb. 1980, *Bridson* 281 (EA!, K!); Akagera NP, pt. 474 to 475, fr., 9 Dec. 2018, *Luke et al.* 18703 (EA!). **TANZANIA.** Bukoba, Rwakarindiri, fl., 28 Sept. 1948, *Ford* 729 (K!); Biharamulo Distr., S of Bukoba, fl., 12 Nov. 1948, *Ford* 828 (K!); Namwele, fr., 24 Feb. 1950, *Bull-ock* 2589 (K!); Biharamulo Distr., Ruiga River Forest Reserve, fl., Oct. 1957, *Procter* 741 (EA!, K!); Lake Province, Bukoba Distr., Ruiga River Forest Reserve, fl., Oct. 1958, *Procter* 1039 (EA!); Biharamulo Distr., Ruiga River Forest Reserve, fr., Dec. 1958, *Procter* 943 (K!); Biharamulo Distr., Ruiga River Forest Reserve, Kikoma Hill, imm. fr., Dec. 1958, *Procter* 1105 (EA!, K!); Mahali Mts, Mt Pasagulu, fr., 28 Jan. 1973, *Uehara* 110 (EA!); Biharamulo Distr., Burigi Game Reserve, fl., 17 Oct. 1973, *Rodgers* 1681 (EA!); Ludewa Distr., Livingstone Mts, Isalo Valley, c. 2 km NE of Nikanda village beach along coastal path and c. 3 km from coast of Lake Nyasa along SW tributary feeding into Isazo R., fl., 30 Nov. 1992, *Harder et al.* 1525 (K!). **ZAMBIA.** Kitwe, Baluba R., fr., 14 Jan. 1959, *Fanshawe* 5075 (K!); *ibid.*, fl., 2 Dec. 1963, *Fanshawe* 8163 (K!, LISC).

**HABITAT.** Riparian and ridgetop thickets as well as in plateau miombo woodland, with an elevation range of 1200 – 1825 m.

**CONSERVATION STATUS.** This subspecies has a wide distribution covering four countries. Based on its EOO of c. 1.2 million km<sup>2</sup>, and the fact that there is still considerable suitable habitat intact within this EOO, we assess it as Least Concern [LC], in agreement with the assessment by Timberlake (2021).

**3b. *Pyrostria lobulata* Bridson subsp. *bridsoniae* Matheka & I. Darbysh. subsp. nov.** Type: Zambia, Muchinga (N) Province, Mutinondo Wilderness Area, Kankonde Camp, fl., 24 June 2015, *Merrett* 1994 (K!).

<https://www.ipni.org/urn:lsid:ipni.org:names:77329781-1>

**RECOGNITION.** Recognisable, compared to subsp. *lobulata*, by its much smaller architecture. Its habit is a scrambling or somewhat climbing shrub, to 3 m tall. The leaves are visibly thicker and waxy, drying blackish-brown; the blade is narrowly elliptic to lanceolate, 2.7 – 7.5 × 0.9 – 3.3 cm, with an acute base, an obtuse apex and tertiary venation faintly visible at least in some leaves. In addition, the anthers are narrowed

and deeply notched at the base, measuring up to 1.1 × 0.5 mm. Figs 3 & 4.

**DISTRIBUTION.** Mutinondo Wilderness Area, Zambia, see Map 2.

**SPECIMENS EXAMINED. ZAMBIA.** Muchinga (N) Province, Mutinondo Wilderness Area, Kankonde Camp, beside Mutinondo R., fr., 26 Feb. 2015, *Osborne* JO 1115 (K!); Mutinondo Wilderness Area, fl., 23 April 2015, *Bidgood et al.* 8347 (K!); *ibid.*, fl., 24 June 2015, *Merrett* 1994 (K!).

**HABITAT.** On the edge of riverine thicket or forest at elevations of 1350 – 1450 m.

**CONSERVATION STATUS.** This subspecies has only been collected recently for the first time and is represented by three specimens, two of which share the same coordinates and can, therefore, be considered as co-located (sensu IUCN 2022a). The EOO is < 10 km<sup>2</sup>, as is the AOO, this subspecies may, therefore, be Critically Endangered [CR] under criteria B1 and 2. However, Mutinondo Wilderness Area, where subsp. *bridsoniae* is found, is protected as a privately run reserve and is not currently considered to be threatened. Nevertheless, there remains a plausible, future threat, from clearance of woodland for firewood and construction materials and a single such event might affect all or significant portions of the population. Therefore, we provisionally consider the subspecies as Vulnerable [VU D2] pending further field research to ascertain its full range.

**ETYMOLOGY.** The name honours Diane Mary Bridson, who preceded this study with her revision of the genus in mainland Africa.

**NOTES.** This taxon is little known and has been described from the cited collections all made in 2015. More field observations and collections are desirable to ascertain other possible differences from subsp. *lobulata*.

#### 4. *Pyrostria* sp. A

*Pyrostria* sp. A sensu Bridson (1991: 889).

**DISTRIBUTION.** Southeast Kenya.

**SPECIMENS EXAMINED. KENYA.** Taita Taveta Distr., Mt Kasigau, fl., Oct. 1938, *Joana* 9403 (EA!, K, photo!); Kajiado Distr., Emali Hill, ridge leading to summit, fl., 19 Dec. 1971, *Faden et al.* 71/932 (EA!, K!); Kitui Distr., Endau Forest, in bud, 11 Jan. 1979, *Owino & Matheenge* 182 (EA!); Emali Hill, imm. fr., 20 Dec. 1986, *Luke & Robertson* 109 (EA!); Kitui Distr., Mutha Hill, fr., 23 Dec. 2001, *Luke & Stone* 8228 (EA!, K!); Mt Kasigau, Kiteghe, going up the main trail to the hotel site and to Siriri R., sterile, 23 June 2006, *Medley* 795 (EA!).

**HABITAT.** Dry evergreen forest at elevations of 850 – 1784 m.

**CONSERVATION STATUS.** This species is known from only four localities, treated as separate locations



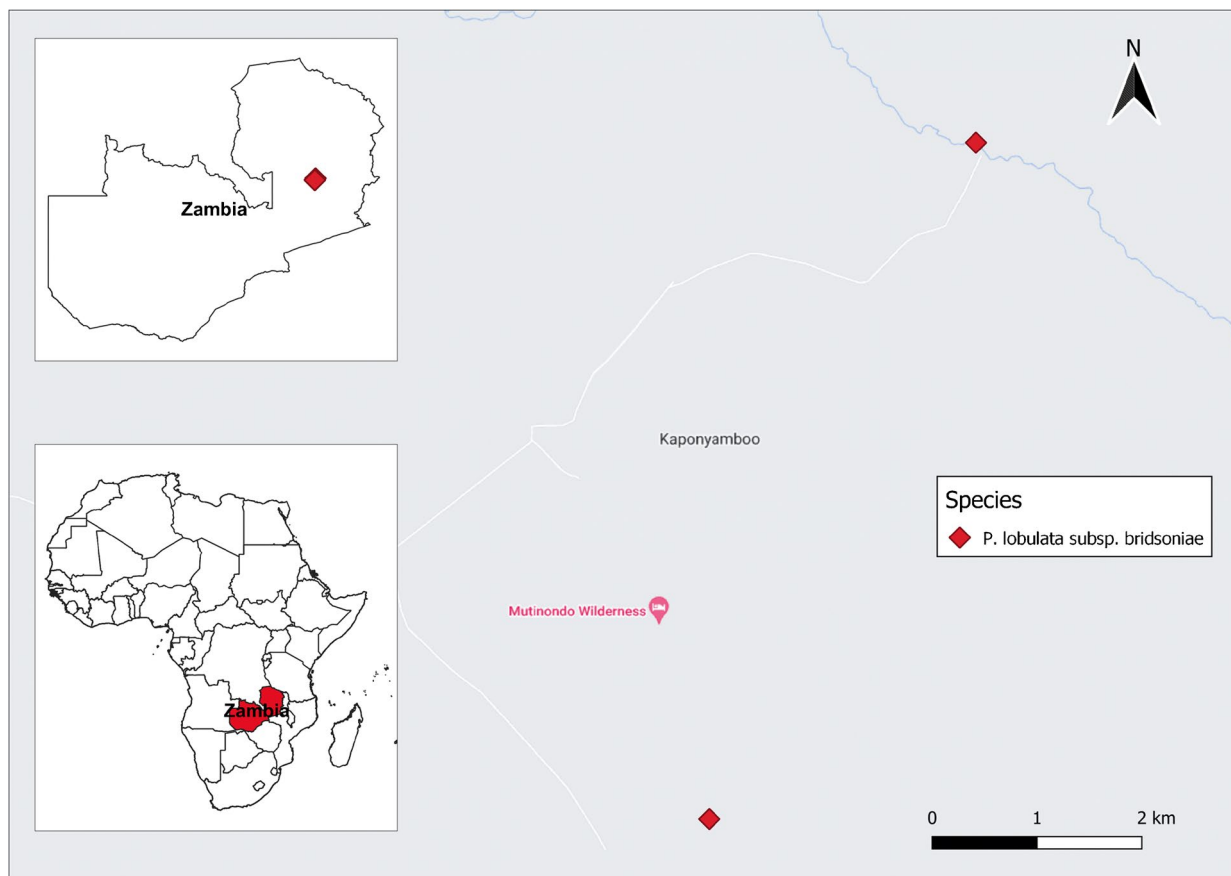
**Fig. 4.** *Pyrostria lobulata* subsp. *bridsoniae* in the field. **A & B** flowering plants; **C & D** fruiting plants, Mutinondo Wilderness, Zambia. PHOTOS: L. MERRETT.

sensu IUCN (2022a), with an EOO of c. 19,000 km<sup>2</sup> and an AOO of 16 km<sup>2</sup>. Due to its restricted range, few known locations and the presence of threats to its favoured forest habitats, in particular agricultural activity and firewood and pole harvesting at Emali Hill and Mt Kasigau, this species is assessed as Endangered [EN B2ab(iii)].

**NOTES.** This species was partially described by Bridson (1991) from a few collections, which were not sufficient for a full description, due to the lack of mature flowers and fruits. It may be confused with *Pyrostria lobulata*, but can be separated by the number of secondary veins, 3–4 (–5) compared to (5–)6 and their disjunct distributions. Two further collections made since Bridson's (1991) description, *Luke & Stone* 8228 and *Medley* 795, have been included in this circumscription,

although inclusion of the former is tentative as it has more broadly elliptic leaves, with a rounded or abruptly acute base, obtuse to rounded apex and more prominent lateral veins compared to the original specimens. Although *Luke & Stone* 8228 bears young fruits, it is not possible to ascertain whether this specimen is a variant of *P. sp. A*, which is known from the same region, or a different taxon. Further field research and collections are highly recommended to enable a full description and understanding of the species' variation and range, thus allowing for a full conservation assessment.

Specimens of this taxon have been included within *Pyrostria bibracteata* in the recent revision of Rubiaceae for the Flora of Kenya (Wang *et al.* 2023) without explanation as to why these authors do not



**Map 2.** Distribution of *Pyrostria lobulata* subsp. *bridsoniae*.

follow Bridson (1991) in separating out this taxon. Therefore, we retain *P. sp. A* as a distinct taxon pending further detailed research.

**5. *Pyrostria chapmanii* Bridson (1998: 343); Burrows (2018: 932).** Type: Malawi, Mt Mulanje, along the Nessa Path, Litchenya Plateau, imm. fr., 7 Sept. 1986, *Chapman & Chapman* 8198 (holotype K! [K000049992]; isotypes FHO, MAL, MO).

*Pyrostria* sp. A sensu Bridson (1987: 627).

*Pyrostria chapmanii* Bridson subsp. A sensu Bridson (1998: 344).

**DISTRIBUTION.** Mt Mulanje in southern Malawi and from the Namuli and Ribáuè-Mepáluè Mountains in northern Mozambique.

**SPECIMENS EXAMINED. MALAWI.** Outer slopes Mt Mulanje, E branch of Chitakale stream, sterile, 30 Nov. 1985, *Chapman & Chapman* 6907 (MAL\*); Mt Mulanje, along the Nessa path, Litchenya Plateau, imm. fr., 7 Nov. 1986, *Chapman & Chapman* 8198 (K!, MAL); Mt Mulanje, Chambe West Face Shelf, fr., 24 Nov. 1987, *Chapman & Chapman* 8972 (K!); Mt

Mulanje, Chisongeli Forest, Muluzi valley, fl., 29 Nov. 1988, *Chapman & Chapman* 9347 (K!); Mulanje Distr., Chambe Peak slopes, fr., 3 April 2009, *Patel* 942 (K!). **MOZAMBIQUE.** Ribáuè, Serra de Ribáuè, Mepáluè, fr., 25 Jan. 1964, *Torre & Paiva* 10251 (LISC\*); Zambézia, Guruè, encosta da serra do Guruè, via fábrica Junqueiro a oeste dos Picos Namuli, próx. do R. Malema, fr., 6 Nov. 1967, *Torre & Correia* 15974 (LISC\*); serra do Guruè, a oeste dos Picos Namuli, próx. da nascente do R. Malema, fl., 8 Nov. 1967, *Torre & Correia* 16002 (LISC\*); Ribáuè, Serra de Mepáluè, fr., 9 Dec. 1967, *Torre & Correia* 16422 (LISC\*); Guruè, encosta da serra do Guruè, próx. do R. Malema, fr., 3 Jan. 1968, *Torre & Correia* 16832 (LISC\*); Zambézia, Mt Namuli, waterfall into small R. Lucongo valley, slopes of Serra Pesse, sterile, 17 Nov. 2007, *Timberlake* 5204b (K!); Zambézia, Mt Namuli, Naconha Plateau, fr., 21 Nov. 2007, *Timberlake* 5262 (K!); Nampula, Ribáuè Mt, fl./imm. fr., 15 Oct. 2017, *Darbyshire* 1117 (K!, LMA!).

