

Two new dioecious species of Vanguerieae (Rubiaceae) from limestone regions in Madagascar

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Abstract

Background and aims – The Paleotropical tribe Vanguerieae (Rubiaceae) is centred in Africa and Madagascar. In Madagascar, many of its ca 150 species are functionally dioecious, belonging to the small genus *Bullockia* and two large genera, *Pyrostria* (~90 species) and *Peponidium* (~50 species). These species estimates include many undescribed species, two of which are formally described here.

Material and methods – A Bayesian inference of ITS sequence data from Vanguerieae was performed to pinpoint the generic placement of the new taxa. Morphological studies were conducted based on standard methods of herbarium taxonomy. The new species are described in detail, illustrated, and compared to morphological similar species. Distribution maps are presented and the preliminary conservation status of the new taxa was evaluated using IUCN criteria.

Key results – Two new species of Malagasy Vanguerieae are described. ITS data place one in the genus *Peponidium* and one in the genus *Pyrostria*. *Peponidium calciphilum* sp. nov. is endemic to the Tsingy of Ankarana in northern Madagascar, while *Pyrostria multilocellata* sp. nov. is restricted to the spiny thickets in dry southern and southwestern Madagascar. Both species occur on limestone and in dry vegetation types, have 4-merous, functionally dioecious flowers, and bilocular fruits. *Peponidium calciphilum* sp. nov. is characterized by ovate, sessile leaves with cordate bases, well-developed subulate stipules, glabrous shoots, ovaries, and calyces, distinct tufts of hairs at the tips of the calyx lobes, and vaulted corolla lobes with well-developed appendages. *Pyrostria multilocellata* sp. nov. is characterized by very small, strongly coriaceous to almost succulent leaves, single-flowered male and female inflorescences, minute flowers, and multilocellate anthers in the male flowers. *Peponidium calciphilum* sp. nov. is considered as Endangered, whereas *Pyrostria multilocellata* sp. nov. is estimated to be Near Threatened.

Keywords

Ankarana, functional dioecy, ITS, multilocellate anthers, new species, *Peponidium*, *Pyrostria*, Toliara

INTRODUCTION

The tribe Vanguerieae (Rubiaceae) is Paleotropical, with ca 650 species in 29 genera (Klackenberg and Razafimandimbison 2024; Razafimandimbison and Rydin 2024a, 2024b) but centred in Africa and Madagascar, with ca 550 species in 23 genera. In Madagascar, the tribe is

represented by six genera (Razafimandimbison et al. 2009) and at least 150 species, many of which remain undescribed (Klackenberg and Razafimandimbison 2024). Members of Vanguerieae are characterized by axillary inflorescences consisting of one to many, usually small flowers, campanulate corollas, valvate aestivation, a cylindrical or knob-like stigma (Igersheim 1993; Tilney

et al. 2014), a single apically attached, pendulous ovule per locule, porate pollen, secondary pollen presentation, a bilocular to plurilocular ovary, drupaceous fruits containing strongly woody pyrenes with apical preformed germination slits, and seeds with large embryos and superior radicles (Robbrecht 1988; Bridson 1998; De Block and Razafimandimbison 2022).

In Madagascar, most Vanguerieae species have functionally dioecious flowers. The large variation in flower and fruit morphology of the Malagasy dioecious Vanguerieae led to the historical description of species in several genera, notably *Pyrostria* Comm. ex A.Juss., *Peponidium* (Baill.) Arènes, *Canthium* Lam., and the endemic genera *Leroya* Cavaco, *Neoleroya* Cavaco, and *Pseudopeponidium* Homolle ex Arènes. Subsequent morphological (e.g. Bridson 1987) and molecular studies (Razafimandimbison et al. 2009) clarified the generic delimitation of the dioecious Vanguerieae group. The Malagasy species are currently accommodated in three genera: *Bullockia* (Bridson) Razafim., Lantz & B.Bremer (two species in Madagascar, as yet undescribed), *Peponidium* (ca 50 species in Madagascar, both named and undescribed), and *Pyrostria* (ca 90 species in Madagascar, both named and undescribed) (Razafimandimbison et al. 2009; Klackenberg and Razafimandimbison 2024). In Madagascar, *Bullockia* is easily recognized because the two Malagasy species are characterized by deciduous leaves (Razafimandimbison et al. 2009). Also present on mainland Africa but there with persistent leaves, *Bullockia* is further characterized by the small, free bracts on the peduncle, the dioecious flowers, the well-defined ring of deflexed hairs inside the corolla tube, the pubescent (but not congested) throat, the anthers without darkly coloured connective or with only the central area of the connective darkly coloured, the stigmatic head which is hollow at its base, and, the bilocular, heart-shaped fruits (Bridson 1987). According to Razafimandimbison et al. (2009), the genera *Peponidium* and *Pyrostria* can be distinguished by the nature of the bracts at the base of the inflorescence. *Peponidium* has small cupular, deciduous bracts that never enclose the young inflorescence, whereas *Pyrostria* has persistent, basally connate, and long-acuminate, paired bracts, completely enclosing the young inflorescence (Razafimandimbison et al. 2009; De Block and Razafimandimbison 2022). Many Malagasy species of *Peponidium* and *Pyrostria* remain unnamed. However, several new dioecious species have recently been described (Lantz et al. 2007; Atalahy et al. 2021; Klackenberg and Razafimandimbison 2024) and a revision of *Pyrostria* is underway (Atalahy 2022).

In this study, we investigated two new Malagasy Vanguerieae species, collected during recent field work. Although their delimitation as distinct species was clear, it was difficult to assign them to genera. We therefore tested their generic placement by adding new ITS sequence data to an existing sequence alignment of Vanguerieae (Razafimandimbison et al. 2009). The goal of this analysis was not to present new hypotheses about the

phylogenetic relationships within the dioecious group or the Vanguerieae tribe, but to place both new species in a genus. The new species are described in detail, illustrated, compared to morphologically similar species, and a distribution map and preliminary IUCN conservation status are given.

MATERIAL AND METHODS

Descriptions are based on dried and alcohol-preserved samples housed in the herbaria BR and P (acronyms according to Thiers 2025). Terminology follows Robbrecht (1988), except for leaf shape, which is described according to the terminology of simple symmetrical plane shapes (Systematics Association Committee for Descriptive Biological Terminology 1962). Methods follow normal practice of herbarium taxonomy (De Vogel 1987). Specimens are cited per region, alphabetically by collector, with localities as given on the specimen labels. An asterisk after the herbarium citation indicates that a duplicate for this herbarium has not yet been distributed. All specimens cited were examined unless indicated differently. Preliminary conservation status was assessed, applying the IUCN Red List Category criteria (IUCN Standards and Petitions Committee 2024) based on metrics (EOO, AOO) produced via GeoCAT (Bachman et al. 2011). The distribution maps were created using QGIS Desktop v.3.4.11 (QGIS Development Team 2025).

