MONOGRAPH



Systematics of the Trembleya sensu stricto clade of Microlicia (Melastomataceae, Lavoisiereae)

Ricardo Pacifico^{1,2}, Frank Almeda², Darin S. Penneys³, Karina Fidanza⁴

I Universidade Estadual de Maringá, Programa de Pós-Graduação em Biologia Comparada. Av. Colombo, 5790, 87020-900 Maringá, Paraná, Brazil 2 California Academy of Sciences, Institute for Biodiversity Science and Sustainability, Department of Botany, 55 Music Concourse Drive, Golden Gate Park, San Francisco, California 94118-4503, USA 3 Department of Biology and Marine Biology, University of North Carolina Wilmington, North Carolina 28403, USA 4 Departamento de Biologia, Universidade Estadual de Maringá, Av. Colombo, 5790, Jardim Universitário, CEP 87020-900, Maringá, Paraná, Brazil

Corresponding author: Ricardo Pacifico (ricardo_b9@hotmail.com)

Academic editor: Marcelo Reginato | Received 29 July 2022 | Accepted 25 October 2022 | Published 20 December 2022

Citation: Pacifico R, Almeda F, Penneys DS, Fidanza K (2022) Systematics of the *Trembleya* sensu stricto clade of *Microlicia* (Melastomataceae, Lavoisiereae). PhytoKeys 126: 1–101. https://doi.org/10.3897/phytokeys.126.91032

Abstract

A systematic monograph of the *Trembleya* s.s. clade is presented, a Brazilian endemic lineage of Melastomataceae comprising 11 species and currently recognised as part of *Microlicia* s.l. (Melastomataceae). First, we investigate phylogenetic relationships within Lavoisiereae using two nuclear markers and two sampling datasets (102 and 134 terminals). Then, we provide a systematic revision and new circumscription of the *Trembleya* s.s. clade, including line drawings, photos of living specimens, leaves and floral parts, distribution maps, a key to the 11 accepted species, comments on morphology, reproductive biology, richness, endemism, biogeography and recommended conservation assessments. A nomenclatural update of all taxa previously treated in *Trembleya* is also provided, including the designation of 45 lectotypes and the proposal of 38 new synonyms.

Keywords

Brazil, Cadeia do Espinhaço, campo rupestre, Endemism, Minas Gerais

Introduction

Melastomataceae Juss. comprises about 5,880 species in 173 genera with about twothirds of this diversity restricted to the neotropics (Ulloa Ulloa et al. 2022). Brazil is the most diverse country with 69 genera and about 1440 species and the family is represented in all Brazilian biomes except for the Caatinga *sensu stricto* (Goldenberg et al. 2020). The most comprehensive treatments of Brazilian Melastomataceae were produced by Cogniaux (1883–1888, 1891) in "Flora Brasiliensis", which were largely based on tribal concepts proposed by Triana (1872). During the last century, the family has been treated in many regional "Floras" and several genera and numerous new species of Brazilian Melastomataceae were described (Goldenberg et al. 2012). Although the work of Cogniaux (1883–1888) has long been the primary global reference for the family, a new familial treatment for Brazil was recently published, including morphological descriptions and keys to all Brazilian genera and species (Goldenberg et al. 2020), as part of the ambitious Brazilian Flora 2020 (BFG 2022).

As compared to the treatment in "Flora Brasiliensis", the most recent infrafamilial classifications of Melastomataceae show significant improvements. Based on DNA sequence data, several new Neotropical tribes have been delimited, i.e. Henrietteeae Penneys, Michelang., Judd & Almeda (Penneys et al. 2010), Marcetieae M.J.Rocha, P.J.F.Guim. & Michelang. (Rocha et al. 2018), Pyramieae Naudin (as Cambessedesieae Bochorny, Almeda, Michelang. & R.Goldenb.) (Bochorny et al. 2019), Rupestreeae Penneys & R.Goldenb., Stanmarkieae Penneys & Almeda (Penneys et al. 2022), Trioleneae Bacci, Michelang. & R.Goldenb. (Bacci et al. 2019), Eriocnemeae Penneys & Almeda and Lithobieae Penneys & Almeda (Penneys et al. 2020). Some new genera have also proposed, for example, Rupestrea R.Goldenb., Almeda & Michelang. (Goldenberg et al. 2015), Physeterostemon R.Goldenb. & Amorim (Goldenberg and Amorim 2006), Brasilianthus Almeda & Michelang. (Almeda et al. 2016) and others were relegated to synonymy (for example, see Penneys and Judd 2013 and Bochorny et al. 2019); and there are still unplaced clades and genera that need to be tested for monophyly (Penneys et al. 2022). Meanwhile, many new species are still being described from little-studied genera and/or resulting from fieldwork in areas that remain poorly known or underexplored botanically.

With about 275-300 species, the near-endemic Brazilian tribe Lavoisiereae DC., which has long been known by the later tribal name Microlicieae Naudin, is one of the richest clades of Neotropical Melastomataceae (Fritsch et al. 2004; Versiane et al. 2021; Pacifico and Almeda 2022). Currently, three genera are accepted, i.e. Rhynchanthera DC. (15 spp.; Renner 1990), Poteranthera Bong. (5 spp.; Kriebel 2012; Almeda and Pacifico 2018) and Microlicia D.Don (ca. 250 spp.; Versiane et al. 2021; Pacifico and Almeda 2022). However, this tribe has a complex taxonomic history and its current generic delimitation has been drastically modified in light of molecular evidence (Fritsch et al. 2004; Rocha et al. 2016; Versiane et al. 2021). Based on rpl16 and nrITS data, Fritsch et al. (2004) found support for the restriction of Lavoisiereae to the six genera previously enumerated by Almeda and Martins (2001). In turn, phylogenetic analyses of Rocha et al. (2016) were decisive in assigning *Poteranthera* to the tribe where it had been placed by Triana (1872) and several other early classifications, thus resulting in the recognition of seven genera in Lavoisiereae. Major taxonomic alterations were proposed by Versiane et al. (2021), who included four traditionally recognised genera (Chaetostoma DC., Lavoisiera DC., Stenodon Naudin, Trembleya DC.) in a broadly

circumscribed *Microlicia* s.l. Versiane et al. (2021) recovered little support for most clades within *Microlicia* s.l., whereas some internal clades were strongly supported and are recognisable morphologically, e.g. the "*Trembleya* s.s." "*Lavoisiera*" and "*Chaetosto-ma*" clades (Koschnitzke and Martins 2006; Martins and Almeda 2017; Pacifico et al. 2019; Versiane et al. 2021). For a complete taxonomic history of the tribe, see Martins and Almeda (2017: 32–34) and Pacifico and Almeda (2022).

Trembleya s.s. is one of the clades currently recognised as part of *Microlicia* s.l. (Versiane et al. 2021; Pacifico and Almeda 2022). We here re-evaluate the status of this lineage in a phylogenetic context and provide a systematic revision and new circumscription of the *Trembleya* s.s. clade. Line drawings, photos of living specimens, leaves and floral parts, distribution maps, a complete nomenclatural update, comments on morphology, reproductive biology, richness, endemism, biogeography and conservation are also provided.

Historical background

Trembleya was named by Augustin Pyramus de Candolle (1778–1841) in honour of the members of the family Trembley for their contributions to several fields of science (Candolle 1828: 125). At that time, the genus was represented by six species, all of which were described, based on the collections made by Carl Friedrich Philipp von Martius in Brazil (Spix and Martius 1824). Candolle (1828: 114) placed *Trembleya* along with other 13 genera in the tribe Rhexieae DC. This arrangement changed about two decades later when Charles Victor Naudin (1818–1889) assigned this genus to the tribe Lavoisiereae (as "Microliciales") (Naudin 1849: 203). *Trembleya* was maintained in the tribe Lavoisiereae (as "Microliciae") in subsequent treatments of Melastomataceae like those by Triana (1872) and Cogniaux (1883–1888, 1891).

Trembleya was recognised as a heterogeneous group of species since it was first delimited by Candolle (1828), who recognised three morpho-groups. Three sections were proposed, two of which were named in honour of members of the Trembley family (Candolle 1828). The section *Jacobia* DC. was named after Jacob Trembley and the section *Abrahamia* DC. was named after Abraham Trembley (Candolle 1828: 125–126). The remaining section, composed of only *Trembleya lycnithis* DC. [= *Microlicia laniflora* (D.Don) Baill.], was named *Erioleuca* DC. in reference to the lanose appearance of this species (Candolle 1828: 126). Candolle (1828b: 38) also claimed that these three sections could one day either be brought together through more nuanced intermediaries or separated into three distinct genera.

Chamisso (1834) followed Candolle's infrageneric classification and described two new species in the genus: *Trembleya pithyoides* Cham. in section *Jacobia* and *Trembleya calycina* Cham. in sect. *Abrahamia*. Naudin (1849: 264) agreed with Candolle (1828) on the polymorphic aspect of *Trembleya*, considering it a "genus habitu specierum omnino *heteromorphum*" [genus in which the habit is highly heteromorphic amongst species]. Naudin (1849) reformulated the infra-generic classification of the genus under two new sections, *Trembleya* sect. *Verae* Naudin and *Trembleya* sect. *Heterogenae* Naudin. In "Flora Brasiliensis", Cogniaux (1883–1888) mostly maintained the sections proposed by Naudin (1849). *Trembleya* sect. *Trembleya* Cogn. contained the same species of *Trembleya* attributed to sect. *Verae*, but included two taxa that were not available for study in Paris by Naudin, *Trembleya chamissoana* Naudin and *Trembleya rosmarinoides* Mart. & Schrank ex DC. In addition, Cogniaux (1883–1888) resurrected Candolle's monotypic section *Erioleuca*, which included only *Trembleya laniflora*. The section *Heterogenae* was also maintained by Cogniaux (1883–1888), who included three additional species that were described after Naudin's monographs, *Trembleya selloana* Cogn., *Trembleya warmingii* Cogn. and *Trembleya pradosiana* Netto.

Renner (1990: 609) stated that *Trembleya* was "an assemblage of species differing greatly in habit and pubescence". Martins (1995) described another species, *Trembleya hatschbachii* Wurdack & E.Martins. In the unpublished monograph of *Trembleya* by Martins (1997), 18 species were recognised (several never validly published) and three dubious taxa were noted. Martins (1997) did not recognise any of the infrageneric sections previously proposed in the genus.

Martins (1997) made a special effort to understand the supra-generic delimitation of *Trembleya*. She emphasised that the number of ovary locules was the only feature used by Cogniaux (1883–1888) to differentiate this genus from *Microlicia* D.Don (3-locular in *Microlicia* and 5-locular in *Trembleya*). In this context, a major objective of Martins (1997) was to clarify the limits between *Trembleya* and *Microlicia*. Based on comparative morphology, Martins (1997) proposed an expanded re-circumscription of *Trembleya*, which was based on characters, such as inflorescence structure, vegetative architecture and leaf venation patterns. However, Martins (1997) recognised that none of these features could differentiate *Trembleya* from *Microlicia* in an effective way (Martins 1997). Besides, Martins (1997) mentioned taxa with overlapping features, such as *Microlicia pabstii* Brade, that has leaves with evident secondary venation, a feature attributed only to *Trembleya* (sensu Martins 1997) and isolated axillary flowers, a typical feature of *Microlicia* (Martins 1997).

Fritsch et al. (2004) confirmed the placement of *Trembleya* in Lavoisiereae using molecular data. Subsequently, new species were described in *Trembleya* by Fidanza et al. (2013), Pacifico and Fidanza (2015) and Pacifico et al. (2019). Additionally, one species was transferred from *Lavoisiera* DC. to *Trembleya* by Almeda and Martins (2001) [*Trembleya elegans* (Cogn.) Almeda & A.B.Martins], and another was transferred from *Trembleya* to *Poteranthera* by Almeda and Pacifico (2018) [*Poteranthera warmingii* (Cogn.) Almeda & R.B.Pacifico]. Pacifico et al. (2019) argued that *Trembleya* was polyphyletic and a new circumscription was necessary in order to reduce this genus to a monophyletic group of 11 species (*Trembleya* s.s.).

Based on an expanded phylogenetic analyses using five molecular markers (atpFatpH, trnS-trnG, nrITS, nrETS and waxy) and 12 morphological characters for 113 taxa in Lavoisiereae, Versiane et al. (2021) transferred all species of *Trembleya* to the enlarged *Microlicia* s.l. In order to accommodate these species in *Microlicia*, Versiane et al. (2021) proposed 13 new combinations [*M. altoparaisensis* (R.B.Pacifico, Fidanza & Almeda) Versiane & R.Romero, *M. calycina* (Cham.) Versiane & R.Romero, *M. chamis*- soana (Naudin) Versiane & R.Romero, *M. inversa* (Fidanza, A.B.Martins & Almeda) Versiane & R.Romero, *M. neopyrenaica* (Naudin) Versiane & R.Romero, *M. parviflora* (D.Don) Versiane & R.Romero, *M. pentagona* (Naudin) Versiane & R.Romero, *M. phlogiformis* (Mart. & Schrank ex DC.) Versiane & R.Romero, *M. pithyoides* (Cham.) Versiane & R.Romero, *M. pradosiana* (Netto) Versiane & R.Romero, *M. rosmarinoides* (Mart. & Schrank ex DC.) Versiane & R.Romero, *M. thomazii* (R.B.Pacifico & Fidanza) Versiane & R.Romero, *M. tridentata* (Naudin) Versiane & R.Romero]] and three new names [*M. acuminifolia* Versiane & R.Romero, *M. flaviflora* Versiane & R.Romero, *M. serratifolia* Versiane & R.Romero], whereas *M. laniflora* (D.Don) Baill. was reinstated. The analyses of Versiane et al. (2021) also supported the recognition of *Trembleya* s.s. as a distinct clade, as previously suggested by Pacifico et al. (2019). Although recognisable morphologically, the *Trembleya* s.s. clade was transferred to *Microlicia* by Versiane et al. (2021) because the recognition of that clade as a distinct genus would make *Microlicia* s.l. paraphyletic. This issue is also re-evaluated in the present study.

Material and methods

Taxa sampling and DNA extraction

To investigate phylogenetic relationships in Lavoisiereae, we used two different datasets including samples from the seven genera traditionally recognised in the tribe (Almeda and Martins 2001; Fritsch et al. 2004). Dataset A comprised samples with complete sequences (i.e. fitting perfectly the alignment on both ends) of both nrITS and nrETS. This dataset had 102 terminals, representing 99 species (ingroup, 91 species; eight species are outgroups). Dataset B comprised samples with complete nrITS and nrETS sequences, but also samples lacking sequences of one of these markers and/or partial sequences, including 134 terminals representing a total of 131 species (ingroup, 127 species; four species are outgroups). Overall, taking the two datasets into consideration, 247 sequences were generated for this study (125 nrITS plus 122 nrETS; total of 131 species). Eight sequences were retrieved from GenBank and added to the alignment (seven nrETS plus one nrITS; total of seven species). For information on specimen vouchers and GenBank accessions, see Suppl. material 1.

Total genomic DNA was extracted from silica-dried leaves or from herbarium specimens. DNA extraction was performed mainly using Qiagen DNeasy plant kits, following the manufacturer's recommendations (https://www.qiagen.com/) or modified to extend the incubation time in AP1 Buffer and RNAase to 1 hour, followed by 1 hour of precipitation in ice. A few samples were extracted using the modified CTAB (hexadecyltrimethylammonium bromide) protocol of Doyle and Doyle (1987). Leaves were ground in a mixer mill, incubated in 1.2 ml CTAB and 5 μ l of Proteinase K for 60–180 minutes at 55 °C. DNA was precipitated overnight in isopropanol and sodium acetate at -20 °C, centrifuged at 13,000 rpm for 20 minutes, washed twice

with 70% ethanol and dried at room temperature. The pellets with DNA were then resuspended in 100 μ l of 1× TE (tris-EDTA buffer, pH 8.5) and incubated at 55 °C for about 30 minutes.

PCR and DNA sequencing

We amplified and sequenced the ribosomal markers nrETS and nrITS. In Melastomataceae, the nrETS region has been used by Kriebel et al. (2015), Rocha et al. (2016), Bacci et al. (2020) and Versiane et al. (2021). The nrITS is widely used in phylogenetic studies of the family (e.g. Ionta et al. 2007; Penneys and Judd 2013; Reginato and Michelangeli 2016; Zhou et al. 2018). Information on the primers used in this study may be found in the aforementioned literature. The PCR recipes were: (1) for nrETS, 1.5 µl of Buffer 10×, 0.9 µl of MgCl, 25 uM, 0.3 µl of each primer (10 uM), 0.3 µl of dNTP (10 uM), 0.3 µl of Hotstart Taq polymerase (1.25 uM) and 1 µl of template, reaching 15 µl of final reaction; (2) for nrITS, the recipe was similar to (1), but differed in including 1.2 µl of BSA (10 uM) and using Invitrogen Taq polymerase to improve the performance. The thermocycler programmes were: (1) for nrETS initial denaturation at 95 °C for 2 minutes, 40 cycles of denaturation at 94 °C for 30 seconds, annealing at 58 °C for 30 seconds; extension at 72 °C for 1 minute and final extension at 72 °C for 7 minutes; (2) for nrITS, initial denaturation at 94 °C for 5 minutes, 40 cycles of denaturation at 94 °C for 10 seconds; annealing at 61 °C for 45 seconds; extension at 72 °C for 40 seconds and final extension at 72 °C for 10 minutes. The quality of amplifications was verified in agarose electrophoresis gel. The amplified fragments were cleaned using 5 µl of PCR products (7 µl for weak bands) and 2 µl of diluted ExoSAP-IT. The PCR cleaning was performed by incubating the samples at 37 °C for 30 minutes and 80 °C for 15 minutes. Cycle sequencing was performed by using the same amplification primers. The thermocycler programme used for cycle sequencing began at 96 °C for 60 sec, followed by 15 cycles of 10 sec at 96 °C, 5 sec at 50 °C and 75 sec at 60 °C; another 5 cycles of 10 sec at 96 °C, 5 sec at 50 °C, 90 sec at 60 °C; 5 sec at 50 °C and 120 sec at 60 °C. The Sanger Sequencing was performed in an ABI 3130 Genetic Analyzer in the Center for Comparative Genomics at the California Academy of Sciences, San Francisco, CA. GenBank accessions for all sequences used in this study are provided in Suppl. material 1.