**HABITAT.** Riverine or wet (sub)montane evergreen forests and in *Newtonia buchananii*-dominated seasonally wet forest and adjacent transitions to montane grassland, at elevations of 1150 – 2000 m.

**CONSERVATION STATUS.** This taxon was recently assessed as Endangered [EN B1ab(iii)+2ab(iii)] and included on the IUCN Red List of Threatened Plants by Timberlake (2020). It is threatened by forest clearance for agriculture, primarily in the Mozambique portion of its range.

**NOTES.** Bridson (1998) proposed that the Mozambique material of this species may be treated as a separate subspecies to the Malawi (Mulanje) material, based on differences in plant habit. The Mulanje specimens are forest trees, (6 –) 10 – 20 m tall, with smooth or winding and fluted trunks and wide-spreading or horizontally inclined branches. The Mozambique specimens, on the other hand, are shrubs or small trees usually 1 – 6 m tall. There is, however, some slight overlap. The current study also notes variation in the young fruit: the young fruits of the Mulanje plants have a tapered base, while fruits from Mozambique plants are rounded at the base. It may also be noteworthy that some leaves and stipules in Mozambican *Pyrostria chapmanii* remain yellowish-green when dried, while those from Mulanje dry blackish, although this may be affected by the post-collection specimen handling. Further collections may confirm two infraspecific taxa to be involved, however, based on the currently available material, we consider this as a single, variable taxon. Fig. 5.

## 6. *Pyrostria* sp. B

*Pyrostria* sp. A sensu Bridson (1998: 344).

**DISTRIBUTION.** One locality in coastal Mozambique.

**SPECIMENS EXAMINED. MOZAMBIQUE.** Zambézia, Maganja da Costa, floresta de Gobene, prox. da praia Raraga, ao 35 km de Vila de Maganja, fr., 10 Jan. 1968, Torre & Correia 17041 (LISC\*).

**HABITAT.** Deciduous coastal forest on sand with, inter alia, *Brachystegia oblonga* Sim, *Scorodophloeus torrei* Lock (misidentified on specimen labels by Torre & Correia as *Cynometra*) and *Albizia* sp. as associated taxa, at an elevation of c. 20 m.

**CONSERVATION STATUS.** This species is known only from one collection, from the Gobene Forest near Maganja (Olinga) along the Mozambique coast. The vast majority of this forest has now been cleared for cultivation of coconut, mango and cashew and the tiny remnants are threatened by cutting for fuelwood and clearance for agriculture (Burrows *et al.* 2018; Darbyshire & Rokni 2020). It is possible that this species is already extinct, given the high rates of habitat loss in the coastal dune formations around Maganja (Olinga). However, similar “chenier” dune units are found in the Zambezi delta to the southwest, some of which retain more intact vegetation (J. Burrows, pers. comm.), and these may offer the best hope of

rediscovering it. On the current evidence, assuming it proves to be a distinct species, we provisionally assess it as Critically Endangered and Possibly Extinct [CR(PE) B2ab(iii)] based on the single known location with an AOO of less than 4 km<sup>2</sup> and ongoing decline in extent and quality of habitat.

**NOTES.** This species may be confused with the newly described *Pyrostria makovui* (sp. 7 below) because of the acute leaf apices and single-fruited peduncles, as well as the congested inflorescences and well-developed calyx lobes (Bridson 1998), but the latter has at least 3-locular fruits and coriaceous leaves, as opposed to 2-locular fruits and papery leaves in *P.* sp. B. *P.* sp. B is only known from the one cited specimen and thus requires further field study.

## 7. *Pyrostria makovui* Matheka & I. Darbysh. sp. nov.

Type: Mozambique, Cabo Delgado Province, Nangade – Palma, fl./fr., 15 Dec. 2003, Luke, Kibure & Nacamo 10148 (holotype K! [K001236763]; isotypes EA! MO, UPS, LMA).

<https://www.ipni.org/urn:lsid:ipni.org:names:77329778-1>

*Pyrostria* sp. D sensu Bridson (1991: 891); Timberlake *et al.* (2011: 131).

*Shrub* to 2.5 m high; young branches square; stems covered with a thin, greyish bark, which peels off to expose a brownish-black inner bark. *Leaves* elliptic to broadly so or slightly ovate, coriaceous, slightly shiny above, drying brownish-green or slightly blackish, 1.2 – 8.8 × 0.6 – 4.9 cm, surfaces glabrous, base rounded to cuneate, sometimes unequal, apex acute or shortly acuminate and apiculate; 4 – 5 main pairs of lateral veins; tertiary veins obscure; *domatia* absent; petiole 1 – 2 (– 4) mm long. *Stipules* triangular-connate at base with a linear lobe, 5 – 7 × 2.8 – 3.1 mm, enclosing dense brownish hairs; ultimately caducous. *Inflorescences* opposite, axillary paired umbels, sometimes drying black; peduncles ± 2 mm long, pedicels 2 – 4 mm long; bracts remaining fused for most of their length with narrowly triangular lobes, enclosing brownish hairs, sometimes partially divided in the middle, ± 6 × 2.6 mm; flowers bisexual, 2 – 7 per umbel, 5-merous. *Calyx* tube not apparent, lobes divided almost to base, narrowly triangular, 1.6 – 3.1 × 0.5 – 1 mm, acute at apex, glabrous. *Corolla* cream-green or yellow-green, tube up to 3.4 × 2.5 mm; lobes triangular with tapering apex, ± 3.4 × 1.7 mm, deflexed when mature to expose dense white hairs on the inner base of the lobes, white-scaly internally. *Anthers* attached between corolla lobes, ± linear with a narrowed cordate base and tapering at apex, ± 1 mm long; pollen yellow. *Pollen presenter* spherical, 0.7 × 0.6 mm; style black-spotted, 3.8 × 0.3





**Fig. 5.** *Pyrostria chapmanii* in the field. **A** habit; **B** flowers with old, discoloured petals; **C** young fruits, Ribáuè Mountains, Mozambique (collected as *Darbyshire* 1117). PHOTOS: I. DARBYSHIRE.

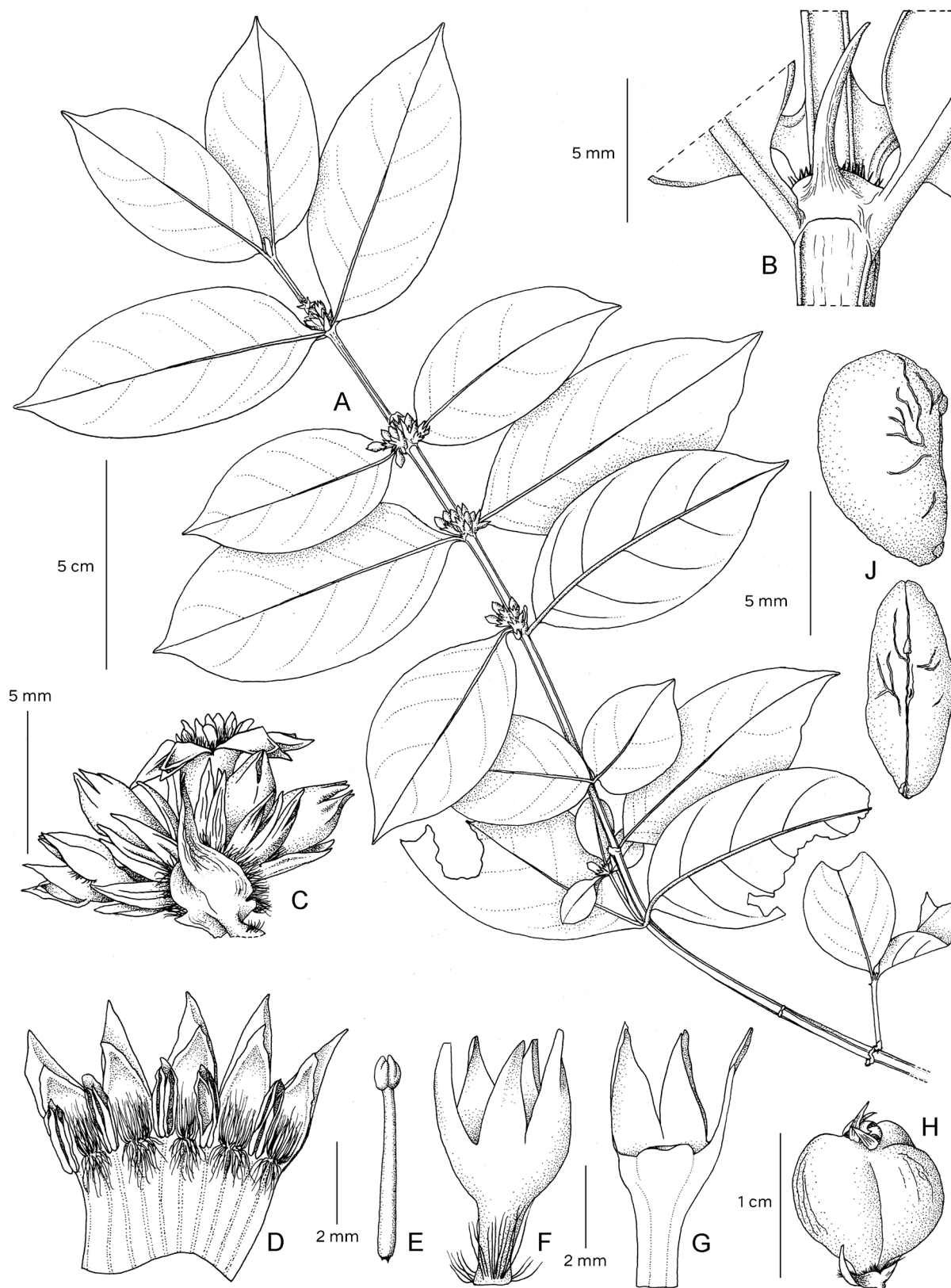
mm. *Fruit* green, globose, with at least 3 well-developed lobes and 1–2 aborted lobes, slightly wider than long, drying blackish,  $0.8 \times 1$  cm; *pyrenes*  $\pm$  kidney-shaped with one end narrowed, surface rugulose; persistent calyx prominent. Figs 6 & 7.

**RECOGNITION.** *Pyrostria makovui* is clearly distinguishable from all other continental African species of *Pyrostria* by having very reduced petioles, usually 1–2 mm long, peduncles  $\pm$  2 mm long and pedicels 2 (–4) mm long. It may be confused with *P. sp. B* (= *Torre & Correia* 17041) due to the similar size ranges of their petioles 2–3 mm long, peduncles 2 mm and pedicels 3–3.5 mm, but the latter species has papery leaves clustered towards the branch tips, while *P. makovui* has coriaceous leaves well-spaced along the branches. In addition, *P. makovui* has at least 3-lobular fruits at maturity, compared to 2-lobular in all the other species

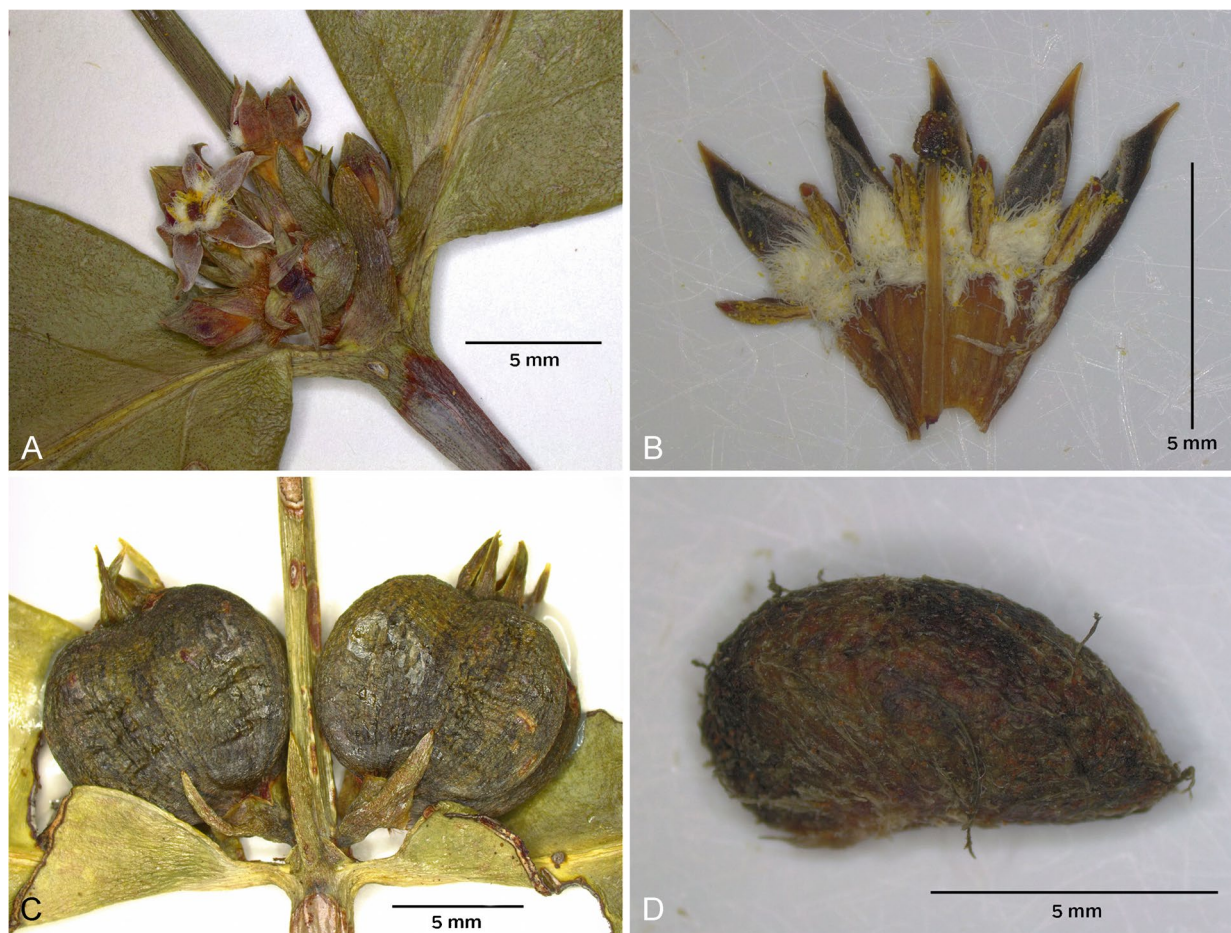
within the study area; this character is otherwise known to occur only in some species in Madagascar.

