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Roquea, a new genus of Lychnophorinae (Vernonieae, Asteraceae) from Brazil and its phylogenetic placement

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Abstract

Lychnophorinae (Vernonieae, Asteraceae) consists of 21 genera and approximately 150 species, primarily distributed in the Brazilian Central Plateau, with several novelties recently described. With new botanical expeditions conducted in Serra da Formosa, state of Minas Gerais, a set of collections that belong to Lychnophorinae but were not easily assigned to a genus was discovered. After morphological and anatomical analyses and phylogenetic studies, we describe and illustrate *Roquea*, a new genus of Asteraceae from Brazil, to accommodate the new species *Roquea multiserialis*. Affinities of the new genus with other genera of Lychnophorinae are discussed along with a preliminary conservation status assessment, and notes on its distribution, ecology and affinities. This new finding contributes to the understanding of the taxonomy and evolution of Lychnophorinae and the campos rupestres and supports the urgent need to preserve Serra da Formosa, currently threatened by human activity.

Key words: campo rupestre, Compositae, endemism, Neotropical flora, taxonomy

Introduction

Asteraceae contains ca. 1,700 genera and nearly 24,700 species with a cosmopolitan distribution (Funk *et al.* 2009, Susanna *et al*. 2020, Palazzesi *et al*. 2022). This monophyletic family is morphologically characterized by flowers arranged centripetally on a receptacle surrounded by bracts, called capitulum, anthers fused in a ring with secondary presentation of pollen grains and cypselae usually with a pappus (Bremer 1994, Funk *et al*. 2009, Palazzesi *et al.* 2022). Within the 16 subfamilies and 51 tribes of Asteraceae (Susanna *et al.* 2020, Gostel *et al.* 2024), the tribe Vernonieae stands out in the Brazilian flora (Loeuille *et al.* 2024) due to the diversity and ecological importance of subtribe Lychnophorinae (Loeuille *et al*. 2015).

Lychnophorinae consists of 21 genera and approximately 150 species, primarily distributed in the Brazilian Central Plateau, which is immersed in the Cerrado Domain, a conservation hotspot (Mittermeier *et al.* 2011). The subtribe is especially diverse in the high elevation *campos rupestres* (Alves & Loeuille 2021). Most members of Lychnophorinae are woody plants, often with a leaf sheath, indumentum primarily composed of 3- to 5-armed trichomes, pappus frequently paleaceous, deciduous to caducous, and common occurrence of syncephaly (secondary or tertiary capitula), although some genera do not show any fusion between heads. In terms of micromorphological characters, the apical anther appendages generally have conspicuous wall thickenings, the style lacks a basal node, and the pollen is always

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sublophate (Robinson 1992, Loeuille *et al*. 2019). Phylogenetic studies (Loeuille *et al*. 2015, Aguilar-Cano *et al.* 2025, Siniscalchi *et al.* in prep.) reshaped the circumscription of the group with the inclusion of some genera, notably *Cololobus* Robinson (1994: 557) (Siniscalchi *et al.* in prep.) and *Piptocoma* Lessing (1829: 315) (Aguilar-Cano *et al.* 2025). The monophyly of the subtribe is now strongly supported by molecular synapomorphies and the presence of heliangolides in the aerial parts (Loeuille *et al.* 2015).

Since the publication of a synopsis for the subtribe (Loeuille *et al*. 2019), several taxonomic novelties have been recently described in Lychnophorinae (Bonfim e Cândido & Loeuille 2020, 2021, 2022, Gomes & Loeuille 2021, 2022, Marques *et al.* 2021, Antar *et al.* 2022, Loeuille *et al.* 2022), underlining the still incomplete knowledge of the group. This is especially true as many of these new taxa are endemic or microendemic species of the *campos rupestres* of the Espinhaço range of mountains in the states of Minas Gerais and Bahia (Alves & Loeuille 2021). Many *campos rupestres* areas are still botanically poorly known or completely unknown and their exploration frequently brings new species to light, such as *Eremanthus ovatifolius* Loeuille & Pirani (2016: 132) in Pico da Aliança in eastern Minas Gerais or in the Ibicoara region in Chapada Diamantina, Bahia: *Lychnophora spiciformis* Loeuille & Siniscalchi in Siniscalchi *et al.* (2016: 49) and *Lychnophorella hindii* Bonfim e Cândido & Loeuille (2020: 379). In the state of Minas Gerais, the main areas of study of *campos rupestres* have been the Diamantina plateau, Serra do Cabral, Grão Mogol, and Serra do Cipó (Giulietti & Pirani 1988, Almeida *et al*. 2023). The area north of Grão Mogol and south of Serra do Sincorá (mostly Espinhaço Septentrional) was neglected until recently (Almeida *et al.* 2023, Antar *et al.* 2024), showing a low collection density for Lychnophorinae (Alves & Loeuille 2021). The recent botanical exploration of the Espinhaço Septentrional led to the description of *Maschalostachys* Loeuille & Roque (2017: 38), a new genus of Lychnophorinae, and a new species, *Anteremanthus piranii* Roque & Santana (2014: 656).

Serra da Formosa is an insufficiently explored area of *campos rupestres* in Espinhaço Septentrional (Zavatin *et al.* 2023, Magri *et al.* 2024). Recent gatherings from that region revealed specimens of an undescribed species of Lychnophorinae that fits none of the current generic concepts (Loeuille *et al.* 2019). Here, with morphological, anatomical analyses and phylogenomics, we describe a new genus, *Roquea*, based on the description and illustration of these new specimens as *Roquea multiserialis*, endemic to Serra da Formosa, Minas Gerais, Brazil. Additionally, we provide a preliminary conservation status assessment, ecological comments, as well as a comparison with other closely related genera, including a photographic plate, a distribution map, and an artificial key to the genera of Lychnophorinae.

Materials and methods

Phylogenetic analysis:—Sequences of the new species were obtained as part of the Plants and Fungal Tree of Life project and sequencing methods largely follow those described in Zuntini *et al.* (2024), except for the use of a double capture strategy, combining both the Angiosperm353 and Compositae1061 probe sets (manufactured by Arbor Biosciences). Only the Compositae1061 gene set was analysed here, to match the sequences available from the past studies. Additional sequences of Lychnophorinae were obtained from Siniscalchi *et al.* (2019, in prep.), available at the Sequence Read Archive under BioProjects PRJNA546287 and PRJNA1108325. Read treatment and assembly follow Siniscalchi *et al.* (2019). Aligned gene matrices were used to generate gene trees in RAxML v8.0.0 (Stamatakis 2014), using 100 bootstraps. Branches with support lower than 10 were collapsed in the gene trees and a species tree was obtained with Astral III (Zhang *et al.* 2018). Branch support values were calculated as local posterior probabilities.

Light and electronic microscopy:—Dry cypselae and leaves from herborised specimens were rehydrated in hot water until completely softened before anatomical procedures. The cypselae and leaves were sectioned crosswise by hand with razor blades. In addition, cypselae were sectioned lengthwise, and unsectioned pieces were also assembled for observation in frontal view. To investigate leaf trichomes, the leaves were also submitted to a dissociation process to separate the epidermal layer of the adaxial surface and the tangle of trichomes by hydrolysing the tissues, according to the Franklin protocol (Franklin 1945), followed by manual separation with tweezers. To prepare histological slides, part of the cypsela was mounted without staining and part was stained with safranin 0.1% (50% ethanol solution). Leaf cross sections were stained in safranin 0.1% (50% ethanol solution), or toluidine blue 0.1% (in water solution) (Sakai 1973); and the trichomes dissociated were stained in Safranin 0.1% (50% ethanol solution). Semi-permanent histological preparations were mounted with glycerol gelatin. Anthers were mounted on a microscope slide with Hoyer's solution (Anderson 1954) for an analysis of microcharacters. Photomicrographs with scale bars were obtained with a Zeiss Axio Imager Z2 microscope.

Scanning electron microscopy (SEM) images of the cypselae were taken. Herborised materials were submitted to platinum metallization using a Quorum Q150TS high vacuum sputter coater (vacuum of 5 × 10−5 mbar). Samples were examined under a Hitachi Regulus 8230 FE scanning electron microscope, under 10KV.

Taxonomic treatment:—The morphological description was based on specimens seen in the following herbaria: K, RB, SAMES and SPF (Thiers 2024 [continuously updated]). Additionally, the online databases Reflora Virtual Herbarium (REFLORA 2024) and SpeciesLink (INCT 2024) were consulted. Digital images of the types of species of Lychnophorinae were obtained on-line from institutional databases (JSTOR 2019).

A 10−60 × magnification stereomicroscope was used to analyse morphological features of the specimens. Terminology follows Harris & Harris (2001) for general morphology and Hickey (1973) for leaf shape, as well as Loeuille *et al.* (2019) for organism-specific terms. The distribution map was produced in QGIS v.3.0.1 (QGIS Development Team 2018). Coordinates were gathered from the labels and if absent, specimens were georeferenced using the locality description. A preliminary conservation status assessment was made based solely on criterion B following the IUCN criteria (2012) and guidelines (IUCN 2019), using the Geospatial Conservation Assessment (GeoCAT) tool (Bachman *et al.* 2011) with the IUCN default values for Extent of Occurrence (EOO) and Area of Occupancy (AOO).