Phylogenetic analyses

Contigs were assembled and edited using Geneious 11.0 (https://www.geneious.com). The same software was employed to align (using Muscle algorithm), concatenate and export the sequences as fasta files. Low-quality sequences were discarded. Final manual edits on the alignment were performed using Mega 7 (Kumar et al. 2016). Maximum Likelihood (ML) and Bayesian Inference (BI) phylogenetic analyses were performed using ML. All analyses were run through the CIPRES online gateway (http://www.phylo.org/; Miller et al. 2012) as four independent partitions (*nrETS*, *ITS1*, *5.8S* and

ITS2). The ML analyses were performed using a fast Maximum Likelihood tree search algorithm (RAxML, Stamatakis 2014) with the GTR+ Γ +I model and 1,000 bootstrap repetitions. The BI analysis was performed with MrBayes version v.3.2.6 using the same model (GTR+ Γ +I), which was employed for being the most parameter-rich (see Abadi et al. 2019). BI analyses consisted of two independent runs, each one with one cold and three heated simultaneous independent Markov chains. A total 15,000,000 generations were carried out, sampling one tree every 1000 generations and discarding 25% of the sampled trees as burn-in. A node was considered to be strongly supported if it showed both a Bayesian Posterior Probability \geq 0.95 and a Bootstrap Support \geq 70%.

Taxonomic study

Specimens of all species of the *Trembleya* s.s. clade were examined. This study was carried out using collections from the following herbaria: BM, BR, C, CAS, CESJ, ESA, F, G, GH, HB, HUEM, INPA, K, L, M, MBM, MO, NY, P, R, RB, S, SPF, UEC, US and W (acronyms follow Thiers 2022). Specimens of some of the mentioned herbaria were examined only through online images (BM, C, CESJ, ESA, G, GH, INPA, L, M, MO and S). All types and their synonyms were examined directly or through online images available from databases, for example, JSTOR Global Plants (https://plants.jstor.org/) and SpeciesLink (http://www.splink.org.br/). A list with all specimens cited in this study is provided in Appendix 1.

Populations of all but two species (*M. rosmarinoides* and *M. trembleyiformis*) of the *Trembleya* s.s. clade were sampled in the field during several expeditions carried out by the authors, mainly in the following regions of Brazil: Serra do Cipó, Serra do Cabral, Serra do Bota, Serra de Grão Mogol, Serra do Caraça, Serra do Gandarela, Serra de Ouro Preto and on the Diamantina Plateau (in Minas Gerais State), Chapada Diamantina (Bahia State), Chapada dos Veadeiros and Serra dos Pirineus (Goiás State) and Parque Estadual do Guartelá (Paraná State). All specimen identifications were carefully checked by the authors. We considered one specimen as a putative hybrid between *M. pentagona* and *M. laniflora* because it clearly intermixes characters between these two species and was collected in an area where they occur sympatrically.

The morphological diagnosis was based on a comparative study of species in the clade and all remaining taxa within Lavoisiereae. Species descriptions, lists of specimens examined and circular histograms of phenology were prepared using the functions "TabletoDescription", "Collector List" and "PhenoHist" (respectively), available from the package monographaR implemented in R (Reginato 2016). Herbarium specimens were also the source of all distributional data used in this study. All coordinates obtained from specimen labels were mapped to verify if they matched the locality described.

SEM images

Scanning Electron Microscope (SEM) photos were taken from herbarium specimens. Sections of leaf blades (all species in the clade), anthers (four species), seeds (five species) and pollen grains (*M. pithyoides*) were affixed using double-stick tape on pin stubs, sputter-coated with gold and examined using a Hitachi SU3500 microscope with coupled digital camera in the SEM Lab of the California Academy of Sciences, San Francisco, CA.

Anatomical studies

Dried leaves of *M. altoparaisensis, M. chamissoana* and *M. flaviflora* were obtained from exsiccatae (housed in HUEM), rehydrated in sodium hydroxide (NaOH) 5% (Anderson 1963, modified) and stored in 70% methyl alcohol (Johansen 1940). Epidermal dissociation was performed either using acetic acid and hydrogen peroxide (1:1) (Franklin 1945) or 10% nitric acid and 10% chromic acid (1:1) (Johansen 1940). Epidermal sections were stained using Safranine and Astra blue (Bukatsch 1972) and mounted in glycerine 50% (Kraus and Arduin 1997). Samples of the leaf blade were embedded in historesin (2-hydroxyethylmethacrylate). Cross and longitudinal sections of the leaf blade (7 μ m) were obtained using a rotary microtome and stained with 0.05% toluidine blue, acetate buffer at pH 4.7 (O'Brien et al. 1965, modified). Light micrographs were taken using a Leica EZ4D digital camera in the Department of Biology of the Universidade Estadual de Maringá.

Biogeography and mapping

Species richness and weight endemism analyses were run in R through the Dinamica Ego platform (http://www.dinamicaego.com) using the tools "SR" and "WE" from the toolkit BioDinamica 2.2 (Oliveira et al. 2019). In both cases, the distributional data were saved as a csv file and analysed by employing a grid of hexagons in which the distances amongst centroids were 1°. We delimited the main area of endemism for the Tremb*leya* s.s clade based on endemicity analyses implemented in the NDM/VNDM software (Szumik et al. 2002; Szumik and Goloboff 2004). A spreadsheet with the distributional data was saved as a csv file and converted into a xyd file using the GeX online tool (http:// gex.mfuhlendorf.com/ (Santos and Fuhlendorf 2018). In NDM/VNDM, we used a grid of 1° cells and searched for Areas of Endemism with 1000 repetitions. Only individual areas of endemism with scores equal to or higher than 2 were considered and overlapping subsets were kept only if they had at least 40% unique species. The consensus area of endemism was obtained using the loose consensus rule and a cut-off value of 40% (see Aagesen et al. 2013). Coordinates of the consensus area were exported from NDM/VNDM as a text file and converted into a shapefile using DIVA-GIS (Hijmans et al. 2001). All maps were prepared using QGIS 3.14 software (QGIS Development Team 2021).

Conservation assessments

Following the guidelines of criterion B of IUCN (2019), we provide informal conservation status recommendations for each species, based on georeferenced data from herbarium material. GeoCAT (Bachman et al. 2011) was used to calculate Extent of Occurrence (EOO) and Area of Occupancy (AOO) for each species using a user-defined cell width of 2 km. We are aware that the AOO is often inappropriately used for conservation assessments, as most plant species are represented in herbaria by only a few specimens, thereby underestimating the AOO (Lughadha et al. 2019). For Lavoisiereae, our field experience showed that most species in this tribe are often represented only by a few populations restricted to rocky outcrops on a shallow layer of white quartzitic soil. These populations usually occupy an area smaller than 4 km²; thus, we believe that the cell width of 2 km is appropriate for these analyses.

Results and discussion

Molecular phylogenetics

The aligned matrix of the combined nrETS+nrITS contains 1435 characters. In all analyses, Lavoisiereae was recovered as monophyletic with strong statistical support, in agreement with the analyses of Fritsch et al. (2004) and Versiane et al. (2021). *Rhynchanthera* was recovered as the first diverging lineage (as reported by Fritsch et al. 2004 and Versiane et al. 2021), followed by *Poteranthera* and *Microlicia* s.l. (in agreement with Versiane et al. 2021; Figs 1, 2). In this context, even with the inclu-



Figure 1. Maximum Likelihood (left) and Bayesian Inference (right) trees of Lavoisiereae, based on analyses of nrITS+nrETS sequences using dataset A. Bootstrap support values \geq 70% and Bayesian Posterior Probability values \geq 0.9 are given at each node.



Figure 1. Continued.

sion of *Poteranthera* by Rocha et al. (2016), the Lavoisiereae can be distinguished amongst other capsular-fruited Melastomataceae by its elongate to reniform seeds with a reticulate-foveolate testa, stamens forming well-developed pedoconnectives and anthers with rostrate thecae (Fritsch et al. 2004; Rocha et al. 2016; Pacifico and Almeda 2022).

Overall, species traditionally recognised in *Trembleya* (for example, by Cogniaux 1883–1888, 1891 and Martins 1997) were recovered in three distinct regions of the Lavoisiereae tree. Using the dataset A, a clade composed exclusively of species of *Trembleya* s.s. was recovered as sister to the rest of *Microlicia* s.l. in the ML tree, with a Bootstrap Support of 70% (Fig. 1). However, this sister relationship was unresolved in the BI tree (Fig. 1). Several clades within *Microlicia* s.l. had low topological resolution in all analyses and especially using dataset B (Fig. 2).

The analyses of nrETS and nrITS resulted in incompletely resolved trees with several weakly-supported clades, making it impossible to evaluate the monophyly of most clades within *Microlicia* s.l. This was expected since these lineages have been recovered with very short branch lengths in family-level phylogenetic analyses, based on the multi-loci approach that used a larger sampling of Melastomataceae (Penneys et al. 2022). However, a clade that is diagnosable morphologically and is a good match to *Trembleya* s.s. of Pacifico et al. (2019) was identified. The recovery of this clade as sister to the remaining *Microlicia* s.l. in the ML tree, based on complete nrETS and nrITS sequences, suggests that this group of species could be treated as a distinct genus. This taxonomic decision was neither confirmed nor refuted by both the BI tree using dataset A and the ML tree using dataset B. Thus, we here tentatively treat the *Trembleya* s.s. clade as part of *Microlicia*. Future studies using enhanced taxonomic characters may provide a definitive assessment of the limits between this clade and *Microlicia* s.l.

General characterisation

Habit and branching

Species of the *Trembleya* s.s. clade are woody and perennial erect shrubs, usually 0.5–2 m tall, small trees 2.5–4 m tall (e.g. *M. laniflora* and *M. parviflora*) or caespitose shrubs (e.g. *M. pithyoides* and *M. rosmarinoides*). Species can be highly variable in habit, like *M. laniflora*, which is typically a small tree (1.7–2.5 m tall), but may also be a shrub up to 0.8 m tall with divaricate branching (Fig. 3). Both forms may occur in the same population. The small trees of *M. laniflora* stand out by having a single trunk with corky bark. Variation in habit is also common in the wide-spread *M. parviflora*, generally from small shrubs ca. 0.5 m tall to small trees to 3–4 m tall. On the Serra do Cipó (Minas Gerais), a "dwarf" specimen of *M. chamis*-



Figure 2. Maximum Likelihood tree of Lavoisiereae, based on analyses of nrITS+nrETS sequences using dataset B. Bootstrap support values ≥ 70% at each node.





soana measuring about 10 cm tall when flowering was collected once (*Giulietti et al CFSC12492*). The branching pattern in the *Trembleya* s.s. clade is consistently di-trichotomic, with quadrangular branchlets that are unwinged or have narrow wings ca. 0.2 mm wide. The branchlets are typically glandular-punctate and may be covered by other types of trichomes of variable type and distribution. Unlike many taxa of the *Lavoisiera* clade of *Microlicia* s.l. (Martins and Almeda 2017), all species in the *Trembleya* s.s. clade do not present conspicuous scars where the leaf has fallen away.



Figure 3. Habit in the *Trembleya* s.s. clade of *Microlicia* **A** Celso de Paiva (ICMBio) taking a picture of a small *M. laniflora* tree **B** *M. parviflora*, small tree **C** *M. laniflora* with divaricate habit **D** *M. chamissoana* with divaricate habit **E** *M. rosmarinoides*, a small, much-branched shrub **F, G** Saxicolous shrubs: **F** *M. fla-viflora* **G** *M. pentagona*. Photos: **A** by O. Graeff **B** by R. Penati **C, E** by L. Pedrosa **D, F, G** by R. Pacifico.

Root and stem anatomy and development

Information on root and stem anatomy and development is limited to the study of Somavilla and Graciano-Ribeiro (2012) on *M. parviflora*. The roots of *M. parviflora* have a uniseriate epidermis with outer periclinal walls and part of the anticlinal walls thickened and the cuticle thinner than the outer periclinal wall. In more developed roots, the epidermis is replaced by exodermis (Somavilla and Graciano-Ribeiro 2012). Likewise, the stems of *M. parviflora* have a uniseriate epidermis with outer periclinal walls slightly thickened and covered by a cuticle (Somavilla and Graciano-Ribeiro 2012). The cortex and the centre of the stems are separated by an endodermis layer and the central part of the cortex has large intercellular spaces (Somavilla and Graciano-Ribeiro 2012). The pericycle consists of 1–2 layers of parenchymatic cells surrounding the vascular system and the pith is parenchymatic (Somavilla and Graciano-Ribeiro 2012).

Microlicia parviflora stands out by having a spiralled aerenchymatous polyderm surrounding the root and stem (Somavilla and Graciano-Ribeiro 2012). In this species, the secondary growth of the stems and roots starts with the development of the vascular cambium, as well as the phellogen from pericycle cells. Derivative cells from phellogen then differentiate externally into two cell types disposed in concentric layers and centrifugally intercalated (Somavilla and Graciano-Ribeiro 2012). The one-layered phelloderm is produced centripetally by the phellogen (Somavilla and Graciano-Ribeiro 2012).

Leaf morphology

Leaf shape is highly variable and, together with indumentum and venation, it is one of the most taxonomically informative characters in the Trembleya s.s. clade (Fig. 4). Leaves are opposite and decussate like most Melastomataceae, highly variable in size along the branches and usually not imbricate. All species of the Trembleya s.s. clade have petiole features that are shared in a consistent way only with Rhynchanthera (see Renner 1990). The leaf blades vary from linear to oblong, lanceolate, narrowlyelliptical, elliptical, ovate or rarely slightly obovate. Leaf consistency varies from papyraceous to chartaceous or coriaceous. In 10 out of 11 species recognised in the Trembleya s.s. clade, the leaf blades become strongly discoloured when dry. The blade is usually plane throughout, although (when dry), the marginal region may become slightly revolute (in three species) or conspicuously revolute in M. calycina. The leaf blade is never keeled like it is in species of the Chaetostoma clade (Koschnitzke and Martins 2006). The leaf margin is entire, slightly serrulate or entire along the basal half and serrulate at the upper half; it lacks the stout glandular trichomes typical of Poteranthera (Almeda and Pacifico 2018). It is also not callose-thickened like in most species of the Lavoisiera clade (Martins and Almeda 2017). The leaves always have 1-3 primary basal veins and two or more pairs of secondary basal acrodromous veins (see Carmo et al. 2019). In most species, the most external pair of acrodromal veins is tenuous and positioned close to the leaf margin. Ten out of 11 species have tertiary veins more or less evident on the abaxial leaf surface, which are arranged nearly perpendicular to the mid-vein and may branch randomly or only apically.



Figure 4. Leaves in the Trembleya s.s. clade of Microlicia in abaxial view A M. tridentata B M. altoparaisensis C-E M. pentagona F M. rosmarinoides G M. pithyoides H M. flaviflora I M. laniflora J M. parviflora K M. trembleyiformis L M. calycina M M. chamissoana. Voucher specimens: A Longhi-Wagner et al. CFCR9184 (SPF, UEC, US) B Glaziou 21300 (F, P, S) C Barreto 10734 (BHCB) D Barreto 7025 (BHCB) E Rapini et al. 296 (HUEM, SP, SPF) F Souza et al. 2584 (BHCB) G Pacifico 295 (CAS, HUEM, SPF) H Hatschbach et al. 52005 (S) I Pacifico 185 (HUEM, SPF) J Pacifico 191 (HUEM) K Romero & Nakajima 3593 (HUFU, K, UEC) L Pacifico 290 (CAS, SPF) M Romero et al. 8627 (HUEM, HUFU, RB).

When mature, the leaf adaxial surface is always glandular-punctate to glabrescent. The abaxial surface is always glandular-punctate and often covered with other types of trichomes.