**DISTRIBUTION.** Southeastern Tanzania on the Rondo Plateau of Lindi District, and northeastern Mozambique within Palma District of Cabo Delgado Province; see Map 1.

**SPECIMENS EXAMINED. TANZANIA.** Lindi Distr., SW end of Rondo Plateau, 15 km NE of Mihima, fl., 12 Nov. 1988, *Mackinder & Lock*, 36 (K!). **MOZAMBIQUE.** Cabo Delgado, Palma Distr., Nangade – Palma, pt. 532, fl./fr., 15 Nov. 2003, *Luke et al* 10148 (K!); Miculumo area, 12 km NW of Palma, in bud, 6 Dec. 2008, *Timberlake et al.* 5651 (K!); Pundanhar to Nangade road, fl., 6 Nov. 2009, *Müller & Clarke* 4160 (K!); Palma – Nangade road, c. 32 km W of junction with road to Nhica do Rovuma, between Pundanhar and Nangade, fl., 8 Nov. 2009, *Goyder et al.* 6033 (K!); Nangade to Pundanhar, pt. 427, fr., 12 Nov. 2009, *Luke & Luke* 13761 (K!);



**Fig. 6.** *Pyrostria makovui*. **A** habit, flowering branch; **B** stem node with stipule and base of leaves and inflorescence; **C** inflorescence; **D** dissected corolla with androecium; **E** style and stigma; **F** calyx; **G** longitudinal section of calyx and hypanthium (functionally male flower); **H** fruit; **J** pyrene, face and edge views. **A** and **C** from Goyder *et al.* 6033 (K); **B**, **H** & **J** from Clarke 122 (K); **D** – **G** from Luke 10148 (K). DRAWN BY ANDREW BROWN.



**Fig. 7.** *Pyrostria makovui* from herbarium specimens. **A** inflorescence; **B** dissected flower (both from *Luke et al.* 10148, K); **C** fruits; **D** pyrene (both from *Clarke* 122, K).

Palma Distr., bicycle track between L. Nompuid/Mikulumu and the Rovuma R., fr., 15 Nov. 2009, *Clarke* 122 (K!).

**HABITAT.** An understorey shrub in dry coastal and escarpment forest or woodland, on sand; at 60 – 750 m elevation.

**CONSERVATION STATUS.** This species is known from one collection from southeastern Tanzania and six from northeastern Mozambique. The stretch from Lindi town (Tanzania) towards the Mozambican border is experiencing ongoing change in land use and the small remnants of coastal forest there are threatened by rural development (*Burrows & Burrows* 2010). At the Rondo Plateau, 2755 ha. of natural forest was cleared during the Rondo Forest Programme in 1952 – 1978 and replaced by commercial plantations of exotic tree species (*Clarke* 2001). However, a sizeable area of forest (some secondary in nature) remains on the western slopes of the plateau (*I. Darbyshire* pers. obs.), and its designation as a Nature Forest Reserve in 2016 may have resulted in its improved protection

and management. In Mozambique, Palma District has experienced a recent surge in development activities as a result of oil and gas discovery, and associated migration into the region (*Burrows & Burrows* 2010; *Timberlake et al.* 2011; *Johnson et al.* 2017; *Darbyshire et al.* 2021) which poses a direct threat to the existence of the species. The recent violent insurgency in this region has temporarily halted some of these activities and led to considerable displacement of local populations, but the longer-term trajectory is likely to be one of continued habitat degradation, given that none of the forests or woodlands here is formally protected. The AOO of this species is 20 km<sup>2</sup> and the EOO is 4,863 km<sup>2</sup>, falling within the thresholds for Endangered using criteria B1 and B2. Given that there are fewer than five locations, an ongoing decline in extent and quality of its habitat, with clear threats, we assess this species as Endangered [EN B1ab(iii) + B2ab(iii)].

**ETYMOLOGY.** The specific epithet is a posthumous recognition of former colleague and EA botanist, Joshua

Makovu Muasya (Polhill & Polhill 2015), who was a mentor and a great inspiration to the first author in his formative years at the EA herbarium.

**NOTES.** *Pyrostria makovui* is the first species on mainland Africa known to bear more than two pyrenes, i.e., to have 3-locular fruits, a character otherwise observed only in some species on Madagascar and surrounding islands. It is also only the second hermaphrodite species known in Africa, after *P. bibracteata*. While *Pyrostria* is known to have 2-locular or plurilocular fruits elsewhere, the species in the study area are mostly 2-locular or rarely 1-locular, as a result of developmental malfunction. Hence, *P. makovui* is suspected to have its lineage with Malagasy species. Although the leaves may be elliptic and acute at the base and apex, like those of *P. sp. B* (= *Torre & Correia* 17041), they are more coriaceous and do not turn black upon drying, except for the young terminal ones. The species also grows to a shrub under 3 m tall, while *P. sp. B* may reach a height of 6 m. A phylogenetic study of these species might establish their precise relationship.

#### 8. *Pyrostria* sp. C

*Pyrostria* sp. D sensu Bridson (1987: 628)

*Pyrostria* sp. C sensu Bridson (1991: 891)

**DISTRIBUTION.** Ulanga District of Tanzania.

**SPECIMENS EXAMINED. TANZANIA.** Ulanga Distr. [Mahenge Distr.], Sali, Muhulu Forest Reserve, on ridge above Mbezi, fr., 24 Jan. 1979, *Cribb et al.* 11177 (K!).

**HABITAT.** The single record of this species is from submontane moist forest at 1350 m elevation.

**CONSERVATION STATUS.** The species is known only from the one cited specimen. It has not been recollected in the intervening 43 years. While the collecting locality lies within the protected Mhulu Forest Reserve, total area 8.08 km<sup>2</sup>, evidence from satellite imagery suggests considerable loss of forest there. There does remain intact forest in the nearby Sali Forest Reserve, total area 10.72 km<sup>2</sup>, but the species is yet to be recorded from there. Based on current evidence, and assuming that it will prove to be a distinct species, we provisionally assess this species as Critically Endangered [CR B2ab(iii)] based on the single known location with an AOO of less than 10 km<sup>2</sup> and ongoing decline in extent and quality of habitat.

**NOTES.** This species may be confused with other related species with acuminate leaves, but it is easily distinguished by the prominent tertiary leaf venation, a character unique to this species in continental Africa.

#### 9. *Pyrostria* sp. D

*Pyrostria* sp. B sensu Bridson (1987: 628, 1991: 888).

**DISTRIBUTION.** East Usambara Mountains of Tanzania.

**SPECIMENS EXAMINED. TANZANIA.** Lushoto Distr., E Usambara mountains, Longuza, fr., 1917, *Zimmermann* 6107 (EA!, K!).

**HABITAT.** With no habitat details given on the specimen, it is presumed to be a moist forest species based on the type locality, and with an approximate elevation of 500 m.

**CONSERVATION STATUS.** This species is known from just one collection. Although the collection date is not given, it was collected by Albrecht Zimmermann between 1902 and 1920 following his arrival at the newly created research institute at Amani a year earlier (Polhill & Polhill 2015). The collecting locality is within an area subject to extensive agricultural activity around Longuza, resulting in much forest loss. In the absence of any information on the habitat requirements for this species, although it is assumed to be a forest species, it is hereby assessed as Data Deficient [DD], although it is likely to prove to be threatened. Targeted field studies are required for this species, to confirm its current status within the Usambara Mountains.

**NOTES.** This species is only known from one specimen collected in 1917 and the material is inadequate to permit a full description. It is recognisable by its papery elliptic leaf blades, 2.6–7 × 1.2–2.7 cm, short petioles of 1–2 mm, linear stipules, narrowly triangular bracts and pedicels of ± 1 cm. These are the main characters that together separate it from *P. uzungwaensis*.

**10. *Pyrostria uzungwaensis* Bridson (1991: 888).** Type: Tanzania, Ulanga Distr., Mwanihana Mts [Udzungwa Mts], Sanje, fl., 19 July 1986, *Lovett & Carr* s.n. (holotype K! [K000352748, K000352749]).

*Pyrostria* sp. C sensu Bridson (1987: 628).

**DISTRIBUTION.** Endemic to the Udzungwa Mountains in Tanzania.

**SPECIMENS EXAMINED. TANZANIA.** Kilombero Distr., Mwanihana Forest Reserve above Sanje, fr., 22 Sept. 1984, *Thomas* 3942 (K!); Mwanihana Mts [Udzungwa Mts], Sanje, fl., 19 July 1986, *Lovett & Carr* s.n. (K!); Udzungwa Mountains National Park, Mt Luhomero, pt. 129–131, sterile, 27 Sept. 2000, *Luke et al.* 6719 (EA!, K!); Udzungwa Mountains National Park, pt. 229–230, imm. fr., 30 July 2001, *Luke et al.* 8004 (K!).

**HABITAT.** Mid-altitude to submontane moist forest, on ridge-tops at an elevation range of 650–1600 m.

**CONSERVATION STATUS.** *Pyrostria uzungwaensis* is known only from four collections from the Udzungwa Mountains and has an EOO of 3483 km<sup>2</sup>. It is, therefore, potentially Endangered, using criterion B1. However, the species occurs entirely within a National Park and this protected area is not considered to face any imminent threats (Luke *et al.* 2015). We, therefore, give a provisional assessment of Least Concern [LC], which

will apply so long as the protection by the National Park remains effective. However, any degradation of the forests there may quickly result in this species becoming threatened.

**NOTES.** At a glance, the species may be confused with *Pyrostria* sp. C, based on leaf shape, but it can be immediately separated, as sp. C has prominent tertiary veins on both leaf surfaces. The other confusable species is *P.* sp. D, which has a similar, but smaller, leaf size, however, sp. D has longer pedicels and shorter stipules compared to *P. uzungwaensis*.

**11. *Pyrostria bispathacea* (Mildbr.) Bridson (1987: 629).** Type: Cameroon, 10 km NW of Jaunde [Yaoundé] Station, fl., Jan. 1914, *Mildbraed* 7840 (isotype K! [K000412482]).

*Plectronia bispathacea* Mildbr. (Mildbraed 1924: 203).

**DISTRIBUTION.** Cameroon. This species is known only from the type locality.

**SPECIMEN EXAMINED. CAMEROON.** 10 km NW of Jaunde [Yaoundé] Station, fl., Jan. 1914, *Mildbraed* 7840 (K!).

**HABITAT.** Mid-altitude mixed and semi-deciduous forest. The elevation range (sourced from Google Earth Pro 2022) is between c. 730 and 1200 m.

**CONSERVATION STATUS.** This species is known only from the flowering, type specimen, collected between 1911 and 1914. Onana (2013) assessed this species (IUCN 2012) as Critically Endangered [CR] or, possibly, Extinct [EX], owing to the degradation of the known habitat as a result of increasing urbanisation around Yaoundé, the capital city of Cameroon. Google Earth Pro (2022) imagery taken on 29 March 2017 shows highly disturbed patches of forest extending in a radius > 20 km from the centre of Yaoundé, which threat, along with the fact that the species has not been recollected for more than a century, serves to support Onana's designation. The species is, therefore, here reassessed and confirmed as Critically Endangered and Possibly Extinct [CR(PE) B2ab(iii)].

**NOTES.** There is no grid reference given for the collection either on the specimen datasheet or in the protologue. However, the locality is described as 10 km NW of Yaoundé. Satellite imagery taken on 29 March 2017 (Google Earth Pro 2022) shows patches of the forest are highly disturbed, even far beyond a radius of 20 km from the centre of the city. A thorough, targeted search for this species in any remnant forest patches is, therefore, highly recommended to ascertain its current status. One possible locality is the Mefou Proposed National Park, although the species was not recorded from there during fairly extensive botanical surveys in the 2000s (Cheek *et al.* 2011). The fruits of this species are unknown, as the type specimen is in flower only.

**12. *Pyrostria affinis* (Robyns) Bridson (1987: 628; 1991: 890).** Type: D. R. Congo, Lesse, aux bords de la Semliki [R.], fl./imm. fr., 23 March 1914, *Bequaert* 3141 (holotype BR\* [BR0000008855480]; isotypes BR\* [BR0000008855206], K! [K000043470]).

*Dinocanthium affine* Robyns (1943:19; 1947: 350).

*Dinocanthium bequaertii* Robyns (1943:19; 1947: 350, pl. 35). Type: D. R. Congo, Lesse, aux bords de la Semliki [R.], fl., 20 March 1914, *Bequaert* 3068 (holotype BR\* [BR0000008855473]; isotypes EA!, K! [K000043471], P\* [P00553444]).

*Canthium affine* (Robyns) Hepper (1962: 338).

*Rytigynia affinis* (Robyns) Hepper (1963a: 171; 1963b: 186).

*Coffea melanocarpa* sensu Good (1926: 27) quoad *Gossweiler* 4453, non Welw. ex Hiern.

**DISTRIBUTION.** Widespread but scattered in west and central Africa: Guinea, Liberia, Ivory Coast, Ghana, Cameroon, Gabon, D. R. Congo, Uganda and Angola.