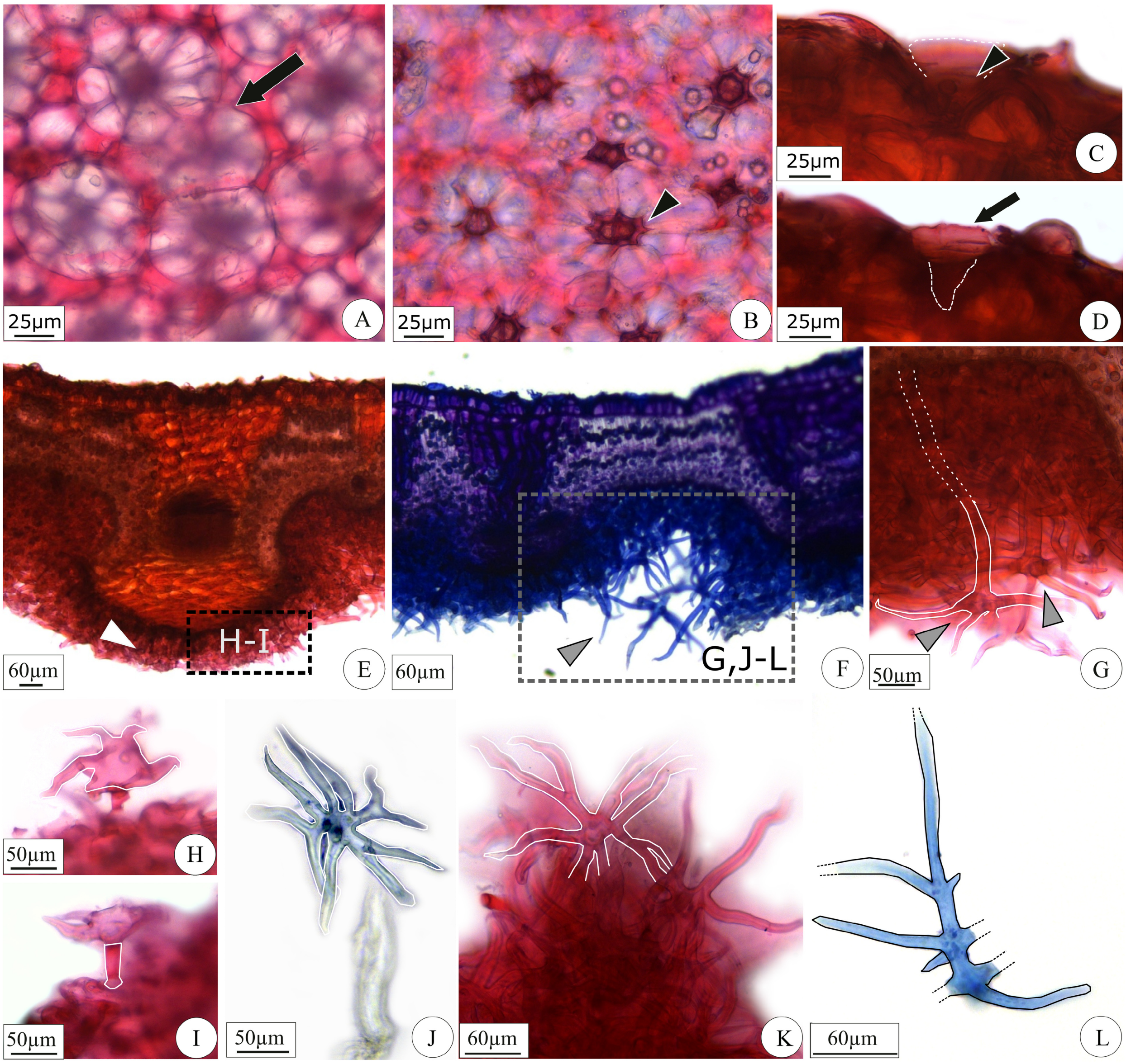

FIGURE 1. Trichomes of *Roquea multiserialis* Loeuille & Antar. **A.** Glandular trichome, showing distended cuticle (black arrow). **B.** Glandular trichome base, showing secretory cells (black arrowhead). **C.** Glandular trichome, showing secretory cells (black arrowhead). **D.** Glandular trichome, showing distended cuticle (black arrow). **E.** Leaf transversal section at midrib region, showing short stalked stellate trichomes (white arrowhead). **F.** Leaf transversal section at inter-vein section, evidencing crypt with long stalked stellate trichomes (grey arrow head). **G.** Long stalked stellate trichome, with unbranched arms (grey arrowhead). **H.–I.** Swollen short stalked stellate trichomes. **J.–K.** Long stalked stellate trichomes, with forked arms. **L.** Geminate long stalked stellate with side-arm trichome.

Results

Anatomy:—Glandular capitate trichomes were found in the adaxial surface of leaves (Fig. 1A, B, C, D), which are sunken in the epidermal layer, with a few glandular cells with sclerified outer walls and basal part of neighbouring cells (Fig. 1B, C); the "head" of these trichomes corresponds to distended cuticle (Fig. 1A, D). The indumentum of stems and leaves is composed of unbranched long trichomes with 4–6 cells restricted to the adaxial surface of the leaf sheath and several subtypes of stellate trichomes (Fig. 1E, F, G, H, I, J, K, L). Short-stalked swollen stellate trichomes are on the stem and in higher density along the leaf midrib and venations (Fig. 1E, H, I). Long stalked stellate trichomes occur in the stem and leaf crypts (Fig. 1F, G), sometimes with forked arms (Fig. 1J, K) or geminate (Fig. 1L).

The anthers are calcarate and tailed (Fig. 2A, B, C). The apical appendage is triangular with sclerified cells (Fig. 2B), and the tails are blunt, broad-based, non-sclerified and papillated at the extremities (Fig. 2C).

FIGURE 2. Anthers of *Roquea multiserialis*. **A.** Anther. **B.** Apical appendage with sclerified cells (black arrowhead). **C.** Tails.

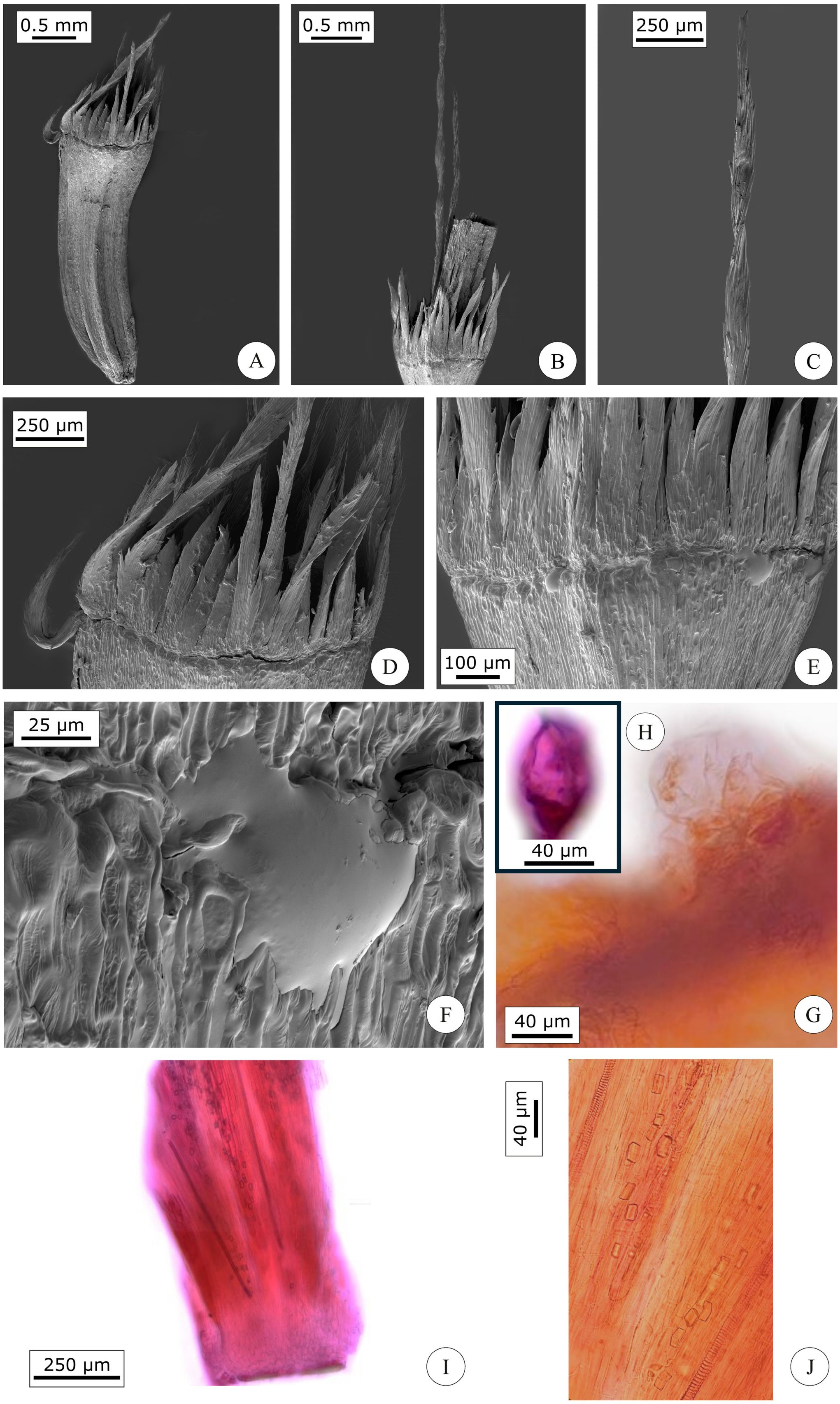

FIGURE 3. Cypsela and pappus of *Roquea multiserialis*. **A.** Cypsela and outer pappus series. **B.** Outer pappus series with two setae of the inner series and base of corolla. **C.** Detail of inner pappus series seta, upper half. **D.** Detail of outer pappus series. **E.** Upper callus with remnants of glandular trichomes as droplet of secretion. **F.** Detail of a droplet of secretion. **G.** Glandular trichome of the upper callus. **H.** Detail of the glandular trichome of the upper callus, showing the secretory cells in trichome base (in red) and the distended cuticle (in pink). **I.** Cypsela, frontal view. **J.** Raphides in the cypsela wall.

The cypsela is prismatic and glabrous (Fig. 3A), except for some glandular trichomes in the upper callus (Fig. 3G, H), which are capitate, with some secretory cells at their base and a cuticle that stretches considerably, giving the trichomes a globose to conical shape. These trichomes were observed only in light microscopy (Fig. 3G, H) whereas in the SEM the trichomes are replaced by droplets of secretion, superficially looking like idioblasts but without well-defined walls, suggesting that the glands are probably caducous. The cypsela wall does not contain phytomelanin but shows subquadrate raphides organized in longitudinal bands (Fig. 3I, J). The pappus is biseriate, with unequally sized (Fig. 3A, B, D), serrulate (Fig. 3D, E), sometimes twisted (Fig. 3D) outer series setae, free or partially fused at base (Fig. 3D, E.). The inner series setae are deciduous, twisted and slightly serrulate (Fig. 3B, C).

Phylogenetic position:—*Roquea* is one of the earliest diverging lineages of Lychnophorinae, emerging as the sister group to all Lychnophorinae except *Centratherum* Cassini (1817: 31), *Cololobus*, *Blanchetia* Candolle (1836: 75) and *Gorceixia* Baker (1882: 225) (Fig. 4). This node has a low statistical support and, as in the previous phylogenies of Lychnophorinae (Loeuille *et al.* 2015, Siniscalchi *et al.* 2019, in prep.), there is still uncertainty in the relationships among these early-diverging lineages. Nonetheless, *Roquea* is not closely related to the two well-supported clades in this part of the tree: the one which contains *Anteremanthus hatschbachii* Robinson (1992: 646), *Hololepis* Candolle (1810: 155, 189) and *Eremanthus crotonoides* (Candolle 1836: 81) Schultz-Bipontinus (1863: 396), and the other with *Chronopappus* Candolle (1836: 84), *Heterocoma* Candolle (1810: 190, t. 7), *Anteremathus piranii* Roque & Santana (2014: 656), *Maschalostachys* Loeuille & Roque (2017: 38) and *Paralychnophora* MacLeish (1984: 106) (Fig. 3). Thus, its phylogenetic position supports the recognition of *Roquea* as a new distinct genus in the subtribe Lychnophorinae.