Leaf anatomy and indumentum

Information on leaf anatomy is available for *M. altoparaisensis* (Pacifico et al. 2019), *M. calycina* (Pflaum 1897), *M. chamissoana* (Carmo et al. 2019, 2020), *M. laniflora* (Pflaum 1897; Silva et al. 2018), *M. parviflora* (Pflaum 1897; Somavilla and Graciano-Ribeiro 2011), *M. flaviflora* (Carmo et al. 2019, 2020), *M. pithyoides*

(Pflaum 1897), M. rosmarinoides (Pflaum 1897) and M. tridentata (Pflaum 1897). A plate with photos of leaf anatomical characters is presented in Fig. 5 (A-F). Overall, the leaf epidermis is uniseriate with outer periclinal walls thicker than the other walls. The adaxial epidermal cells have straight to slightly sinuous walls in top view, while the abaxial epidermal cells have walls varying from straight to sinuous (Fig. 5C). Microlicia altoparaisensis has amphistomatic leaves, while the remaining four species have hypostomatic leaves. Cuticle striation was reported for M. chamissoana and M. flaviflora. In cross-section, the petiole has an ovate or arched shape, 3-5 bicollateral or amphicribal vascular bundles (Fig. 5E) and collenchyma in the cortical region. The mesophyll varies from isobilateral (Fig. 5B) to dorsiventral or mixed, always with palisade parenchyma as the cortical tissue and the mid-rib projected. The shape of the mid-rib varies from arched to open arched, with bicollateral or amphicribral vascular bundles (Fig. 5A) and parenchyma and/ or collenchyma at the cortical region. Sclereids and crystalliferous cells generally occur in the petiole, mesophyll and mid-rib. In M. flaviflora and M. chamissoana, the veinlets have imperfect areoles and terminal sclereids and the apical venation is not ramified (fig. 5C in Carmo et al. 2019). In the marginal region, the venation is incomplete in *M. flaviflora* and arch-shaped in *M. chamissoana* (fig. 5E in Carmo et al. 2019).

All species of the *Trembleya* s.s. clade have some type of trichome on the leaves, branchlets and abaxial leaf surfaces. Scanning Electronic Microscopy images showing details of the leaf surface in the clade are presented in Figs 6–7. The common glandular-punctate indumentum consists of a set of glandular trichomes with a multicellular head and a stalk that is too short to be seen with a typical stereomicroscope (Carmo et al. 2019; Figs 5F, 6A, B, F, 7D-F). This type of glandular trichome was initially described by Pflaum (1897), but only illustrated in detail by Mentink and Baas (1992; as "bladder-like glandular hairs"). Similar trichomes were commonly referred to as "sessile glands", "sessile glandular trichomes" or "unforrowed sessile glands" (for example, by Wurdack 1986) across the taxonomic literature. As these trichomes are not sessile, they have been treated as typical glandular trichomes in anatomical studies (Reis et al. 2005; Cassiano et al. 2010; Romero and Castro 2014; Silva et al. 2018; Carmo et al. 2019, 2020). In a more detailed investigation, Carmo et al. (2019) proposed new names for trichomes and epidermal appendages, based on the structure of the stalk, head and cuticle. Carmo et al. (2019) included two species of the Trembleya s.s. clade in their study (M. chamissoana and M. flaviflora). Together with the anatomical descriptions and figures provided by Somavilla and Graciano-Ribeiro (2011), Silva et al. (2018) and Pacifico et al. (2019), the following types of trichomes were reported for the Trembleya s.s. clade:

1. Reduced glandular trichomes with apex consisting of 2–4 globular cells, distended cuticle and pluricellular stalk, in *M. chamissoana* and *M. flaviflora* (Carmo et al. 2019);

2. Uniseriate elongated eglandular trichomes, narrow at the base and truncated at the apex, with circular depressions in *M. chamissoana* (Carmo et al. 2019; Fig. 6C);

3. Short-stalked glandular trichomes with pluricellular clavate apex, with or without a distended cuticle, in *M. parviflora* (Somavilla and Graciano-Ribeiro 2011) and *M. altoparaisensis* (Pacifico et al. 2019; Fig. 6A);

4. Woolly eglandular trichomes in *M. laniflora* (Silva et al. 2018; Fig. 6E).



Figure 5. Anatomical features of leaves in the *Trembleya* s.s. clade of *Microlicia* **A–C** *Microlicia altoparaisensis*: **A** cross section of the mid-vein, showing an amphicribral arch-shaped vascular bundle **B** cross section of the leaf, showing the isobilateral mesophyll, the wavy epidermis and a glandular trichome in a depression **C** Adaxial surface of the epidermis in frontal view, with stomata and glandular trichomes **D**, **E** *Microlicia chamissoana*: **D** leaf stomatal crypt in cross section, with glandular trichomes **E** petiole in cross section, showing an amphicribral vascular bundle **F** *Microlicia flaviflora*, cross section of the leaf blade showing a reduced glandular trichome. AB: Abaxial surface; AD: Adaxial surface; CE: Common epidermal cells; GT: Glandular trichome; PP: Palisade parenchyma; SP: Spongy parenchyma; ST: Stomata. All photos by A.A.O. Carmo. Voucher specimens: **A–C** Pacifico & Bressan 380 (CAS, HUEM, SPF) **D**, **E** Pacifico & Carmo 154 (HUEM, UEC) **F** Mello-Silva et al. 509 (SPF).



Figure 6. SEM images showing details of the leaf surface in the *Trembleya* s.s. clade of *Microlicia* **A** *Microlicia altoparaisensis*, glandular trichomes and stomata on the leaf abaxial surface **B** *Microlicia calycina*, glandular trichomes and stomata on the leaf abaxial surface **C** *Microlicia chamissoana*, eglandular trichomes and stomata on the leaf abaxial surface **C** *Microlicia chamissoana*, eglandular trichomes and stomata on the leaf abaxial surface **C** *Microlicia chamissoana*, eglandular trichomes and stomata on the leaf abaxial surface **D** *Microlicia flaviflora*, stomata on the leaf abaxial surface **F** glandular trichomes on the leaf abaxial surface **F** glandular trichomes; on the leaf adaxial surface. ET: Eglandular trichomes; GT: Glandular trichomes; ST: Stomata. Voucher specimens: **A** Pacifico & Bressan 380 (CAS, HUEM, SPF) **B** Pacifico 290 (CAS, SPF) **C** Pacifico & Carmo 154 (HUEM, UEC) **D** Mello-Silva et al. 509 (SPF) **E**, **F** Almeda et al. 9179 (CAS, UEC).

Inflorescence

Given the diversity of inflorescence types and the presence of many similar structures which are not guaranteed homologous, efforts have been made to establish natural systems for the flower-bearing parts of the Angiosperms (e.g. Briggs and Johnson 1979; Weberling 1988; Prusinkiewicz et al. 2007; Kirchoff and Claßen-Bockhoff 2013).



Figure 7. SEM images of leaves in the *Trembleya* s.s. clade of *Microlicia* **A** *Microlicia parviflora*, abaxial surface in frontal view **B–D** *Microlicia pithyoides*: **B** abaxial surface in frontal view **C** pore on the leaf abaxial surface **D** glandular trichome on the leaf adaxial surface **E** *Microlicia trembleyiformis*, glandular trichome on the abaxial surface **F** *Microlicia tridentata*, detail of a glandular trichome on the adaxial surface. All photos by R. Pacifico. Voucher specimens: **A** Almeda et al. 8483 (CAS, HUFU, NY) **B**, **C** Pacifico 295 (CAS, HUEM, SPF) **E** Romero & Nakajima 3593 (HUFU, UEC) **F** Pacifico 290 (CAS, HUEM, SPF).

Inflorescences found in Lavoisiereae always have a terminal flower, which means that they are determinate, i.e. monotelic *sensu* Weberling (1988) and anthotelic *sensu* Briggs and Johnson (1979). Overall, inflorescences in the *Trembleya* s.s. clade are similar in structure to those of the *Lavoisiera* clade, which were described in detail by Martins and Almeda (2017). In both clades, the inflorescences always consist of a proliferation or reduction, based on a 3-flowered dichasial unit, with opposite branching like that of sterile branches (Fig. 8). The dichasial unit consists of a terminal flower subtended by



Figure 8. Inflorescences in the *Trembleya* s.s. clade of *Microlicia* **A** *M. altoparaisensis* **B** *M. chamissoana* **C** *M. laniflora* **D–F** *M. flaviflora* **G** *M. parviflora* **H** *M. tridentata.* Photos: **A** by V. E. Bressan **B** by F.A.O. Silveira **C** by L. Pedrosa **D, E** by R. Pacifico **F** by A.V. Scatigna **E** by F. Almeda **F** by F.A. Michelangeli.

a pair of modified leaves (bracts). Two lateral branches originate from the axils of the bracts to produce lateral flowers, which are, in turn, subtended by a pair of bracteoles. The proliferation of this pattern produces biparous cymes in a compound inflorescence. In some cases, only one lateral branch develops from the axil of a bract. This pattern is associated with production of uniparous cymes at the distal portion of the inflorescence and is here reported for a few species.

In the *Trembleya* s.s. clade, seven species have simple or compound dichasia (*M. altoparaisensis, M. calycina, M. chamissoana, M. flaviflora, M. laniflora, M. parviflora* and *M. tridentata*) and the remaining four have inflorescences reduced to solitary flowers at the apical region of the branches (*M. pentagona, M. pithyoides, M. ros-marinoides* and *M. trembleyiformis*). Floral pedicels are usually evident and measure 0.3–4 mm long. These are inconspicuous to 0.2 mm long only in *M. altoparaisensis*. Like some species of the *Lavoisiera* clade (Martins and Almeda 2017), a tendency of inflorescence reduction to congested clusters occurs in *M. chamissoana* and *M. laniflora* (Fig. 8B–C). The degree of inflorescence development, as well as the shape, size and venation of the bracteoles, are characters of taxonomic significance at the species level.

Hypanthium and calyx

The hypanthium that envelops the superior ovaries is campanulate to urceolate and its length varies between 1.7 and 6.5 mm. The external surface is light green, reddish or golden and has (8)10(12) longitudinal vascular ribs that terminate apically in a circular ring where the hypanthium and calyx lobes meet. In Melastomataceae, this region is usually referred to as the torus (Wurdack 1953; Almeda 1978; Martins and Almeda 2017). In two species (*M. tridentata* and *M. pentagona*), the hypanthium could be described as glabrous, although it is minutely granulose and covered by a glutinous substance. In four species, the external surface is only glandular-punctate (*M. altoparaisensis, M. calycina, M. pithyoides* and *M. rosmarinoides*), while, in the other three, eglandular or gland-tipped trichomes usually occur associated with the glandular-punctate indumentum (*M. chamissoana, M. parviflora* and *M. trembleyiformis*). An atypical indumentum is found in *M. laniflora*, which has the external surface of the hypanthium totally hidden by a dense lanose indumentum of eglandular trichomes and in *M. parviflora*, which has a hypanthium that is usually pruinose, eventually sparsely to densely covered with gland-tipped trichomes.

The calyx lobes that develop above the torus are united at the base and that union forms the calyx tube, which, in the *Trembleya* s.s. clade, varies in length between 0.1 and 0.7 mm. The calyx lobes are either oblong, triangular, narrowly triangular or subulate, with the apex acute or acuminate and between 0.7 and 9.7 mm long. The indumentum of both calyx tube and calyx lobes is usually similar to that of the hypanthium. Differences in the shape, size and indumentum of the calyx lobes are generally useful diagnostic characters at the species level in this clade.

Corolla

Flowers are generally 5-merous (Fig. 9) with petals convolute in bud. Rarely, one or a few 4-merous or 6-merous flowers are found in inflorescences predominantly with 5-merous flowers. The corolla is always radially symmetrical at anthesis. The petals are free, attached to the torus alternating with calyx lobes and opposing the smaller set of stamens. They vary between 4.5 and 26.0 mm in length, exceeding 20 mm only in *M. laniflora*. The shape is obovate with the apex rounded or acute, varying in colour from white (*M. altoparaisensis, M. laniflora*) to magenta (*M. calycina, M. chamissoana, M. pentagona, M. pithyoides, M. trembleyiformis, M. tridentata*) or yellow



Figure 9. Diversity of flowers in the *Trembleya* s.s. clade of *Microlicia* A *M. chamissoana* B *M. parviflora*C *M. flaviflora* D *M. laniflora* E, F *M. pentagona* G *M. rosmarinoides* H *M. tridentata.* Photos: A by F.A.O. Silveira B and D–F by F. Almeda C by A.V. Scatigna G by L. Pedrosa H by F.A. Michelangeli.

(*M. flaviflora*, *M. rosmarinoides*) (Fig. 9). In *M. parviflora*, both magenta and white petals occur in distinct populations. These petals are more commonly described as white with pink stains. A rare form of *M. lanifora* with pink-flushed petals was once reported from Serra do Cipó, Minas Gerais. Both surfaces of the petals are generally glabrous and the margin varies from entire to glandular-punctate (*M. chamissoana*) or ciliate (*M. laniflora*, sometimes in *M. parviflora*).

Androecium

Flowers are diplostemonous and, therefore, generally have ten stamens, which are organised in an antesepalous whorl of larger stamens and an antepetalous whorl of smaller stamens. In all but one species of the clade (M. altoparaisensis), the pedoconnectives of the antepetalous stamens are much shorter than those of the antepetalous stamens, forming a yellow ventral appendage that measures about 0.1(-0.5) mm and is often inconspicuous. The pedoconnectives of the antesepalous stamens are generally well-developed, forming yellow ventral appendages (0.1-)0.7-3.0 mm long that are usually emarginate at the apex. In the majority of species, the antesepalous stamens have purple to vinaceous anthers in strong contrast to the yellow anthers of the antepetalous whorl. The exception is *M. altoparaisensis*, which has subisomorphic stamens with all anthers yellow. The filaments are filiform, glabrous, measuring 1.5-6.3 mm long, usually similar in colour to the petals. The anthers are oblong (Fig. 10A, B), 0.7–3.8 mm in length (excluding rostra), with a smooth external surface and 2-celled tetrasporangiate thecae. Each anther tapers to a rostrum measuring 0.2–0.5(–0.7) mm long with a ventrally inclined apical pore (Figs 10C–F, 11A–D). A remarkable difference between the two sets of stamens is that the anther pores of the antepetalous whorl are always narrower than those of the antesepalous set. This distinction is usually only evident when anthers are examined with Scanning Electron Microscopy (Figs 10C-F, 11A-D). Overall, in this clade, the androecium is radially symmetrical at bud and bilaterally symmetrical at anthesis (see Fig. 9). For notes on reproductive strategies, see the topic "Reproductive Biology, Pollination and Phenology."

Pollen

Pollen grains in Melastomataceae are small, generally tricolporate, radially symmetrical and isopolar (Patel et al. 1984; Renner 1993). Apparently of little taxonomic use, these characters have rarely been described in taxonomic studies of the family (Almeda and Robinson 2011; Alvear and Almeda 2019). Based on SEM photos of four species of the *Trembleya* s.s. clade taken during this study (*T. altoparaisensis, M. calcyina, M. chamissoana* and *M. pithyoides*), the pollen grain structure of the clade is apparently not informative taxonomically and matches the descriptions provided in the above-cited references. SEM images of pollen grains of *M. pithyoides* are presented in Fig. 11E, F.



Figure 10. SEM images of anthers and anther rostra in the *Trembleya* s.s. clade of *Microlicia* **A** *Microlicia parviflora*, anther of an antesepalous stamen **B** *Microlicia tridentata*, anther of antesepalous stamen **C** *Microlicia flaviflora*, anther rostrum of an antesepalous stamen **D** *Microlicia flaviflora*, anther rostrum of an antesepalous stamen **F** *Microlicia parviflora*, anther rostrum of an antesepalous stamen **F** *Microlicia parviflora*, anther rostrum of an antesepalous stamen **F** *Microlicia parviflora*, anther rostrum of an antesepalous stamen **F** *Microlicia parviflora*, anther rostrum of an antesepalous stamen **F** *Microlicia parviflora*, anther rostrum of an antesepalous stamen. Voucher specimens: **A**, **E**, **F** Pirani et al. CFSC 12361 (SPF) **B** Pacifico & Bressan 290 (CAS, HUEM) **C**, **D** Hatschbach et al. 54239 (CAS, INPA, MBM).

Gynoecium and capsule

The ovary is always superior, glabrous and completely enclosed by the hypanthium. Ovaries are 5-locular in most species, 3(-4)-locular only in *M. altoparaisensis* and vary from 3–5-locular only in *M. trembleyiformis*. These differences in ovary locule number



Figure 11. SEM images of anther rostra and pollen grains in the *Trembleya* s.s. clade of *Microlicia* **A** *Microlicia pentagona*, anther rostrum of an antesepalous stamen **B** *Microlicia pentagona*, anther rostrum of an antesepalous stamen **C** *Microlicia tridentata*, anther rostrum of an antesepalous stamen **D** *Microlicia tridentata*, anther rostrum of an antesepalous stamen **D** *Microlicia tridentata*, anther rostrum of an antesepalous stamen **D** *Microlicia tridentata*, anther rostrum of an antesepalous stamen **D** *Microlicia tridentata*, anther rostrum of an antesepalous stamen **D** *Microlicia tridentata*, anther rostrum of an antesepalous stamen **D** *Microlicia tridentata*, anther rostrum of an antesepalous stamen **D** *Microlicia tridentata*, anther rostrum of an antesepalous stamen **D** *Microlicia tridentata*, anther rostrum of an antesepalous stamen **D** *Microlicia tridentata*, anther rostrum of an antesepalous stamen **D** *Microlicia tridentata*, anther rostrum of an antesepalous stamen **D** *Microlicia tridentata*, anther rostrum of an antesepalous stamen **D** *Microlicia tridentata*, anther rostrum of an antesepalous stamen **E**, **F** *Microlicia pithyoides*, pollen grains. Voucher specimens: **A**, **B** Irwin et al. 20486 (CAS, MO, NY, US) **C**, **D** Pacifico & Bressan 290 (CAS, HUEM) **E**, **F** Pacifico 295 (CAS, HUEM, SPF).

are additional characters that can be used for species recognition. The ovaries are ovoid to globose or cylindrical, measuring between 0.9 and 4.1 mm in length. Placentation is axile with numerous tiny anatropous ovules attached to subpeltate placental intrusions. The style is filiform (3–10 mm long) and incurved distally to sigmoid at anthesis, glabrous, similar in colour to the petals and the stigma is punctiform to truncate.