**SPECIMENS EXAMINED. GUINEA.** Sérédou (Mecenta), fr., 20 April 1956, *Adam* 12011 (K!); Préfecture de Macenta, Massif de Ziama, village Boo sud ouest de Ziama piste cotia, fl., 15 Feb. 2014, *Haba* 1042 (HNG, K!).

**LIBERIA.** Without precise locality, fl., 13 Jan. 1951, *Harley* s.n. (WAG\*).

**IVORY COAST.** Mont Mafa, fl., 14 March 1967, *Aké Assi* 9535 (K!).

**GHANA.** Donkoto near Bibiani, fl., 4 Feb. 1954, *Darko* 854 (K!); Nyanao Hill, near Nsawam, fl., 12 May 1968, *Hall & Bowling* GC 37187 (K!); Begoro, by R. Abrum, just above falls, fl., 23 Dec. 1977, *Hall & Siaw* GC 46162 (K!).

**CAMEROON.** 5 km W Bateba Malemle, village situi a 24 km NE of Moloundou, fr., 16 April 1971, *Villiers* 655 (K!); [indecipherable], a 80 km au SSE de Yokadouma, fl., 1 April 1973, *Letouzey* 12235 (K!).

**GABON.** Woleu-Ntem, Minkébé National Park, fr., 7 May 2003, *Ngok Banak* 1699 (WAG\*).

**DEMOCRATIC REPUBLIC OF THE CONGO.** Lesse, aux bords de la Semliki [R.], fl., 20 March 1914, *Bequaert* 3068 (K!); *ibid.*, fl./imm. fr., 23 March 1914, *Bequaert* 3141 (K!); Haut-Zaïre, Mont Hoyo, au-dessus des Escaliers de Venus, fl., 23 April 1973, *Lisowski* 18667 (K!); Zone de Mambasa, Ituri Forest, Mont Mbia, fl., 12 Feb. 2000, *Amsini* 236 (K!).

**UGANDA.** Kigezi Distr., South Maramagambo C.F.R., Bitereke Track, imm. fr., 18 Sept. 1969, *Lock et al.* 69/280 (EA!); South Maramagambo, halfway along Bitereke road, fr., 11 Oct. 1969, *Synnott* 401 (EA!).

**ANGOLA.** Loanda, Cazengo, fr., July 1908, *Gossweiler* 4453 (BM!, K!).

**HABITAT.** Mixed forest at 70 – 1200 m elevation.

**CONSERVATION STATUS.** The species is the most widely distributed *Pyrostria* in mainland Africa, occurring in seven countries. With an EOO of more than 3.7 million km<sup>2</sup>, it is assessed as Least Concern [LC].

**NOTES.** This species may be confused with *Pyrostria bispathacea* based on similar leaf appearance and the conspicuously protruding style and pollen presenter

above the corolla throat. *Pyrostria affinis* is, however, unique as the only species within the genus where the anthers are reflexed in mature flowers.

**13. *Pyrostria phyllanthoidea*** (Baill.) Bridson (1987: 629; 2006: 91, fig. 55). Type: Kenya, Mombasa, without date, *Boivin* s.n. (holotype P n.v.; isotype K! [K000412481, fragments]).

*Canthium phyllanthoideum* Baill. (Baillon 1879b: 220).

*Plectronia bogosensis* Martelli (1886: 42). Type: Eritrea, Keren, Luglio, 1870, *Beccari* 155 (holotype FT\* [FT003436]).

*Canthium bogosense* (Martelli) Penzig (1892: 344); Hutchinson & Bruce (1941: 149); Cufodontis (1965: 1008).

*Rytigynia phyllanthoidea* (Baill.) Bullock (1932: 389).

*Rytigynia* sp. nov. sensu Dale & Greenway (1961: 471), quoad *Bally* 5735 & 6607, *Dale* 3873, *Gisau* in EA 10979 (Sok 3), *Swynnerton* K 45, EAH 10979 & 10981.

**DISTRIBUTION.** Eritrea, Ethiopia, Somalia, Kenya and Tanzania. Outside the study area, it is also recorded in southern Arabia.

**SPECIMENS EXAMINED. ERITREA.** Aidereso, fl., 5 – 10 April 1892, *Schweinfurth & Riva* 1425 (K!); environs d'Acrou, fl., 18 April 1892, *Schweinfurth & Riva* 1722 (K!). **ETHIOPIA.** Harar Prov., Uadendeo Plateau, 36 km ESE of Harar on road to Djigdjigga (Jijiga) and 20 km S, fl., 21 April 1962, *Burger* 1662 (K!); Errer Valley, 22 km SE of Harar on highway to Djigdjigga (Jijiga), fr., 24 June 1962, *Burger* 1994 (K!); Marda Pass W of Djigdjigga, fl., 24 Aug. 1962, *Burger* 2115 (K!); Sidamo, 38 km S of Neghelle, along the road to Melka Guba, S slope of Cure Liban, fr., 17 May 1982, *Friis et al.* 3036 (K!); Sidamo, 1 km N of Harekelo, along the road to Kebre Mengist, fr., 24 May 1982, *Friis et al.* 3274 (K!); Bale, 13 km from Ghinir on road to Robi via Sof Omar, fr., 29 May 1983, *Gilbert et al.* 7873 (K!); Tigray, c. 6 km above the foot of the escarpment where the new road from Angula to Berhale and the Afar Depression enters the plains, fl., 13 Oct. 2001, *Friis et al.* 10642 (K!). **SOMALIA.** Duwi, fl., 21 Oct. 1932, *Gillett* 4405 (K!); Al Madu Range, Geldin, fr., 15 Oct. 1956, *Bally* B 11121 (EA!, K!); foot of NE cliffs behind Galgallo, fl., 27 Nov. 1971, *Lavranos* 9021 (K!); Sheikh, fl., May 1972, *Wood* 5/72/34 (EA!, K!); L 67, 61 km SW of Erigavo, fr., 25 Nov. 1980, *Hemming & Watson* 3261 (EA!, K!); Narok Distr., on a small hill 15 km NE of Maji Moto, in bud, 11 Jan. 1981, *Muchiri* 605 (EA!); Narok Distr., Oliopa, steep north-facing slope, imm. fr., 14 Jan. 1981, *Kuchar* 14068 (EA!); Narok Distr., Loita Plains, fr., 16 Jan. 1981, *Kuchar* 14192 (EA!); Northern Somalia, Site A/12, fr., 25 June 1981, *Gillett & Watson* 23632 (EA!, K!); 09°52'N, 43°28'E, [between El Bardale and Ruqi],

fr., 5 July 1981, *Beckett* 1223 (EA!); Duwi lower site, fr., 12 July 1981, *Gillett & Beckett* 23877 (K!, EA!); 4 km NNW of Ngong, N of circular road, fr., 8 Feb. 1985, *Beentje & Kabuye* 1907 (EA!); halfway up Siria Escarpment, in bud, 20 Sept. 1986, *Luke* 8 (EA!); Mathew's Range, Wamba, Uarges, in bud, 30 June 1987, *Bronner* 223 (EA!); Shabeellaha Dhexe, 0.5 – 2 km on track towards Warshiek starting 1 km S of Balad, fr., 20 May 1989, *Thulin* 6358 (K!); Laikipia, Ol Ari Nyiro Ranch, sterile, 20 Aug. 1990, *Muasya* 2208 (EA!); Mfangano Island, S of Nyakweri, fr., 2 Aug. 2000, *Kirika* 296 (EA!). **KENYA.** Mombasa, without date, *Boivin* s.n. (K!); Kilifi, Sokoke, fr., without date, *Gisau* EAH 10979 (EA!, K!); ibid., fr., without date, *Gisau* EAH 10981 (EA!); ibid., fl., without date, *Gisau* SOK 3 (EA!); Witu, fl., June 1900, *Thomas* 137 (BM!), Ngong – Rift Valley, fl., 29 Dec. 1932, *Napier* 2387 (EA!, K!); Kilifi, in bud, Sept. 1936, *Swynnerton & Swynnerton* K 45 (EA!); Malindi Distr., Arabuko Forest, fl., April 1938, *Dale* 3873 (EA, 3 sheets!, K!); Lake Victoria, Maboko Island, fl., 19 Dec. 1939, *Hornby* 1054 (EA!, K!); Rift Valley, Mt Margaret Estate, Kedong, foot of hill, sterile, June 1940, *Bally* 967 (K!); Port Victoria, fr., 26 Sept. 1945, *Glasgow* 45/34 (EA!); Ngong Escarpment, fl., 21 Dec. 1947, *Bally* 5735 (K!); Port Victoria, fl., 5 Nov. 1948, *Glasgow* 48/10 (EA!, K!); Nairobi Game Park [National Park], in bud, 1 March 1949, *Bally* 6607 (EA!, K!); Dandu, fl., 11 April 1952, *Gillett* 12764 (EA!, K!); Moyale, fr., 12 Aug. 1952, *Gillett* 13712 (EA!, K!); Ngong Escarpment, fl., 6 Feb. 1953, *Bally* 5735 (EA!); Kwale Distr., near Taru, between Samburu and Mackinnon road, fl., 5 Sept. 1953, *Drummond & Hemsley* 4170 (EA!, K!); Baringo, Churo, in bud, 17 Sept. 1957, *Pasture Research, Marigat* s.n. (EA!); Katumani Farm, in bud, May 1959, *Thomas* 1007 (EA!); Athi River Game Park, fr., Jan. 1960, *Birch* 60/56 (EA, 2 sheets!); Narok Distr., Aitong hillside, imm. fr., 1 April 1961, *Glover et al.* 292 (EA!); Suswa, on a lava ridge at the NE foot of the mountain, fr., 27 Jan. 1964, *Glover & Oledone* 4046 (EA!); Kisumu, Nyahera Hills, fr., 17 April 1965, *Kokwaro* 91 (EA!); Near Busia Hills, fr., Sept. 1965, *Makin* 154 (BM!, EA!, K!); Kajiado Distr., SW of Ngong Hills, fl./fr., 25 Dec. 1965, *Gillett* 16970 (EA!, K!); Tsavo West NP, Kevat hillside, fr., 10 April 1967, *Gillett* 1211 (EA!); Kilifi Distr., Sokoke Forest, road to Jilore Forest Station, 3.2 km from turnoff on Kilifi – Malindi road, fr., 28 July 1971, *Faden & Evans* 71/712 (EA!, K!); Masai Mara Game Reserve, Angata Mosee, sterile, 16 Aug. 1971, *Taiti* 1330 (EA!); Lukenya, fr., 16 Feb. 1972, *Kokwaro* 3038 (EA!); Tana River Distr., 20 km N of Hola, fl., 26 Oct. 1972, *Robertson* 1770 (EA!, K!); 60 miles before Garissa, fr., 15 April 1973, *Oxtoby* EA 15350 (EA!); N side of Lolokwe Mt, 28 km NNW of Archers post, fr., 20 April 1973, *Gillett* 20200 (EA!, K!); Nairobi National Park, opposite Masai Lodge, fr., 28 March 1974, *Mbuvi* 327 (EA!); Kajiado Distr., Bissil, fl., 6 Dec. 1975, *Galaty* 167

(EA!); Mathew's Range, fr., 20 Nov. 1976, *Chikawa* 51 (EA!); *ibid.*, imm. fr., 24 Nov. 1976, *Chikawa* 132 (EA!); *ibid.*, fr., 22 Dec. 1976, *Chikawa* 257 (EA!); between Timau and Isiolo, Lewa Downs, imm. fr., 1977, *Blackwell* 6 (EA!); Kajiado Distr., Enkorika area SE of Kajiado, imm. fr., 25 Nov. 1977, *Kuchar et al.* 7951 (EA!); Nairobi National Park, Hydrax cliffs above Embakasi R., fr., 4 Jan. 1978, *Gillett* 21654 (EA!, K!); Baringo Distr., just W of Tikamur Hill, in bud, 1 April 1978, *Kuchar* 8703 (EA!); Masai Mara Game Reserve, Ol Oloitikoishi, Croton bushland on north-facing slope, fr., 22 Oct. 1978, *Kuchar* 9947 (EA!); Marsabit Distr., Mt Kulal, near lower Gatab airstrip, fr., 20 Nov. 1978, *Hepper & Jaeger* 6950 (EA!, K!); N slopes of Mt Kenya, fl./imm. fr., Dec. 1978, *Blackwell* 1 (EA!); Morijo, fl., 18 Feb. 1979, *Bamps* 6604 (K!); Narok Distr., c. 9 km directly N of Sekenani Hill, fr., 20 March 1979, *Kuchar* 10980 (EA!); Masai Mara Game Reserve, Olentoroto, lower-most hillslope, in bud, 2 June 1979, *Costich & Kuchar* 533 (EA!); Laikipia Distr., Luoniek Ranch, about 13 km NW of Sukuta Mugie, fr., 29 July 1980, *Muchiri* 415 (EA!); Machakos Distr., Mbiuni Location, Utithini Village, imm. fr., 2 Dec. 1980, *Fliervoet* 642 (EA!); Narok Distr., 9 km S of Ewaso Nyiro, hill S of Masandare R., in bud, 11 Jan. 1981, *Kuchar* 13888 (EA!); Laikipia Distr., Loldaiga Hills, sterile, 26 June 1981, *Olson* 93 (EA!); South Nyanza, Sindo, fr., 4 Dec. 1981, *Gachathi & Opon* 189/81 (EA!, K!); Kilifi, imm. fr., 18 Dec. 1981, *Meester* 259 (EA!); Turkana Distr., sterile, 1982, *Ohla* 270 (EA!); Coast Province, W part of Tana R., sterile, 15 Jan. 1982, *Ochung* 18 (EA!); Kilifi Distr., Gede Forest, Gedi National Monument, fr., 5 May 1985, *Gerhardt & Steiner* 40 (EA!); Machakos Distr., Kanzui area, about 5 km S of Tawa Shopping Centre, 32 km E of Machakos Town, Tulimani Location, sterile, 22 Aug. 1985, *Muasya* 647 (EA, 2 sheets!); Mt Suswa, in bud, 1985, *Store* 13 (EA!); Kwale Distr., Tiwi Kaya, by DC's rest house on N bank of Mwachema R. mouth, fr., 29 May 1987, *Robertson* 4686 (EA!, K!); Laikipia, Ol Ari Nyiro Ranch, sterile, 17 July 1988, *Muasya* 1868 (EA!); Lamu Distr., Ras Tenewi, in bud, 22 Nov. 1988, *Luke & Robertson* 1435 (EA!, K!); Baringo, Narokwe, fr., 3 July 1990, *Kajos* 842 (EA!); Kwale Distr., Taru Old Quarry, sterile, 18 Nov. 1990, *Robertson & Khayota* 6418 (EA!); Kwale Distr., Kaya Lunguma, fl., 11 Nov. 1992, *Luke* 3350 (EA!); Taita-Taveta Distr., Bura, in bud, 24 Nov. 1997, *Mwachala et al.* EW 182 (EA!); Taita Hills, Secho, in bud, 13 Aug. 1999, *Mungai et al.* 2599 (EA!); Mt Kasi-gau, Kiteghe, sterile, 22 June 2006, *Medley* 778 (EA!); *ibid.*, fr., 8 Dec. 2006, *Medley* 855 (EA!). **TANZANIA.** Hadeni Distr., Zindeni, imm. fr., 13 Sept. 1933, *Burt* 4832 (EA!); Mbulu Distr., Lake Manyara National Park, sterile, 22 Jan. 1962, *Dingle* HD 159 (EA!); *ibid.*, above Msasa, imm. fr., 4 Dec. 1963, *Greenway & Kirrika* 11134 (EA!, K!); Bagamoyo Distr., Kikoka Forest Reserve, fr., April 1964, *Semsei* 3819 (EA!, K!); Iringa Distr., Lukosi