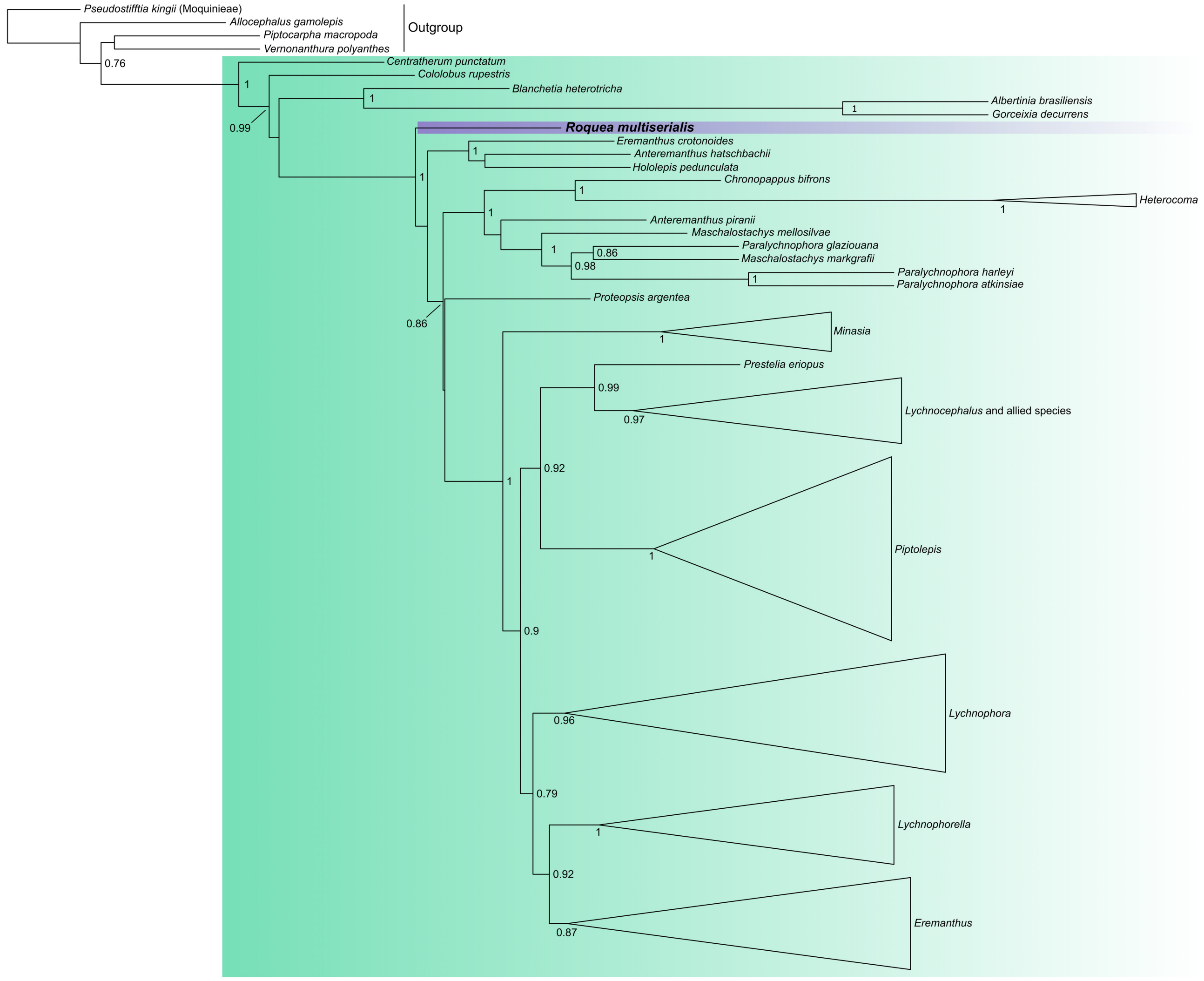

FIGURE 4. Phylogenetic relationships among *Roquea multiserialis* (bold and purple) and members of Lychnophorinae (green) from multispecies coalescent phylogenetic reconstruction of Lychnophorinae. Support values are local posterior probabilities, values below 0.75 not shown.

Taxonomic treatment

Roquea Loeuille & Antar, ***gen. nov.***

Type:—*Roquea multiserialis* Loeuille & Antar.

Diagnosis:—*Compositarum, tribus Vernonieae, subtribus Lychnophorinae. Frutices vel arbusculae. Indumentum ex pilis variabiliter stellatis nec non eramosis compositum. Folia petiolata, vaginis semiamplexicaulibus instructa. Inflorescentiae in ramis axillaribus, capitula in corymbum disposita. Capitula 130–150-flora; squamae involucri 7–9-seriatae, imbricatae, persistentes. Corollae lilacinae ad subroseas, lobis dense villosis; antherae calcaratae, caudatae; basi stylorum non noduliferi. Cypselae prismaticae, glabrae; carpopodia obsoleta; pappus biseriatus; setae pallidae stramineae, paleaceae, saepe leviter tortiles, seriei exterioris breves, basin leviter connatae, persistentes, seriei interioris caducae.*

Etymology:—The generic name honors Dr. Nadia Roque (1970-2024), a Brazilian professor and researcher at Universidade Federal da Bahia, in Salvador, Brazil. She made outstanding contributions to the knowledge of Asteraceae, especially of Neotropical and Brazilian species. She first started her career working with the tribes Barnadesieae and Mutisieae, but soon expanded her studies to Eupatorieae and Heliantheae. She authored more than 100 scientific papers, contributed to ca. 20 book chapters as well as two books: "*Asteraceae. Caracterização e Morfologia Floral*" (Roque & Bautista 2008) and "*A família Asteraceae no Brasil: classificação e diversidade*" (Roque *et al.* 2017b), which have become important references for new students working in Asteraceae taxonomy in Brazil. She also advised numerous graduate students engaged in the study of Asteraceae and other families and led the treatment of Asteraceae in the collaborative project *Flora e Funga do Brasil* (Roque *et al.* 2020).

Roquea multiserialis Loeuille & Antar **sp. nov.**, adhuc unica.

Type:—BRASIL. Minas Gerais: Monte Azul, Pico da Serra da Formosa, 15º14′17.66″S, 42º49′15.47″W, 1070–1805 m, 3 Mar 2023, *R.B. Almeida et al. 1070* (holotype SPF!, isotypes K!, SAMES!) (Figs. 5, 6).

Treelet or shrub up to 2 m tall. Stems moderately branched, greyish, blackish towards base, pubescent, indumentum composed of long-stalked stellate trichomes, sometimes with forked arms or geminate or short-stalked and swollen stellate trichomes. Leaves shortly petiolate, 3–5 mm long, leaf sheath semi-amplexicaul, 2.2–4.1 × 2.9–5 mm, adaxially densely white pilose (unbranched long trichomes); blade rhombic, wide obovate, rarely wide elliptic, 2.6–4.9 × 1.4–2.7 cm, venation eucamptodromous, midrib thick and flattened, furrowed, prominent abaxially, sunken adaxially, including secondary veins, chartaceous to subcoriaceous, conspicuously discoloured, adaxial surface green, dark green or nearly black *in sicco*, glabrescent with sparse short-stalked swollen stellate trichomes, tomentose in the midrib, especially near the base, glandular-punctate, abaxial surface greyish lanate, older leaves dark greyish, lanate, indumentum composed of dense short-stalked swollen stellate trichomes along midrib and venation and sparse darker long-stalked stellate trichomes in stomatal crypts, sometimes with forked arms or geminate, margin slightly thickened, entire or sinuate to crenate, especially near apex, apex obtuse or acute, sometimes retuse or acuminate, base attenuate or cuneate. Inflorescence axillary, capitula organised in a dense corymb; flowering branch 7.7–20.5 cm long, cylindrical or slightly flattened and four-angled, mostly near base of capitula, greyish, sometimes blackish, pubescent, indumentum composed of stellate trichomes with long- or short-stalked trichomes, leaf-like bracts 0.9–2.9 × 0.5–1.4 cm. Capitula 3–6 per corymb, pedunculate, associated to 1–2 leafy spatulate tomentose subinvolucral bract erect or slightly conduplicate towards apex, peduncle 1.4–3.2 cm long, flattened, costate, greyish, sometimes blackish, with similar indumentum as branches; involucre 9.5–13.1 mm tall, 12–18.5 mm in diam., campanulate; phyllaries imbricate, 7–9-seriate, densely light greyish to ochraceous, indumentum of short-stalked stellate and unbranched trichomes, apex dark brown and sparsely tomentose, outer phyllaries ovate to elliptic, 3.4–4.3 × 1.6–2.1 mm, apex acute and recurved, inner phyllaries elliptic to narrowly oblanceolate, 4.8–6.7 × 1.1–1.9 mm long, acute to acuminate and straight to slightly recurved; receptacle fimbrillate, fimbria up to 0.5 mm. Florets 130–150 per capitulum; corolla lilac to pale pink, usually actinomorphic but sometimes asymmetric due to a higher number of lobes and size variation of sinuses, corolla tube 4.5–5.8 × 0.3–0.6 mm, glabrous, sparsely glandular-punctate, corolla lobes 5(–8), 3.2–4.1 × 0.3–0.5 mm, glabrous or sparsely pubescent, apex acute, densely villous; anthers 5(–8), purple, apical anther appendage triangular, anther base calcarate and tailed; style lacking a basal node, style shaft 8.1– 8.9 mm long, whitish to lilac, glabrous throughout except for pubescence upper ca. 1.5–2 mm beneath style-arms, style-arms 1.9–2.5 mm long.

Cypsela prismatic, 3.2–4.1 × 0.7–1.1 mm, 10-ribbed, brownish usually with darker extremities, glabrous; carpopodium inconspicuous; pappus setae biseriate, light stramineous, paleaceous, outer series setae 0.9–1.1 mm long, of unequal sizes, slightly fused at base or free, serrulate, sometimes twisted, persistent, apex erose, inner series setae 3.5–4.4 mm, free, slightly serrulate, twisted, deciduous, apex acute.

Etymology:—The specific epithet refers to the high number of series of phyllaries. The Lychnophorinae taxa typically have fewer than the 7–9 series as in *Roquea multiserialis*.

Distribution, habitat, and phenology:—*Roquea multiserialis* is currently considered endemic to the locality of Serra da Formosa, in the municipality of Monte Azul, in the northern portion of the Espinhaço Range, Minas Gerais, Brazil (Fig. 7). The species is only found in elevations above 1700 m, in *campo rupestre* vegetation, where it can be dominant amongst other species, e.g. *Baccharis platypoda* Candolle (1836: 409), *Begonia grisea* Candolle (1859: 138), *Clusia burle-marxii* Bittrich (1996: 76), *Declieuxia cacuminis* Müller Argoviensis (1876: 438), *Lippia hederifolia* Martius & Schauer in Schauer (1847: 593), *Miconia sclerophylla* Triana (1872: 119), *Mimosa aurivillus* Martius (1838: 52), and *Symphyopappus cuneatus* (Candolle 1836: 149) Sch.Bip. ex Baker (1876: 367). It grows between rocks in rocky-sandy soils. The species was found flowering in March and April and with old capitula and fruits in October.

Preliminary conservation status:—*Roquea multiserialis* is currently known from just four collections, although it is described as dominant in the higher part of Pico da Formosa. Both EOO and AOO are 4 km². The species has a very limited distribution, probably restricted to this single mountain, a general pattern seen with microendemic species in the *campos rupestres* (Vasconcelos *et al.* 2020). *Roquea multiserialis* does not occur in protected areas. Serra da Formosa has been under human-induced threats, including fires, quartzite mining, and road construction for the installation of wind turbine generators. If these threats continue to advance within its potential range, it could negatively impact the species, leading to habitat degradation and decline. Considering the species restricted distribution, potential threats, and AOO value (IUCN 2012, 2019), *Roquea multiserialis* could be assessed as Critically Endangered CRB2a,b[iii].

Additional specimens examined (paratypes):—BRAZIL. Minas Gerais: Monte Azul, Pico da Formosa, 15º14′20″S, 42º49′16″W, 1800 m, 23 Oct 2018, *G. Martinelli et al.* 20471 (HUFU, RB!, SPF!); ibid., 15º14′11″S, 42º49′16″W, 1713 m,08 Apr 2022, *M. Verdi et al. 9096* (HUEFS, RB!, SPF!); ibid., 1802 m, 08 April 2022, *M. Verdi et al. 9110* (HUEFS, RB!, SPF!).