Figure 12. Capsules and infructescences in the *Trembleya* s.s. clade of *Microlicia* A *Microlicia laniflora*, infructescence B *Microlicia parviflora*, capsule enveloped by the hypanthium C–E *Microlicia pentagona*:
C capsule enveloped by the hypanthium D infructescence E capsules enveloped by reddish mature hypanthia. Photos: A by F. Almeda B, C by F.A. Michelangeli E, F by R. Pacifico.

The brownish capsules are loculicidal measuring 2.3–8.0 mm in length, initially enveloped by the hypanthium and calyx that rupture and flake away tardily with age (Fig. 12). The shape of the capsule is ovoid to globose. The enveloping hypanthium is little or markedly constricted at the apex (torus). The capsules dehisce from the apex to the base (basipetal) into 3–5 valves with a deciduous columella. Both calyx tubes (0.2–3.1 mm long) and calyx lobes (1.2–11.5 mm long) may become elongated in fruit. The apex of the mature capsule never exceeds the torus, like it does in several species of *Microlicia* s.s. In fruit, the calyx lobes become sharply thicker only in *M. pentagona* (Fig. 12C–E).

Seed structure and germination

Seed micromorphological characters have been traditionally used in the tribal and generic classification of Melastomataceae (Cogniaux 1883–1888; Baumgratz 1983; Fritsch et al. 2004; Ocampo et al. 2014; Goldenberg et al. 2015; Penneys et al. 2022). In fact, one of the synapomorphies attributed to the Lavoisiereae is the presence of ellipsoid to reniform seeds with a reticulate-foveolate testa (Almeda and Martins 2001; Fritsch et al. 2004; Rocha et al. 2016; Martins and Almeda 2017; Pacifico and Almeda

2022). The use of seed morphology to recognise species from closely-related species groups is limited in Melastomataceae, although some investigations have revealed promising seed characters that could be used together with macromorphology for species circumscriptions (Ocampo and Almeda 2013; Martins and Almeda 2017; Ocampo et al. 2022). In the *Trembleya* s.s. clade, the six species for which mature seeds were available are similar in shape and testa sculpturing and typical of Lavoisiereae (Fig. 13).



Figure 13. SEM images of seeds in the *Trembleya* s.s. clade of *Microlicia* **A** *Microlicia calycina* **B** *Microlicia laniflora* **C**, **D** *Microlicia parviflora* **E** *Microlicia pentagona* **F** *Microlicia rosmarinoides*. All photos by R. Pacifico. Voucher specimens: **A** Pacifico & Bressan 296 (CAS, HUEM, SPF) **B** Almeda et al. 7726 (CAS, UEC) **C**, **D** Almeda et al. 8483 (CAS, HUFU, NY) **E** Irwin et al. 20178 (CAS, MO, NY, UEC, US) **F** Occhioni et al. s.n. (US [US001900109]).

Overall, they are slightly curved to reniform with the raphal zone oblong, occupying ca. 30-70% of the total length of the seed (total length = 0.2-0.8 mm) and the testa cells are arranged in an aligned pattern.

Information on seed germination in the clade is limited to studies of *M. parviflora* and *M. laniflora*. According to Silveira et al. (2012), seeds of these two species are non-dormant. For *M. laniflora*, the optimum temperature range for germination is 20–25 °C, which matches the onset of the rainy season (Rodrigues and Silveira 2013). Seeds of *M. laniflora* are viable after 42 months of storage (Rodrigues and Silveira 2013) and for being easily buried, they are likely easily incorporated into soil seed banks (Rodrigues and Silveira 2013). According to the investigations by Giotto (2015), seeds of *M. parviflora* usually take 5–14 days to germinate and germination occurs more quickly when the seeds are exposed to variations in temperature. Germination is higher for seeds that are stored for more than a month after collection, and they continue to be viable for at least 15 months after being collected (Giotto 2015).

Reproductive biology and pollination

Flowers are hermaphroditic with a strongly dimorphic (rarely subisomorphic) and roecium and poricidal anthers. Plants of this clade provide pollen as a primary resource to reward pollinators and apparently developed floral traits to protect the pollen, select pollinating agents and precisely deposit pollen on the body of the pollinator. These characteristics are usually understood as strategies to deal with the "pollen dilemma", in which pollen grains fulfil two main functions, i.e. to transport the male gamete and to reward flower visitors with resource supply (Westerkamp 1996; Luo et al. 2008). In Melastomataceae, nectar production is apparently restricted to a few genera (see Varassin et al. 2008) and has never been reported in Lavoisiereae. During anthesis, the large anthers are generally positioned almost parallel to each other, serving as a "landing platform", while the smaller anthers are more erect and positioned to serve as the feeding set; a clustering of the yellow anthers of the antepetalous stamens, together with the yellow connective appendages of the antesepalous stamens, apparently acts as a visual sign to pollinators in most species. As usual in Melastomataceae (Renner 1989; Dellinger et al. 2022), the pollen is collected by bees that perform buzz pollination. The bees position themselves over the androecium and perform rapid distortions of the thoracic box and produce a characteristic buzzing sound (Renner 1989).

By having flowers with vibrant colours and diurnal anthesis, most species of Lavoisiereae seem to meet the requirements of the classic melittophily syndrome (Faegri and van Der Pijl 1979). The exception is *M. laniflora*, whose white flowers are the largest in the clade and open at night and dusk (Soares and Morellato 2018). The reproductive success of *M. laniflora* seems to be highly dependent upon large bees of the genus *Xylocopa* that perform crepuscular foraging (Soares and Morellato 2018). Flowers of *M. laniflora* are self-incompatible and depend on cross-pollination; this behaviour suggests that pollinator-mediated interbreeding is a strategy to promote genetic variability of populations naturally isolated on rocky outcrops (Soares and Morellato 2018). There is no evidence of apomixis in *M. laniflora* (Soares and Morellato 2018). The widely-distributed *M. parviflora* has been reported as a facultative apomict (Silva 2001) or non-apomictic (Maia et al. 2016) and self-compatible (Silva 2001; Maia et al. 2016). Still, Maia et al. (2016) reported reduced speed of pollen tube growth in self-pollination treatments. Both staminal whorls have fertile pollen (Santos et al. 2012). Functional dimorphism of stamens in *M. parviflora* is still possible because germination for each type of pollen has not been tested (Santos et al. 2012). Natural vegetative reproduction, probably from rhizomes, was reported by Campos (2005) and Baumgratz et al. (2007). The occasional apomictic behaviour of *M. parviflora* is consistent with the general pattern found in Melastomaceae, a family in which apomictic species generally have wider distributions than non-apomictic taxa (Santos et al. 2012; Caetano and Oliveira 2022). Silva et al. (2012) reported that *M. parviflora* is one of the native plant species most visited by the pollinating bee *Eulaema negrita* in an agroecosystem in Uberlândia (Minas Gerais), indicating that this species performs significant ecosystem services in that region.

Populations of Microlicia parviflora from different localities may be distinct in phenological behaviour, with annual or episodic flowering and continuous or annual fruiting; this species is commonly reported from both typical campo rupestre and gallery forests (Brito et al. 2017). Overall, a tendency to produce flowers during the dry season and seed dispersal at the beginning of the rainy season has been reported in phenological studies for shrubby Melastomataceae from campo rupestre (Le Stradic 2012) and especially in *M. laniflora* (Rodrigues and Silveira 2013; Soares and Morellato 2018). This tendency is believed to be an adaptation for effective pollination and seed dispersal (Salazar et al. 2011; Silveira et al. 2012; Soares and Morellato 2018). Our histograms of flowering and fruiting periods, based on herbarium specimens (Fig. 14), agree with what has been described for *M. laniflora* and suggest a similar tendency for *M. calycina*, M. chamissoana and M. flaviflora. Three other species (M. altoparaisensis, M. pithyoides and *M. rosmarinoides*) could have a distinct phenological pattern, flowering and fruiting mainly during the wet season (Fig. 14A, H, I), although field observations are necessary to confirm this hypothesis. *Microlicia pentagona* and *M. trembleyiformis* apparently produce flowers and fruits more evenly throughout the year (Fig. 14G, J). Additional phenological studies of this clade and the Lavoisiereae, in general, are desirable.

Chemical characters

Knowledge of secondary metabolites of Lavoisiereae is largely restricted to the work by Bomfim-Patrício et al. (2001), who provided leaf flavonoid profiles for 33 species of the tribe, including four species from the *Trembleya* s.s. clade (*M. chamissoana*, *M. laniflora*, *M. parviflora* and *M. pentagona*). They reported 116 flavonoids for the tribe with a predominance of flavonol glycosides. Species of the *Trembleya* s.s. clade do not form a coherent group with respect to a flavonoid profile. A predominance of flavonols in *M. laniflora* and *M. parviflora* resembles *Microlicia* s.s., while 6-methoxylation found in *M. chamissoana* and *M. pentagona* resembles species of the *Lavoisiera* clade (Bomfim-Patrício et al. 2001).



Figure 14. Circular histograms of phenology for species of the *Trembleya* s.s. clade of *Microlicia*. Information on flowering and fruiting periods were obtained from herbarium specimens.

Information on histochemical tests is available only for *M. parviflora* and *M. lani-flora*. Regarding the first, phenolic compounds were reported from the endodermis and parenchyma (Somavilla and Graciano-Ribeiro 2011), histochemical tests performed

on the exodermis cells of the roots were positive for suberin and negative for lignin (Somavilla and Graciano-Ribeiro 2012), oil droplets were found in the mesophyl of the leaves (Somavilla and Graciano-Ribeiro 2011), coumarins, steroids, triterpenes, flavonoids and tannins were also reported, with the following major compounds present in the volatile oils: α -terpineol, α -pinene, β -pinene, sabinene, acetoxyeudesman-4- α -ol and 2,4a-8,8-tetramethyldecahydrocyclopropanaphtalene (Farias et al. 2018). Alkaloids probably occur in *M. parviflora* as well (Raffauf 1996). In *M. laniflora*, phenolic compounds were reported from the leaf palisade parenchyma, collenchyma, vascular bundle sheath (Silva et al. 2018), as well as saponins, triterpenes, tannins, flavonoids (Ventura et al. 2007a) and a flavanone (Ventura et al. 2007b).

Chromosome numbers

Only about 10% of the species of Melastomataceae are known cytologically, but some patterns of chromosomal evolution are evident. Chromosome number stasis at the diploid level and recurrent cycles of polyploidy and dysploidy are common (Almeda 2013; Almeda and Penneys 2022). The base number attributed to the family is x = 12 (Almeda 2013). Lavoisiereae is quite uniform with x = 12 and tetraploidy based on that number, while *Rhynchanthera* differs in having x = 10 and tetraploidy on that base number (Almeda and Penneys 2022). In the *Trembleya* s.s. clade, chromosome counts are available only for two species. The diploid *M. parviflora* has n = 12 and the tetraploid *M. pentagona* has n = 24 (Almeda and Penneys 2022).

Geographic distribution, biogeography and endemism

The *Trembleya* s.s. clade is restricted to Brazil (Fig. 15). Both richness and weight endemism are concentrated in the Minas Gerais State (southern Cadeia do Espinhaço), where 10 species occur (Fig. 16). The only two other States with more than one species are Goiás (*M. altoparaisensis* and *M. parviflora*) and Rio de Janeiro (*M. parviflora* and *M. trembleyiformis*). *Microlicia parviflora* has the widest distribution in the clade and is reported for the states of Bahia, Minas Gerais, Goiás, Distrito Federal, Espírito Santo, Rio de Janeiro, São Paulo and Paraná.

Endemicity analyses detected one consensus area of endemism for the *Tremb-leya* s.s. clade, which resulted from the merging of four individual areas of endemism (Fig. 17). The consensus area consisted of five cells and is a good match for the Southern Espinhaço biogeographic Province (Colli-Silva et al. 2019), which is also a major area of endemism for the Lavoisiereae (Pacifico et al. 2020). The highest endemicity score of the consensus area is 4.93 (at the southern region) and the lowest endemicity score 3.30 (at the northern region). *Microlicia calycina*, *M. chamissoana*, *M. laniflora*, *M. pentagona*, *M. rosmarinoides* and *M. tridentata* were recovered as endemic species and their endemicity scores are presented in Fig. 17.

The region with highest richness and weight endemism of the clade is the Iron Quadrangle (Quadrilátero Ferrífero), located in the Municipalities of Barão dos Cocais, Belo Horizonte, Brumadinho, Caeté, Catas Altas, Congonhas, Itabirito, Mariana,



Figure 15. Geographic distribution of the Trembleya s.s. clade of Microlicia in Brazil.



Cl: Serra do Cipó. CN: Serra da Canastra. Dl: Diamantina plateau. GM: Grão-Mogol. IQ: Iron Quadrangle. MA: Serra da Mantiqueira. VE: Chapada dos Veadeiros.

Figure 16. Richness and weight endemism maps of the *Trembleya* s.s. clade of *Microlicia* **A** species richness map **B** species weight endemism map.



Figure 17. The area of endemism of the *Trembleya* s.s. clade of *Microlicia*, based on Endemicity Analysis **A** grid cells corresponding to the Southern Espinhaço area of endemism **B** the Southern Espinhaço area of endemism manually drawn, based on distribution of species of *Trembleya* s.s. clade of *Microlicia*.

Nova Lima, Ouro Branco, Ouro Preto, Raposos, Rio Acima, Sabará and Santa Bárbara (Minas Gerais State). The Iron Quadrangle is one of the world's largest mineral provinces, consisting of rocks associated with the Archean and Paleoproterozoic periods and includes mountain ranges, such as the Serra de Ouro Branco, Serra de Ouro Preto, Serra da Moeda, Serra da Piedade, Serra do Gandarela, Sera do Garimpo, Serra do Rola-Moça and Serra do Caraça (Ruchkys and Machado 2013). It has been recognised as a distinct biogeographic district associated with campo rupestre in the Southern Espinhaço Province (Colli-Silva et al. 2019) and an area of endemism for the tribe Lavoisiereae (Pacifico et al. 2020). Eight species of the clade have been reported for the Iron Quadrangle region: M. calycina, M. laniflora, M. parviflora, M. pentagona, M. pithyoides, M. rosmarinoides, M. tridentata and M. trembleviformis. Another relevant endemism centre of the clade is the Serra do Cipó, where four narrow endemics can be found (M. chamissoana, M. laniflora, M. pentagona and M. tridentata). Only two narrow endemics are not associated to the regions described above: Microlicia flaviflora, which is restricted to northern Minas Gerais, in Grão Mogol, Botumirim and Rio Pardo de Minas and M. altoparaisensis, restricted to Chapada dos Veadeiros, Goiás.

The richness and endemism of the *Trembleya* s.s. clade are concentrated in the campo rupestre, a biodiversity-rich mosaic of mountaintop vegetation where about 15% of Brazilian vascular plant species occur in an area smaller than 1% of its territory (Vasconcelos 2011; Alves et al. 2014; Fernandes 2016; Silveira et al. 2016).

In Brazil, this azonal peinobiome is found mainly on the Cadeia do Espinhaço (also referred to as "Espinhaço Range"), along the States of Bahia and Minas Gerais and in the Brazilian Central Plateau in the State of Goiás (Giulietti et al. 1997; Vasconcelos 2011; Alves et al. 2014). Its vegetation occurs mostly on mountains from about 900–2000 m, on lithosols associated with outcrops of Precambrian quartzites, sandstones and ironstones (Giulietti et al. 1997; Vasconcelos 2011; Alves et al. 2014; Silveira et al. 2016). All species of the *Trembleya* s.s. clade occur on quartzitic soils (for example, at the Serra do Caraça). Three species were also reported from ironstone outcrops known as cangas (*M. laniflora*, *M. rosmarinoides* and *M. tridentata*). Some species have non-overlapping elevational ranges, suggesting an elevated specificity in their habitat preferences, for example, *M. chamissoana* (1154–1462 m), *M. rosmarinoides* (1609–1807 m) and *M. pithyoides* (1827–2072 m). The most widely distributed species, *M. parviflora*, also has the widest elevational range in the clade (560–2223 m), extending into the Cerrado Biome in savannahs and gallery forests.

The traditional hypothesis for plant diversification in campo rupestre postulates that repeated retraction-expansion events driven by Pleistocene climatic changes would have worked as an evolutionary pump, creating a scenario where mountaintops functioned as long-term refuges and maintained lineages despite climatic alterations (Conceição et al. 2016). In this context, populations isolated on mountaintops would have been susceptible to genetic drift and inbreeding depression, which would have favoured speciation (Rapini et al. 2008). The evolutionary pump hypothesis has been recently challenged by Rapini et al. (2020), who argue that the long-term fragmentation, combined with recurrent extinctions and sporadic events of adaptive radiation, may provide a better explanation for the current diversity and endemism in campo rupestre, in accordance with the "escape-to-radiate model". Another non-excluded hypothesis is that mountains with campo rupestre are old climatically-buffered infertile landscapes (OCBILs) (Hopper 2009; Silveira et al. 2016; Zappi et al. 2017), consisting of both a cradle of continuing diversification and a museum of ancient lineages (Silveira et al. 2016; Zappi et al. 2017; Vasconcelos et al. 2020).