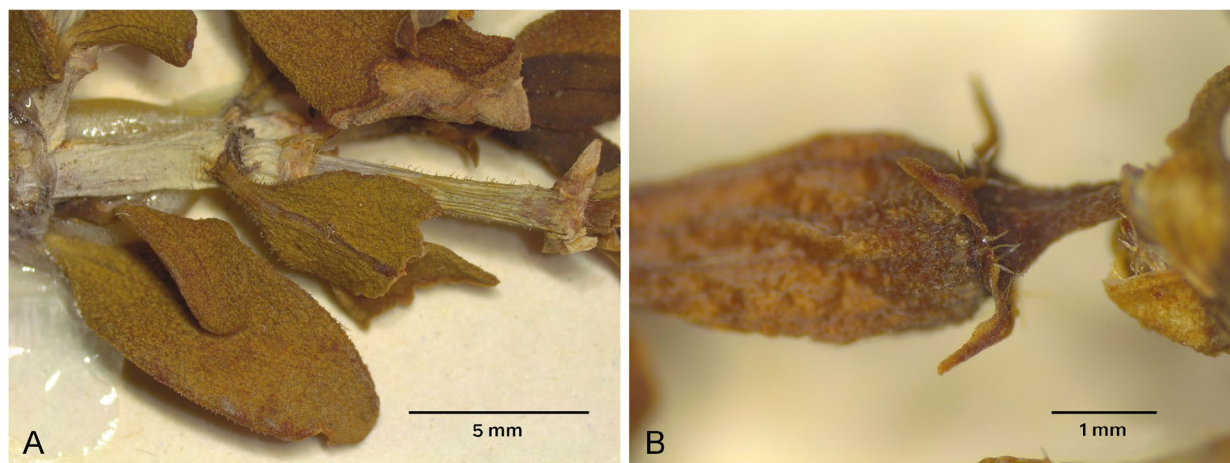
Valley, 6 mile on Iringa – Morogoro road, fl., Nov. 1964, *Procter* 2684 (EA!, K!); Mbulu Distr., Lake Manyara National Park, Msasa R. Gorge, fl./fr., 20 Jan. 1965, *Greenway & Kamuri* 12058 (EA!, K!); Masai Distr., Kijungu, sterile, 22 June 1965, *Leippert* 5970 (EA!); Masai Distr., 10 km Kikuletwa – Naberera, fr., 6 July 1965, *Leippert* 5985 (EA!, K!); Kunduchi, 18 km NNW of Dar es Salaam, fl., 25 Jan. 1969, *Harris* BJH 2766 (EA!, K!); Handeni Distr., Kwa Mkono, fl./imm. fr., 20 June 1973, *Archbold* 1701 (EA!); Kwa Mkono, fr., 28 April 1981, *Archbold* 2816 (K!); *ibid.*, fl., 1 May 1981, *Archbold* 2834 (K!); Same Distr., Same plot nost., 26 Aug. 1987, *Ruffo* 2582 (K!); Iringa Distr., along the Morogoro road and Lukosi R. at bottom of Kitonga gorge, 6 km W of Mahenge village at milepost 253 km from Morogoro, fr., 9 Jan. 1989, *Taylor et al.* 8486 (K!); Arusha, Monduli Distr., Longido Forest Reserve, SE side of Longido Peak, fr., 29 March 2000, *Simon et al.* 439 (K!).

**HABITAT.** *Acacia* and *Commiphora* bushland, often in rocky places, or in *Brachystegia* (miombo) woodland; at altitudes between 0 – 2050 m.

**CONSERVATION STATUS.** This species has recently been assessed and included on the IUCN Red List (2022b) as Vulnerable [VU B2ab(iii)], based on being known from fewer than 10 locations and being threatened by habitat loss and degradation due to human pressures (Crowley 2022). However, this assessment appears to have been made using only a subset (18 specimens) of the available data for this species compared to our 109 studied specimens. The current study reveals it to have a large EOO, of c. 2 million km<sup>2</sup> and to occur in a wide range of habitats, with many more locations. In addition, it is also known to occur within a number protected areas in its native range, such as Nairobi National Park and Arabuko Sokoke Forest in Kenya. It is, therefore, assessed here as Least Concern [LC].

**NOTES.** This species is recognisable vegetatively by its reduced lateral branches, short petioles and oblong-elliptic to linear-oblong leaves which usually lack discernible secondary and tertiary venation. The species most likely to be confused with *Pyrostria phyllanthoidea* are *P. hystrix* and *P. namacubiensis*, the latter is newly described below. However, *P. hystrix* has branches reduced to short spiny shoots in addition to smaller, slightly obovate or elliptic leaves, again with both the secondary and tertiary veins obscure. *Pyrostria namacubiensis* differs in its larger, obovate or elliptic leaves, with 3 pairs of conspicuous secondary veins, but obscure tertiary veins.

A few specimens from northern Kenya have puberulous young branches and minutely ciliate to puberulous leaf margins (Fig. 8A), which may also appear minutely dentate under microscopic examination. Moreover, a few long hairs were also observed at the sinuses between the calyx lobes (e.g. *Gillett* 12764 &



**Fig. 8.** *Pyrostria phyllanthoidea* from herbarium specimens: variant from northern Kenya. **A** pubescent branch and ciliate petiole and leaf margin; **B** hairs in the sinuses of the calyx lobes (both from Gillett 12764, K).

20200; Fig. 8B). However, these characters do not seem to be consistent among all specimens, or even all parts of the same specimen, and consequently need further investigation.

#### 14. *Pyrostria* sp. E

*Pyrostria* sp. B sensu Bridson (1998: 344).

**DISTRIBUTION.** Mozambique.

**SPECIMENS EXAMINED. MOZAMBIQUE.** [António Enes] Angoche, in bud, 17 Oct. 1965, Mogg 32296 (LISC\*); *ibid.*, in bud, 18 Oct. 1965, Mogg 32331 (LISC\*; K photo!).

**HABITAT.** The littoral zone of coastal dunes at c. 0 – 5 m elevation.

**CONSERVATION STATUS.** This species is known only from the two cited collections from the same location. An AOO of 4 km<sup>2</sup> is estimated. The Angoche area is subject to a range of threats including expanding settlement and agriculture, charcoal production, and extensive mining of mineral-rich sands, with much of the coastal vegetation there having been destroyed (Darbyshire *et al.* 2019b; Mucaleque 2020). This species is therefore assessed as Critically Endangered and Possibly Extinct [CR(PE) B2ab(iii)].

**NOTES.** This species is similar to the newly described *Pyrostria namacubiensis* (below) due to the small leaf size, 1.2 – 3.6 × 0.4 – 1.6 cm. However, it differs in having leaves crowded near the tips of the branches, as opposed to arranged on short lateral branches as in *P. namacubiensis*. It is known from only two specimens collected from the same locality that lack mature flowers or fruits for full description.

#### 15. *Pyrostria namacubiensis* Matheka & I. Darbysh. sp. nov.

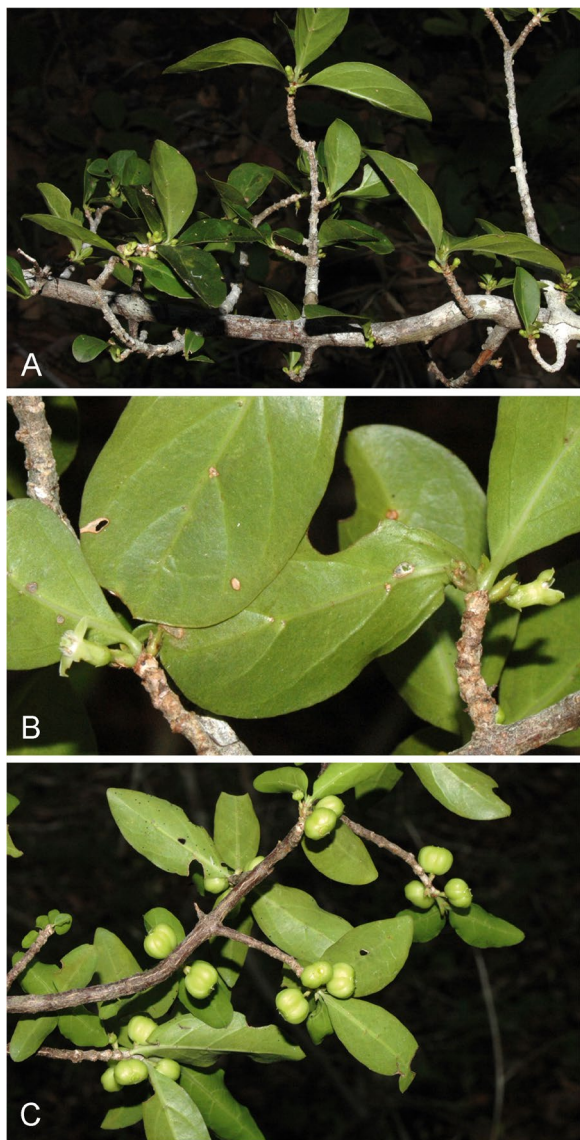
Type: Mozambique, Cabo Delgado Prov., Namacubi Forest (the Banana Forest), W of Quiterajo, fl., 25 Nov. 2008, Burrows & Burrows 10776B (holotype K! [K000738636]; isotypes BNRH, LMA).

<https://www.ipni.org/urn:lsid:ipni.org:names:77329784-1>

*Pyrostria phyllanthoidea* sensu Burrows (2018: 933), pro parte.

*Shrub or tree*, 1.5 – 8 m tall; lateral flowering branches short and almost at right angles to main stem; bark smooth and grey. *Leaves* clustered on short lateral branches, drying brownish-green except when young, then drying blackish; blades elliptic or slightly obovate, 1.2 – 3.6 × 0.4 – 1.6 cm, base acute, apex obtuse to rounded, mucronate; mostly 3 pairs of lateral veins visible; tertiary veins obscure; *domatia* present as ciliate hairs; petiole 1 – 3.5 mm long, petiole and much of midrib whitish. *Stipules* triangular with a central tapering lobe, 0.8 – 2.1 mm long, housing brownish hairs (?colleters); caducous. *Inflorescences* borne near end of short lateral branches, peduncles ± 1.5 mm long, pedicels 1.5 – 2.5 mm long, extending somewhat in fruit; bracts remaining fused for most of their length, attenuate at apex, up to 4 × 3.5 mm, hairs inside brownish; flowers unisexual, 2 – 4 per inflorescence, 4-merous. *Calyx* tube short, lobes triangular, ± 1 × 0.9 mm, uniting at base in a U-shape, acute at apex. *Corolla* cream-green or yellow-green, tube ± 3.1 × 1.2 mm; lobes triangular, ± 1.5 mm long, acute at apex, throat densely white-hairy. *Anthers* attached between corolla lobes, notched at base, slightly widening above, ± 1.1 × 0.5 mm; pollen pale yellow. *Pollen presenter* ellipsoid, surface rugulose or lobed, ± 0.7





**Fig. 9.** *Pyrostria namacubiensis* in the field. **A** habit; **B** flowering branch (both collected as Burrows & Burrows 10776 B); **C** fruiting branch (collected as Burrows & Burrows 10817), Namacubi Forest, Quiterajo, Mozambique. PHOTOS: J. E. BURROWS.

× 0.5 mm; style attached at the base of knob, ± 1.6 mm long. *Fruit* green, ribbed and shiny, globose to slightly obovate, 2-lobed, drying blackish, only seen in immature state. Figs 9, 10 & 11.