Comments:—The position of *Roquea* in Lychnophorinae is strongly supported by our phylogenetic analysis (Fig. 4) and fits into the concept of the subtribe by its woody habit, the presence of apical anther appendages with conspicuous wall thickenings (Fig. 2B), style without a basal node, presence of leaf sheath and paleaceous, deciduous pappus (Loeuille *et al.* 2019). *Roquea* can be distinguished from the other genera in Lychnophorinae by the following combination of characters: shrub or treelet, indumentum composed of stellate trichomes, capitulum with 130–150 florets, involucre with 7–9 series of phyllaries and tailed anthers. Tailed anthers are rare in Lychnophorinae and found only in *Minasia*, *Hololepis* and *Roquea* (Robinson 1992, 1999); the ones in *Roquea* are unsclerified like in *Minasia* (Fig. 2C). The dense indumentum is composed of several types of tector trichomes, mostly stellate, but unbranched trichomes were found in the adaxial surface of the leaf sheath. Stellate trichomes are more frequent in early-diverging lineages, being replaced by 3- to 5-armed trichomes in the derived Lychnophorinae (Wagner *et al.* 2014, Loeuille *et al.* 2015). The short-stalked swollen trichomes of *Roquea* are uncommon, found in *Chronopappus bifrons* (DC. ex Persoon 1807: 391) Candolle (1836: 84) and *Eremanthus crotonoides*, but also sporadically in more derived genera. Two types of trichomes were thought to occur exclusively in a single genus but also occur in *Roquea*: the geminate long-stalked trichomes of *Chronopappus bifrons* (Wagner *et al.* 2014) and the long-stalked trichomes with forked arms of *Blanchetia* (Loeuille *et al.* 2014). The glandular trichomes of the adaxial surface of leaf are similar to those found in *Gorceixia decurrens*, also in the adaxial surface. The ones found in *Eremanthus crotonoides* are larger (higher number of secretory cells), not sunken, and occur in the abaxial surface (Lusa, ined.). Some glandular trichomes were also found in the upper callus region of the cypsela (Fig. F, G, H). Unlike the glandular trichomes previously found in cypselae of Lychnophorinae (*Lychnophora semirii* D.Marques & J.N.Nakaj. in Marques *et al.* 2018: 1051; *Piptolepis* spp.) (Marques *et al.* 2018, 2022), they are caducous.

The high number of florets and phyllary series is rare in the subtribe, found only in *Proteopsis* Mart. & Zucc. ex Schultz-Bipontinus (1864: 378), which has 80–140 florets and 5–10-seriate phyllaries. *Proteopsis* differs from *Roquea* mostly by the caulirosulate habit, indumentum composed of unbranched trichomes, and untailed anthers. *Minasia* Robinson (1992: 648) also shares some characteristics with *Roquea*: a high number of phyllary series (5–8) and tailed anthers; however it differs by its caulirosulate habit and indumentum composed of T-shaped swollen trichomes (Loeuille *et al.* 2019).

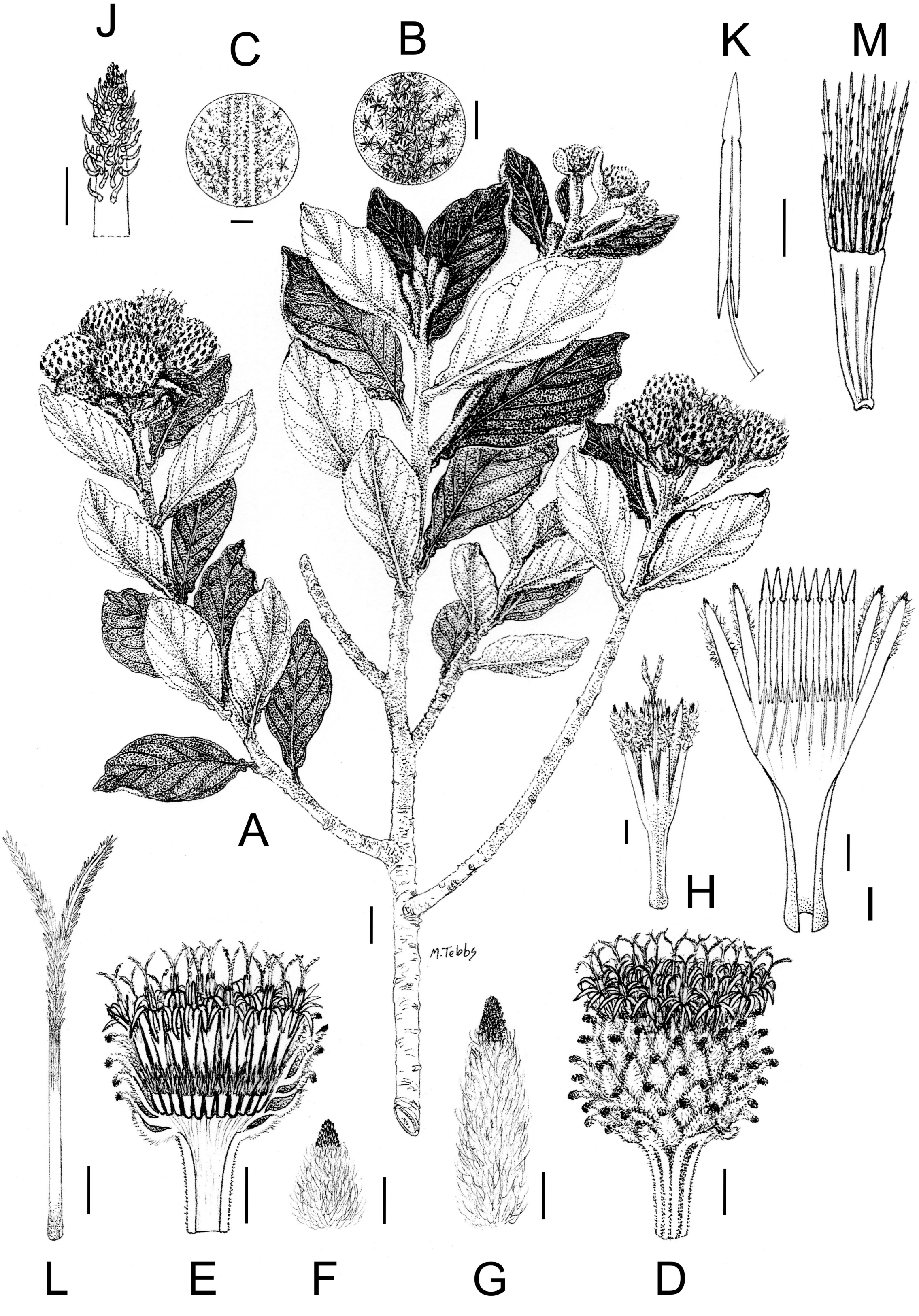

FIGURE 5. *Roquea multiserialis* Loeuille & Antar. **A.** Flowering branch. **B.** Detail of abaxial leaf midrib indumentum composed of stellate trichomes (some indument removed). **C.** Detail of adaxial leaf midrib indumentum composed of stellate trichomes. **D.** Capitulum. **E.** Longitudinal section of capitulum. **F.** Outer phyllary. **G.** Inner phyllary. **H.** Abnormal corolla with 8 lobes. **I.** Abnormal corolla opened and showing 8 anthers. **J.** Apex of corolla lobe. **K.** Anther. **L.** Style. **M.** Cypsela with a pappus. **A.–I.** Illustration by Margaret Tebbs based on *R.B. Almeida et al. 1070* (K).

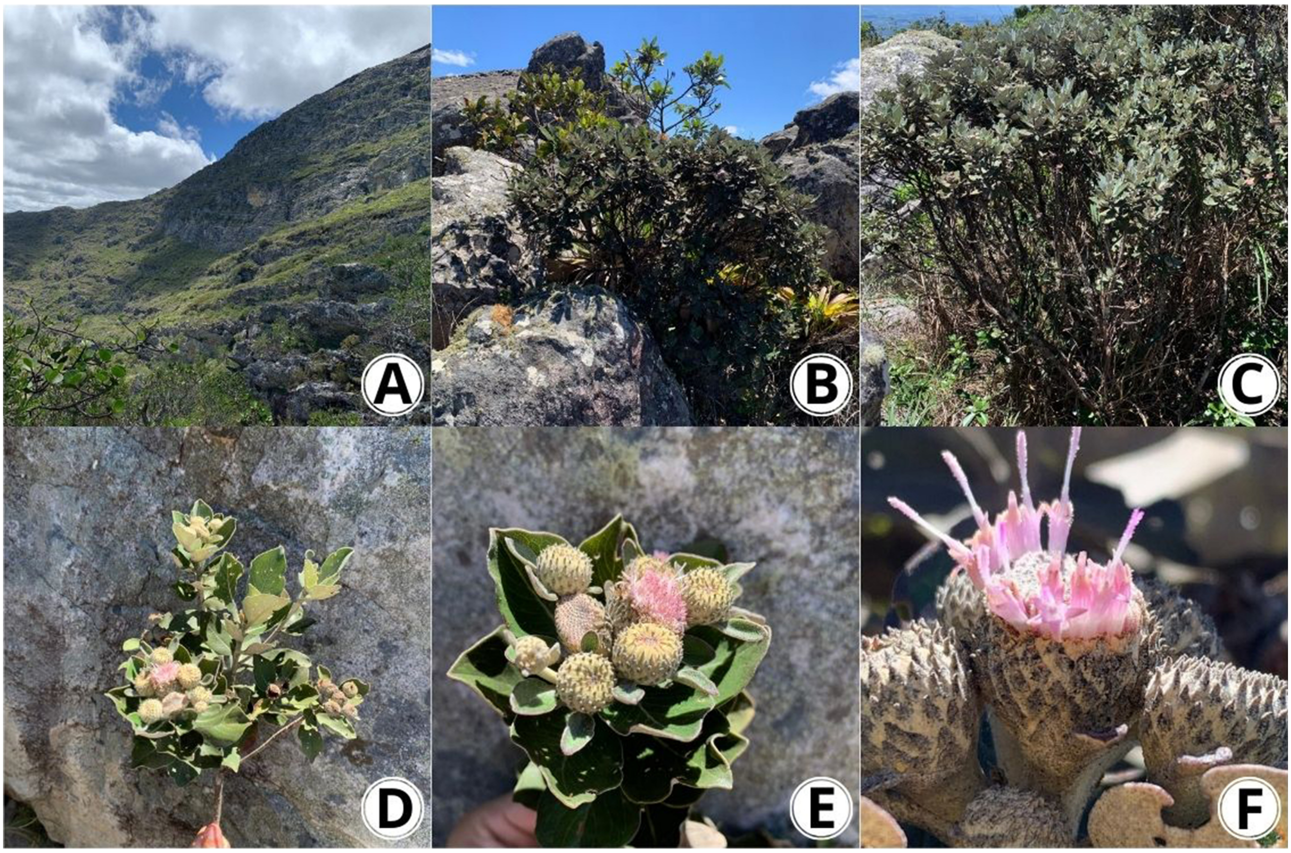

FIGURE 6. *Roquea multiserialis* Loeuille & Antar. **A.** Habitat. **B.** Habitat and habit. **C.** Habit. **D, E.** Branch in flower. **F.** Capitula detail. **A–F.** Photos by R.B. Almeida.