In situ diversification apparently played an important role during the evolutionary history of the *Trembleya* s.s. clade, along with several other plant lineages (Fritsch et al. 2004; Pacifico et al. 2020; Vasconcelos et al. 2020). Major diversification of *Microlicia* s.l. may have occurred during the Pliocene (Fritsch et al. 2004) associated with the acquisition of xeromorphic features, for example, fire-resistant woody xylopodia (Simon et al. 2009), physiologically dormant seeds (Silveira et al. 2012), petiole shortening, stomatal crypts (Fig. 5D), reduction in leaf blade area, densification of palisade parenchyma, thickening of the outer periclinal wall of the epidermal cells (Carmo et al. 2020) and aluminium accumulation mechanisms (Jansen et al. 2002). These are all possible innovations which could have favoured a shift from mesophytic to xerophytic environments and the occupation of the diverse microhabitats found in campo rupestre (Fritsch et al. 2004; Silveira et al. 2012; Carmo et al. 2020).

Conservation

Overall, vascular plant lineages restricted to campo rupestre are highly vulnerable to disturbances and their conservation deserves special attention (Conceição et al. 2016; Silveira et al. 2016). Given their high phylogenetic conservatism, these lineages are not expected to adapt quickly to new conditions and are usually unable to colonise new habitats (Conceição et al. 2016; Silveira et al. 2016). Additionally, most of them would be very unlikely to reach distant suitable areas because of their low dispersal capability (Conceição et al. 2016; Silveira et al. 2016).

The historical stability of campo rupestre vegetation in the face of climatic changes is still under debate (Antonelli et al. 2010; Bitencourt et al. 2016; Conceição et al. 2016; Rapini et al. 2020). According to the OCBIL theory, mountaintops with campo rupestre have been buffered for a long time from climatic alterations and rapid changes could greatly reduce their biodiversity (Hopper 2009; Silveira et al. 2016). In global warming scenarios, Bitencourt et al. (2016) estimated that the Espinhaço Range may lose up to 56% of its plant diversity and 97% of microendemic species by 2080.

Most species of the *Trembleya* s.s. clade have narrow distributions limited to one or a few mountains and several of them also have narrow elevational ranges. The Brazilian Government already recognises three species of this clade as Endangered (EN), i.e. *M. calycina*, *M. chamissoanai* and *M. flaviflora* and one as Critically Endangered (CR), *M. pithyoides* (Brasília 2014). In this study, based on AOO and EOO values and criterion B of IUCN (2019), our informal conservation status recommendations agree with those assigned to these species by the Brazilian Government. We also recommend that four additional species should be recognised as Endangered (EN), *M. altoparaisensis*, *M. pentagona*, *M. rosmarinoides* and *M. tridentata*, *M. laniflora* should be considered as Vulnerable (VU) and *M. parviflora* and *M. trembleyiformis* as Least Concern (LC).

Systematic treatment

Trembleya s.s. clade of Microlicia s.l.

Diagnosis. Perennial shrubs or treelets. Leaves petiolate, not imbricate, not keeled, the adaxial surface glandular-punctate to glabrescent, venation basal acrodromous, impressed on the adaxial surface and prominent on the abaxial surface, consisting of amphicribral or bicollateral vascular bundles. Flowers usually 5-merous, diplostemonous, pedicellate, subtended by a pair of bracteoles. Hypanthia not fused to the ovary, lacking a crown of trichomes at the apex. Stamens strongly dimorphic or subisomorphic, anthers 2-celled, tetrasporagiate. Ovaries superior, (3–4–)5-locular. Capsules dehiscent from the apex to the base, columella deciduous.

Description. Perennial erect shrubs or small trees (0.1-)0.3-4 m tall, woody, sometimes densely branched. Distal branches quadrangular, usually light green (when fresh) and glutinous, glandular-punctate, sometimes granulose or pruinose, eventually covered

with eglandular or gland-tipped trichomes, internodes 0.1–4.5 cm long, angles unwinged or narrowly winged, nodes thickened. Old branches terete, brownish and defoliating towards the base. Leaves decussate, petiolate, not imbricate, not keeled, papyraceous, chartaceaous or coriaceous, usually discoloured when dry. Petioles 0.3-17 mm long. Blades 0.4-11.7 cm long, 0.05-5 cm wide, oblong, lanceolate, elliptic, narrowly elliptic, ovate or linear, entire to slightly serrulate, sometimes entire along the basal half and serrulate on the upper half, rarely ciliate, lacking support tissue on the leaf margin. Adaxial surface green (when fresh), becoming pale green, pale brown, or darkened (when dry), glutinuous, glandular-punctate to glabrescent, glandular trichomes (when present) appearing sessile (i.e. on peduncles too short to be seen with a 40× magnification stereoscope). Abaxial surface usually green (when fresh), becoming pale green (when dry), always lighter than the adaxial surface, glandular-punctate to covered with eglandular or gland-tipped trichomes, or totally concealed by a lanose indumentum. Venation composed of 1-7 basal acrodromous veins, mid-vein stout, lateral veins becoming faint towards the leaf margin, impressed on the adaxial surface and prominent on the abaxial surface, consisting of amphicribral or bicollateral vascular bundles, tertiaries usually evident, nearly perpendicular to the mid-vein and branching towards the leaf margin. Inflorescences simple or compound dichasia, consisting of biparous cymes throughout or proximally biparous and distally uniparous cymes or reduced to solitary flowers on the apical region of the branches. Inflorescence bracts 0.7-5.0 cm long, 0.1-2.0 cm wide, petiolate, usually similar to the principal leaves in shape and indumentum, 1-5-nerved from the base. Bracteoles sessile or with petioles up to 6 mm long, blades 2.2-11 mm long, 0.5-5.5 mm wide, linear, elliptic, lanceolate, ovate, narrowly elliptic, oblong or oblanceolate, 1-3(-5)-nerved from the base, entire to slightly serrulate, rarely ciliate, usually differing in shape, but similar in indumentum to the principal leaves. Flowers (4–)5(–6)-merous, diplostemonous, pedicellate, subtended by a pair of bracteoles. Hypanthia 1.7-6.5 mm long, 1.5-5.2 mm wide at the torus, campanulate to urceolate, not fused to the ovary, externally glandular-punctate, sometimes covered with eglandular or gland-tipped trichomes, rarely completely concealed by a lanose indumentum, lacking a crown of trichomes at the apex. Calyx tubes 0.1-1.2 mm long, externally like the hypanthia. Calyx lobes 0.7-9.7 mm long, 0.4-3.2 mm wide at the base, oblong, triangular, narrowly triangular or subulate, entire or rarely sparsely ciliate, apex acute to acuminate, rarely terminating in an apical eglandular trichome, similar to the hypanthia in indumentum. Petals 4.5-26 mm long, 2.4-15 mm wide, obovate, entire, eventually ciliate, white, magenta or yellow (when fresh), apex acute, rounded, acuminate or emarginate, both surfaces glabrous or rarely sparsely glandular-punctate on the adaxial surface. Stamens (8)10(12), strongly dimorphic or subisomorphic, glabrous throughout, filaments linear, white, pink or yellow, pedoconnectives well-developed, anthers oblong, 2-celled (tetrasporangiate), rostrate, apical pores circular and ventrally inclined. Larger (antesepalous) stamens (4-)5(-6), filaments 1.5-6.3 mm long, pedoconnectives 1.3-7.3 mm long, ventral appendages 0.1-3.0 mm long, the apex usually emarginate to bilobate, thecae (excluding rostra) 0.8-3.8 mm long, purple, red, vinaceous or rarely yellow, rostra 0.2–0.7 mm long, pores 0.1–0.3 mm wide. Smaller (antepetalous) stamens (4-)5(-6), filaments 1.5-5.4 mm long, pedoconnectives
0.2–1.9 mm long, ventral appendages usually up to 0.1 mm long, apex truncate to emarginate, thecae (excluding rostra) 0.8–3.2 mm long, yellow to orange, rostra 0.2–0.6 mm long, pores ca. 0.2 mm wide. Ovaries 0.9–4.1 mm long, 0.7–3.1 mm wide, ovoid, cylindrical or globose, superior, (3–4–)5-locular, glabrous. Styles 3–10 mm long, filiform, sigmoid to incurved, white, pink or yellow, glabrous, stigmas punctiform. Capsules loculicidal, 2.3–8.0 mm long, 2.3–6.0 mm wide, ovoid or globose, the torus initially constricted at the apex, dehiscent from the apex to the base, columella deciduous. Fruiting calyx tubes 0.2–3.1 mm long. Fruiting calyx lobes 1.2–11.5 mm long, rarely thickened. Seeds 0.3–0.9 mm long, reniform, the testa foveolate-reticulate.

Nomenclatural notes

Based on collections housed in the herbarium at Paris (P), Martin and Cremers (2007) selected types for Melastomataceae described by Charles Victor Naudin (1815–1889), including six names for taxa that are part of the *Trembleya* s.s. clade (*Microlicia calycina, M. paniculata, M. pentagona, M. stenophylla, M. trembleyiformis* and *M. tridentata*). More than one specimen corresponding to the types cited by Martin and Cremers (2007) were found at P for the six names. These type citations were here treated as first-step lectotypifications. Thus, second-step lectotypes were designated in these cases following Article 9.17 of the Shenzhen Code (Turland et al. 2018). Overall, our nomenclatural update of this clade includes the designation of 34 lectotypes for names at specific and infraspecific ranks and 25 new synonyms.

Key to the species of Trembleya s.s. clade of Microlicia

1	Leaves 0.5–2 mm wide, 1-nerved from the base2
_	Leaves 3–50 mm wide, 3–7-nerved from the base
2	Leaf blades linear; petals magenta; larger (antesepalous) stamens with anthers
	magenta to purple and smaller (antepetalous) stamens with yellow anthers
-	Leaf blades narrowly-lanceolate to narrowly-elliptic; petals yellow; all stamens
	with anthers yellow to pale brown
3	Plants with a dense whitish lanose indumentum covering branchlets, leaf abaxial
	surfaces and hypanthia; petals 19–26 mm long
_	Plants lacking a whitish lanose indumentum; petals 4.5–13 mm long4
4	Leaves with the abaxial surface entirely concealed by the indumentum, tertiary
	venation "foveolate-like" (Fig. 4M)
_	Leaves with the abaxial surface exposed, tertiary venation (if present) not "fove-
	olate-like"
5	Leaves 3-nerved from the base (including a tenuous inframarginal pair of
	veins) M. calycina
_	Leaves 5-7-nerved from the base (including a tenuous inframarginal pair of
	veins)6

6	Abaxial leaf venation with tertiaries absent or little evident (Fig. 4B-E)7
_	Abaxial leaf venation with tertiaries evident (Fig. 4A, H–M)8
7	Calyx lobes subulate, 6.2-8.5 mm long in flower, becoming stout and thick
	in fruit (Fig. 12C-E); petals magenta; stamens strongly dimorphic (Minas
	Gerais)
_	Calyx lobes oblong to triangular, 2.8–3.4 mm long in flower, tenuous in fruit;
	petals white; stamens subisomorphic (Chapada dos Veadeiros, Goiás)
	M. altoparaisensis
8	Leaf margins entire along the basal half, sharply serrulate on the upper half
	(Fig. 4A), tertiary veins surrounding stout depressions on the abaxial leaf sur-
	face; bracteoles 8.1–11.0 mm long
_	Leaf margins entire or slightly serrulate throughout, tertiary veins not surround-
	ing stout depressions on the abaxial surface; bracteoles 2.2-6.1 mm long9
9	Calyx lobes 4–4.9 mm long; petals yellow; all anthers yellow to pale brown
	M. flaviflora
_	Calyx lobes 0.7-3 mm long; petals white, light pink or magenta; anthers of
	larger (antesepalous) stamens pink to magenta10
10	Branchlets with narrow wings ca. 0.2 mm wide; flowers solitary; calyx lobes
	narrowly-triangular; ovaries 3–5-locular
_	Branchlets unwinged; flowers disposed in compound or simple dichasia; calyx
	lobes triangular; ovaries 5-locular

1. Microlicia altoparaisensis (R.B.Pacifico, Almeda & Fidanza) Versiane & R.Romero, Bot. J. Linn. Soc. 197: 52. 2021.

Fig. 18

Trembleya altoparaisensis R.B.Pacifico, Almeda & Fidanza, Phytotaxa 391(5): 291. 2019. basionym. Type: Brazil. Goiás, Alto Paraíso de Goiás, Parque Nacional Chapada dos Veadeiros, próximo da cachoeira do Rio Preto, perto do povoado de São Jorge, 6 February 1987, J.R. Pirani 1663, R.M. Harley, B.L. Stannard, A. Furlan & C. Kameyama (holotype: SPF!; isotypes: HUEM!, K!, UEC!, US!).

Description. Erect shrubs 0.8–1.8 m tall. Branchlets quadrangular, glandular-punctate, light green to golden (when fresh). Internodes 1.0–2.1 cm long, angles unwinged. Petioles 2.0-5.5 mm long. Leaf blades 14-45 mm long, 3-9 mm wide, papyraceous (when dry), oblong to lanceolate, both surfaces green (when fresh), pale green (when dry), concolorous (when dry), base attenuate, apex rounded to acute, margin flat or slightly revolute, slightly serrulate and glandular-punctate, 5-nerved from the base, one pair of acrodromous veins and one pair of tenuous veins close to the margin, tertiaries little or not evident on the abaxial surface, adaxial surface densely glandular-punctate, abaxial surface densely glandular-punctate. Inflorescences compound dichasia consisting of proximally biparous, distally uniparous cymes, not congested. Bracts (including petioles) 1.0-4.0 cm long, 0.1-0.7 cm wide, 1-nerved, oblong to lanceolate, indumentum like that of the principal leaves. Bracteoles (at anthesis) sessile or with petioles up to 0.1-0.8 mm long, blades 5.0-6.7 mm long, 0.9-1.8 mm wide, oblong to oblanceolate, base acute, apex rounded to emarginate, margin entire and glandular-punctate, 1-nerved, indumentum like that of the principal leaves. Flowers (4–)5-merous, pedicels (at anthesis) inconspicuous up to 0.2 mm long. Hypanthia (at anthesis) 2.5–5.5 mm long, 3.1–3.2 mm wide at the torus, campanulate, light green to golden (when fresh), externally glandular-punctate. Calyx tubes 0.1-0.3 mm long. Calyx lobes (at anthesis) 2.8-3.4 mm long, 3.1-3.2 mm wide at the base, oblong to triangular, apex acute, eventually terminating in an eglandular trichome 0.1–0.4 mm long, margin entire, (when fresh) light green to golden, externally glandular-punctate. Petals 8.1-10.2 mm long, 3.2-4.5 mm wide, white, obovate, apex acuminate, margin entire and glabrous, both surfaces glabrous. Stamens (8)10, subisomorphic. Larger (antesepalous) stamens (4-)5, filaments 3.3-3.5 mm long, white, pedoconnectives 1.3-1.5 mm long, white, appendages ca. 0.1 mm long, white, apex emarginate, thecae (excluding rostra) 2.7-3.8 mm long, yellow, oblong, rostra 0.3-0.5 mm long, the circular pores ca. 0.2 mm wide. Smaller (antepetalous) stamens (4-)5, filaments 2.7-2.8 mm long, white, pedoconnectives 0.7-1.0 mm long, white, inconspicuous appendages ca. 0.1 mm long, white, apex truncate, thecae (excluding rostra) 2.5–3.2 mm long, yellow, oblong, rostra 0.3–0.5 mm long, the circular pores ca. 0.2 mm wide. Ovary 2.4-2.5 mm long, 1.4-1.6 mm wide, cylindrical, 3(-4)-locular. Style ca. 10 mm long, white. Capsules (at maturity) 4.5–5.3 mm long, 2.8–3.2 mm wide, ovoid, initially enveloped by the hypanthium, torus constricted at the apex, fruiting calyx tubes 0.4–0.5 mm long, fruiting calyx lobes 3.2–3.4 mm long, not thickened. Seeds not seen.

Recognition and affinities. Microlicia altoparaisensis can be recognised by its oblong-lanceolate leaf blades $(1.4-4.5 \times 0.3-0.9 \text{ cm})$, papyraceous, 3-5-nerved from the base, glandular-punctate on both surfaces, tertiary veins not evident, inflorescences composed of proximally biparous and distally uniparous cymes, white petals, yellow subisomorphic stamens and 3(-4)-locular ovaries. The subisomorphic androecium is the most distinctive feature of *M. altoparaisensis* as it is unique in the clade. *Microlicia* altoparaisensis is also the only species with amphistomatic leaves, attenuate thecae rostra and a distribution restricted to Goiás (Pacifico et al. 2019). Ovaries with 3-4 locules occur only in the apparently distantly related *M. trembleyiformis*, which differs in having leaves with tertiaries evident (vs. not evident), discoloured when dry (vs. concolorous), solitary flowers (vs. developed inflorescences), petals magenta (vs. white) and dimorphic stamens (vs. subisomorphic). Another possible relative is the widespread M. parviflora with a range that extends from Paraná to Bahia and Goiás and the only representative of the clade that grows with M. altoparaisensis at the Chapada dos Veadeiros. Microlicia altoparaisensis differs from M. parviflora by the leaves with tertiaries not evident (vs. evident), concolorous when dry (vs. discoloured), amphistomatic (vs. hipostomatic), inflorescences with distally uniparous cymes (vs. biparous cymes), subisomorphic stamens (vs. dimorphic) and 5-locular ovaries (vs. 3-4-locular).