For scanning electron microscopy (SEM), material was washed twice in 70% ethanol for 5 minutes, transferred to a 1:1 mixture of dimethoxymethane and 70% ethanol for 5 minutes and, then placed in 100% dimethoxymethane for 20 minutes. The material was subsequently critical point dried with liquid CO₂ using a Balzers CPD 030 critical point dryer (BAL-TEC, Balzers, Liechtenstein). The dried samples were mounted on aluminium stubs with Leit-C carbon adhesive tape and coated with a platinum palladium mixture using a Cressington JFC-2300/208HR sputter coater. SEM images were obtained with a JEOL JSM7100F field emission scanning electron microscope (JEOL Ltd., Tokyo, Japan).

Genomic DNA was extracted from silica-dried leaf samples of the new species using an adapted CTAB protocol (Doyle and Doyle 1987). DNA quantity and purity were assessed with a Fragment Analyzer system (Agilent Technologies, Inc.) and NanoDrop (Thermo Scientific), respectively. The ITS region was amplified using the primers mentioned in De Block et al. (2015) and sent for sequencing to Macrogen, Inc. (Amsterdam, the Netherlands). The ITS sequences of other members of the Vanguerieae tribe were retrieved from Razafimandimbison et al. (2009) and Wikström et al. (2010). Voucher information and GenBank accession numbers can be found in Supplementary material 1.

All sequences were automatically aligned with MAFFT v.7.490 (Katoh and Standley 2013), as a plugin in Geneious Prime v.2025.1.3 (<https://www.geneious.com>). The best-fit nucleotide substitution model was determined using

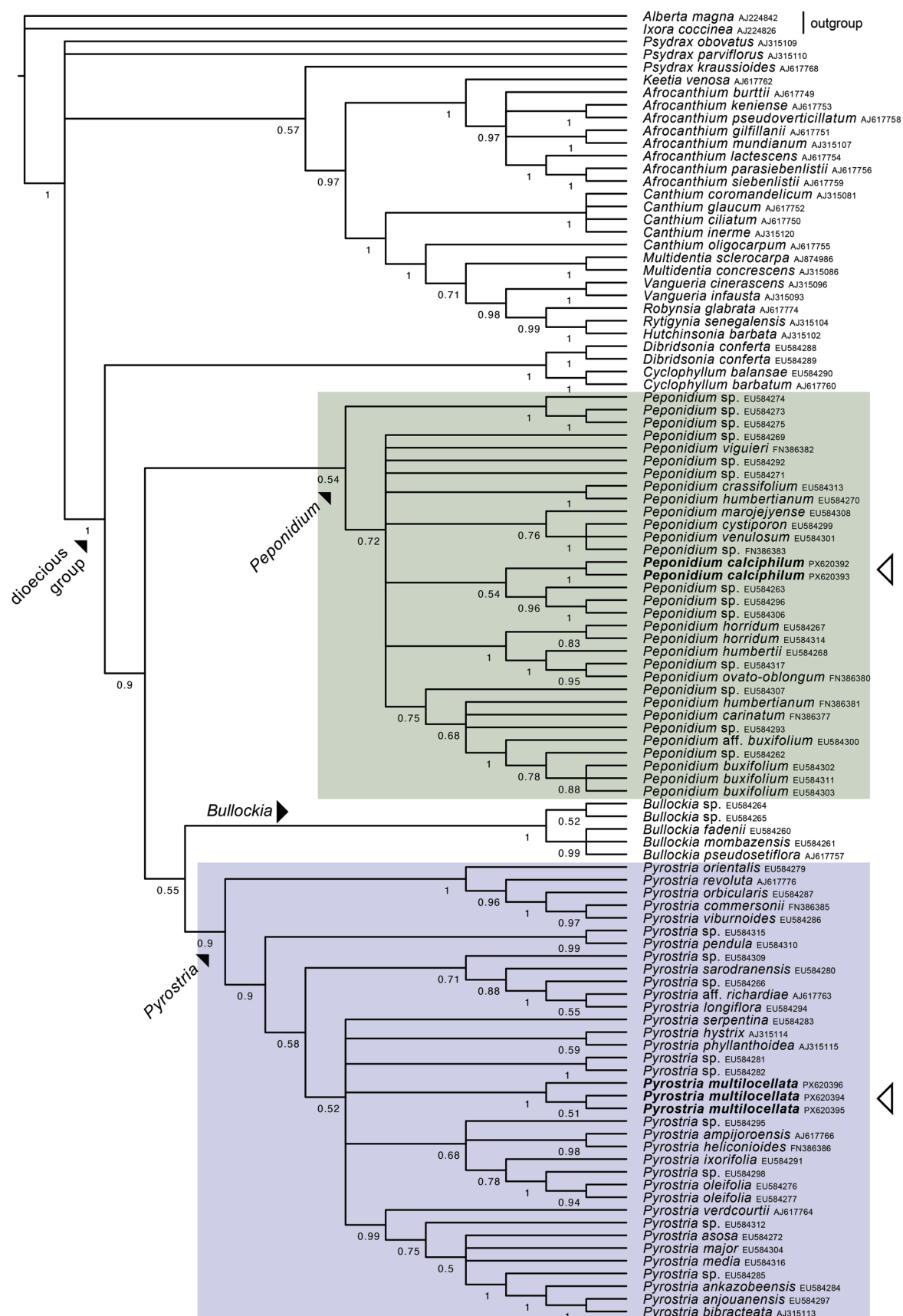


Figure 1. Bayesian inference phylogram of tribe Vanguerieae based on ITS sequence data. Bayesian posterior probabilities are indicated at the nodes. Representatives of *Peponidium* are indicated in green, those of *Pyrostria* in blue. Accessions of the two new species are given in bold and indicated with an arrowhead.

the Akaike information criterion in jModelTest v.2.1.10 (Darriba et al. 2012) and the GTR+I+G model was shown to be the most optimal model. The ITS alignment was analysed with MrBayes v.3.2.7 (Ronquist and Huelsenbeck 2003), running for 1 million generations and sampling every 1000th generation. Chain convergence and ESS parameters were checked with Tracer v.1.7.2 (Rambaut et al. 2018) and the 50% majority rule consensus tree was calculated with a burn-in of 10%. The tree with the posterior probabilities was displayed using Tree v.1.4.4 (Rambaut 2018).

RESULTS AND DISCUSSION

The two new species are functionally dioecious, placing them within the dioecious Vanguerieae lineage. Generic delimitation within the dioecious Malagasy Vanguerieae has long been problematic. Important characters once used to delimit genera included the number of locules, the shape and size of the fruit, and the shape, size and deciduousness of the bracts supporting the inflorescence. However, subsequent analyses have shown that the number of locules is homoplasious within the dioecious Malagasy Vanguerieae, having evolved independently multiple times, and fruit size and shape show a continuous variation (Razafimandimbison et al. 2009). Consequently, these characters are unreliable for distinguishing the genera of the dioecious Malagasy Vanguerieae. According to Razafimandimbison et al. (2009), *Peponidium* and *Pyrostria* can be distinguished by the nature of the bracts at the base of the inflorescence: small, cupular, deciduous bracts that never enclose the young inflorescence (*Peponidium*) vs persistent, basally connate, long-acuminate bracts, completely enclosing the young inflorescence (*Pyrostria*). In addition, ongoing morphological and phylogenomic studies of *Peponidium* reveal that the distinct tuft of hairs at the tips of the calyx lobes are a morphological synapomorphy that unites all *Peponidium* species (Sylvain Razafimandimbison pers. obs.; see also Lantz et al. 2007; Klackenberg and Razafimandimbison 2024). While the presence of persistent, connate bracts is a good field character for recognizing *Pyrostria* species, this salient trait is not detected in the two new species. Inflorescence bracts can be observed in both taxa when flowers are open, suggesting the bracts are not deciduous, nor can their shape and size be unambiguously classified as small and cupular or long-acuminate. The lack of plant material with inflorescences in early developmental stages is a complicating factor. Moreover, the adaptation to an extreme dry environment, i.e. the reduction of the inflorescences in *Pyrostria multilocellata* sp. nov., may further obscure the observation of key characters.