The presence of stellate trichomes links *Roquea* to some of the early-diverging lineages like *Gorceixia*, *Blanchetia* and *Eremanthus crotonoides*. Only *Blanchetia* and *Roquea* share the stellate trichomes with forked arms, but the former differs from *Roquea* by its smaller shrubby habit (never a treelet), sheathless leaves (vs. semi-amplexicaul leaf sheath), ovoid capitula (vs. campanulate), phyllaries 3–4-seriate (vs. 7–9-seriate) and 5–10 florets (130–150) (Loeuille *et al.* 2014). *Roquea* has long-stalked stellate, sometimes geminate trichomes like *Eremanthus crotonoides*, which is placed as *incertae sedis* in Loeuille *et al.* (2019), and *Gorceixia*. *Eremanthus crotonoides* and *Gorceixia* are trees or treelets (1–4 m tall and 5–7 m tall, respectively), whereas *Roquea* hardly reaches 2 m, they have sheathless leaves (vs. semi-amplexicaul leaves), smaller capitula (3–5 vs. 130–150 florets) and lower number of phyllary series (3 for *Gorceixia*, 5–6 for *E. crotonoides* vs. 7–9) (Hind *et al.* 2006, Loeuille *et al.* 2019) (Table 1).

TABLE 1. Diagnostic morphological characters of *Roquea* Loeuille & Antar and related genera.

Character	*Roquea*	*Anteremanthus*	*Gorceixia*	*Hololepis*	*Paralychnophora*
Leaf sheath	Semi-amplexicaul	Semi-amplexicaul	Absent	Absent	Semi-amplexicaul
Leaf trichomes	Stellate and unbranched	T-shaped	Stellate	Inverted Y-shaped	3- to 5-armed and unbranched
Syncephalium	No	No	Yes	No	Yes
Number of phyllary series	7–9	4–5	3	4–5	(3–)4–5(–6)
Number of florets	130–150	20–60	5	30–40	2–26
Anther base	Calcarate, tailed	Calcarate, not tailed	Calcarate, not tailed	Calcarate, not tailed	Calcarate, not tailed
Carpopodium	Inconspicuous	Prominent	Inconspicuous	Prominent	Prominent or inconspicuous
Pappus type	Biseriate, paleaceous	Biseriate, paleaceous	Uniseriate, laciniate collar	Biseriate, subpaleaceous	Biseriate or triseriate, setose to subpaleacous

Roquea shares the habit, the presence of semi-amplexicaul leaf sheath and biseriate pappus with *Anteremanthus* and *Paralychnophora*. However, the latter differs from *Roquea* by the capitula organised into a syncephalium (vs. absence of syncephalium), the indumentum composed of 3- to 5-armed trichomes, swollen or not, and unbranched trichomes (vs. stellate and unbranched trichomes). *Anteremanthus* shares with *Roquea* the absence of syncephalium, but its indument is composed of T-shaped trichomes and the carpopodium is prominent (vs. inconspicuous). *Anteremanthus* and *Paralychnophora* have capitula with a smaller number of phyllary series (3–6 vs. 7–9) and a smaller number of florets (2–26 vs. 130–150) (Loeuille *et al.* 2019) (Table 1).

Geographically, *Roquea* occurs in sympatry with *Paralychnophora glaziouana* Loeuille in Loeuille *et al.* (2012: 290) and *Maschalostachys mellosilvae* Loeuille & Roque (2017: 42); the latter is easily distinguishable from *Roquea* by the habit (monopodial treelet) and capitula organised in axillary loose spikes of syncephalia or rarely a cyme of syncephalia (Loeuille & Roque 2017).

It is worth noting that abnormal florets were found in some capitula of *Roquea multiserialis*, with six to eight corolla lobes and stamens (Fig. 5H, I). While tetramerous florets are relatively widespread in the family and have been identified in more than 80 taxa from disparate lineages (initially listed for disc florets by Gardner 1977), the increase in the number of corolla lobes and stamens is extremely rare. To our knowledge, only cases of up to hexamerous florets have been found in wild species as *Aster prainii* (Drummond 1907: 91) Chen (1981: 1314) (Small 1927), *Flaveria trinervia* Sprengel (1800: 63) Mohr (1901: 810) (Misra 1957), and some Barnadesioideae (Svoma *et al.* 2020). Fusion of florets has been reported in *Flaveria trinervia* (nine corolla lobes, nine stamens, two styles or eight corolla lobes, eight abortive stamens and two abortive styles) (Misra 1957) and *Helianthus annuus* (Linnaeus 1753: 904) (Joshi 1934). The abnormal florets of *Roquea multiserialis* have a single style and normal stamens, but the high number of florets densely compacted in the capitulum may eventually lead to some kind of fusion, a hypothesis that should be tested with developmental studies.

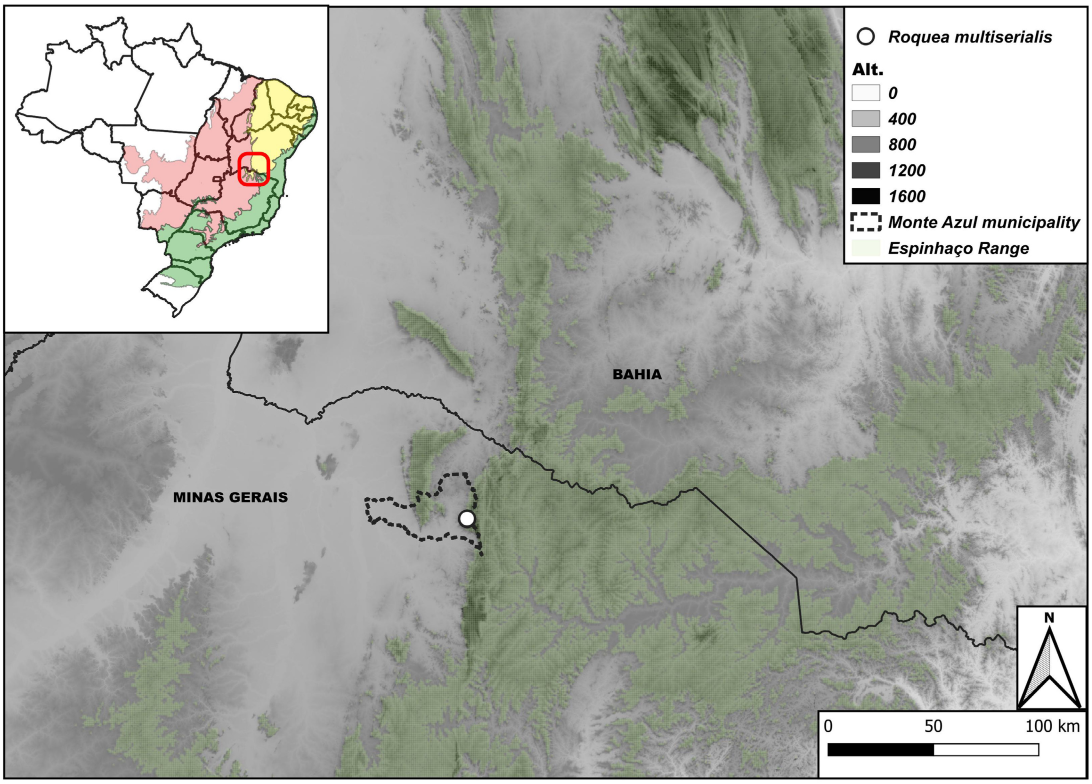

FIGURE 7. Distribution map of *Roquea multiserialis* Loeuille & Antar. Upper left corner inset highlights Brazilian phytogeographic domains (Cerrado, pink; Mata Atlântica, green; Caatinga, yellow).

Artificial Key to the Genera of Lychnophorinae (modified from Loeuille *et al.* 2019)

1. Caulirosula life-forms 2
\- Trees, treelets, shrubs, subshrubs or herbs 4
2. Capitula arranged in a syncephalium; phyllaries in 3–4 series; cypselae with an inconspicuous carpopodium........................ *Prestelia*
\- Capitula arranged in a solitary glomerule or panicle of glomerules; phyllaries in 5–6 series; cypselae with a prominent carpopodium 3

3. Leaf indumentum composed of T-shaped swollen trichomes; capitula with 20–50 florets; phyllary apices without spiny appendages; anthers tailed .... *Minasia*
- Leaf indumentum composed of unbranched trichomes; capitula with 80–140 florets; phyllary apices with spiny appendages; anthers not tailed .... *Proteopsis*
4. Herbs, rarely subshrubs and then outermost phyllaries foliaceous; anthers ecalcarate .... *Centratherum*
- Shrubs, treelets or trees, rarely subshrubs and then outermost phyllaries not foliaceous; anthers calcarate 5
5. Leaf sheath absent 6
- Leaf sheath present, pad-like to amplexicaul 12
6. Receptacle deeply alveolate; style with basal node; leaf indumentum composed of symmetric T-shaped trichomes with long arms .... *Albertinia*
- Receptacle naked, areolate to fimbrillate; style without basal node; leaf indumentum composed of unbranched, 3–5-armed, stellate and T-shaped trichomes with short arms or asymmetric long arms 7
7. Capitulum solitary with foliaceous trinerved subinvolucral bracts .... *Hololepis*
- Capitula arranged in an inflorescence (glomerule, syncephalium, cyme or panicle) or, when solitary, capitulum with pinnate subinvolucral bracts 8
8. Leaf margins serrate to dentate; leaf indumentum composed of stellate trichomes with a long multicellular stalk 9
- Leaf margins entire, rarely serrulate; leaf indumentum composed of trichomes T-shaped or 3–5-armed, with a short stalk when stellate 10
9. Shrubs; stems not winged; capitula arranged in a panicle with short internodes; involucre ovoid .... *Blanchetia*
- Trees or treelets; stems winged; capitula arranged in a syncephalium; involucre cylindrical .... *Gorceixia*
10. Leaf margins flat; capitula arranged in corymb, panicle, glomerule or a cyme of glomerules or syncephalia 11
- Leaf margins revolute; capitula arranged in a solitary syncephalium or rarely in a congested spike .... *Lychnophora*
11. Capitula arranged in a cyme of glomerules or syncephalia; pappus 2–5-seriate, both series setose or paleaceous, outer series shorter than the inner series, rarely subequal (Brazil, Bolivia) .... *Eremanthus*
- Capitula arranged in a corymb, panicle or glomerules; pappus (1–)2-seriate, rarely absent, outer pappus of c. 10 short squamellae, free to connate (pseudocoroniform), inner pappus of 0–14 elongate scales (West Indies to Central America and northern South America) .... *Piptocoma*
12. Leaves usually with pad-like sheath; if sheath semi-amplexicaul then phyllaries caducous 13
- Leaves with semi-amplexicaul to amplexicaul sheath; phyllaries persistent, rarely deciduous 14
13. Phyllaries strongly imbricate and persistent (state of Bahia) .... *Lychnophorella*
- Phyllaries weakly imbricate and caducous (state of Minas Gerais) .... *Piptolepis*
14. Capitula arranged in a syncephalium 15
- Capitula variously arranged in a glomerule, corymb, thyrse or panicle or rarely solitary 17
15. Third-order syncephalium; inner series pappus setae apices narrowed .... *Lychnocephalus*
- Second-order syncephalium; inner series pappus setae apices not narrowed 16
16. Branched sympodial trunk; leaf indument composed of 3–5-armed and unbranched trichomes; syncephalium long-pedunculate .... *Paralychnophora*
- Unbranched monopodial trunk; leaf indument composed of T-shaped and unbranched trichomes; syncephalium sessile .... *Maschalostachys*
17. Cypselae glabrous; capitula with foliaceous subinvolucral bracts; leaf indument composed of stellate and/or 3–5-armed trichomes, commonly geminate 18
- Cypselae pubescent; capitula rarely with foliaceous subinvolucral bracts; leaf indument composed of T-shaped trichomes 20
18. Leaf adaxial surface strongly muricate, not marcescent; involucre ovoid; capitula with 8–11 florets .... *Chronopappus*
- Leaf adaxial surface smooth, not muricate; involucre campanulate; capitula with 20–150 florets 19
19. Leaf marcescent; capitula with 20–75 florets; cypselae walls with phytomelanin .... *Heterocoma*
- Leaf not marcescent; capitula with 130–150 florets; cypselae walls without phytomelanin .... *Roquea*
20. Phyllaries with recurved tips (at least the inner series); corolla lobes short and glabrous; style with a basal node .... *Cololobus*
- Phyllaries without recurved tips; corolla lobes long and pubescent; style lacking a basal node 21
21. Leaf petiolate; capitula pedunculate, with 20–60 florets; cypselae with a prominent carpopodium .... *Anteremanthus*
- Leaf sessile; capitula sessile, with 8–12 florets; cypselae with an inconspicuous carpopodium .... *Vinicia*