Distribution, habitat, and elevation range. Probably endemic to Chapada dos Veadeiros in Alto Paraíso de Goiás Municipality, Goiás, Brazil (Fig. 19A). It occurs in



Figure 18. *Microlicia altoparaisensis* **A** habit **B** detail of the glandular-punctate indumentum on the branches **C** leaf abaxial surface **D** bracteole adaxial surface **E** floral bud **F** flower in lateral view **G** petal adaxial surface **H** antepetalous (left) and antesepalous (right) stamens. Drawn from Pirani et al. 1663 (UEC). Copyright Magnolia Press. Reproduced with permission from copyright holder.



Figure 19. Geographic distribution of species of the *Trembleya* s.s. clade of *Microlicia* **A** distributions of *M. altoparaisensis*, *M. calycina*, *M. chamissoana* and *M. flaviflora* **B** distributions of *M. laniflora* and *M. trembleyiformis*.

transitional formations between Cerrado and campo rupestre, on rocky quartzitic soils partially exposed to sun, at elevations of 1043–1086 m.

Conservation. *Microlicia altoparaisensis* is known from less than 10 collections. The EOO is 7.025 km² and the AOO is 16 km². Based on IUCN (2019) recommendations and criteria, we believe that this species should be classified as Endangered (EN): B1ab(iii). The majority of the populations of *M. altoparaisensis* occur inside Parque Nacional da Chapada dos Veadeiros, where this species is afforded some protection.

Notes. The collection *Glaziou 21300* was listed under the name *Trembleya debilis* by Glaziou (1908: 250). Following the proposal by Mansano and Pederneiras (2016), the catalogue of collections by Glaziou (1908) was included in the List of Suppressed Works for all taxonomic ranks in the Shenzhen Code (Turland et al. 2018). New names at specified ranks included in publications listed as suppressed works are not validly published according to Article 34 of the Code.

Specimens examined. BRAZIL. Goiás: Alto Paraíso de Goiás Municipality, Chapada dos Veadeiros, Drummond et al. 321 (MBM, NY, RB), Klein et al. 2465 (HUFU, UFG), Machado et al. 153 (HUFU), Meyer 1171 (UEC, UPCB), Pacifico & Bressan 380 (CAS, HUEM, SPF), Pirani et al. 1663 (holotype: SPF; isotypes: HUEM, K, UEC, US), Pirani et al. 1694 (K, SPF, UEC); Unknown municipality, Fazenda da Boa-Vista, près Morro do Salto, Glaziou 21300 (F[photo], P, S).

2. *Microlicia calycina* (Cham.) Versiane & R.Romero, Bot. J. Linn. Soc. 197: 52. 2021. Fig. 20

- Trembleya calycina Cham., Linnaea 9(4): 430. 1835. basionym. Type: Brazil. "Brasilia, Itacolumi" [Minas Gerais, Ouro Preto], F. Sellow s.n. (lectotype, designated here: K [K00530658]!; isolectotypes: BR [BR0000005227020]!, F [neg. 16634]!, K [K00530659]!; image of lectotype is available at http://specimens.kew.org/herbarium/K000530659).
- *Trembleya revoluta* Naudin, Ann. Sci. Nat., Bot. Sér. 3, 2: 155. 1844. Type: Brazil. "Minas Gerais, Capanema" [Minas Gerais, Santa Bárbara], 1841, *P. Claussen 10* (lectotype, first-step designated by Martin and Cremers (2007), second-step designated here: P [P00723384]!; isolectotypes: G [G00368001]!, P [P00723507]!; image of lectotype is available at http://coldb.mnhn.fr/catalognumber/mnhn/p/ p00723384).
- Trembleya stenophylla Naudin, Ann. Sci. Nat., Bot. Sér. 3, 12: 265. 1849. syn. nov. Type: Brazil. "Minas Gerais, Capanema" [Minas Gerais, Santa Bárbara], 1843, *P. Claussen 368* (lectotype, first-step designated by Martin and Cremers (2007), second-step designated here: P [P00723385]!; isolectotype: P [P00723386]!; image of lectotype is available at http://coldb.mnhn.fr/catalognumber/mnhn/p/ p00723385).

Description. Erect shrubs 0.65–1.5 m tall. Branchlets quadrangular, glandularpunctate and sparsely covered with glandular trichomes 0.1–0.2 mm long, light green (when fresh). Internodes 1.5-3.0 cm long, angles with narrow wings 0.2-0.4 mm wide. Petioles 0.8-1.8 mm long. Leaf blades 10-26 mm long, 2-9 mm wide, chartaceous (when dry), elliptic to narrowly elliptic, both surfaces green (when fresh), adaxial surface blackened and abaxial surface pale green (when dry), discoloured (when dry), base attenuate, apex rounded to acute, margin revolute, entire along the basal half, appearing entire to slightly serrulate on the upper half and minutely granulose and becoming glabrescent with age, 3-nerved from the base, one tenuous pair of acrodromal veins, tertiaries evident on the abaxial surface, nearly perpendicular to the mid-vein, little reticulate and branching apically, foveolate-like, adaxial surface sparsely glandular-punctate, appearing glabrous when dry, abaxial surface densely glandular-punctate. Inflorescences simple dichasia or reduced to solitary flowers, not congested. Bracts (including petioles) 1.0–1.3 cm long, 0.3–0.4 cm wide, 3-nerved, elliptic to narrowly elliptic, indumentum like that of the principal leaves. Bracteoles (at anthesis) sessile or with petioles up to 1.0 mm long, blades 4.0-5.0 mm long, 1.3-1.8 mm wide, elliptic, base attenuate, apex rounded to acute, margin entire and glandular-punctate, 1-nerved, indumentum like that of the principal leaves. Flowers 5-merous, pedicels (at anthesis) 0.5-0.7 mm long. Hypanthia (at anthesis) 2.6-3.5 mm long, 1.9-2.2 mm wide at the torus, campanulate, light green or reddish (when fresh), externally glandular-punctate. Calyx tubes 0.4–0.7 mm long. Calyx lobes (at anthesis) 3.5–5.2 mm long, 0.5-0.7 mm wide at the base, subulate, apex acuminate, margin entire, (when



Figure 20. *Microlicia calycina* **A** habit **B** leaf abaxial surface **C** bracteole abaxial surface **D** floral bud **E** flower in lateral view **F** flowering hypanthium **G** petal adaxial surface **H** antesepalous stamen **I** antesepalous stamen **J** gynoecium **K** capsule. Drawn from Barreto 9019 (UEC).

fresh) light green or reddish, externally glandular-punctate. Petals 7.8–10 mm long, 5.0–6.2 mm wide, magenta, obovate, apex acuminate, margin entire and glabrous, both surfaces glabrous. Stamens 10, strongly dimorphic. Larger (antesepalous) stamens 5, filaments 4.7–4.9 mm long, pink, pedoconnectives 5.9–6.2 mm long, pink, appendages 1.4–1.6 mm long, yellow, apex truncate to slightly emarginate, thecae (excluding rostra) 2.3–2.6 mm long, purple, oblong, rostra 0.4–0.7 mm long, the circular pores ca. 0.2 mm wide. Smaller (antepetalous) stamens 5, filaments 3.8–4.1 mm long, pink, pedoconnectives 0.6–0.8 mm long, yellow, inconspicuous appendages ca. 0.1 mm long, yellow, apex truncate, thecae (excluding rostra) 2.1–2.3 mm long, yellow, oblong, rostra 0.4–0.6 mm long, the circular pores ca. 0.2 mm wide. Ovary 2.0–2.2 mm long, 1.9–2.1 mm wide, globose, 5-locular. Style ca. 6.5 mm long, pink. Capsules (at maturity) 2.3–2.7 mm long, 2.3–2.7 mm wide, globose, initially enveloped by the hypanthium, torus constricted at the apex, fruiting calyx tubes 0.7–0.8 mm long, fruiting calyx lobes 5.5–6.0 mm long, not thickened. Seeds ca. 0.8 mm long, reniform.

Recognition and affinities. Microlicia calycina may be recognised by its elliptic to narrowly elliptic leaf blades with revolute margins, 3-nerved from the base, simple dichasia or solitary flowers and subulate calyx lobes 3.5–5.2 mm long. In morphology, M. calycina resembles narrow-leaved forms of M. pentagona (see notes under this species). Both species share the glandular-punctate indumentum, inflorescences reduced to solitary flowers (sometimes perfect dichasia only in *M. calycina*), subulate calyx lobes, magenta petals, and bicoloured anthers. Microlicia calycina differs by the leaf blades that are 3-nerved from the base (vs. 5-nerved) and calyx lobes 3.5-5.2 mm long (vs. 6.2–8.5 mm long) that become thick in fruit (vs. tenuous). These two species may occur sympatrically in the seasonally dry grasslands of Parque Estadual do Itacolomi (Rolim 2011) and at Serra do Caraça. Microlicia parviflora is also morphologically similar to *M. calycina*, which may be distinguished by leaves 3-nerved from the base (vs. 5-nerved) and subulate calyx lobes (vs. triangular). Additionally, *M. parviflora* is distinct in having openly ramified inflorescences that are sometimes reduced to simple dichasia. In turn, the inflorescences of *M. calycina* consist of simple dichasia that are frequently reduced to solitary flowers. The distributions of Microlicia calycina and M. parviflora overlap in Caeté, Ouro Preto and Catas Altas, where sympatry is likely to occur. *Microlicia calycina* is also similar to *M. pithyoides* (see notes under this species).

Distribution, habitat and elevation range. Endemic to central and southern Minas Gerais (Fig. 19A), at Serra do Caraça, Serra do Itacolomi and Serra da Piedade. It occurs on quartzitic campo rupestre exposed to full sun at elevations between 1692 and 1920 m.

Conservation. *Microlicia calycina* is known from about 20 collections. The EOO is 481 km² and the AOO is 20 km². This species is currently recognised as endangered (EN) by the Brazilian Government (Brasília 2014). Based on IUCN (2019) recommendations and criteria, we recommend a similar assessment: (EN): B1ab(iii). The conservation units of Parque Estadual do Itacolomi and RPPN Serra do Caraça (Natural Heritage Private Reserve) are of major importance for the long-term conservation of *M. calycina*.

Notes. We agree with Cogniaux (1883–1888) and treat *Trembleya revoluta* as a synonym of *M. calycina*. The type of *Trembleya revoluta* (*P. Claussen 10*) differs from typical *M. calycina* collections only by its revolute leaf margins, a feature that appears to be an artefact of drying. Likewise, we consider *Trembleya stenophylla* a narrow-leaved form of *M. calycina*. Specimens of *M. calycina* with leaf blades conspicuously revolute have also been confused with *M. pithyoides*. For a comparison of *M. calycina* and *M. pithyoides*, see the notes under the latter.

Specimens examined. BRAZIL. Minas Gerais: Caeté Municipality, Serra da Piedade, Grandi et al. 6593 (BHCB, HUFU); Catas Altas Municipality, Serra do Caraça, Castro et al. 283 (HUFU), Oliveira & Giacomin 47 (BHCB), Oliveira & Giacomin 84 (BHCB), Oliveira et al. 480 (BHCB), Pacifico & Bressan 296 (CAS, HUEM, SPF); Ouro Preto Municipality, Serra do Itacolomi, Barreto 9019 (BHCB, ESA, FUEL, HUFU, SP, SPF, UEC, UPCB), Damazio s.n. (RB [48391]), Glaziou 14745 (P), Glaziou 18232 (K, P, R), Pacifico & Bressan 291 (CAS, HUEM, SPF), Peron 220 (RB), Peron 268 (RB), Peron 269 (RB), Riedel s.n. (K [K00530657], NY [NY00941982], W [18890019737]), Rolim 366 (HUFU, NY, RB, VIC), Schwacke 9368 (RB, W); Unknown municipality, Claussen 10 (P [P00723384, P00723507]), "capanema", Claussen 368 (P [P00723385, P00723386]), Sellow s.n. (lectotype: K [K00530659]; isolectotypes: BR [BR0000005227020], F [neg. 16634], K [K00530658]).

3. *Microlicia chamissoana* (Naudin) Versiane & R.Romero, Bot. J. Linn. Soc. 197: 53. 2021.

Fig. 21

Trembleya chamissoana Naudin, Ann. Sci. Nat., Bot. Sér. 3, 12: 270. 1849. basionym. Type: Brazil. "Brasilia, Itambé" [Minas Gerais, probably Santo Antônio do Itambé], F. Sellow s.n. [b. 1171 c. 1156] (lectotype, designated here: K [K00530656]!; isolectotype: P [P00723508]!; image of lectotype is available at http://specimens. kew.org/herbarium/K000530656).

Description. Erect shrubs (0.1–)0.3–1.5 m tall. Branchlets quadrangular, glandularpunctate and covered with gland-tipped trichomes 0.2–0.4 mm long, light green (when fresh). Internodes 0.3–1.5 cm long, angles unwinged. Petioles 1.0–4.9 mm long. Leaf blades 10–28 mm long, 4–18 mm wide, chartaceous (when dry), elliptical, both surfaces green (when fresh), adaxial surface blackened and abaxial surface pale green (when dry), discoloured (when dry), base attenuate, apex obtuse to acute, margin flat or slightly revolute, entire throughout or slightly serrulate on the upper half and glandular-punctate, 7-nerved from the base, two pairs of acrodromous veins and one tenuous pair of veins close to the margin, tertiaries evident on the abaxial surface, nearly perpendicular to the mid-vein, reticulate and randomly branching, adaxial surface sparsely glandular-punctate, appearing glabrous when dry, abaxial surface densely glandular-punctate and covered with gland-tipped trichomes 0.2–0.4 mm long.



Figure 21. *Microlicia chamissoana* **A** habit **B** leaf abaxial surface **C** bracteole abaxial surface **D** floral bud **E** Flower in lateral view **F** flowering hypanthium **G** detail of the indumentum of the hypanthium **H** petal adaxial surface **I** gynoecium **J** antepetalous (behind) and antesepalous (in front) stamens. Drawn from Barreto 6745 (SPF, UEC).

Inflorescences simple or compound congested dichasia consisting of biparous cymes, or reduced to solitary flowers. Bracts (including petioles) 0.8-1.0 cm long, 0.6-0.7 cm wide, 5-nerved, elliptical, indumentum like that of the principal leaves. Bracteoles (at anthesis) with petioles 1.6-2.0 mm long, blades 4.2-4.9 mm long, 1.4-2.1 mm wide, narrowly elliptic, base attenuate, apex acuminate, margin entire along the basal half, sparsely serrulate on the upper half, 3–5-nerved, indumentum like that of the principal leaves. Flowers 5-merous, pedicels (at anthesis) 2-4 mm long. Hypanthia (at anthesis) 2.5–3.7 mm long, 1.9–2.1 mm wide at the torus, campanulate, reddish (when fresh), externally glandular-punctate and sparsely to densely covered with gland-tipped trichomes 0.2-0.4 mm long. Calyx tubes 0.9-1.2 mm long. Calyx lobes (at anthesis) 4.5–6.7 mm long, 1.9–2.1 mm wide at the base, narrowly triangular, apex acuminate, margin entire and sparsely ciliate with gland-tipped trichomes 0.2–0.4 mm long, (when fresh) reddish, externally glandular-punctate and covered with gland-tipped trichomes 0.2-0.4 mm long. Petals 11.5-13 mm long, 5.8-6.2 mm wide, magenta, obovate, apex acuminate, margin entire and glandular-punctate, adaxial surface sparsely glandularpunctate, abaxial surface glabrous. Stamens 10, strongly dimorphic. Larger (antesepalous) stamens 5, filaments 5.2-6.0 mm long, pink, pedoconnectives 5.5-6.5 mm long, pink, appendages 1.2–1.8 mm long, yellow, apex bilobate, thecae (excluding rostra) 1.7–2.6 mm long, purple, oblong, rostra 0.3–0.6 mm long, the circular pores ca. 0.3 mm wide. Smaller (antepetalous) stamens 5, filaments 4.7-5.0 mm long, pink, pedoconnectives 1.0-1.2 mm long, yellow, inconspicuous appendages ca. 0.1 mm long, yellow, apex truncate, thecae (excluding rostra) 1.5–2.0 mm long, yellow, oblong, rostra 0.4–0.6 mm long, the circular pores ca. 0.2 mm wide. Ovary 2.2–2.8 mm long, 1.6-1.8 mm wide, cylindrical, 5-locular. Style ca. 6.3 mm long, pink. Capsules (at maturity) 2.5-3.2 mm long, 2.3-3.0 mm wide, ovoid, initially enveloped by the hypanthium, torus constricted at the apex, fruiting calyx tubes 1.5-1.7 mm long, fruiting calyx lobes 5.2-6 mm long, not thickened. Seeds ca. 0.5 mm long, reniform.

Distribution, habitat and elevation range. Largely restricted to the Serra do Cipó in central Minas Gerais (Fig. 19A), but extending to the Serra dos Alves and probably to Pico do Itambé. Most of the recent collections were made at Serra do Cipó; only one collection studied came from Serra dos Alves, *Souza & Miranda 1639* (BHCB). Considering Sellow's itinerary in Brazil (see Rego et al. 2013), the type series was probably collected at the Pico do Itambé region. It occurs on quartzitic campo rupestre exposed to full sun at elevations between 1154 and 1462 m.