In the ITS analysis (Fig. 1), the two new species clearly fall within the dioecious group, which is a monophyletic clade (PP 1). Both species are shown to be monophyletic.

One is nested within the genus *Peponidium*, while the other is part of *Pyrostria*.

TAXONOMIC TREATMENT

Peponidium calciphilum De Block, sp. nov.

urn:lsid:ipni.org:names:77378621-1

Figs 2D, E, 3

Type. MADAGASCAR – **Antsiranana province, Diana region, Ambilobe District** • Ankarana, road from campement des Anglais towards campement des Américains (not beyond first savanna); 82 m; 13 Jan. 2002; fl. (functionally male); *De Block, Rakotonasolo & Randriamboavonjy 1182*; holotype: BR [BR0000020242732]; isotypes: BR [BR0000020242749, BR0000009757653, BR0000009757554], G*, K*, MO*, P*, S*, TAN.

Diagnosis. *Peponidium calciphilum* resembles *P. sessile* Klack. & Razafim. by the sessile, ovate leaves with cordate bases, the glabrous calyx with distinct tufts of hairs at the tips of the lobes, the vaulted corolla lobes with well-developed appendages at the tips, and the preference for growing on limestone, but differs from it by the glabrous young shoots (vs covered with \pm orange-brown erect hairs), the larger size of the leaves ($6\text{--}9.5 \times 2.5\text{--}5$ cm vs $3\text{--}5.5 \times 1.5\text{--}3.5$ cm) and stipules ($6\text{--}9$ vs $1.5\text{--}2.5$ mm long), the higher number of flowers in the female inflorescences ($3\text{--}8$ vs $1\text{--}2$), the larger flowers (functionally male flowers with corolla tube ca 2.5 mm long and lobes $3.2\text{--}3.5$ mm long vs tube ca 0.7 mm long and lobes ca 1.6 mm long), and the shorter pedicels in fruiting stage ($2\text{--}6$ mm vs up to 16 mm long).

Description. Shrub 1–2 m tall; young internodes laterally flattened, glabrous, brown, smooth, first becoming orange to reddish brown and glossy, later pale cream or grey, flaking; branches terete, glabrous, with greyish brown bark, somewhat corky. Leaves opposite, sessile; blades ovate, $6.0\text{--}9.5 \times 2.5\text{--}5.0$ cm, subcoriaceous to thinly coriaceous, glabrous and glossy on both surfaces, drying brown to dark brown and not discoloured; base cordate; apex subacute to shortly acuminate, with acumen ≤ 1 cm long, its tip obtuse to rounded; margin flat to somewhat revolute; midrib raised on both surfaces when dry, $6\text{--}7$ secondary nerves on each side of midrib, hardly raised on either surface; small hairy pit domatia sometimes present in axils of basal secondary nerves. Stipules caducous, $6\text{--}9$ mm long, subulate, consisting of a triangular basal sheath $2.5\text{--}3.5$ mm long and a robust awn $3.0\text{--}5.5$ mm long, glabrous externally except for some patches of short, appressed, orange-brown hairs at the base of the sheath on both sides and sometimes with a few hairs at the tip. Species functionally dioecious; female inflorescences (only seen in fruiting stage) delicate, sessile, with $1\text{--}3$ flowers, subtended by a cup-like structure consisting of fused bracts; male inflorescences pluriflorous, with short, robust, $1\text{--}2$ mm long peduncle, one part of the

inflorescence consisting of flower remnants such as remains of pedicels and bracteoles (Fig. 3C), the other part consisting of 3–8 flowers in different developmental stages (anthetic or immature flowers, flowers with corolla fallen, and undeveloped buds, the latter only visible in the compact inflorescence structure as orange-brown hairs), the whole inflorescence as well as the group of open/developing flowers subtended by 1 or 2 cup-like structures consisting of fused bracts; bracts fused into cup-like structures, up to $1\text{--}2 \times 3\text{--}4$ mm, glabrous outside, glabrous and with a continuous ring of colleters at the base inside, margins (sparsely) ciliate, hairs \pm short, orange-brown, unicellular, stiff; higher order bracts and bracteoles unknown, included in the compact basal part of the inflorescence (bracteoles not present on the visible part of the pedicels or on the ovary); pedicels 2–6

mm long in both flowering and fruiting stage, glabrous. Flowers 4-merous, functionally dioecious; corolla aestivation valvate. Functionally male flowers with calyx tube 0.4–0.6 mm long, glabrous outside, glabrous and without colleters inside; calyx lobes interspaced with sinuses at least as wide as the width of the lobes, triangular, 0.3–0.5 mm long, glabrous inside, with a tuft of \pm short, orange-brown, unicellular, stiff hairs at the tip outside, tips acute; corolla apiculate in bud; corolla tube broadly cylindrical to campanulate, ca 2.5 mm long, ca 2 mm wide at the base and 2.3–2.5 mm wide at the throat, glabrous outside and inside but with a dense ring of long, soft, unicellular, white hairs in the throat, conspicuous from the outside at anthesis; corolla lobes 3.2–3.5 mm long, ca 1.3 mm wide at the base, vaulted with well-developed appendages, margins thickened and papillate, tip acute



Figure 2. Field photographs of *Pyrostria multilocellata* De Block (A–C) and *Peponidium calciphilum* De Block (D, E). **A.** Habit. **B–C.** Flowering branch (functionally female flowers). **D.** Flowering branch (functionally male flowers). **E.** Fruiting node. Photos: Inge Groeninckx (A–C), Petra De Block (D–E).