Final remarks

Roquea joins a growing list of genera of Asteraceae recently described from Brazil, e.g. *Maschalostachys*, *Lapidia* Roque & S.C.Ferreira in *Roque et al.* (2017a: 6), *Lychnophorella* Loeuille *et al.* (2019: 73), *Archidasyphyllum* (Cabrera 1959: 44) Ferreira *et al.* (2019: 13) and *Vickia* Roque & Sancho (2020: 670). Although description of new genus based on new collections in the 21st century might be surprising, several aspects of Brazil, such as the high plant diversity and endemism and the gaps in botanical collection in several areas, are surely related to this pattern, which is also seen in other tropical countries.

The first known collection of *Roquea multiserialis* dates from 2018 by G. Martinelli, during an expedition mostly focused on collecting Bromeliaceae. Fortunately, the area is now being systematically collected with efforts both from *Centro Nacional da Conservação da Flora* and by a group led by the project “Plano de Ação Territorial Espinhaço

Mineiro", which aims to publish a book detailing the flora of the region. These efforts, which have led to the description of new species (e.g. Cardoso *et al*. 2022; Almeda & Pacifico 2023; Pacifico *et al*. 2023; Silva *et al*. 2023; Zavatin *et al*. 2023, Magri *et al*. 2024, Antar *et al*. 2024) and this new genus, are aimed at the creation of a new protected area.

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The opportunity to honour Nádia Roque by naming this new genus is bittersweet, as she suddenly passed away on 10th of October 2024, during the review process of this manuscript. She was not only a specialist in Asteraceae but also a good friend, sharing with us her enthusiasm for life. She had a fundamental role in keeping the Asteraceae community in Brazil moving towards common goals, and her eagerness to help everybody and joy on bringing people together will be sorely missed. Her legacy leaves on the hundreds of students she advised and researchers she collaborated with, and we hope this small gesture celebrates it (Fig. 8).

FIGURE 8. Dr Nádia Roque (1970–2024) (courtesy of Maria Liris Barbosa da Silva).

References

Aguilar-Cano, J., Siniscalchi, C.M., Lucas, E., Malakasi, P. & Loeuille, B. (2025) Further disintegration of Piptocarphinae, an amplified concept of *Critoniopsis* and notes on the occurrence of paleae in *Piptocarpha* (Compositae: Vernonieae). *Kew Bulletin.* [in press]

Almeida, R.B.P., Murer, B.M. & Sano, P.T. (2023) What is being published on floristics? An overview of floristic studies carried out in the

Espinhaço Range. *Acta Botanica Brasilica* 37: e20220267.
https://doi.org/10.1590/1677-941x-abb-2022-0267

Alves, F.V.S & Loeuille, B. (2021) Geographic distribution patterns of species of the subtribe Lychnophorinae (Asteraceae: Vernonieae). *Rodriguésia* 72: e02072019.
https://doi.org/10.1590/2175-7860202172072

Almeda, F. & Pacifico, R. (2023) New species of *Microlicia* (Melastomataceae) from the Espinhaço Meridional and Septentrional of Minas Gerais, Brazil. *Phytotaxa* 600: 184–194.
https://doi.org/10.11646/phytotaxa.600.3.5

Anderson, L.E. (1954) Hoyer's solution as a rapid permanent mounting medium for bryophytes. *The Bryologist* 57: 242–244.
https://doi.org/10.1639/0007-2745(1954)57[242:HSAARP]2.0.CO;2

Antar, G.M., Monge, M., Nakajima, J.N. & Loeuille, B. (2022) *Lychnophora pseudovillosissima* (Asteraceae: Vernonieae: Lychnophorinae), a new species restricted to Minas Gerais, Brazil. *Webbia* 77: 257–266.
https://doi.org/10.36253/jopt-13250

Antar, G.M., Harley, R.M., Pastore, J.F.B., Verdi, M. & Soares, A.S. (2024) *Eplingiella sanoi* sp. nov. (Hyptidinae-Lamiaceae) supports the urgent need for campos rupestres conservation in the Serra do Espinhaço Septentrional, Minas Gerais state, Brazil. *Webbia* 79: 191–200.
https://doi.org/10.36253/jopt-15902

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. *ZooKeys* 150: 117–126.
https://doi.org/10.3897/zookeys.150.2109

Baker, J.G. (1876) Compositae III. Asteroideae. *In*: Martius†, C.F.P. von & Eichler, A.W. (Eds.) *Flora brasiliensis*, 6 (3). Fried. Fleischer, Münich, Vienna, Leipzig, pp. 1–100.

Baker, J.G. (1882) On *Gorceixia*, a new genus of Vernoniaceae. *Journal of Botany, British and Foreign* 20: 225–227, tab. 232.

Bittrich, V. (1996) Três novas espécies do gênero Clusia (Guttiferae) do Brasil. *Boletim de Botânica da Universidade de São Paulo* 15: 73–82.
https://doi.org/10.11606/issn.2316-9052.v15i1p73-82

Bonfim e Cândido, J. & Loeuille, B. (2020) Two new species of *Lychnophorella* (Vernonieae, Asteraceae) from the Chapada Diamantina, Bahia state, Brazil. *Systematic Botany* 45: 379–386.
https://doi.org/10.1600/036364420X15862837791320

Bonfim e Cândido, J. & Loeuille, B. (2021) Three new species of *Piptolepis* (Vernonieae, Asteraceae) from the Diamantina Plateau, Minas Gerais, Brazil. *Systematic Botany* 46: 493–503.
https://doi.org/10.1600/036364421X16231782047578

Bonfim e Cândido, J. & Loeuille, B. (2022) Reestablishment of the name *Piptolepis pseudomyrtus* (Vernonieae, Asteraceae). *Phytotaxa* 531: 136–142.
https://doi.org/10.11646/phytotaxa.531.2.6

Bremer, K. (1994) *Asteraceae. Cladistics & classification*. Timber Press, Portland, Oregon, 752 pp.

Cabrera, A.L. (1959) Revisión del género *Dasyphyllum* (Compositae). *Revista Museo de La Plata* 38: 21–108.

Candolle, A.L.P. de (1859) Mémoire sur la famille des Bégoniacées. *Annales des Sciences Naturelles, Botanique* 11: 93–149.

Candolle, A.P. de (1810) Observations sur les plantes composées, ou syngenèses. Second mémoire. Monographies de quelques genres de Cinarocéphales. *Annales du Muséum d'Histoire Naturelle* 16: 181–208, pl. 6–15.

Candolle, A.P. de (1836) *Prodromus Systematis Naturalis Regni Vegetabilis, sive enumeratio contracta ordinum generum, specierumque plantarum hucusque cognitarum, juxta methodi naturalis normas digesta*, vol. 5. Treutel & Würtz, Paris, 706 pp.

Cardoso, P.H., Moroni, P., Antar, G.M., Neto, L.M. & Trovó, M. (2022) Two new Brazilian species of Verbenaceae from the Espinhaço Range: *Stachytarpheta olearyana* and *S. vianae*. *Kew Bulletin* 77: 729–736.
https://doi.org/10.1007/s12225-022-10045-0

Cassini, H. (1817) *Centratherum*. *In*: Cuvier, F. (Ed.) *Dictionnaire des Sciences Naturelles dans lequel on traite méthodiquement des différents êtres de la Nature*, ed. 2, vol. 7. Levrault, Strasbourg & Le Normant, Paris, pp. 383–384.

Chen, Y.-L., Liang, S.-Y. & Pan, K.-Y. (1981) Taxa nova Compositarum e flora Xizangensi (Tibetica). *Acta Phytotaxonomica Sinica* 19: 85–106.

Drummond, J.R. (1907) Chlamydites: a new genus of Compositae. *Bulletin Miscellaneous Information (Royal Botanic Gardens, Kew)* 1907 (3): 90–92.

Ferreira, P. de L., Saavedra, M.M. & Groppo, M. (2019) Phylogeny and circumscription of *Dasyphyllum* (Asteraceae: Barnadesioideae) based on molecular data with the recognition of a new genus, *Archidasyphyllum*. *PeerJ* 7: e6475.
https://doi.org/10.7717/peerj.6475

Franklin, G. (1945) Preparations of thin sections of synthetic resin and wood-resin composites and a new macerating method for wood. *Nature* 155: 51.
https://doi.org/10.1038/155051a0

Funk, V.A., Susanna, A., Stuessy, T.F. & Bayer, R.J. (Eds.) (2009) *Systematics, evolution, and biogeography of Compositae*. IAPT, Vienna, 965 pp.

Gardner, R.C. (1977) Observations on tetramerous disc florets in the Compositae. *Rhodora* 79 (817): 139–146.

Giulietti, A.M. & Pirani, J.R. (1988) Patterns of geographic distribution of some species from the Espinhaço Range, Minas Gerais and Bahia, Brazil. *In*: Vanzolini, P.E. & Heyer, W.R. (Eds.) *Proceedings of a workshop on Neotropical distribution patterns*. Academia Brasileira de Ciências, Rio de Janeiro, pp. 39–69.

Gomes, F.M.B. & Loeuille, B. (2021) Three new species of *Lychnocephalus* (Asteraceae: Vernonieae) from the Serra do Cipó, Minas Gerais, Brazil. *Systematic Botany* 46: 476–485.
https://doi.org/10.1600/036364421X16231782047587

Gomes, F.M.B. & Loeuille, B. (2022) Taxonomic revision of *Lychnocephalus* (Lychnophorinae, Vernonieae, Asteraceae), an endemic genus of the Espinhaço Range, Minas Gerais, Brazil. *Phytotaxa* 547: 119–146.
https://doi.org/10.11646/phytotaxa.547.2.1

Gostel, M.R., Loeuille, B., Santana, M.H., Kelloff, C.L., Chan, R., Simões, A.R.G., Larridon, I. & Funk, V.A. (2024) Molecular phylogenetics of *Distephanus* supports the recognition of a new tribe, Distephaneae (Asteraceae). *Botanical Journal of the Linnean Society* boae025.
https://doi.org/10.1093/botlinnean/boae025

Harris, J.G. & Harris, M.W. (2001) *Plant identification terminology: an illustrated glossary*, ed. 2. Spring Lake Publishing, Spring Lake, USA, 206 pp.