Conservation. *Microlicia chamissoana* is known from fewer than 20 collections. The EOO is 885.927 km² and the AOO is 32 km². This species was collected on Pico do Itambé only in the 19th century and the local extinction of that population is a possibility. Several populations found more recently are protected in the Parque Nacional da Serra do Cipó. This species is already recognised as endangered (EN) by the Brazilian Government (Brasília 2014). Our study based on IUCN (2019) recommendations and criteria reached a similar conclusion regarding its conservation status (EN): B1ab(iii).

Recognition and affinities. Microlicia chamissoana may be recognised by its elliptic leaf blades with tertiaries densely reticulate and randomly branching, congested inflorescences or solitary flowers and narrowly triangular calyx lobes 4.5–5.7 mm long. It is probably more closely related to *M. laniflora* and *M. pentagona*, both of which may occur sympatrically with M. chamissoana at Serra do Cipó. Microlicia chamissoana differs from M. laniflora by the shorter height (0.1-)0.5-0.8 m tall (vs. 0.5-3.5 m tall), absence of lanose indumentum on branchlets, abaxial leaf surfaces and hypanthia (vs. present), leaves with shorter petioles 1.0-4.9 mm long (vs. 6-11 mm long), blades with tertaries densely reticulate and randomly branching (vs. little reticulate and branching apically), bracteoles with apices acuminate (vs. rounded), shorter hypanthia 2.5-3.7 mm long (vs. 5.0-6.5 mm long), shorter calvx lobes 4.5-6.7 mm long (vs. 7.9–9.7 mm long) and petals magenta (vs. white) 11.5–13.0 mm long (vs. 19.0–26.0). In turn, Microlicia chamissoana differs from M. pentagona by the branchlets, abaxial surfaces of the leaves and hypanthia that are densely glandular-punctate and covered with gland-tipped trichomes (vs. appearing glabrous, vernicose and minutely granulose), leaf blades with tertiaries densely reticulate and randomly branching (vs. parallel or little reticulate and branching apically) and calyx lobes tenuous (vs. thickened) 5.2–6.0 mm long (vs. 6.5–11.0 mm long).

Notes. Major variation in *M. chamissoana* involves habit and degree of inflorescence development. This species is usually a shrub about 1 m tall, although an atypical specimen from Serra do Cipó is about 10 cm tall (*A.M. Giulietti et al. CFSC12492*). This specimen was described as a herb, but it has woody branches. Most of the specimens examined have congested, many-flowered inflorescences (e.g. *Barreto 6745*), although in some of the inflorescences, these are reduced to solitary flowers (e.g. *Pacifico* & Carmo 154, Almeda et al. 8580).

Based on *F. Sellow s.n.*, Chamisso (1834: 396–397) provided a detailed description for *M. chamissoana* under *Microlicia* sp., indicating his uncertainty of its generic position, especially because of its 5-valvate capsules. Naudin (1849: 270) proposed the epithet *chamissoana* for this species mentioning the description of Chamisso (1834: 396–397). Even preceded by a short description that is not diagnostic (5-valvate capsules), the name *Trembleya chamissoana* Naudin is still valid because Naudin (1849) made reference to Chamisso's decription.

The type specimens of *M. chamissoana*, as cited by Cogniaux (1883–1888), have two collection numbers indicated on each of their labels (*F. Sellow 1171* and 1156). Both collection numbers were cited by Cogniaux in "Flora brasiliensis". At least one set of Sellow's duplicates of *M. chamissoana* was housed at B and probably destroyed during World War II. As the *Sellow* duplicate at K is in good shape, it is here designated as the lectotype for this species.

Specimens examined. BRAZIL. Minas Gerais: "Itambé" [probably Santo Antônio do Itambé Municipality], Sellow s.n. (lectotype: K [K00530656]; isolectotype: P [P00723508]); Conceição do Mato Dentro Municipality, Serra do Cipó, Kameyama et al. CFSC10403 (SPF), Sheperd & Kirzenzaft 10214 (SP); Itabira Municipality, Serra do SAlves, Souza & Miranda 1639 (BHCB); Jaboticatubas Municipality, Serra do Cipó,

Giulietti et al. CFSC12560 (SPF); Morro do Pilar Municipality, Serra do Cipó, Silveira s.n. (HUFU [56533]); Santana do Riacho Municipality, Serra do Cipó, Almeda et al. 8580 (CAS, HUEM, UEC), Escaramai et al. 52 (SPF), Giulietti et al. CFSC12492 (HUEM, SPF), Pacifico & Carmo 154 (HUEM), Pena & Viana 417 (SPF), Rocha 694 (BHCB), Romero et al. 8627 (HUEM, HUFU, RB), Semir CFSC5607 (SP); Unknown municipality, Serra do Cipó, Barreto 6745 (BHCB, HUFU, NY, SP, SPF, UEC, UPCB), Damazio 2026 (RB), Sena s.n. (W [W19110004181]).

4. *Microlicia flaviflora* Versiane & R.Romero, Bot. J. Linn. Soc. 197: 53. 2021. Fig. 22

Trembleya hatschbachii Wurdack & E.Martins, Bol. Bot. Univ. São Paulo 14: 40. 1995. original name. Type: Brazil. Minas Gerais, Grão Mogol, Rio das Mortes, 15 May 1988, G. Hatschbach, M. Hatschbach & O. Ribas 52005 (holotype: MBM!; isotypes: BHCB!, C!, CAS!, CTES, ESA!, G!, HUFSJ, K!, MO!, RB!, S, SPF!, US!, VIC, VIES).

Description. Erect shrubs 0.8–2.5 m tall. Branchlets quadrangular, appearing glabrous, vernicose and minutely granulose, light green (when fresh). Internodes 0.6-3.0 cm long, angles with narrow wings 0.2-0.4 mm wide. Petioles 3.9-17 mm long. Leaf blades 37–90 mm long, 17–50 mm wide, coriaceous (when dry), elliptic to slightly ovate, both surfaces green (when fresh), adaxial surface blackened and abaxial surface pale brown (when dry), discoloured (when dry), base cuneate to attenuate, apex acute, margin flat, entire and minutely granulose and becoming glabrescent with age, 5-nerved from the base, one pair of acrodromous veins and one pair of tenuous veins close to the margin, tertiaries evident on the abaxial surface, nearly perpendicular to acute to the mid-vein, little reticulate and branching apically, adaxial surface glabrous to minutely granulose, vernicose, abaxial surface glabrous to minutely granulose. Inflorescences compound dichasia consisting of biparous cymes, not congested. Bracts (including petioles) 3.2-5.0 cm long, 1.4-2.0 cm wide, 5-nerved, elliptical, appearing glabrous, vernicose. Bracteoles (at anthesis) with petioles 1.6-1.9 mm long, blades 3.5-6.0 mm long, 1.3-1.9 mm wide, narrowly elliptic, base attenuate, apex acute, margin entire, 1–3-nerved, indumentum appearing glabrous, vernicose. Flowers 5-merous, pedicels (at anthesis) 1.8–2.2 mm long. Hypanthia (at anthesis) 3.3–4.1 mm long, 3.0–3.2 mm wide at the torus, campanulate, light green (when fresh), externally glabrous, minutely granulose, vernicose. Calyx tubes inconspicuous, 0.1-0.2 mm long. Calyx lobes (at anthesis) 4.0-4.9 mm long, 1.3-1.9 mm wide at the base, narrowly triangular, apex acute, margin entire, (when fresh) light green, externally glabrous, minutely granulose, vernicose. Petals 6.0-8.8 mm long, 5.2-7 mm wide, yellow, obovate, apex rounded, margin entire and glabrous, both surfaces glabrous. Stamens 10, strongly dimorphic. Larger (antesepalous) staments 5, filaments 3.4-4.0 mm long, yellow, pedoconnectives 3.7-4.0 mm long, yellow, appendages 1.0-1.2 mm long, yellow, apex truncate



Figure 22. *Microlicia flaviflora* **A** habit **B** leaf abaxial surface **C** bracteole abaxial surface **D** floral bud **E** flower in lateral view **F** flowering hypanthium **G** petal adaxial surface **H** antesepalous (left) and antepetalous (right) stamens **I** gynoecium **J** capsule enveloped by the hypathium. Drawn from Meireles et al. 1124 (UEC).

to slightly emarginate, thecae (excluding rostra) 1.4–1.6 mm long, brownish, oblong, rostra 0.3–0.4 mm long, the circular pores ca. 0.2 mm wide. Smaller (antepetalous) stamens 5, filaments 2.7–2.9 mm long, yellow, pedoconnectives 1.2–1.4 mm long,

yellow, short appendages ca. 0.5 mm long, yellow, apex truncate, thecae (excluding rostra) 1.4–1.6 mm long, yellow-brownish, oblong, rostra 0.3–0.5 mm long, the circular pores ca. 0.2 mm wide. Ovary 3.5–4.1 mm long, 2.9–3.1 mm wide, globose, 5-locular. Style 4–4.2 mm long, yellow. Capsules (at maturity) 3.4–3.6 mm long, 3.5–4.2 mm wide, globose, initially enveloped by the hypanthium, torus constricted at the apex, fruiting calyx tubes 0.2–0.4 mm long, fruiting calyx lobes 3.7–4.0 mm long, not thickened. Seeds ca. 0.6 mm long, reniform.

Distribution, habitat and elevation range. Endemic to northern Minas Gerais (Fig. 19A), at Serra de Grão Mogol, Serra de Botumirim and Serra Nova. It occurs on quartzitic campo rupestre exposed to full sun at elevations between 760 and 1243 m. The distribution of *M. flaviflora* is a good match to the Grão Mogol biogeographic district (Colli-Silva et al. 2019).

Conservation. This species is known from about 20 collections. The EOO is 468,668 km² and the AOO is 32 km². Most of the populations of *M. flaviflora* occur within the following conservation units: Parque Estadual de Grão Mogol, Parque Estadual de Botumirim and Parque Estadual da Serra Nova, where this species is afforded protection. The Brazilian Government assigned a conservation status of Endangered (EN) to this species (Brasília 2014). Based on IUCN (2019) recommendations and criteria, we concur with that conclusion (EN): B1ab(iii).

Recognition and affinities. Microlicia flaviflora may be recognised by its leaves and hypanthia that appear to be glabrous, but are vernicose and minutely granulose, leaf blades 3.7-9.0 cm long, elliptic to slightly ovate, compound dichasia and yellow petals. In overall vegetative morphology, M. flaviflora resembles M. tridentata. In turn, its yellow petals, staminal filaments and styles are shared only with M. rosmarinoides. Microlicia flaviflora differs from M. tridentata by its leaves that have entire margins throughout (vs. serrulate along the upper half), abaxial surfaces appearing glabrous (vs. glandular-punctate), shorter bracteoles with blades 3.5–6.0 mm long (vs. 8.1-11.0 mm long) and apex acute (vs. rounded to obtuse) and yellow petals (vs. magenta or rarely white) that are 6.0-8.8 mm long (vs. 11.5-13.0 mm long). Microlicia flaviflora differs from M. rosmarinoides by its taller habit 0.8-2.0 m tall (vs. 0.3-0.6 m tall), branchlets, abaxial surfaces of the leaves and hypanthia appearing glabrous (vs. glandular-punctate), leaf blades 3.7-9.0 cm long (vs. 0.4-1.0 cm long) that are elliptic to slightly ovate (vs. linear to lanceolate) and have 5 basal acrodromous veins (vs. 1-nerved from the base), compound dichasia (vs. solitary flowers), longer calyx lobes 4.0-4.9 mm long (vs. 2.2-2.8 mm long) and longer petals 6.0-8.8 mm long (vs. 5.0–5.3 mm long).

Specimens examined. BRAZIL. Minas Gerais: Botumirim Municipality, Estrada para o Rio do Peixe, Forzza et al. 4897 (NY, RB, SPF), Serra da Canastra, Mello-Silva et al. 509 (HUEM, SPF, UEC), Nakajima et al. 4764 (HUFU), Scatigna & Galvão 376 (UEC); Grão Mogol Municipality, Serra de Grão Mogol, Bidá et al. CFCR11951 (SPF, US), Cerati et al. 246 (K, SP, UEC), Furlan et al. CFCR771 (SPF, UEC, US), Hatschbach & Hatschbach 52005 (holotype: MBM; isotypes: BHCB, C, CAS, CTES, ESA, G, HUFSJ, K, MBM, MO, S, SPF, US, UPCB, VIC, VIES), Hatschbach 41337 (ESA, FLOR, HCF, HUEFS, MBM, NY, RB, SPF, UPCB, US), Hatschbach et al. 54239 (CAS,

INPA, MBM), Hatschbach et al. 68067 (MBM), Hensold et al. CFCR3525 (SPF, US), Kral et al. 72723 (SP, SPF), Leitão Filho et al. 7893 (MBM, UEC), Meireles et al. 1124 (CAS, HUEM, UEC), Oliveira et al. CFCR12997 (SPF, US), Pacifico & Simoes 353 (CAS, HUEM), Pacifico 565 (CAS, HUEM, RB); Pirani & Mello-Silva CFCR10814 (HUEM, SPF, UEC, US), Zappi et al. CFCR9903 (SPF, UEC); Rio Pardo de Minas Municipality, Serra Nova, Araújo et al. 2043 (BHCB), Rocha et al. 497 (BHCB, NY).

5. *Microlicia laniflora* (D.Don) Baill., Adansonia 12: 95. 1877. Fig. 23

- Melastoma laniflora D.Don, Mem. Wern. Nat. Hist. Soc. 4: 292. 1823. basionym. Type: Brazil. "in Brazilia", F. Sellow s.n. (lectotype, designated here: K [K00957812]!; probable isolectotypes: K [K00957818]!, P [P005317063]!, P [P005317064]!, P [P005317070]!; image of lectotype is available at http://specimens.kew.org/herbarium/K000957812).
- *Trembleya lychnitis* Schrank & Mart. ex DC., Prod. 3: 126. 1828. Type: Brazil. "In Brasiliae lapidosis apricis ad latera montium prov. Min. gener." [Minas Gerais], *C.F.P. Martius s.n.* (lectotype, designated here: G [G00368004]!; isolectotype: M [M0165875]!).
- *Trembleya laniflora* (D.Don) Cogn. in Martius et al., Fl. Bras. 14(3): 130. 1883.Type: Based on *Melastoma laniflora* D.Don.
- Trembleya laniflora var. acutifolia Cogn. in Martius et al., Fl. Bras. 14(3): 131. 1883. syn. nov. Type: Brazil. "Brasilia meridionalis, ad Serra da S. Antonio" [Minas Gerais], 1878, F. Sellow 1727 (lectotype, designated here: K [K00530655]!; isolectotype: P [P00723419]!; image of lectotype available at http://specimens.kew.org/ herbarium/K000530655).
- Trembleya laniflora var. genuina Cogn. in Martius et al., Fl. Bras. 14(3): 130. 1883. syn. nov. Type: Brazil. "Minas Geraes" [Minas Gerais], 1840, P. Claussen 332A (lectotype, designated here: BR [BR0000005228225]!, isolectotype: BR [BR0000005227891]!).
- Trembleya laniflora var. grandifolia Cogn. in Martius et al. Fl. Bras. 14(3):131. 1883.
 syn. nov. Type: Brazil. "ad Pico d'Itabira et ad Caxoeira do Campo" [Minas Gerais, Itabira and Cachoeira do Campo], *C.F.P. Martius 930* (lectotype, designated here: P [P005317085]!; isolectotypes: BM [BM00516949]!, G [G00368005]!, G [G00318589]!, GH [GH00053137]!, L [L00056323]!, L [L00056324]!, M [M0165876]!, M [M0165877]!, M [M0165878]!, P [P005317086]!, S [S09-12961]!; image of lectotype is available at http://coldb.mnhn.fr/catalognumber/mnhn/p/p05317085).
- Trembleya laniflora var. intermedia Cogn. in Martius et al., Fl. Bras. 14(3):130. 1883. syn. nov. Type: Brazil. "In prov. Minas Geraës loco haud indicato" [Minas Gerais], G. Gardner 4601 (lectotype, designated here: BM [BM00525899]!; isolectotypes: G [G00318586]!, GH [GH00053136]!, NY [NY00245856]!, P [P005317081]!,

R [R000168426]! US [US00623967]!; image of isolectotype at P is available at http://coldb.mnhn.fr/catalognumber/mnhn/p/p05317081).