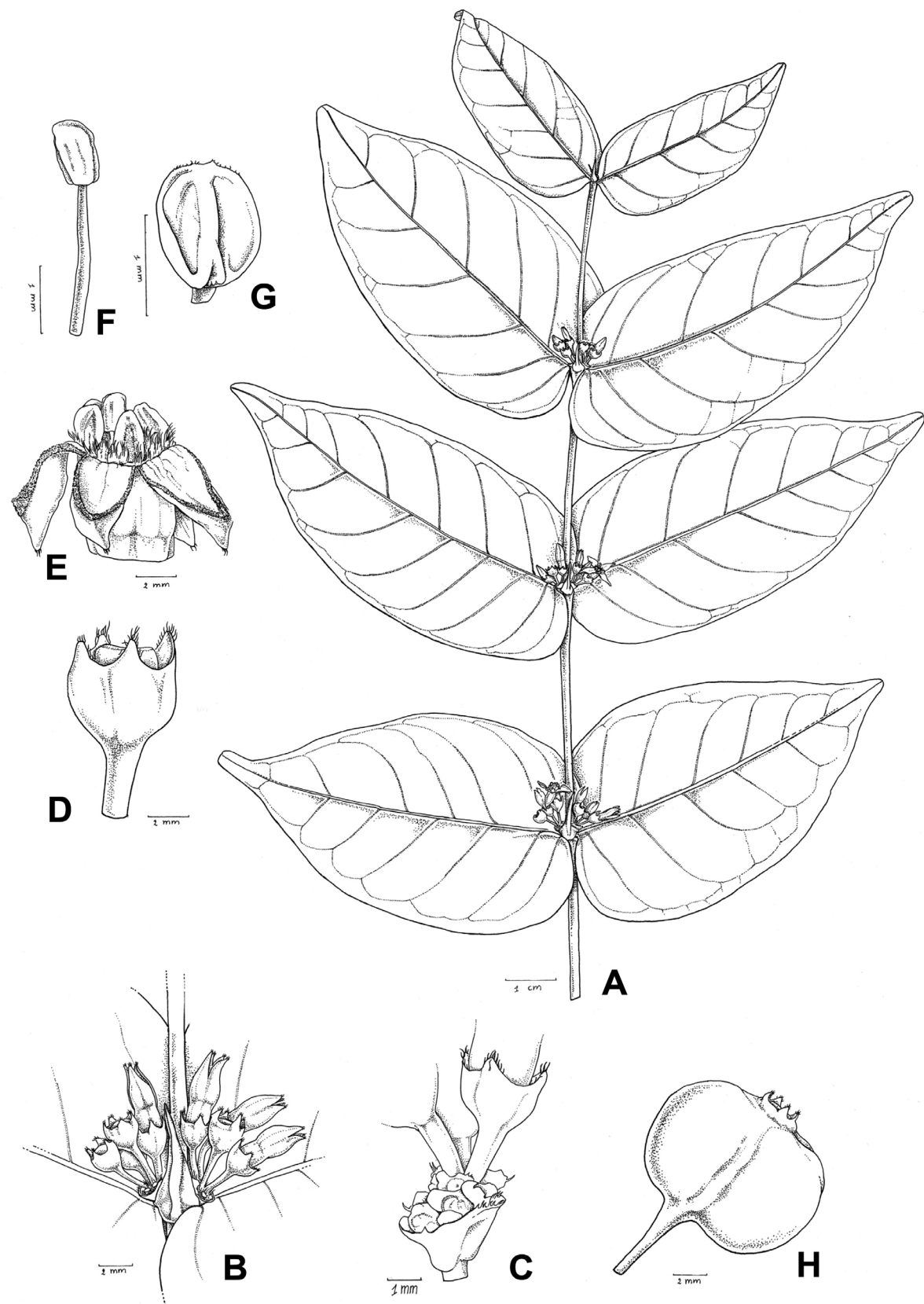


Figure 3. *Peponidium calciphilum* De Block (functionally male specimen). **A.** Habit. **B.** Flowering node, showing stipule and axillary inflorescences. **C.** Inflorescence, side view. **D.** Pedicel, ovary, and calyx. **E.** Corolla, anthers, style, and stigma. **F.** Style and stigma. **G.** Stamen, adaxial view. **H.** Fruit. A–G from *De Block et al. 1182* (BR); H from *De Block et al. 997* (BR). Drawn by Hilde Orye.

to shortly acuminate, conspicuously thickened, distinctly appendiculate, topped by a single hair or a small tuft of hairs (\pm short, orange-brown, unicellular, stiff); stamens inserted at the throat, anthers erect and completely exerted just above the throat at anthesis, $1.0\text{--}1.3 \times 0.5\text{--}0.7$ mm, basifixed, tip rounded, papillate, base not sagittate but sometimes somewhat unequal, filaments $0.2\text{--}0.3$ mm long, connective drying dark brown abaxially; style ca 2.5 mm long, glabrous, stigma knob-like, ca 0.5 mm long, exerted from the corolla tube at anthesis but topped by the exerted anthers; ovary ca 0.5 mm long, bilocular, glabrous, either with a single underdeveloped pendulous ovule per locule or locules empty or not formed; disc ca 1 mm high at anthesis. Functionally female flowers unknown. Fruits with persistent calyx, bilobed, wider than high, ca $11\text{--}12 \times 7\text{--}8$ mm, glabrous, dark or reddish pink when ripe; pyrenes ca 6×5 mm, thick and stony, dark brown, with apical longitudinal ridge at abaxial side and running down the abaxial side to the middle; seeds \pm bean-shaped, $4.5 \times 3.5 \times 3.0$ mm, dark brown.

Distribution. Restricted to the Antsiranana Province, the Diana Region, the Ambilobe District; only known from the Tsingy of the Ankarana Special Reserve (Fig. 4).

Habitat. Dry semi-deciduous or deciduous forest, on limestone covered by red sand; elevation 50–200 m.

Phenology. Flowers in December–January and fruits in February–May.

Etymology. The specific epithet means “limestone loving” and is chosen because the species only grows in the Tsingy of Ankarana on limestone.

Preliminary IUCN conservation assessment. *Peponidium calciphilum* is only known from the

Ankarana Special Reserve. Detailed coordinates are not available for all specimens, so we choose the surface of the reserve as the maximum AOO, notably ca 240 km². With five known specimens, the AOO is at most 20 km². Both AOO and EOO comply with the Endangered category under, respectively, criterion B1 and B2. The species is collected from less than five locations in the Ankarana Special Reserve, which again complies with the Endangered category under subcriterion ‘a’ of criterion B2. The Ankarana Special Reserve is protected legally, which would suggest the absence of any threat. In reality, however, infringements into the Ankarana Special Reserve are common: bushfires, clearing for slash-and-burn agriculture, illegal logging for hardwood, firewood, and the production of charcoal, hunting, collection of plant species for medicinal or subsistence use, and illegal mining for sapphires all occur within its boundaries (De Block 2022). Because of these facts, a reduction in the extent and quality of the habitat of *P. calciphilum* is inferred. This threat, in combination with the AOO, EOO, and the low number of locations, qualifies the species for Endangered status: EN B1ab(iii)+2ab(iii).

Additional material examined. MADAGASCAR – Antsiranana Province, Diana region, Ambilobe District • Réserve Spéciale d’Ankarana, piste vers le lac Vert, à partir de la plaque de Tsingy; 180 m; 19 Feb. 1994; fr.; Andrianarisata, Lewis, McDonagh, Andriatsiferana, Randriambololona & Andrianantoanina 33; MO n.v., P [P00274292] • Matsaborimanga, Réserve d’Ankarana, piste Grim à proximité du camp des Anglais; 9 Dec. 1997; fl. (functionally male); Bardot-Vaucoulon & Toly 1036; K*, MO*, P (unmounted) • Ankarana, close