**RECOGNITION.** This species may be confused with *Pyrostria hystrix* and *P. phyllanthoidea* because of its similar growth habit, with right-angled lateral branching, and some similar leaf characters. However, it differs as it has 3 main pairs of lateral veins visible;

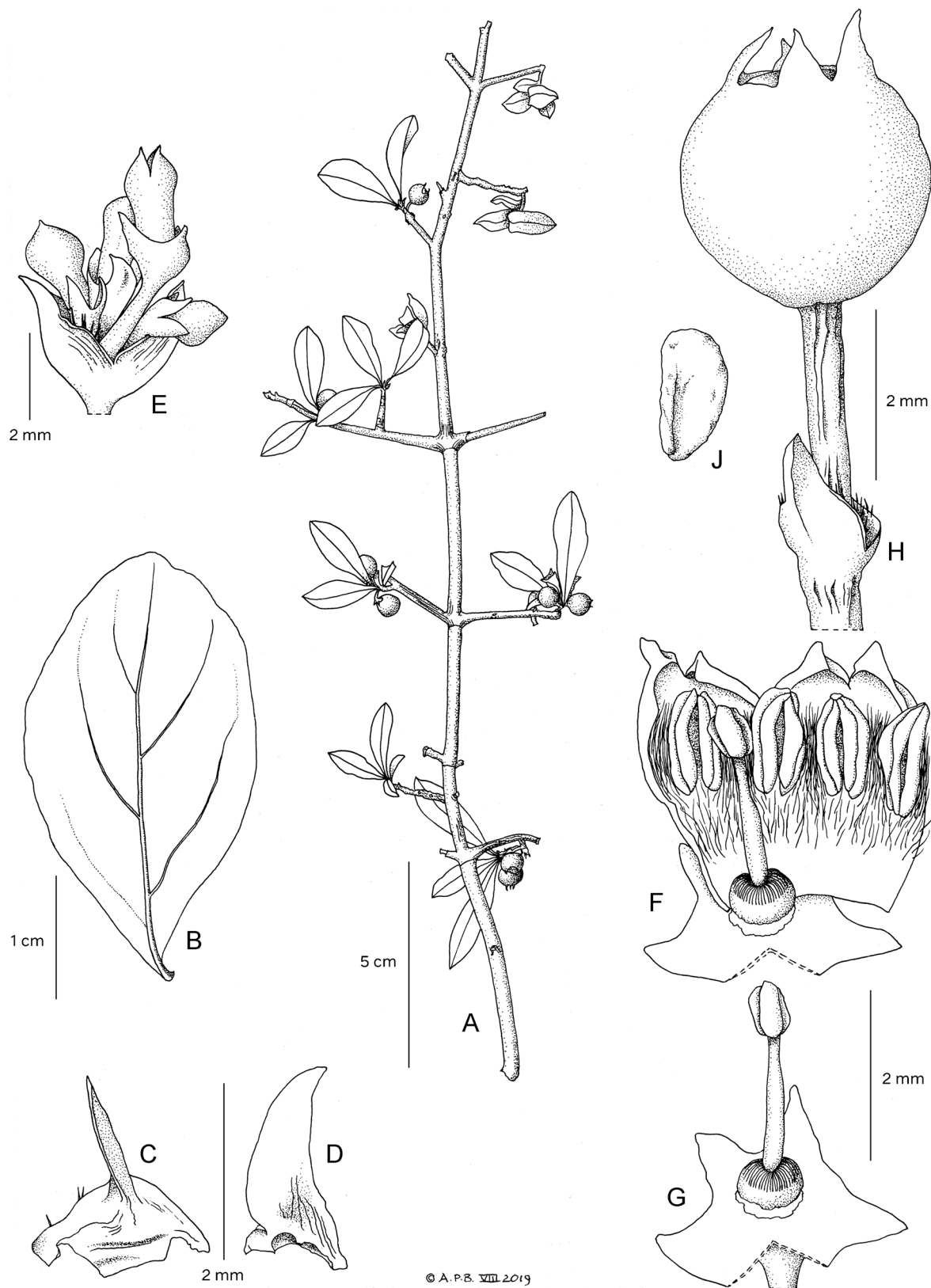
they are indistinct in those two species. In addition, both peduncles and pedicels are clearly visible in *P. namacubiensis* but the pedicels in *P. hystrix* are almost absent while the peduncles are longer and visible and vice versa in *P. phyllanthoidea*. Finally, the bracts in *P. namacubiensis* are larger, 4 × 3.5 mm, remaining fused for most of their length but sometimes partially subdivided with 1 – 2 lobes, whereas in *P. hystrix* they are very reduced and in *P. phyllanthoidea* they are narrow and the pairs are divided to the base when dry.

**DISTRIBUTION.** Northeastern Mozambique, where it occurs near Quiterajo in Palma District of Cabo Delgado Province, as well as near Memba in Nampula Province, see Map 1.

**SPECIMENS EXAMINED. MOZAMBIQUE.** Cabo Delgado Prov., Pangane, fr., Dec. 2006, Schmidt 4127 B (BNRH\*); Namacubi Forest (the Banana Forest), W of Quiterajo, fl., 25 Nov. 2008, Burrows & Burrows 10776 B (K!, BNRH\*); Quiterajo, Miparawa Forest, NE Escarpment area of Banana Forest overlooking Messalo R. floodplain, fr., 26 Nov. 2008, Burrows & Burrows 10817 (BNRH\*, K!); Quiterajo, close to margin of Namacubi Forest above Messalo R. floodplain, fr., 23 Nov. 2009, Crawford *et al.* FC 702 (K!, P\*); Nampula Distr., W of turnoff to Memba on the Cava to Nacala Velho road, fl., 8 Jan. 2012, Burrows & Burrows 12596 (BNRH\*).

**HABITAT.** An understorey shrub or tree in dry, mixed, coastal sand forest and on rocky outcrops; at 20 – 123 (– 150) m elevation.

**CONSERVATION STATUS.** This species faces similar threats to *Pyrostria makovui* in northeastern Mozambique due to a shared habitat. It is only known from the five cited collections. The EOO based on these five collections is 1,470 km<sup>2</sup>, while the AOO is 20 km<sup>2</sup>. The full extent of the Namacubi Forest is approximately 23.5 km<sup>2</sup>, it is currently unprotected and threatened by a number of factors, including timber exploitation, expanding subsistence agriculture, settlement and increased frequency of wildfires (Burrows & Burrows 2010; Timberlake *et al.* 2011; Johnson *et al.* 2017; Darbyshire *et al.* 2021). Timberlake *et al.* (2014) estimate a c. 10% reduction in forest cover at Namacubi between 1999 and 2013, and encroachment, into the southern portion of the forest in particular, is clearly evident on satellite imagery. A significant threat arose in the mid-2010s, from the proposed construction of a new road from Mocimboa da Praia to Pemba, associated with oil and gas industrial activity, which would have run through the Namacubi Forest. However, this project did not proceed, and the threat from it appears to have abated. There is also significant and ongoing habitat loss in the vicinities of Pangane and Memba, the other two locations for this species. With three known locations, the estimates of EOO and AOO, and a continuing decline in the extent and quality of



**Fig. 10.** *Pyrostria namacubiensis*. **A** habit, fruiting branches; **B** leaf, abaxial surface; **C** stipule, detached, face view; **D** stipule, detached, side view; **E** inflorescence; **F** dissected flower; **G** ovary, style and stigma in situ on partially dissected hypanthium and calyx; **H** fruit; **J** pyrene. **A** from Burrows & Burrows 10817 (K); **B** – **G** from Burrows & Burrows 10776 B (K); **H** & **J** from Crawford 702 (K). DRAWN BY ANDREW BROWN.



**Fig. 11.** *Pyrostria namacubiensis* from herbarium specimens. **A** inflorescences in situ; **B** inflorescences showing bracts; **C** calyx, style and pollen presenter (all from *Burrows & Burrows* 10776 B); **D** fruits (*Crawford et al.* FC 702).

habitat, this species is hereby assessed as **Endangered** [EN B1ab(iii)+B2ab(iii)].

**ETYMOLOGY.** The specific epithet ‘*namacubiensis*’ is derived from the type locality, Namacubi Forest.

**NOTES.** The species is a new addition to the *Pyrostria* of continental Africa which was only recently discovered at its type locality. *Burrows* (2018) cited this species as a coastal variant of *P. phyllanthoidea*, because of its larger leaves. However, the leaves tend to be smaller and more narrowly elliptic in collections with immature leaves (*Burrows & Burrows* 10817; *Crawford et al.* 702), where they dry blackish rather than green. More field observations and collections are necessary to better understand the variation within this species. The floral measurements presented here are based on observation of a few flowers.

**16. *Pyrostria hystrix*** (*Bremek.*) *Bridson* (1987: 629); *Coates Palgrave* (1988: 16k); *Pooley* (1993: 480);

*Burrows* (2018: 932). Type: South Africa, Transvaal [Limpopo Prov.], Pietersburg, [Polokwane], between Leipzig and Bochum [Senwabarwana], fl., 19 Jan. 1931, *Bremekamp* [*& Schweickerdt*] 147 (holotype PRE\* [PRE0144097-0]).

*Dinocanthium hystrix* *Bremek.* (*Bremekamp* 1933: 259).

**DISTRIBUTION.** South Africa: Limpopo, Mpumalanga and KwaZulu-Natal. Eswatini, southern Mozambique.

**SPECIMENS EXAMINED. MOZAMBIQUE.** Moamba, fr., 1 Dec. 1942, *Mendonça* 1525 (LISC\*); Lourenço Marques [Maputo], Manjacaze ao km 30, fr., 3 Dec. 1942, *Mendonça* 1581 (LISC\*). **ESWATINI.** Stegi Distr., Sicusha, fl., 3 April 1962, *Compton*, 31434 (K!). **SOUTH AFRICA.** [KwaZulu] Natal, fr., without date, *Gerard* 1619 (BM!, K!); KwaZulu Natal, Ubombo, Biala, sterile, 28 Aug. 1937, *Gerstner* 2299 (K!); KwaZulu Natal, Zululand, Biala, fr., 17 Jan. 1939, *Gerstner* 3289 (K!); KwaZulu Natal, Ubombo Distr., between Mhlosinga and Biala, fr., 8 July 1948, *Gerstner* 6971 (K!); Kruger National

**Table 2.** Characters for distinguishing *Pyrostria namacubiensis* from morphologically similar species.

Character	<i>P. namacubiensis</i>	<i>P. hystrix</i>	<i>P. phyllanthoidea</i>
<b>Branching</b>			
Lateral branches	90° or slightly less to main stem; not spiny	always at ± 90° to main stem; often spiny	usually less than 90° to main stem; not spiny
<b>Leaves</b>			
Leaf shape and size (cm)	elliptic or narrowly obovate, 1.2 – 3.6 × 0.4 – 1.6	slightly obovate or elliptic, 0.8 – 2.2 × 0.4 – 1	oblong-elliptic to linear-oblong, 0.5 – 3.6 (– 4.5) × 0.3 – 1.3 (– 1.7)
Leaf venation	secondary veins conspicuous, usually 3 per side	secondary veins obscure	secondary veins obscure
<b>Inflorescence</b>			
Peduncle (mm)	≤ 1.5	1 – 2	1 – 2
Pedicel (mm)	1.5 – 2.5	≤ 1	1.5 – 3
Bracts	fused for most of their length, attenuate at apex	ovate, obtuse at apex	ovate, acuminate at apex
Corolla colour and length (mm)	cream-green or yellow-green, tube ± 3.1	white or yellowish, tube ± 1.5	cream-coloured, tube 2 – 5

Park, Skukuza Gastehuis, sterile, 31 March 1952, *van der Schyff* 456 (K!); KwaZulu Natal, Umfolozi Game Reserve, bank of Tobothi R., fr., 20 March 1969, *Ross*

2042 (K!); KwaZulu Natal, Ndumu Game Reserve, in bud, 3 Nov. 1969, *Moll* 4243 (K!); Mpumalanga/Limpopo, Kruger National Park, on N<sup>o</sup> Watimihiri



**Fig. 12.** *Pyrostria hystrix*. **A** stem habit, Chokwe, Mozambique; **B** flower branch, Ingwavuma, South Africa; **C** fruiting branches, Ohrigstad, South Africa. PHOTOS: J. E. BURROWS.

Causeway, 780 m after intersection with Lower Sabie Road, in direction of Lower Sabie, sterile, 15 Sept. 2005, *Maurin et al.* OM 234 (K!).

**HABITAT.** Low-elevation *Acacia* woodland. The elevation range, inferred from data labels on herbarium specimens, is c. 60 – 350 m.

**CONSERVATION STATUS.** This species is widespread and frequent in northeastern South Africa, although it appears to be much more localised in southern Mozambique and Eswatini. The EOO is > 160,000 km<sup>2</sup>, including South African data from GBIF, but excluding a record from south of Durban. Quite a number of the localities fall within the Kruger National Park, where it is likely to be secure. It is, therefore, assessed here as Least Concern [LC].

**NOTES.** This is one of the three twiggy species of *Pyrostria* in continental Africa but the only one with sometimes spiny, short shoots. In addition, it has visibly smaller leaves when compared to the other two species (*P. phyllanthoidea* and *P. namacubiensis*; see Table 2) and the distributions of the three are disjunct. Fig. 12.

### Acknowledgements

This study formed a part of the first author's MSc. in Plant and Fungal Taxonomy, Diversity and Conservation at Queen Mary University (QMUL), London and Royal Botanic Gardens, Kew and was made possible thanks to the B. A. Krukoff Fellowship in Systematics awarded by the Bentham Moxon Trust; our thanks go to Jennifer Alsop and Colin Clubbe for administering the award. We greatly appreciate the staff at Kew and QMUL who assisted during the course of this study and in particular Aaron Davis (for Rubiaceae literature), Lari Merrett (field photographs), Kaj Vollesen (additional recent collections of *Pyrostria*), Martin Cheek, Peter Petoe, Toral Shah (literature and encouragement), and Nina Davies (herbarium support). In addition, we thank Ranee Prakash who provided access to the collections at BM, Diane Bridson who provided essential advice and opinion on the revision, and Quentin Luke, Lari Merrett and John Burrows who provided field photographs and helpful advice on eastern African species of *Pyrostria*. Finally, we particularly thank Andrew Brown for the line illustrations and Kevin Odhiambo of EA for producing the species distribution maps for the new taxa.