Hickey, L.J. (1973) Classification of the architecture of dicotyledonous leaves. *American Journal of Botany* 60: 17–33.
https://doi.org/10.1002/j.1537-2197.1973.tb10192.x

Hind, D.J.N., Giulietti, A.M. & Harley, R.M. (2006) *Gorceixia decurrens* (Compositae: Vernonieae): new for Bahia State, Brazil. *Sitientibus Série Ciências Biológicas* 6: 129–132.
https://doi.org/10.13102/scb8167

INCT (2024) Herbário Virtual da Flora e dos Fungos. Available from: http://inct.splink.org.br/ (accessed 18 May 2021)

IUCN (2012) *IUCN Red List categories and criteria*. Version 3.1. Second edition. IUCN, Gland, Switzerland and Cambridge, UK, 33 pp.

IUCN (2019) *Guidelines for using the IUCN Red List Categories and Criteria*, version 14. Cambridge. Available from: http://www.iucnredlist.org/documents/RedListGuidelines.pdf (accessed 18 May 2021)

Joshi, A.C. (1934) Some abnormal flowers of *Helianthus annus* L. *The Journal of the Indian Botanical Society* 13: 237–239.

JSTOR (2019) Jstor Global Plants, Ithaka. Available from: https://plants.jstor.org/ (accessed 18 May 2021)

Lessing, C.F. (1829) De synanthereis herbarii regii berolinensis dissertatio prima. Vernonieae. *Linnaea* 4: 240–356.

Linnaeus, C. (1753) *Species plantarum*. Laurentius Salvius, Holmiae [Stockholm], 1200 pp.

Loeuille, B. & Pirani, J.R. (2016) Two new syncephalous species of *Eremanthus* (Asteraceae: Vernonieae) from southeastern Brazil. *Phytotaxa* 243: 128–136.
https://doi.org/10.11646/phytotaxa.243.2.2

Loeuille, B. & Roque, N. (2017) *Maschalostachys*, a new genus of Vernonieae (Asteraceae) from Brazil. *Phytotaxa* 295: 35–48.
https://doi.org/10.11646/phytotaxa.295.1.3

Loeuille, B., Semir, J. & Pirani, J.R. (2012) A new species of *Paralychnophora* (Asteraceae: Vernonieae), and comments on the identity of *Paralychnophora bicolor*. *Brittonia* 64: 289–295.
https://doi.org/10.1007/s12228-012-9245-1

Loeuille, B., Siniscalchi, C.M. & Pirani, J.R. (2014) New names in Vernonieae (Asteraceae) of Northeastern Brazil. *Phytoneuron* 2014-9: 1–11.

Loeuille, B., Semir, J., Lohmann, L.G. & Pirani, J.R. (2015) A phylogenetic analysis of Lychnophorinae (Asteraceae: Vernonieae) based on molecular and morphological data. *Systematic Botany* 40: 299–315.
https://doi.org/10.1600/036364415X686585

Loeuille, B., Semir, J. & Pirani, J.R. (2019) A synopsis of Lychnophorinae (Asteraceae: Vernoniae). *Phytotaxa* 398: 1–139.
https://doi.org/10.11646/phytotaxa.398.1.1

Loeuille, B., Bringel Jr., J.B.D., Faria Jr., JE.Q. & Valls, J.F.M. (2022) Three new species of Lychnophorinae from the Brazilian Central Plateau (Asteraceae: Vernonieae). *Phytotaxa* 531: 249–266.
https://doi.org/10.11646/phytotaxa.531.3.5

Loeuille, B., Castro, M.S., Monge, M., Marques, D., Saavedra, M.M., Angulo, M.B., Volet, D.P., Siniscalchi, C.M., Nakajima, J., Via do

Pico, G.M., Souza-Souza, R.M.B., Soares, P.N., Picanço, W.L., Roque, N., Lorencini, T.S., Rivera, V.L., Semir, J.†, Ribeiro, R.N., Fernandes, F., Esteves, R.L., Dematteis, M. & Heiden, G. (2024) Vernonieae. *In*: *Flora e Funga do Brasil*. Jardim Botânico do Rio de Janeiro. Available from: https://floradobrasil.jbrj.gov.br/FB25247 (accessed 27 June 2024)

MacLeish, N.F.F. (1984) *Argyrovernonia* and *Paralychnophora*: New Names in the Tribe Vernonieae (Asteraceae/Compositae). *Taxon* 33: 105–106.
https://doi.org/10.2307/1222046

Magri, R.A., Cabral, A., Prado, J. & Lopes, J.C. (2024) Two new critically endangered species of *Vellozia* (Velloziaceae) from the *campos rupestres* of Espinhaço Range, Brazil. *Phytotaxa* 652: 1–9.
https://doi.org/10.11646/phytotaxa.652.1.1

Marques, D., Via do Pico, G.M. & Nakajima, J.N. (2018) A new species of *Lychnophora* Mart. (Vernonieae: Asteraceae) from Minas Gerais state, Brazil. *Systematic Botany* 43: 1051–1058.
https://doi.org/10.1600/036364418X697715

Marques, D., Quaresma, A.S., Meyer, P.B. & Nakajima, J. (2021) Flowers to Òsanyìn: *Lychnophora osanyiniana* (Asteraceae: Vernonieae), a new "arnica da serra" from Minas Gerais, Brazil. *Phytotaxa* 491: 57–64.
https://doi.org/10.11646/phytotaxa.491.1.6

Marques, D., Bonfim e Cândido, J., Loeuille, B. & Marzinek, J. (2022) Comparative morphology and anatomy of cypselae in *Piptolepis* (Vernonieae, Asteraceae) with emphasis on the pappus systematic significance. *Flora* 287: e151988.
https://doi.org/10.1016/j.flora.2021.151988

Misra, S. (1957) Floral morphology of the family Compositae. I. The flower and the gametophytes of *Flaveria repanda* Lag. *The Journal of the Indian Botanical Society* 36: 502–512.

Mittermeier, R.A., Turner, W.R., Larsen, F.W., Brooks, T.M. & Gascon, C. (2011) Global biodiversity conservation: the critical role of hotspots. *In*: Zachos, E. & Habel, J.C. (Eds.) *Biodiversity hotspots*. Springer Publishers, London, pp. 3–22.
https://doi.org/10.1007/978-3-642-20992-5_1

Mohr, C. (1901) Plant Life of Alabama. *Contributions from the United States national Herbarium* 6: 1–921.

Müller Argoviensis, J. (1876) Rubiaceae brasilienses novae. *Flora* 59: 433–438.

Pacifico, R., Almeda, F. & Kriebel, R. (2023) *Microlicia delicata* and *Microlicia pumila* (Melastomataceae), two new species from unprotected mountains with *campo rupestre* vegetation in eastern Brazil. *Phytotaxa* 599: 207–224.
https://doi.org/10.11646/phytotaxa.599.4.1

Palazzesi, L., Pellicer, J., Barreda, V.D., Loeuille, B., Mandel, J.R., Pokorny, L., Siniscalchi, C.M., Tellería, M.C., Leitch, I.J. & Hidalgo, O. (2022) Asteraceae as a model system for evolutionary studies: from fossils to genomes. *Botanical Journal of the Linnean Society* 200: 143–164.
https://doi.org/10.1093/botlinnean/boac032

Persoon, C.H. (1807) *Synopsis plantarum: seu enchiridium botanicum complectens enumerationem systematicam specierum hucusque cognitarum*, vol. 2 (2). C.F.Cramer, Paris & J.G.Cotta, Tübingen, 656 pp.

QGIS Development Team (2018) QGIS Geographic Information System. Open Source Geospatial Foundation Project. Available from: https://qgis.org/en/site/ (accessed 23 May 2024)

REFLORA (2024) Reflora-Herbário Virtual Available from: http://reflora.jbrj.gov.br/reflora/herbarioVirtual (accessed 15 May 2024)

Robinson, H. (1992) Notes on Lychnophorinae from Minas Gerais, Brazil, a synopsis of *Lychnophoriopsis* Schultz-Bip., and the new genera *Anteremanthus* and *Minasia* (Vernonieae: Asteraceae). *Proceedings of the Biological Society of Washington* 105: 640–652.

Robinson, H. (1994) *Cololobus*, *Pseudopiptocarpha*, and *Trepadonia*, three new genera from South America (Vernonieae: Asteraceae). *Proceedings of the Biological Society of Washington* 107: 557–568.

Robinson, H. (1999) Generic and subtribal classification of American Vernonieae. *Smithsonian Contributions to Botany* 89: 1–116.
https://doi.org/10.5479/si.0081024X.89

Roque, N. & Bautista, H. (2008) *Asteraceae. Caracterização e Morfologia Floral*. EDUFBA, Salvador, 69 pp.

Roque, N. & Santana, F.A. (2014) A new species for a monotypic genus: *Anteremanthus* (Asteraceae: Vernonieae). *Systematic Botany* 39: 656–661. [http://www.bioone.org/doi/full/10.1600/036364414X680771]

Roque, N. & Sancho, G. (2020) *Vickia*, a new genus of tribe Gochnatieae (Compositae). *Taxon* 69: 668–678.
https://doi.org/10.1002/tax.12283

Roque, N., Ferreira, S.C. & van den Berg, C. (2017a) *Lapidia*, a new monotypic genus of Asteraceae (Eupatorieae) from Brazil, and its phylogenetic placement. *Phytotaxa* 291: 1–16.
https://doi.org/10.11646/phytotaxa.291.1.1

Roque, N., Teles, A.M. & Nakajima, J.N. (2017b) *A família Asteraceae no Brasil: classificação e diversidade*. EDUFBA, Salvador, 260 pp.
https://doi.org/10.7476/9788523219994

Roque, N., Nakajima, J., Heiden, G., Monge, M., Ritter, M.R., Loeuille, B.F.P., Christ, A.L., Rebouças, N.C., Castro, M.S., Saavedra, M.M., Teles, A.M., Gandara, A., Marques, D., Bringel Jr., J.B.A., Angulo, M.B., Santos, J.U.M.D., Souza-Buturi, F.O., Alves, M., Sancho, G., Reis-Silva, G.A., Volet, D.P., Hattori, E.K.O., Plos, A., Simão-Bianchini, R., Rivera, V.L., Magenta, M.A.G., Silva, G.H.L., Abreu, V.H.R., Grossi, M.A., Amorim, V.O., Schneider, A.A., Carneiro, C.R., Borges, R.A.X., Siniscalchi, C.M., Bueno, V.R., Via do Pico, G.M., Almeida, G.S.S., Freitas, F.S., Deble, L.P.; Moreira, G.L.; Contro, F.L., Gutiérrez, D.G., Souza-Souza, R.M.B., Viera Barreto, J.N., Soares, P.N., Quaresma, A.S., Picanço, W.L., Fernandes, F., Mondin, C.A., Salgado, V.G., Kilipper, J.T., Farco, G.E., Ribeiro, R.N., Walter, B.M.T., Lorencini, T.S., Fernandes, A.C., Silva, L.N., Barcelos, L.B., Barbosa, M.L., Bautista, H.P., Casas, J.C., Dematteis, M., Ferreira, S.C., Hiriart, F.D., Moraes, M.D. & Semir, J. (2020) *Asteraceae. In: Florae Funga do Brasil*. Jardim Botânico do Rio de Janeiro. Available from: http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB55 (Accessed 17 August 2024)

Sakai,W.S. (1973) Simple method for differential staining of paraffin embedded plant material using toluidine blue O. *Stain Technology* 48: 247–249.
https://doi.org/10.3109/10520297309116632

Schauer, J.C. (1847) Ordo CXLVII. Verbenaceae. *In:* Candolle, A.L.P. de (Ed.) *Prodromus Systematis Naturalis Regni Vegetabilis, sive enumeratio contracta ordinum generum, specierumque plantarum hucusque cognitarum, juxta methodi naturalis normas digesta*, vol. 11, Victor Masson, Paris, L. Michelsen, Leipzig, pp. 522–700.