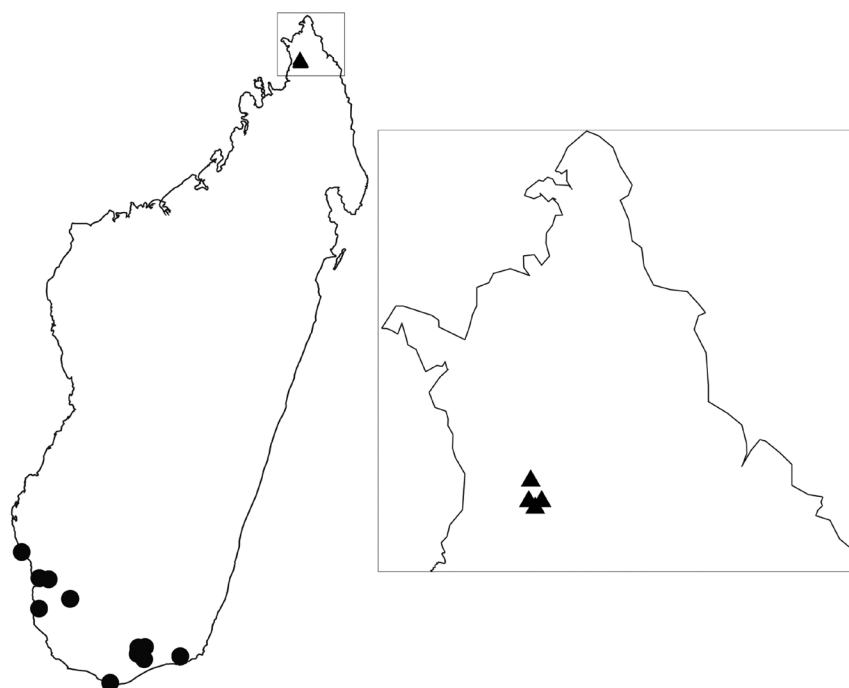


Figure 4. Distribution map of *Peponidium calciphilum* De Block (▲) and *Pyrostria multilocellata* De Block (●).

to campement des Anglais, 82 m; 25 May 1999; fr.; De Block, Rapanarivo & Randriamboavonjy 997; BR [BR0000009758025, BR0000009757929], G*, MO*, P*, TAN • Ankarana, road from campement des Anglais towards campement des Américains (not beyond first savanna); 82 m; 13 Jan. 2002; fl. (functionally male); De Block, Rakotonasolo & Randriamboavonjy 1182; BR [BR0000020242732, BR0000020242749, BR0000009757653, BR0000009757554], G*, K*, MO*, P*, S*, TAN • Réserve Spéciale d'Ankarana, sur le Tsingy, piste vers le village Matsaborimanga; 180 m; 19 Feb. 1994; fr.; Rahajasoa, Lewis, McDonagh, Andrianantoanina, Ravelonarivo & Rasoavimbahoaka 176; MO n.v., P [P00274293].

Notes. In living plants with functionally male inflorescences, the leaves are dark green above. The bracts, bracteoles, pedicels, ovaries and calyces are pale green. The corolla tubes and lobes are greenish white outside and the lobes white inside. The anthers and filaments, style and stigma are white. Ripe fruits are dark to reddish pink in colour.

Peponidium calciphilum and *P. sessile* (Klackenberg and Razafimandimbison 2024) share most of their salient characters, notably the sessile, ovate leaves with cordate bases, the glabrous calyx, the distinct tufts of hairs at the tips of the calyx lobes, and the vaulted corolla lobes with well-developed appendages. Furthermore, both occur in dry semi-caducous or caducous forest on limestone. They differ in quantitative or minor characters such as leaf size ($6\text{--}9.5 \times 2.5\text{--}5$ cm in *P. calciphilum* vs $3\text{--}5.5 \times 1.5\text{--}3.5$ cm in *P. sessile*), stipule size ($6\text{--}9$ vs $1.5\text{--}2.5$ mm long), flower size (corolla tube ca 2.5 mm and lobes $3.2\text{--}3.5$ mm long vs tube ca 0.7 mm and lobes ca 1.6 mm long in functionally male flowers), the higher number of flowers in the male inflorescences ($3\text{--}8$ vs $1\text{--}2$), the shorter pedicels in fruiting stage ($2\text{--}6$ vs up to 16 mm long), the higher number of fertile nodes on functionally male flowering branches (up to 5 vs $1\text{--}2$) and by the absence/presence of pubescence on the young shoots (absent in *P. calciphilum*, present in *P. sessile*). These quantitative differences raise the question whether to consider the two taxa as subspecies or as species. However, *P. calciphilum* is only known from the Tsingy d'Ankarana in the north, while *P. sessile* is restricted to the Tsingy de Bemaraha in the west. The distance between these two locations is at least ca 750 km as the crow flies. We therefore hypothesize that the two taxa are reproductively isolated and treat them here as separate species.

Three hair types occur in the reproductive structures of this species. The hairs on the tip of the calyx lobes, the tip of the corolla lobes, and the cilia on the bracts are orange-brown, unicellular, relatively short, and stiff. The hairs forming the dense ring in the throat are also unicellular, but much longer than the first type, translucent, and soft. This is in contrast to *P. sessile* for which the hairs at the throat are described as moniliform (Klackenberg and Razafimandimbison 2024). However, within the compact base of the male inflorescences, next to hairs of the first

type (cilia on bracts and hairs at the tip of corolla lobes of undeveloped flowers), a third hair type was observed, consisting of long, translucent, soft, moniliform hairs.

***Pyrostria multilocellata* De Block, sp. nov.**

urn:lsid:ipni.org:names:77378622-1

Figs 2A–C, 5, 6

Type. MADAGASCAR – Toliara Province, Atsimo-Andrefana Region, Toliara II District • La Table, 15 km from Toliara on Route Nationale 7; 4 Jan. 1999; fl. (functionally male); De Block, Leyman, Dessein, Rakotonasolo & Randriamboavonjy 544; holotype: BR [BR0000009125025]; isotypes: MO*, P*, S*, TAN.

Diagnosis. The species resembles *Pyrostria serpentina* Lantz, Klack. & Razafim. by the habit (densely branched shrub), the very small coriaceous to somewhat succulent leaves, the extremely pauciflorous inflorescences (both male and female), and the small flowers and fruits, but differs from it by the following characters: branches erect (vs tortuously twisting), ovary (if developed) densely pubescent (vs glabrous), calyx lobes triangular with acute tips and bases not overlapping (vs calyx lobes low and rounded, overlapping at the base), or, calyx with an uneven, \pm truncate, ciliate margin (vs margin glabrous), and the multilocellate anthers in the functionally male flowers (vs anthers non-multilocellate).