### Declarations

**Conflict of Interest** The authors declare that they have 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

- Alejandro, G. J. D., Arenas, E. H., Cremen, C. M. & Arriola, A. H. (2013). A new record of *Pyrostria* (Vanguerieae – Rubiaceae) from the Philippines inferred from molecular and morphological data. *Philipp. J. Syst. Biol.* 7: 1 – 12. <https://asbp.org.ph/wp-content/uploads/2016/09/3230-11880-1-PB.pdf>
- \_\_\_\_\_, Magdaleno, C. M. M., Pacia, J. A. T., Paraguison, L. D., Quiogue, K. K. C., Wong, A. E. D., Yayen, K. M. R. & Arriola, A. H. (2014). Generic affiliations of *Canthium* species placed under *Pyrostria* group B sensu Bridson (Vanguerieae, Rubiaceae) inferred from morphology and molecular data. *Bot. Stud.* 55: 1 – 8. <https://doi.org/10.1186/s40529-014-0065-3>.
- Arènes, J. (1960). A propos de quelques genres Malgaches de Rubiacées. *Notul. Syst. (Paris)* 16: 6 – 41. <https://www.biodiversitylibrary.org/page/12869532#page/12/mode/1up>.
- Arriola, A. H., Camacho, P. D., Calaramo, M. J. A. & Alejandro, G. J. D. (2015). *Pyrostria triflora*, a new species of Vanguerieae (Rubiaceae) from Luzon, Philippines. *Bangladesh J. Pl. Taxon.* 22: 55 – 58. <https://doi.org/10.3329/bjpt.v22i1.23868>.
- \_\_\_\_\_, Meve, U. & Alejandro, G. J. D. (2016). *Canthium elmeri* Merr. lectotypified and transferred to *Pyrostria* (Rubiaceae). *Ann. Bot. Fenn.* 53: 216 – 218. <https://doi.org/10.5735/085.053.0409>.
- Bachman, S., Moat, J., Hill, A. W., de la Torre, J. & Scott, B. (2011). Supporting Red List threat assessments with GeoCAT: Geospatial Conservation Assessment Tool. In: V. Smith & L. Penev (eds), e-Infrastructures for data publishing in biodiversity science. *ZooKeys* 150: 117 – 126. <https://doi.org/10.3897/zookeys.150.2109>.
- Baillon, H. (1879a). Mémoire sur les genres *Canthium* et *Hyprobathrum*. *Adansonia* 12: 179 – 213. <https://www.biodiversitylibrary.org/item/25865#page/191/mode/1up>.
- \_\_\_\_\_. (1879b). Stirpes Exoticae Novae (cont.). *Adansonia* 12: 220 – 254. <https://www.biodiversitylibrary.org/item/25865#page/232/mode/1up>.
- \_\_\_\_\_. (1880). *Histoire des Plantes. Monographie des Rubiacées, des Valérianiacées et des Dipsacacées* 7. Librairie

- Hachette, Paris. <https://bibdigital.rjb.csic.es/idurl/1/15026>.
- Baker, J. G. (1877). *Flora of Mauritius and the Seychelles*. L. Reeve & Co., London. <https://doi.org/10.5962/bhl.title.139960>.
- Balfour, I. B. (1877). Aspects of the phaenogamic vegetation of Rodriguez, with descriptions of new plants from the island. *J. Linn. Soc., Bot.* 16: 7 – 25. <https://doi.org/10.1111/j.1095-8339.1877.tb00167.x>.
- Beentje, H. J. (1994). *Kenya Trees, Shrubs and Lianas*. National Museums of Kenya, Nairobi.
- \_\_\_\_ (2016). *The Kew Plant Glossary: An Illustrated Dictionary of Plant Terms*. Royal Botanic Gardens, Kew.
- Bremekamp, C. E. B. (1933). New or otherwise noteworthy plants from the Northern Transvaal. *Ann. Transvaal Mus.* 15: 233 – 264.
- Bremer, B., Andreasen, K. & Olsson, D. (1995). Subfamilial and tribal relationships in the Rubiaceae based on *rbcL* sequence data. *Ann. Missouri Bot. Gard.* 82: 383 – 397. <https://www.jstor.org/stable/2399889>.
- \_\_\_\_, Jansen, R. J., Oxelman, B., Backlund, M., Lantz, H. & Kim, K.-J. (1999). More characters or more taxa for a robust phylogeny — case study from the coffee family (Rubiaceae). *Syst. Biol.* 48: 413 – 435. <https://doi.org/10.1080/106351599260085>.
- Brenan, J. P. M. (1949). *Check-lists of the forest trees and shrubs of the British Empire. No. 5, Tanganyika Territory. Part II*. Imperial Forestry Institute, Oxford.
- Bridson, D. M. (1985). The Reinstatement of *Psydrax* (Rubiaceae, subfam. Cinchonoideae tribe Vanguerieae) and a revision of the African Species. *Kew Bull.* 40: 687 – 725. <https://www.jstor.org/stable/4109853>.
- \_\_\_\_ (1987). Studies in African Rubiaceae – Vanguerieae: a new circumscription of *Pyrostria* and a new subgenus, *Canthium* subgen. *Bullockia*. *Kew Bull.* 42: 611 – 639. <https://www.jstor.org/stable/4110068>.
- \_\_\_\_ (1991). *Pyrostria*. In: R. M. Polhill (ed.), *Flora of Tropical East Africa, Rubiaceae* (Part 3): 885 – 892. A. A. Balkema, Rotterdam / Brookfield.
- \_\_\_\_ (1998). Rubiaceae (Tribe Vanguerieae). In: G. V. Pope (ed.), *Flora Zambesiaca* 5 (2): 227 – 377. Royal Botanic Gardens, Kew.
- \_\_\_\_ (2006). *Pyrostria*. pp. 90 – 91. In: M. Thulin (ed.), *Flora of Somalia. Vol. 3*. Royal Botanic Gardens, Kew.
- \_\_\_\_ (2009). *Pyrostria lobulata*. In: U. Bloesch, G. Troupin & N. Derungs (eds), *Les plantes ligneuses du Rwanda. Flore ecologie et usages*: 530. Shaker Verlag, Aachen.
- \_\_\_\_ & Troupin, G. (1982). *Rubiaceae*. In: G. Troupin & D. M. Bridson, *Flore des plantes ligneuses du Rwanda*. Musée Royal de l'Afrique Centrale, Tervuren.
- Bullock, A. A. (1932). *Canthium* in British East Africa. *Bull. Misc. Inform., Kew* 1932: 353 – 389. <https://doi.org/10.2307/4113481>.
- Burgess, N. D., Butynski, T. M., Cordeiro, N. J., Doggart, N. H., Fjeldså, J., Howell, K. M., Kilahama, F. B., Loader, S. P., Lovett, J. C., Mbilinyi, B., Mengon, M., Moyer, D. C., Nashanda, E., Perkin, A., Rovero, F., Stanley, W. T. & Stuart, S. N. (2007). The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. *Biol. Conservation* 134: 209 – 231. <https://doi.org/10.1016/j.biocon.2006.08.015>.
- Burrows, J. E. (2018). Rubiaceae. In: J. E. Burrows, S. M. Burrows, M. C. Lötter & E. Schmidt, *Trees and Shrubs Mozambique*: 890 – 1018. Publishing Print Matters (Pty) Ltd, Noordhoek, Cape Town.
- \_\_\_\_ & Burrows, S. M. (2010). A new species of *Didymosalpinx* and a new species of *Oxyanthus* from Mozambique and Tanzania. *Bothalia* 40: 200 – 204. <https://doi.org/10.4102/abc.v40i2.221>.
- \_\_\_\_, Burrows, S. M., Lötter, M. C. & Schmidt, E. (2018). *Trees and Shrubs Mozambique*. Publishing Print Matters (Pty) Ltd, Noordhoek, Cape Town.
- \_\_\_\_ & Timberlake, J. (2011). Mozambique's centres of endemism, with special reference to the Rovuma Centre of Endemism of NE Mozambique and SE Tanzania. *S. African J. Bot.* 77: 518. <https://www.sciencedirect.com/journal/south-african-journal-of-botany/vol/77/issue/2>.
- de Candolle, A. P. (1830). *Prodromus systematis naturalis regni vegetabilis* 4. Sumptibus Sociorum Treuttel et Würtz, Paris. <https://doi.org/10.5962/bhl.title.286>.
- Capuron, R. (1969). A propos des Rubiacées–Vanguériées de Madagascar. *Adansonia, sér. 2*, 9: 47 – 55. <https://www.biodiversitylibrary.org/item/281041#page/49/mode/1up>.
- Cavaco, A. (1966). Contribution à l'étude des Vanguériées (Rubiaceae) de Madagascar. *Bull. Mus. Natl. Hist. Nat., sér. 2*, 38: 700 – 702. <https://www.biodiversitylibrary.org/item/242583#page/724/mode/1up>.
- \_\_\_\_ (1968). Espèces nouvelles de Rubiacées de Madagascar. *Bull. Mus. Natl. Hist. Nat., sér. 2*, 39: 1015 – 1019. <https://www.biodiversitylibrary.org/item/242405#page/1039/mode/1up>.
- \_\_\_\_ (1969). Contribution à l'étude des genres *Pseudopeponidium* et *Peponidium* (Rubiaceae – Vanguériées). *Adansonia, sér. 2*, 9: 43 – 46. <https://www.biodiversitylibrary.org/item/281041#page/45/mode/1up>.
- \_\_\_\_ (1970). *Leroyia*, nouveau genre de Rubiaceae. *Adansonia, sér. 2*, 10: 333 – 337. <https://www.biodiversitylibrary.org/item/281009#page/39/mode/1up>.
- \_\_\_\_ (1971a). Remarques sur quelques *Pyrostria* (Rubiaceae – Vanguériées) de Madagascar. *Adansonia, sér.*

- 2, 11: 393 – 396. <https://www.biodiversitylibrary.org/item/281039#page/175/mode/1up>.
- Cavaco, A. (1971b). *Neoleroia*, nouveau genre de Rubiaceae-Vanguerieae. *Adansonia*, sér. 2, 11: 19 – 123. <https://www.biodiversitylibrary.org/item/281006#page/121/mode/1up>.
- CEPF (2022). Critical Ecosystems Partnership Fund. Coastal Forests of Eastern Africa. Available at: <https://www.cepf.net/our-work/biodiversity-hotspots/coastal-forests-eastern-africa>. [Accessed 25 March 2022].
- Cheek, M., Harvey, Y. & Onana, J. M. (2011). *The Plants of Mefou Proposed National Park, Yaoundé, Cameroon: A Conservation Checklist*. Royal Botanic Gardens, Kew.
- Clarke, G. P. (2001). The Lindi centre of endemism in southeastern Tanzania. *Syst. Geogr. Pl.* 71: 1063 – 1072. <https://doi.org/10.2307/3668738>.
- Coates Palgrave, K. (1988). *Trees of Southern Africa. Third Edition*. C. S. Struik Publishers, Cape Town.
- Crowley, D. (2022). *Pyrostria phyllanthoidea*. The IUCN Red List of Threatened Species 2022: e.T164051952A164059365. <https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T164051952A164059365.en>. [Accessed 18 Aug. 2022].
- Cufodontis, G. (1965). Enumeratio Plantarum Aethiopiae Spermatophyta (sequentia). *Bull. Jard. Bot. État. Bruxelles* 35 (1) suppl.: 979 – 1010. <https://doi.org/10.2307/3667270>.
- Dale, I. R. & Greenway, P. J. (1961). *Kenya Trees and Shrubs*. University Press, Glasgow.
- Darbyshire, I., Goyder, D. J., Wood, J. R. I., Banze, A. & Burrows, J. E. (2020). Further new species and records from the coastal dry forests and woodlands of the Rovuma Centre of Endemism. *Pl. Ecol. Evol.* 153: 427 – 445. <https://doi.org/10.5091/plecevo.2020.1727>.
- \_\_\_\_\_, \_\_\_\_\_, \_\_\_\_\_, \_\_\_\_\_ & \_\_\_\_\_ (2021). Further new species and records from the coastal dry forests and woodlands of the Rovuma Centre of Endemism - Erratum. *Pl. Ecol. Evol.* 154: 316. <https://doi.org/10.5091/plecevo.2021.1878>
- \_\_\_\_\_, Richards, S., Osborne, J., Matimele, H., Langa, C., Datizua, C., Massingue, A., Rokni, S., Williams, J., Alves, T. & de Sousa, C. (2023). *The Important Plant Areas of Mozambique*. Royal Botanic Gardens, Kew.
- \_\_\_\_\_ & Rokni, S. (2020). *Scorodophloeus torrei*. The IUCN Red List of Threatened Species 2020: e.T149257100A153685894. <https://doi.org/10.2305/iucn.uk.2020-2.rlts.t149257100a153685894.en>. [Accessed 19 March 2021].
- \_\_\_\_\_, \_\_\_\_\_, Alves, M. T., Burrows, J. E., Chelene, I., Datizua, C., Sousa, C. de, Fijamo, V., Langa, C., Massingue, A. O., Massunde, J., Matimele, H. A., Mucalque, P. A., Osborne, J. & Siteo, P. (2019b). *Memecylon sessilicarpum*. The IUCN Red List of Threatened Species 2019b: e.T32162A136538253. <https://doi.org/10.2305/IUCN.UK.2019-2.RLTS.T32162A136538253.en>. [Accessed 19 March 2021].
- \_\_\_\_\_, Timberlake, J., Osborne, J., Rokni, S., Matimele, H., Langa, C., Datizua, C., Sousa, C. de, Alves, T., Massingue, A., Hadj-Hammou, J., Dhanda, S., Shah, T. & Wursten, B. (2019a). The endemic plants of Mozambique: diversity and conservation status. *PhytoKeys* 136: 45 – 96. <https://doi.org/10.3897/phytokeys.136.39020>.
- Davis, A. P., Govaerts, R., Bridson, D. M., Ruhsam, M., Moat, J., & Brummitt, N. A. (2009). A global assessment of distribution, diversity, endemism, and taxonomic effort in the Rubiaceae. *Ann. Missouri Bot. Gard.* 96: 68 – 78. <https://doi.org/10.3417/2006205>.
- \_\_\_\_\_ & Razafimandimbison, S. G. (2010). Three species of Madagascan *Peponidium* transferred to *Peponidium* (Vanguerieae, Rubiaceae). *Phytotaxa* 10: 46 – 48. <https://doi.org/10.11646/phytotaxa.10.1.7>.
- Fosberg, F. R. & Renvoize, S. A. (1980). The Flora of Aldabra and neighbouring islands. *Kew Bull. Addit. Ser.* 7. HMSO, London.
- Friedmann, F. (1994). *Flore des Seychelles. Dicotylédones*. IRD Éditions / Publications Scientifiques du Muséum, Marseilles. Available from: [http://horizon.documentation.ird.fr/exldoc/pleins\\_textes/divers12-09/010052287.pdf](http://horizon.documentation.ird.fr/exldoc/pleins_textes/divers12-09/010052287.pdf).
- Gmelin, J. F. (1791). *Pyrostria commersonii*. In: C. Linné, *Systema Natura, Ed. 13 [bis]* 2 (1): 246, aucta, reformata. Cura Jo. Frid. Gmelin ... Lipsiae, impensis G. E. Beer. <https://doi.org/10.5962/bhl.title.36932>.
- Good, R. D. (1926). Rubiaceae. Mr John Gossweiler's plants from Angola and Portuguese Congo. *J. Bot.* 64 suppl. 2: 1 – 175.
- Google Earth Pro (2022). Google Earth Pro version 7.3.n. Available from: <https://earth.google.com/web>. [Accessed throughout 2022].
- Hepper, F. N. (1962). Notes on tropical African Rubiaceae: III. *Kew Bull.* 16: 329 – 339. <https://doi.org/10.2307/4118841>.
- \_\_\_\_\_ (1963a). Tropical African plants: XXVII. Rubiaceae. *Kew Bull.* 17: 170 – 171. <https://doi.org/10.2307/4118712>.
- \_\_\_\_\_ (1963b). *Rytigynia*. In: F. N. Hepper (ed.), *Flora of West tropical Africa Edition 2*, 2: 185 – 186. Crown Agents for Oversea Governments and Administrations, London.
- Hiern, W. P. (1877). Order LXX. Rubiaceae. In: D. Oliver (ed.), *Flora of Tropical Africa* 3: 33 – 247. L. Reeve & Co., London. <https://www.biodiversitylibrary.org/item/125#page/39/mode/1up>.
- Hutchinson, J. & Bruce, E. A. (1941). Enumeration of the plants collected by Mr. J. B. Gillett in Somaliland