Schultz-Bipontinus, C.H. (1863) [1864] *Lychnophora* Martius und einige benachbarte Gattungen. *Jahresbericht der Pollichia, eines Naturwissenschaftlichen Vereins der bayerischen Pfalz* 20/21: 321–439.
https://doi.org/10.5962/bhl.title.46952

Silva, D.N. da, Antonicelli, M.C.A. & Guimarães, P.J.F. (2023) Taxonomic novelties from the Espinhaço Septentrional: two new species of *Pleroma* and the first records of Melastomataceae from the Morro das Marombas, Minas Gerais, Brazil. *Systematic Botany* 48: 44–54.
https://doi.org/10.1600/036364423X16758873924090

Siniscalchi, C.M., Loeuille, B., Semir, J. & Pirani, J.R. (2016) *Lychnophora spiciformis* (Asteraceae: Vernonieae), a new species from Bahia, Brazil. *Phytotaxa* 253: 48–56.
https://doi.org/10.11646/phytotaxa.253.1.3

Siniscalchi, C.M., Loeuille, B., Funk, V.A., Mandel, J.R. & Pirani, J.R. (2019) Phylogenomics yields new insight into relationships within Vernonieae (Asteraceae). *Frontiers in Plant Sciences* 10: 1224.
https://doi.org/10.3389/fpls.2019.01224

Sprengel, [C.]K.[P.J.] (1800) *Der botanische Garten der Universität zu Halle im Jahre 1799*. Bei C.A. Kümmel, Halle, 108 pp.

Small, J. (1927) *Wardaster*: a new genus of the Compositae from the Marches of Yunnan-Szechuan. *Transactions of the Botanical Society of Edinburgh* 29: 230–234.

Stamatakis, A. (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313.

Susanna, A., Baldwin, B.G., Bayer, R.J., Bonifacino, J.M., Garcia Jacas, N., Keeley, S.C., Mandel, J.R., Ortiz, S., Robinson, H. & Stuessy, T.F. (2020) The classification of the Compositae: A tribute to Vicki Ann Funk (1947–2019). *Taxon* 69: 807–814.
https://doi.org/10.1002/tax.12235

Svoma, E., Mayer, V., Stuessy, T.F. & Urtubey, E. (2020) Staminal features in Barnadesioideae (Asteraceae): description, evolution and function. *Botanical Journal of the Linnean Society* 192: 474–497.
https://doi.org/10.1093/botlinnean/boz091

Thiers, B. (2024) 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 2 March 2024).

Triana, J.J. (1871) [1872] Les Mélastomatacées. *Transactions of the Linnean society of London* 18 (1): 1–188.

Vasconcelos, T.N.C., Alcantara, S., Andrino, C.O., Forest, F., Reginato, M., Simon, M.F. & Pirani, J.R. (2020) Fast diversification through a mosaic of evolutionary histories characterizes the endemic flora of ancient Neotropical mountains. *Proceedings of the Royal Society B: Biological Sciences* 287: e20192933.
https://doi.org/10.1098/rspb.2019.2933

Wagner, M. de A., Loeuille, B.P.F., Siniscalchi, C.M., Melo-de-Pinna, G.F. & Pirani, J.R. (2014) Diversity of non-glandular trichomes in subtribe Lychnophorinae (Asteraceae: Vernonieae) and taxonomic implications. *Plant Systematics and Evolution* 300: 1219–1233.
https://doi.org/10.1007/s00606-013-0957-9

Zavatin, D.A., Almeida, R.B.P., Ramos, R. & Lombardi, J.A. (2023) *Chionanthus monteazulensis* (Oleaceae), a new species from the *campo rupestre* of Espinhaço Range, Brazil. *Phytotaxa* 603: 289–296.
https://doi.org/10.11646/phytotaxa.603.3.8

Zhang, C., Rabiee, M., Sayyari, E. & Mirarab, S. (2018) ASTRAL-III: polynomial time species tree reconstruction from partially resolved

gene trees. *BMC Bioinformatics* 19 (Suppl. 6): 153.
https://doi.org/10.1186/s12859-018-2129-y

Zuntini, A.R., Carruthers, T., Maurin, O., Bailey, P.C., Leempoel, K., Brewer, G.E., Epitawalage, N., Françoso, E., Gallego-Paramo, B., McGinnie, C., Negrão, R., Roy, S.R., Simpson, L., Toledo Romero, E., Barber, V.M.A., Botigué, L., Clarkson, J.J., Cowan, R.S., Dodsworth, S., Johnson, M.G., Kim, J.T., Pokorny, L., Wickett, N.J., Antar, G.M., DeBolt, L., Gutierrez, K., Hendriks, K.P., Hoewener, A., Hu, A.-Q., Joyce, E.M., Kikuchi, I.A.B.S., Larridon, I., Larson, D.A., de Lírio, E.J., Liu, J.-X., Malakasi, P., Przelomska, N.A.S., Shah, T., Viruel, J., Allnutt, T.R., Ameka, G.K., Andrew, R.L., Appelhans, M.S., Arista, M., Ariza, M.J., Arroyo, J., Arthan, W., Bachelier, J.B., Bailey, C.D., Barnes, H.F., Barrett, M.D., Barrett, R.L., Bayer, R.J., Bayly, M.J., Biffin, E., Biggs, N., Birch, J.L., Bogarín, D., Borosova, R., Bowles, A.M.C., Boyce, P.C., Bramley, G.L.C., Briggs, M., Broadhurst, L., Brown, G.K., Bruhl, J.J., Bruneau, A., Buerki, S., Burns, E., Byrne, M., Cable, S., Calladine, A., Callmander, M.W., Cano, Á., Cantrill, D.J., Cardinal-McTeague, W.M., Carlsen, M.M., Carruthers, A.J.A., de Castro Mateo, A., Chase, M.W., Chatrou, L.W., Cheek, M., Chen, S., Christenhusz, M.J.M., Christin, P.-A., Clements, M.A., Coffey, S.C., Conran, J.G., Cornejo, X., Couvreur, T.L.P., Cowie, I.D., Csiba, L., Darbyshire, I., Davidse, G., Davies, N.M.J., Davis, A.P., van Dijk, K.-j., Downie, S.R., Duretto, M.F., Duvall, M.R., Edwards, S.L., Eggli, U., Erkens, R.H.J., Escudero, M., de la Estrella, M., Fabriani, F., Fay, M.F., de L. Ferreira, P., Ficinski, S.Z., Fowler, R.M., Frisby, S., Fu, L., Fulcher, T., Galbany-Casals, M., Gardner, E.M., German, D.A., Giaretta, A., Gibernau, M., Gillespie, L.J., González, C.C., Goyder, D.J., Graham, S.W., Grall, A., Green, L., Gunn, B.F., Gutiérrez, D.G., Hackel, J., Haevermans, T., Haigh, A., Hall, J.C., Hall, T., Harrison, M.J., Hatt, S.A., Hidalgo, O., Hodkinson, T.R., Holmes, G.D., Hopkins, H.C.F., Jackson, C.J., James, S.A., Jobson, R.W., Kadereit, G., Kahandawala, I.M., Kainulainen, K., Kato, M., Kellogg, E.A., King, G.J., Klejevskaja, B., Klitgaard, B.B., Klopper, R.R., Knapp, S., Koch, M.A., Leebens-Mack, J.H., Lens, F., Leon, C.J., Léveillé-Bourret, É., Lewis, G.P., Li, D.-Z., Li, L., Liede-Schumann, S., Livshultz, T., Lorence, D., Lu, M., Lu-Irving, P., Luber, J., Lucas, E.J., Luján, M., Lum, M., Macfarlane, T.D., Magdalena, C., Mansano, V.F., Masters, L.E., Mayo, S.J., McColl, K., McDonnell, A.J., McDougall, A.E., McLay, T.G.B., McPherson, H., Meneses, R.I., Merckx, V.S.F.T., Michelangeli, F.A., Mitchell, J.D., Monro, A.K., Moore, M.J., Mueller, T.L., Mummenhoff, K., Munzinger, J., Muriel, P., Murphy, D.J., Nargar, K., Nauheimer, L., Nge, F.J., Nyffeler, R., Orejuela, A., Ortiz, E.M., Palazzesi, L., Peixoto, A.L., Pell, S.K., Pellicer, J., Penneys, D.S., Perez-Escobar, O.A., Persson, C., Pignal, M., Pillon, Y., Pirani, J.R., Plunkett, G.M., Powell, R.F., Prance, G.T., Puglisi, C., Qin, M., Rabeler, R.K., Rees, P.E.J., Renner, M., Roalson, E.H., Rodda, M., Rogers, Z.S., Rokni, S., Rutishauser, R., de Salas, M.F., Schaefer, H., Schley, R.J., Schmidt-Lebuhn, A., Shapcott, A., Al-Shehbaz, I., Shepherd, K.A., Simmons, M.P., Simões, A.O., Simões, A.R.G., Siros, M., Smidt, E.C., Smith, J.F., Snow, N., Soltis, D.E., Soltis, P.S., Soreng, R.J., Sothers, C.A., Starr, J.R., Stevens, P.F., Straub, S.C.K., Struwe, L., Taylor, J.M., Telford, I.R.H., Thornhill, A.H., Tooth, I., Trias-Blasi, A., Udovicic, F., Utteridge, T.M.A., Del Valle, J.C., Verboom, G.A., Vonow, H.P., Vorontsova, M.S., de Vos, J.M., Al-Wattar, N., Waycott, M., Welker, C.A.D., White, A.J., Wieringa, J.J., Williamson, L.T., Wilson, T.C., Wong, S.Y., Woods, L.A., Woods, R., Worboys, S., Xanthos, M., Yang, Y., Zhang, Y.-X., Zhou, M.-Y., Zmarzty, S., Zuloaga, F.O., Antonelli, A., Bellot, S., Crayn, D.M., Grace, O.M., Kersey, P.J., Leitch, I.J., Sauquet, H., Smith, S.A., Eiserhardt, W.L., Forest, F. & Baker, W.J. (2024) Phylogenomics and the rise of the angiosperms. *Nature* 629: 843–850.
https://doi.org/10.1038/s41586-024-07324-0