Description. Subshrub or shrub, 0.5–2(–3) m tall, creeping to erect, hard-wooded, densely branched, each branch with many brachyblasts up to 2–3 cm long; young internodes laterally flattened, pale straw-coloured and densely covered with short erect to spreading hairs, rapidly flaking and then glabrous; branches terete, older branches with greyish bark, younger branches with smooth, dark reddish brown or blackish bark. Leaves opposite, usually grouped terminally on brachyblasts, the lower parts of the brachyblasts with leaves fallen and only stipules remaining (stipules densely positioned without any stem surface visible), more rarely on longer shoots with extended internodes; blades elliptic to obovate, $3\text{--}8 \times 1.5\text{--}3.5\text{--}(4.0)$ mm, thickly coriaceous to succulent, glabrous on both surfaces or sparsely to densely covered with short erect to appressed hairs on the upper surface and with somewhat longer appressed hairs on the lower surface, drying brown and dull above, somewhat paler below; base cuneate to acute; apex mucronulate, blunt with a short point or rounded; margin flat to somewhat revolute, sometimes sparsely ciliate; only midrib visible, faintly impressed on upper surface, faintly raised on lower surface; rarely (1–)2–4 hairy pit domatia present on lower leaf surface, either opposite or alternately positioned. Petioles articulate, 0.5–1.0 mm long, canaliculate above, glabrous or sparsely to densely covered with erect or appressed hairs. Stipules triangular, ca 1 mm long, keeled, tip acute to obtuse, glabrous or sparsely to densely covered with erect or appressed hairs outside. Species functionally dioecious; female and male inflorescences uniflorous, sessile; pedicels 0–1 mm long in both flowering and fruiting stage, glabrous or pubescent; bracteoles fused

into a cup-like structure 0.5–0.6 mm long, glabrous outside, glabrous but with a dense ring of large colleters at the base inside, margins ciliate with \pm long hairs. **Flowers** 4-merous, functionally dioecious; corolla aestivation valvate and somewhat induplicate; calyx tube 0.3–0.5 mm long, glabrous outside, glabrous and without colleters inside, unevenly truncate with ciliate margin or calyx lobes triangular, 0.2–0.4 mm long, glabrous outside, glabrous or with appressed hairs inside, margins ciliate, bases not overlapping, tips acute; corolla tube glabrous outside, with a ring of long deflexed white hairs at the level of insertion of the anthers but otherwise glabrous inside, hairs not visible from outside; corolla lobes rounded triangular, glabrous inside and outside but margins thickened and papillate, tip acute to shortly acuminate and hood-like, with one or a few short hairs at the tip; stamens inserted at the throat, anthers erect, partly exerted from the corolla tube at anthesis, medifixed, filaments 0.2–0.3 mm long, base sagittate, tip rounded, papillate; style glabrous, stigma completely exerted from the corolla tube at anthesis, $0.3\text{--}0.5 \times 0.3\text{--}0.65$ mm long; ovary densely covered with \pm long whitish appressed hairs, bilocular. **Functionally male flowers** with corolla tube cylindrical, 1.2–1.5 mm long, ca 0.8 mm wide at base and ca 1 mm wide at throat; corolla lobes 1.2–1.5 mm long, ca 1 mm wide at base; anthers $0.6\text{--}0.8 \times 0.3\text{--}0.5$ mm, exerted from the corolla tube for $4/5^{\text{th}}$ of their length at anthesis, multilocellate; style ca 1.5 mm long, stigma knob-like, reaching the same height as the anthers or somewhat topped by them at anthesis; ovary $0.5\text{--}0.6 \times \text{ca } 0.3$ mm, either with a single underdeveloped pendulous ovule per locule or locules empty or not formed. **Functionally female flowers** with corolla tube campanulate, ca 1 mm long, ca 0.9 mm wide at base and ca 1.4 mm wide at throat; corolla lobes 0.8–1 mm long, ca 0.8 mm wide at base; anthers $0.5\text{--}0.8 \times \text{ca } 0.3$ mm, upper half exerted from the corolla tube at anthesis, not producing viable pollen; style 1.3–1.5 mm long, stigma positioned above the level of the anthers at anthesis, knob-like when young, opening into two broad lobes, much wider than long, curved and folded, with papillae present on the adaxial surface and in a broad band on the margins of the lobes (Fig. 6D); ovary $0.8\text{--}1.2 \times \text{ca } 1$ mm, with a single pendulous ovule per locule. **Fruits** with persistent calyx, bilobed, wider than high, somewhat laterally flattened, $6\text{--}7 \times 4.0\text{--}4.5$ mm, moderately covered with short appressed hairs all over, normally bilocular but ca half the fruits on all specimens seen unilocular because of abortion of one locule; pyrenes $\text{ca } 4.0 \times 3.5$ mm, thick and stony, brown, with unexplicit apical longitudinal ridge in upper half at adaxial surface and running down ca $1/4^{\text{th}}$ on abaxial surface, functioning as preformed germination slit; seeds \pm bean-shaped, $3.5 \times 2.5 \times 2.5$ mm, brown, with apical longitudinal ridge in upper half at adaxial surface and running down ca $1/4^{\text{th}}$ on abaxial surface; abaxial side convex, adaxial side convex in upper half, flat in lower half.

Distribution. Occurring in the Toliara Province, in the Atsimo-Andrefana, Androy, and Anosy Regions;

seemingly widespread in the southern part of Madagascar from Taolagnaro in the east, to Cap Sainte Marie in the south, and Manombo (north of Toliara) in the west. Occurring in the Tsimanampetsotse National Park and Cap Sainte Marie Special Reserve (Fig. 4).

Habitat. Dry deciduous forest, spiny forest, dry scrub sometimes as low as 0.5 m, on limestone covered by white sand; elevation 20–200 m.

Phenology. Flowers in November–April and fruits in January–April.

Etymology. The species is named for the multilocellate anthers in the male flowers, a feature hitherto not known in the genus *Pyrostria* nor in the tribe Vanguerieae.

Preliminary IUCN conservation assessment. This assessment is based on 14 herbarium specimens collected between 1955 and 2010. The EOO of *Pyrostria multilocellata* is estimated to be 33240 km², exceeding the upper limit of the Vulnerable category under criterion B1. The AOO is 44 km², which complies with the Endangered category under criterion B2. The species occurs in 11 locations, which exceeds the Vulnerable category under subcriterion ‘a’ of criterion B2. *Pyrostria multilocellata* occurs in two protected areas: Tsimanampetsotse National Park and Cap Sainte Marie Special Reserve but both are threatened to a certain extent by human activities, notably an overexploitation of natural resources by local populations (Waeber et al. 2020; Protected Areas of Madagascar 2025). According to the IUCN Red List of Ecosystems, a global reference framework to assess the vulnerability of ecosystems, the southern and southwestern Malagasy dry woody vegetation on limestone is considered endangered because of a very strong observed (between 1975 and 2025) and future estimated decline in geographic distribution (Carré et al. 2022). The dry forests in western and southern Madagascar have suffered high deforestation rates (Harper et al. 2007) as a result of subsistence farming, charcoal production, pastoral land use, and over-exploitation of essential resources. Furthermore, potential mining, oil and agribusiness concessions threaten the dry forest region (Waeber et al. 2015). Because of these facts, a reduction in the extent and quality of the habitat of *P. multilocellata* is inferred. This threat, in combination with the AOO and the number of locations, qualifies the species for Near Threatened status: NT.