- and Eastern Abyssinia. *Bull. Misc. Inform., Kew* 1941: 76 – 199. <https://www.jstor.org/stable/4102534>
- IUCN (2012). *IUCN Red List Categories and Criteria, version 3.1*. IUCN Species Survival Commission, Gland and Cambridge.
- IUCN (2022a). *Guidelines for Using the IUCN Red List Categories and Criteria, version 15.1*. Prepared by the Standards and Petitions Committee. International Union for Conservation of Nature, Gland and Cambridge. Available from: <https://www.iucnredlist.org/documents/RedListGuidelines.pdf>.
- IUCN (2022b). *The IUCN Red List of Threatened Species. Version 2021-3*. Available from: <https://www.iucnredlist.org>. [Accessed 25 March 2022].
- Johnson, D. M., Luke, Q., Goyder, D. J. & Murray, N. A. (2017). New species of *Xylopia* (Annonaceae) from East Africa. *Kew Bull.* 72 Article 11: 1 – 13. <https://doi.org/10.1007/s12225-017-9681-x>
- Jussieu, A. L. de (1789). *Genera Plantarum Secundum Ordines Naturales Disposita, juxta methodum in Horto regio parisiensi exaratum, anno M.DCC.LXXIV*. Apud Viduam Herissant et Theophilum Barrois, Paris. <https://doi.org/10.5962/bhl.title.284>.
- Kainulainen, K. & Razafimandimbison, S. G. (2016). New taxonomic combinations in West Indian Ocean Vanguerieae (Rubiaceae). *Phytotaxa* 282: 267 – 272. <https://doi.org/10.11646/phytotaxa.282.4.3>
- Lantz, H., Andreasen, K. & Bremer, B. (2002) Nuclear rDNA ITS sequence data used to construct the first phylogeny of Vanguerieae (Rubiaceae). *Pl. Syst. Evol.* 230: 173 – 187. <https://doi.org/10.1007/s006060200003>.
- \_\_\_\_ & Bremer, B. (2004). Phylogeny inferred from morphology and DNA data: characterizing well-supported groups in Vanguerieae (Rubiaceae). *Bot. J. Linn. Soc.* 146: 257 – 283. <https://doi.org/10.1111/j.1095-8339.2004.00338.x>.
- \_\_\_\_, Klackenberg, J., Razafimandimbison, S. G. & Mouly, A. (2007). Three new species of Vanguerieae (Rubiaceae) from Madagascar. *Adansonia* 29: 129 – 136. <https://sciencepress.mnhn.fr/en/periodiques/adansonia/29/1/trois-nouvelles-especes-de-vanguerieae-rubiaceae-de-madagascar>.
- Lovett, J. C., Ruffo, C. K., Gereau, R. E. & Taplin, J. R. D. (2006). *Field Guide to the Moist Forest Trees of Tanzania*. The Society for Environmental Exploration, UK and the University of Dar es Salaam.
- Luke, W. R. Q., Bangirinama, F., Beentje, H. J., Darbyshire, I., Gereau, R., Kabuye, C., Kalema, J., Kelbessa, E., Kindeketa, W., Malombe, I., Minani, V., Mwangoka, M. & Ndangalasi, H. (2015). *Mimulopsis marronia*. The IUCN Red List of Threatened Species 2015: e.T48154051A48154989. <https://doi.org/10.2305/IUCN.UK.2015-2.RLTS.T48154051A48154989.en>. [Accessed 19 March 2021].
- Madagascar Catalogue (2022). *Catalogue of the plants of Madagascar*. Missouri Botanical Garden, St. Louis & Antananarivo. Available at: <http://legacy.tropicos.org/Project/Madagascar>. [Accessed 25 April 2022].
- Martelli, U. (1886). *Florula Bogosensis: enumeration delle piante dei Bogos raccolte dal Dott. O. Beccari*. Tipografia di Mariano Ricci, Firenze. <https://hdl.handle.net/2027/chi.086800292>.
- Mildbraed, J. (1924). Additamenta africana I. Rubiaceae. *Notizbl. Bot. Gart. Berlin-Dahlem* 9: 200 – 207. <https://doi.org/10.2307/3994337>
- Mucaleque, P. A. (2020). *Ammannia moggii*. The IUCN Red List of Threatened Species 2020: e.T149257990A153685939. <https://doi.org/10.2305/IUCN.UK.2020-3.RLTS.T149257990A153685939.en>. [Accessed 19 March 2021].
- Onana, J. M. (2013). *Synopsis des espèces végétales vasculaires endémiques et rares du Cameroun. Check-liste pour la gestion durable et la conservation de la biodiversité*. In J. M. Onana (ed.), *Flore du Cameroun* 40. Ministère de la Recherche Scientifique et de l'Innovation (MIN-RESI), Cameroon.
- \_\_\_\_ & Cheek, M. (2011). *Red data book of the flowering plants of Cameroon*. Royal Botanic Gardens, Kew.
- Penzig, O. (1892). *Atti del Congresso Botanico Internazionale di Genova 1892*. Tipografia del R. Istituto Sordomuti, Genoa. <https://babel.hathitrust.org/cgi/pt?id=hvd.32044106401094&seq=355>.
- Plant List (2013). *The Plant List. Version 1.1*. Published on the Internet. Available from: <http://www.theplantlist.org>. [Accessed 22 Jan. 2018].
- Polhill, D. & Polhill, R. (2015). *East African Plant Collectors*. Royal Botanic Gardens, Kew.
- Pooley, E. (1993). *The Complete Field Guide to Trees of Natal, Zululand and Transkei*. Natal Flora Publications Trust, Natal Herbarium, Durban.
- POWO (2021, continuously updated). *Plants of the World Online*. Royal Botanic Gardens, Kew. Published on the Internet. Available from: <http://www.plantsoftheworldonline.org>. [Accessed 26 March 2021].
- Razafimandimbison, S. G., Lantz, H. & Bremer, B. (2007). New combinations and names in *Pepionidium* and *Pyrostria* (Rubiaceae, Vanguerieae). *Novon* 17: 516 – 521. [https://doi.org/10.3417/1055-3177\(2007\)17\[516:ncanip\]2.0.co;2](https://doi.org/10.3417/1055-3177(2007)17[516:ncanip]2.0.co;2).
- \_\_\_\_, \_\_\_\_ , Mouly, A. & Bremer, B. (2009). Evolutionary trends, major lineages and new generic limits in the Dioecious group of the tribe Vanguerieae (Rubiaceae): Insights into the evolution of functional dioecy. *Ann. Missouri Bot. Gard.* 96: 161 – 181. <https://doi.org/10.3417/2006191>.
- Robyns, W. (1943). Sympétales nouvelles de la région du Parc National Albert (Congo Belge). *Bull. Jard. Bot. État. Bruxelles*. 17: 65 – 107. <https://doi.org/10.2307/3666735>.
- \_\_\_\_ (1947). *Flore des spermatophytes du Parc National Albert. 2. Gymnospermes et Chloripétales*. Institut des Parcs Nationaux du Congo Belge, Bruxelles.



- Schatz, G. E. (2001). *Generic Tree Flora of Madagascar*. Royal Botanic Gardens, Kew & Missouri Botanical Garden, Missouri.
- Smith, A. C. & Darwin, S. P. (1988). Family 168. *Rubiaceae*. Pp. 146 – 362. In: A. C. Smith (ed.), *Flora Vitiensis Nova. A New Flora of Fiji (spermatophytes only)*, Vol. 4, *Angiospermae: Dicotyledones, Families*, 164 – 169. Pacific Tropical Botanical Garden, Kauai. <https://doi.org/10.5962/bhl.title.44033>.
- Stearn, W. T. (2004). *Botanical Latin. Fourth Edition*. Timber Press, Portland.
- Stuessy, T. F. (2009). *Plant Taxonomy: The Systematic Evaluation of Comparative Data*. Columbia University Press, New York.
- Thiers, B. (2020, continuously updated). *Index Herbariorum: A global directory of public herbaria and associated staff*. New York Botanical Garden's Virtual Herbarium. Available from: <http://sweetgum.nybg.org/science/ih/>. [Accessed 26 March 2021].
- Timberlake, J. (2020). *Pyrostria chapmanii*. *The IUCN Red List of Threatened Species* 2020: e.T146653136A146819456. <https://doi.org/10.2305/iucn.uk.2020-2.rlts.t146653136a146819456.en>. [Accessed 26 Aug. 2021].
- \_\_\_\_\_. (2021). *Pyrostria lobulata*. *The IUCN Red List of Threatened Species* 2021: e.T168474175A169378328. <https://doi.org/10.2305/IUCN.UK.2021-3.RLTS.T168474175A169378328.en>. [Accessed 18 Aug. 2022].
- \_\_\_\_\_, Goyder, D., Crawford, F., Burrows, J., Clarke, G. P., Luke, Q., Matimele, H., Müller, T., Pascal, O., de Sousa, C. & Alves, T. (2011). Coastal dry forests in northern Mozambique. *Pl. Ecol. Evol.* 144: 126 – 137. <https://doi.org/10.5091/plecevo.2011.539>.
- \_\_\_\_\_, Matimele, H. & Massingue, A. (2014). *Environmental assessment of proposed road alignment – Pemba to Mocimboa da Praia, northern Mozambique: plants and vegetation*. Unpubl. report prepared for ERM (Southern Africa).
- 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. (eds) (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>.
- Utteridge, T. M. A. & Davis, A. P. (2009). Two new combinations in *Pyrostria* (Rubiaceae – Vanguerieae) from Thailand. *Kew Bull.* 64: 751 – 752. <https://doi.org/10.1007/s12225-009-9158-7>.
- Verdcourt, B. (1983). Notes on Mascarene Rubiaceae. *Kew Bull.* 37: 521 – 574. <https://doi.org/10.2307/4109725>.
- \_\_\_\_\_. (1987). Notes on African Rubiaceae: Vanguerieae. *Kew Bull.* 42: 123 – 199. <https://doi.org/10.2307/4109900>.
- \_\_\_\_\_ & Bridson, D. M. (1991). Rubiaceae (Part 3). In: R. M. Polhill (ed.), *Flora of Tropical East Africa*. A. A. Balkema, Rotterdam/ Brookfield.
- Wang, Q. F., Mwachala, G., Zhou, Y. D., Zhang, C. F. & Hu, G. W. (eds) (2023). *Flora of Kenya. Rubiaceae (Vol. 23)*. Nature Kenya — The East African Natural History Society & Hubei Science and Technology Press.
- White, F. (1983). *Vegetation of Africa. A Descriptive Memoir to Accompany the UNESCO/AETFAT/UNSO Vegetation Map of Africa*. UNESCO, Paris.
- Wong, K. M., Mahyuni, R., Ng, X. Y. & Neo, L. (2018). Flora of Singapore precursors, 8. Systematy of the new Southeast Asian genera *Canthiumera* and *Dibridsonia* (Rubiaceae: Vanguerieae), with notes on plant architecture and reproductive ecology. *Reinwardtia* 17 (2): 101 – 124. <https://doi.org/10.14203/reinwardtia.v17i2.3648>.

#### Publisher's Note

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