Additional material examined. MADAGASCAR – Toliara province, Atsimo-Andrefana region • près d’Ambatry, S de Betioky; 14 Jan. 1962; fl. (functionally male); Capuron 20692-SF; BR [BR0000009311268], P • La Table, 15 km from Toliara on Route Nationale 7; 4 Jan. 1999; fl. (functionally male); De Block, Leyman, Dessein, Rakotonasolo & Randriamboavonjy 544; BR [BR0000009125025], MO*, P*, S*, TAN • La Table, 15 km from Toliara on Route Nationale 7; 4 Jan. 1999; fl. (functionally female), fr.; De Block, Leyman, Dessein, Rakotonasolo & Randriamboavonjy 545; BR [BR0000009125018], MO*, TAN • Road from La Table to Sept Lacs; 2 Feb. 2007; fl. (functionally male); De Block,

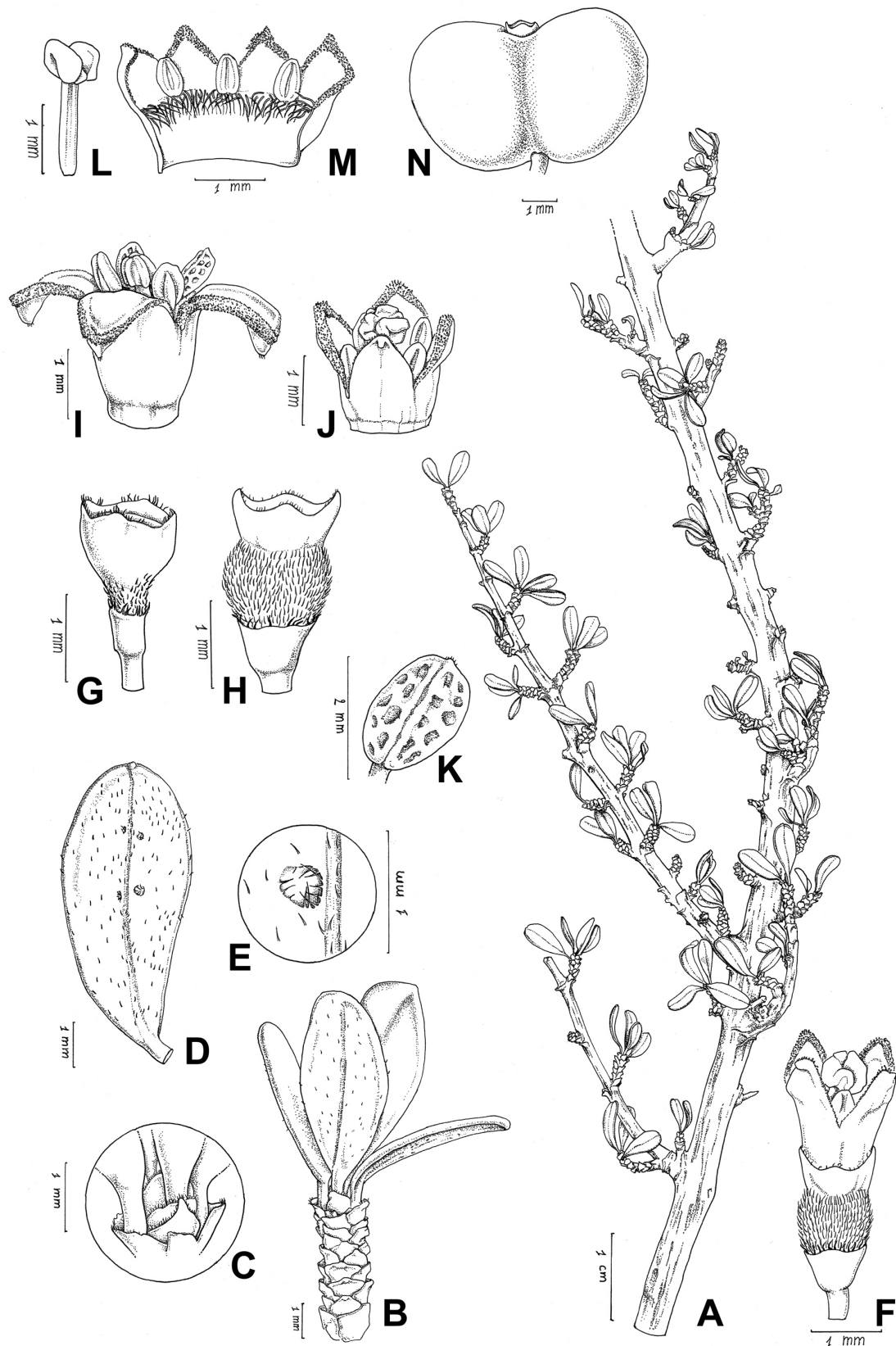


Figure 5. *Pyrostria multilocellata* De Block. A. Habit. B. Brachyblast, showing stipules and terminal leaf pairs. C. Brachyblast, detail. D. Leaf, showing lower surface with domatia. E. Domatium. F, H, J, L, M. Functionally female flower. G, I, K. Functionally male flower. G, H. Pedicel, bracteolar cone, ovary, and calyx. I, J. Corolla, anthers, style, and stigma. K. Stamen, adaxial view, showing multilocellate anther. L. Style and stigma. M. Longitudinally opened corolla. N. Fruit. A–E, G, I, K from De Block et al. 2307 (BR), F, H, J, L, M from Groeninckx et al. 323 (BR); N from Groeninckx et al. 325 (BR). Drawn by Hilde Orye.

Groeninckx & Rakotonasolo 2307; BR [BR0000006745622], MO*, P*, TAN • Lac Tsimanampetsotsa; 5 Feb. 2007; fl. (functionally female); *Groeninckx, De Block & Rakotonasolo* 217; BR [BR0000005272235], MO*, P*, TAN • Route Nationale 10, km 111, entre Betioky & Ejeda; 190 m; 4 Feb. 1990; fl. (functionally male), fr. (separate branches); *Labat, Du Puy & Phillipson* 2066; BR [BR0000017834490], MO n.v., P online • 9 km N of Manombo along coast near Fiserenamasay; 20 m; 23 Feb. 1993; fl. (functionally female); *Phillipson & Raharilala* 4124; BR [BR0000009139244], MO n.v. – **Toliara province, Androy region** • Sur les pentes du massif de l'Angavo, E d'Antanimora; Nov. 1955; fl. (functionally male); *Capuron* 11731-SF; BR [BR0000009222373], P • 43 km from Ambovombe on road to Betroka; 2 Feb. 2007; fl. (functionally male); *De Block, Groeninckx & Rakotonasolo* 2330; BR [BR0000006745325], MO*, P*, TAN • Sakamasy forest, route de Tsihombe à Ambovombe, ca 8 km de

Tsihombe; 4 Apr. 2010; fl. (functionally male); *De Block, Groeninckx & Rakotonasolo* 2439; BR [BR0000005444724], K*, MO*, TAN • Fort-Dauphin, Ambovombe district, commune Ambohimalaza, N of fokotany Mahatomotsy; 29 Mar. 2010; fr.; *Groeninckx, De Block & Rakotonasolo* 301; BR [BR0000005512096], MO*, P*, TAN • Fort-Dauphin, close to Cap Sainte Marie National Park; 3 Apr. 2010; fl. (functionally female); *Groeninckx, De Block & Rakotonasolo* 323; BR [BR0000005561933, BR00000020242756], MO*, TAN • Fort-Dauphin, Cap Sainte Marie National Park; 3 Apr. 2010; fl. (functionally female), fr.; *Groeninckx, De Block & Rakotonasolo* 325; BR [BR0000005561735], TAN. – **Toliara province, Anosy region** • On Route Nationale 13 from Fort-Dauphin to Ambovombe, pk 40 from Fort Dauphin; 26 Mar. 2010; fl. (functionally male); *De Block, Groeninckx & Rakotonasolo* 2381; BR [BR0000005518845], TAN.

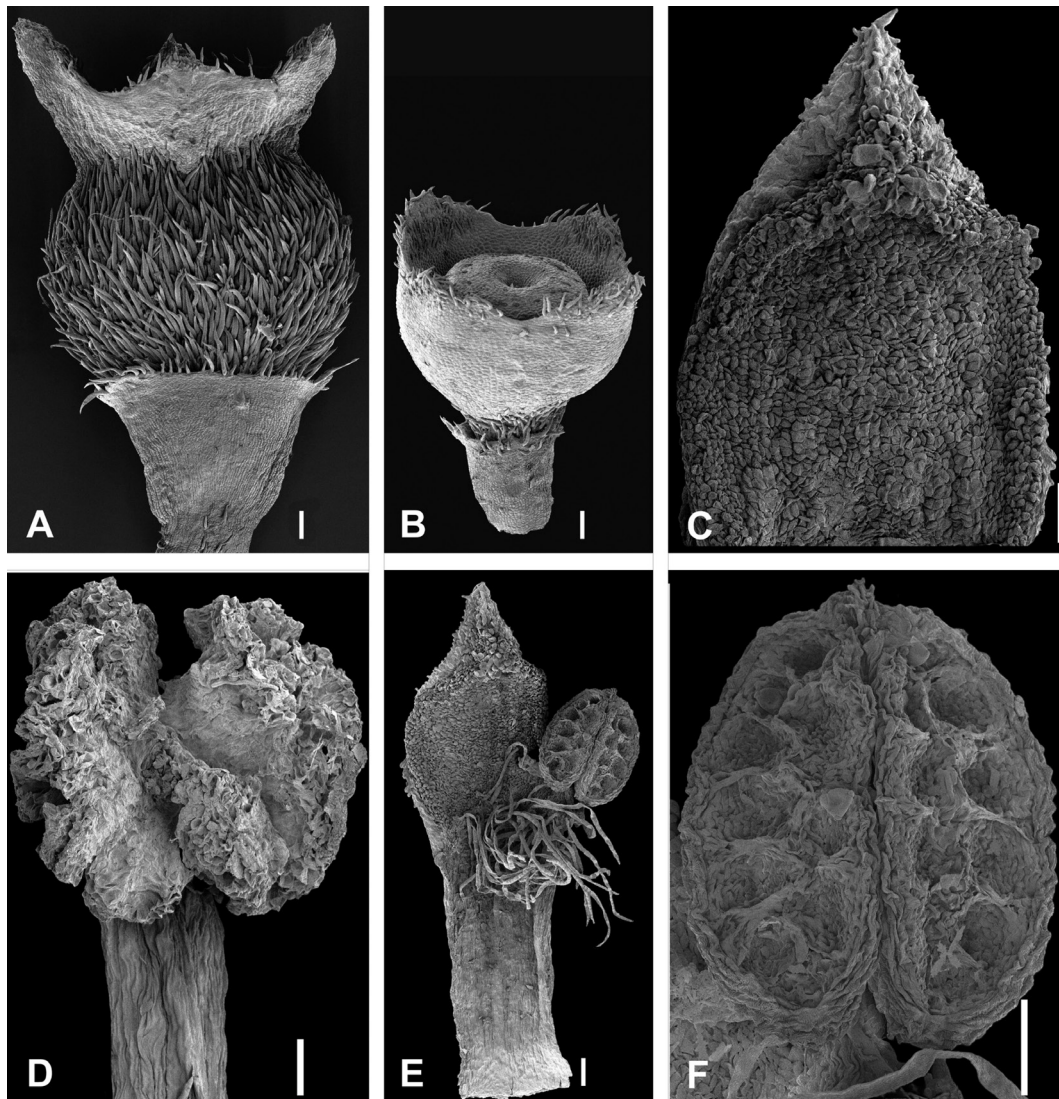


Figure 6. SEM micrographs of flowers of *Pyrostria multilocellata*. A, C, D. Functionally female flower. B, E, F. Functionally male flower. A, B. Fused bracteoles, ovary, and calyx. C. Inner surface of corolla lobe. D. Stigma. E. Corolla tube and lobe, stamen and ring of deflexed hairs at the level of insertion of the stamens. F. Detail of anther. A, D from *Groeninckx et al.* 323 (BR); B, C, E, F from *De Block et al.* 2307 (BR). Scale bars: 100 μ m

Notes. In living plants, the leaves are dark green or green above and somewhat paler below. Fruits were only observed when green, even though seeds seem mature when dissecting these green fruits. Ovary, calyx tube and calyx lobes are green, the ovary with whitish appressed pubescence. The corolla is pale green, white or yellowish at anthesis. Anthers and filaments are described as white, with anthers turning brownish with age. Style and stigma are described as white or pale green.

Functionally male and female flowers differ in the shape and size of the corolla tube (cylindrical, 1.2–1.5 mm long in functionally male flowers vs campanulate, ca 1 mm long in functionally female flowers), the length of the corolla lobes (1.2–1.5 vs 0.8–1.0 mm long), and the position of the stigma (at the level of the anthers or somewhat topped by them vs stigma positioned above the anthers). Anthers of functionally male flowers are somewhat more exerted from the corolla tube than those of functionally female flowers. Furthermore, the anthers are multilocellate vs not producing viable pollen. Also, the ovary is larger (0.8–1.2 × ca 1.0 mm vs 0.5–0.6 × ca 0.3 mm) with normal-sized ovules developing in functionally female flowers (vs ovules underdeveloped or locules empty or not formed). There are no differences between male and female inflorescences; they are both uniflorous.

Multilocellate anthers have hitherto not been reported from *Pyrostria* nor from the tribe Vanguerieae. They are known to occur sporadically in scattered genera of Rubiaceae, such as *Aidia* Lour. (Gardenieae), *Calycosiphonia* Pierre ex Robbr. (Coffeeae), *Isertia* Schreb. (Judkevich et al. 2021) and *Kerianthera* J.H.Kirkbr. (Oliveira et al. 2011) (Isertiaeae), *Leptactina* Hook.f. and *Pavetta* L. (Pavetteae), *Sherbournia* G.Don (Sherbournieae) (Robbrecht 1988). The function of the septa occurring in multilocellate anthers is not yet known. Historically, a nutritive function was suggested, with the septa conveying nutrients to large pollen masses (Lersten 1971). However, Lersten (1971) suggested an alternative function, notably the reduction of the number of sporogeneous cells. This would take place “In species with very effective pollination mechanisms, and particularly where the entire plant has undergone a general reduction in size ... under selective pressure for the anther to contribute to the general reduction.” This last hypothesis seems to be the correct one for *P. multilocellata*, which has effectively undergone a considerable reduction in size of all plant organs as an adaptation to drought. The need for additional nutrition secreting tissues to reach all pollen inside the minute anthers of the species seems untenable.

CONFLICT OF INTEREST

BV is the editor in chief of Plant Ecology and Evolution but was not involved in the editorial process of the manuscript and had no influence on the final decision.

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SUPPLEMENTARY MATERIAL

Supplementary material 1

List of GenBank accession numbers for sequences used in the analysis and information on voucher specimens.

<https://doi.org/10.5091/plecevo.177167.suppl1>