Description. Erect shrubs or treelets 0.5–3.5 m tall. Branchlet surfaces concealed by a lanose indumentum of eglandular trichomes 0.1–0.5 mm long, whitish (when fresh). Internodes 0.7-4.5 cm long, angles unwinged. Petioles 6-11 mm long. Leaf blades 20-39 mm long, 9-25 mm wide, coriaceous (when dry), ovate, elliptic or narrowly elliptic, adaxial surface green and partially covered by a thin layer of whitish indumentum, abaxial surface totally concealed by the white lanose indumentum (when fresh), adaxial surface blackened, abaxial surface hidden by the white to pale brown lanose indumentum (when dry), discoloured (when dry), base cuneate to rounded, apex acute to rounded, margin flat, entire and minutely granulose and becoming glabrescent with age, 5-nerved from the base, one pair of acrodromous veins and one pair of tenuous veins close to the margin, tertiaries evident on the abaxial surface, nearly perpendicular to the mid-vein, little reticulate and branching apically, adaxial surface glandular-punctate, usually pruinose and becoming glabrescent with age, abaxial surface densely covered with lanose eglandular trichomes 0.1-0.5 mm long. Inflorescences simple dichasia or reduced to solitary flowers, usually congested. Bracts (including petioles) 1-1.9 cm long, 0.3-0.8 cm wide, 3-nerved, ovate, elliptical or narrowly elliptic, indumentum like that of the major leaves. Bracteoles (at anthesis) with petioles 4-6 mm long and blades eventually linear and rudimentary, blades (when well-developed) 2.2-4.4 mm long, 1.5-2 mm wide, linear to elliptic, base attenuate, apex rounded, margin entire, 1-nerved, indumentum like that of the principal leaves. Flowers 5(-6)-merous, pedicels (at anthesis) 0.7-2.0 mm long. Hypanthia (at anthesis) 5.0-6.5 mm long, 4.5-5.2 mm wide at the torus, campanulate to urceolate, surface hidden by the whitish lanose indumentum composed of eglandular trichomes 0.1–0.5 mm long. Calyx tubes 1.0–2.0 mm long. Calyx lobes (at anthesis) 7.9-9.7 mm long, 2.0-2.7 mm wide at the base, subulate, apex acute, margin entire, (when fresh) surface hidden by the whitish lanose indumentum composed of eglandular trichomes 0.1-0.5 mm long. Petals 19-26 mm long, 10-15 mm wide, white, rarely with pink stains at the apical region, obovate, apex emarginate, margin entire and ciliate with eglandular trichomes 0.1–0.4 mm long at the apical region, both surfaces glabrous. Stamens 10(-12), strongly dimorphic. Larger (antesepalous) stamens 5(-6), filaments 5.2-6.3 mm long, white, pedoconnectives 6.1-7.3 mm long, white to light yellow, appendages 1.9–3.0 mm long, yellow, apex emarginate, thecae (excluding rostra) 2.3-2.7 mm long, vinaceous, oblong, rostra 0.4-0.6 mm long, the circular pores ca. 0.2 mm wide. Smaller (antepetalous) stamens 5(6), filaments 4.0-5.4 mm long, white, pedoconnectives 0.8–1.1 mm long, yellow, inconspicuous appendages ca. 0.1 mm long, yellow, apex emarginate, thecae (excluding rostra) 2.4-2.6 mm long, yellow, oblong, rostra 0.3-0.6 mm long, the circular pores ca. 0.2 mm wide. Ovary 2.5-4.0 mm long, 1.7-2.0 mm wide, globose to cyclindrical, 5-locular. Style 6.5-8.0 mm long, white. Capsules (at maturity) 5.0-8.0 mm long, 5.0-6.0 mm wide, globose, initially enveloped by the hypanthium, torus constricted at the apex, fruiting



Figure 23. *Microlicia laniflora* **A** habit **B** leaf abaxial surface **C** bracteole abaxial surface **D** flower in lateral view **E** flowering hypanthium **F** petal adaxial surface **G** detail of indumentum on the apex of the petal **H** antepetalous (behind) and antesepalous (in front) stamens **I** gynoecium **J** ovary in cross-section **K** capsule enveloped by the hypanthium. Drawn from Almeda et al. 7726 (UEC) and Almeda et al. 9197 (UEC).

calyx tubes 2.0–3.1 mm long, fruiting calyx lobes 9.0–11.5 mm long, not thickened. Seeds ca. 0.8 mm long, reniform.

Distribution, habitat and elevation range. Endemic to central and southern Minas Gerais (Fig. 19B), mainly at Serra de Ouro Branco, Serra do Itacolomi, Serra do Cipó, Serra da Piedade, Serra da Moeda, Serra do Caraça, Serra do Gandarela, Serra de Lavras Novas, Serra dos Alves, Serra de Itabirito, Serra do Rola-Moça, Serra do Curral, Serra de Taquaril, Serra do Garimpo, Serra do Belo Vale, Diamantina Plateau and mountains in the Municipalities of Brumadinho and Mariana. It occurs on quartzitic or ferrugineous campo rupestre exposed to full sun at elevations between 868 and 1540 m.

Ecology. *Microlicia laniflora* has a symbiotic relationship with arbuscular mycorrhizae (Abrahão et al. 2019). This is likely related to phosphorus and nitrogen acquisition strategies (Abrahão et al. 2019). This species easily colonises degraded campo rupestre areas and has been recommended for ecological restoration (Amaral et al. 2013). According to Pereira (2011), its leaves develop increased asymmetry when damaged by insects. Vasconcelos et al. (2001) reported the use of *M. laniflora* for nesting by the endemic hummingbird, Hyacinth Visorbearer (*Augastes scutatus*), in campo rupestre at the Serra do Cipó.

Uses. Leaf and stem extracts from *Microlicia laniflora* have antimicrobial activity against *Staphylococcus aureus* and *Micrococcus luteus* (Cota et al. 2002; Ventura et al. 2007a).

Conservation. This species is known from more than 100 herbarium specimens making it one of the better sampled species in the *Trembleya* s.s. clade. However, this sampling is geographically biased towards the surroundings of the MG-010 highway, where more than a half of these collections were made. The MG-010 highway is the main road crossing the mountains at south-eastern Serra do Cipó and provides easy access to large populations of *M. laniflora*. The EOO is 19,113.356 km² and the AOO is 248 km². Based on IUCN (2019) recommendations and criteria, we suspect that this species would be classified as Vulnerable (VU): B2ab(iii). Several populations of *M. laniflora* occur within the following conservation units: Parque Estadual Serra do Ouro Branco, Parque Estadual do Biribiri, Parque Estadual de Itacolomi, Monumento Natural Estadual Serra da Piedade, Monumento Natural Estadual Serra da Gandarela, Parque Nacional da Serra do Cipó and RPPN Serra do Caraça (Natural Heritage Private Reserve), where *M. laniflora* is afforded protection.

Recognition and affinities. *Microlicia laniflora* may be recognised by its branches, abaxial surfaces of the leaves and hypanthia that are densely covered by a lanose indumentum, white petals (rarely flushed with pink) that are 19.0–26.0 mm long and subulate calyx lobes 7.9–9.7 mm long. It appears to be most closely related to *M. pentagona* and *M. chamissoana. Microlicia laniflora* differs from *M. pentagona* by the branches, abaxial foliar surfaces and hypanthia densely covered by the lanose indumentum (vs. appearing glabrous, vernicose and minutely granulose), leaves with longer petioles 6.0–11.0 mm long (vs. 0.4–2.5 mm long) and margins entire throughout (vs. serrulate on the upper half), longer hypanthia 5.0–6.5 mm long (vs. 2.5–3.5 mm long) and longer petals 19.0–26.0 mm long (vs. 11.8–13.8 mm long), that are white, rarely

flushed with pink (vs. magenta). For additional comparisons, see comments under *M. chamissoana*.

Notes. The four varieties proposed by Cogniaux (1883–1888) were based mainly on differences in petiole length, leaf size and leaf shape. An examination of Cogniuax's varieties and many additional collections showed these purported differences to be inconsistent with much size overlap in the characters he used to delimit his infraspecific taxa. The ovate leaf shape that Cogniuax (1883–1888) attributed only to var. *genuina* is present in most of the individuals examined, along with a great deal of variation in leaf and petioles sizes. *Cavalcanti et al. CFSC10628* (UEC), for example, has ovate leaves (a feature attributed only to var. *genuina*) and well-developed petioles (a feature attributed to the varieties *intermedia*, *grandifolia* and *acutifolia*). This specimen could be identified as var. *intermedia* since its leaf measurements match those of the protologue (3–4 cm long). However, when comparing the *Cavalcanti* specimen with the type of var. *intermedia* (*Gardner 4601*), it is clear that this variety has lanceolate leaves that are very distinct from the ovate leaves of *Cavalcanti et al. CFSC10628*. Characters, such as leaf shape and size, also vary along branches of a single individual and, thus, do not constitute good diagnostic features to delimit varieties of this species.

According to Cogniaux (1883–1888), some of Glaziou's collections of *M. laniflora* (his numbers *14740* and *14741*) were made "in prov. Rio de Janeiro" [Rio de Janeiro State]. On the other hand, Glaziou (1908: 251) asserts that his number *14740* came from "Serra do Caraça, au Morro do Inficionado" and the number *14741* came from "Campo de São Sebastião, prés Ouro Preto", both sites located in Minas Gerais State. The labels of *Glaziou 14740* and *14741* from P had annotations of collections' sites similar to those shown in Glaziou (1908), while a duplicate of *Glaziou 14740* from K has a label that says "14741 the same" and the location site is cited as "Environs de Rio de Janeiro et Ouro Preto". Due to these contradictions, the cited collections were not used for the geographical distribution summary of *M. laniflora*. The discordant data on Glaziou's collections of Melastomataceae have been noted by Wurdack (1970) for other collections of Melastomataceae, such as *Clidemia, Leandra, Macairea, Miconia, Rhynchanthera, Tibouchina* and *Tococa*. This is the first report of dubious geographic information for a species of *Microlicia*. We found similar contradictory information on labels of *Glaziou 14746* which is discussed in the comments under *M. pithyoides*.

Specimens examined. BRAZIL. Minas Gerais: Barão de Cocais Municipality, Serra do Garimpo, Hensold 778 (SPF, US), Semir et al. 28809 (UEC), Souza 1606 (BHCB); Belo Horizonte Municipality, Serra do Taquaril – Serra do Curral, Barreto 6769 (SP), Ducke s.n. (RB [241970]), Ferreira 5544 (HUFU), Roth s.n. (BHCB, CESJ, CTES, ESA, R, RB, SP, UB, UPCB), Morro do Chapéu, Brandão 28574 (HUFU), Brumadinho Municipality, Serra do Rola-Moça, Carmo 4819 (BHCB), Serra da Calçada, Martens 7 (SPF), Martens 383 (SPF), Retiro das Pedras, Carvalho s.n. (HUFU [39992]), Stehmann & Morais 2650 (BHCB); Caeté Municipality, Serra do Gandarela, Damazio 1025 (RB); Catas Altas Municipality, Serra do Caraça, Vasconcelos s.n. (SPF [145870, 145871]); Conceição do Mato Dentro Municipality, Serra do Cipó, Macedo 3758 (S), Martinelli & Tavora 2583 (RB); Diamantina Municipality, "Dia-

mantina Plateau", Araújo et al. 323 (HUFU, RB, UEC), Brade 13735 (NY, RB, US), Franco et al. 1270 (HUFU), Hatschbach et al. 27400 (K, MBM, UPCB), Hatschbach et al. 68138 (MBM, UPCB), Leitão et al. 17281 (RB, UEC), Lima et al. 49 (SPF), Maguire et al. 49140 (NY), Marques et al. 274 (HUFU), Mello et al. 61 (HUFU), Vauthier 37 (P); Itabira Municipality, Martius 930 (GH, K, NY, P), Torres s.n. (RB [241965]); Itabirito Municipality, Serra do Itabirito, Irwin 19974 (NY), Irwin et al. 19974 (K, NY, US), Krieger 10641 (CESJ, ESA, HUFU, MBM), Lima et al. 1443 (RB), Teixeira s.n. (BHCB [21783], HUFU [19443]); Jaboticatubas Municipality, Serra do Cipó, Goldenberg & Silveira 1573 (UPCB); Mariana Municipality, Collo et al. s.n. (SPF [62806]), Messias et al. 1922 (OUPR, RB); Nova Lima Municipality, Serra do Curral, Nakajima & Romero 3040 (HUFU), Pereira & Pabst 3107 (RB), Sampaio 7194 (BHCB), Williams & Assis 6352 (GH, NY); Ouro Branco Municipality, Serra de Outro Branco, Almeda et al. 7726 (CAS, UEC), Almeda et al. 8395 (CAS, UEC), Alves & Almeida-Lafetá 5573 (R), Alves et al. 6925 (R), Araújo et al. 334 (ESA, RB), Arbo et al. 3906 (CTES, MBM, RB, SPF, UB), Delfini et al. 78 (ESA, HUFU, RB), Forzza et al. 993 (SPF), Nakajima et al. 4547 (HUFU), Paula et al. 136 (HUFU, VIC), Paula et al. 295 (HUFU, VIC), Paula et al. 8 (HUFU, VIC), Pereira & Pabst 2944 (RB), Pirani et al. CFCR11211 (SPF), Rocha et al. 602 (BHCB, NY), Saraiva et al. 85 (OUPR, RB); Ouro Preto Municipality, Barreto & Viégas s.n. (IAC [6389]), Damazio 1540 (NY, US), Ferreira et al. 433 (HUFU), Fontana et al. 2288 (RB), Forzza et al. 6344 (OUPR, RB, UPCB), Forzza et al. 6359 (NY, OUPR, RB, UPCB), Groppo & Ulwin 676 (SPF), Lima et al. 1296 (RB), Meireles et al 1362 (HUEM, UEC), Messias et al. 2151 (OUPR, RB), Rolim et al. 329 (HUFU, RB, VIC), Rolim et al. 386 (RB, VIC), Rolim et al. 61 (HUFU, VIC), Teixeira s.n. (SPF [114173]), Valente et al. 2574 (RB, VIC); Raposos Municipality, Tameirão Neto & Mansur 4874 (BHCB); Rio Acima Municipality [Gandarela], Emygdio 3314 (NY), Emygdio 3353 (NY); Sabará Municipality, Barreto 6771 (BHCB), Barreto 6772 (NY); Santa Bárbara Municipality, Serra do Caraça, Almeda et al. 7753 (CAS, UEC), Almeda et al. 8862 (CAS, UEC), Arbo et al. 4030 (SPF), Barreto 706 (NY, UEC), Fraga et al. 3333 (NY, RB), Fraga et al. 3341 (NY, RB), Marcondes-Ferreira et al. 281 (SPF), Pirani & Yano 696 (CAS, SPF), Pirani et al. 696 (SP, SPF), Rocha et al. 672 (BHCB, RB), Romero et al. 5307 (CAS, UEC), Tales et al. 17 (BHCB, HUFU), Temponi & Vasconcelos s.n. (BHCB [36249], HUFU [19313]), TSMG & Tales 81 (BHCB, HUFU), Valente et al. 1229 (HUFU, VIC), Valente et al. 1230 (HUFU, VIC), Valente et al. 535 (HUFU, VIC); Santana do Riacho Municipality, Serra do Cipó, Almeda et al. 8549 (CAS, UEC), Almeda et al. 9179 (CAS, UEC), Alves et al. 2109 (SPF), Andrade et al. 374 (BHZB, HUFU), Antar et al. 1662 (SPF), Borges et al. 153 (HUEFS, K, NY, SPF), Bruniera et al. 37 (HUFU, SPF), Castro et al. s.n. (HUEM [24842], HUFU [2254]), Ceccantini et al. 3914 (SPF), Chuckr et al. s.n. (HUEM [24776]), Cordeiro et al. CFSC10504 (SPF), Escaramai et al. 65 (SPF), Faria & Mazucato 105 (SPF), Farinaccio et al. 36 (MBM, RB), Fernandes et al. 1468 (BHZB, HUFU), Forero et al. 7700 (SPF), Forero et al. 7831 (SPF), Giulietti et al. CFSC12564 (UEC), Kral et al. 72997 (CEN, SP), Kubo et al. 109 (SPF), Kubo et al. 125 (SPF), Maguire et al. 49016 (NY),

Mattos & Rizzini 107 (RB, US), Mattos & Rizzini 480 (RB), Monge et al. 384 (UEC), Ordones et al. 1856 (BHZB, HUFU), Pacifico 185 (HUEM, SPF), Pena & Viana 365 (SPF), Pereira & Pabst 152 (HUEM), Pirani et al. 5082 (NY, SPF), Pires & Braga s.n. (CESJ [21520]), Reginato et al. 1401 (NY, UPCB), Sakuragui & Souza 38 (ESA), Salatino et al. 14 (NY, SPF), Salatino et al. 18 (NY, SPF), Souza et al. 11565 (ESA, RB), Souza et al. 25181 (ESA), Stehmann & Morais 2354 (SPF), Verdi et al. 6501 (RB), Zappi et al. CFSC9353 (SPF); Santana do Riacho Municipality ["Conceição do Mato Dentro"], Serra do Cipó, Marquete et al. 3817 (RB); Santana do Riacho Municipality ["Jaboticatubas"], Serra do Cipó, Joly CFSC2405 (SPF), Joly CFSC82 (SPF), Mantovani 99 (SP, SPF), Semir CFSC2005 (SP, SPF), Semir CFSC4133 (SPF), Semir CFSC5001 (SPF), Semir CFSC5068 (SPF); Serro, Semir et al CFCR230 (SPF); Unknown municipality, Bunge s.n. (P [P005317069]), Claussen 1 (BR, CAS), Claussen 1645 (P), Claussen 332A (BR), Claussen 554 (P), Claussen 640 (BR), Claussen 923 (CAS), Claussen s.n. (K [K00957804, K00957810, K00957811, K00957816], NY [NY00941988], P [P005317066, P005317067, P005317071, P005317072]), Gardner 4601 (BM, G, GH, K, NY, P, R, US), Glaziou 11953 (K), Glaziou 14740 (K, P), Glaziou 14741 (K, P), Glaziou s.n. (P [P005317096]), Gounelle s.n. (P [P005317089]), Lund 135 (C), Martius 930 (BM, G, GH, L, M, P, S), Martius s.n. (P [P005317088]), Netto s.n. (BR [BR0000005520688]), Raben 428 (S), Riedel s.n. (K [K00957817], P [P005317084]), Saint-Hilaire 216 (P), Sellow 1446 (BR, US), Sellow 1727 (P [P00723419]), Sellow s.n. (lectotype: K [K00957812]; probable isolectotypes: K [K00957818], P [P005317063, P005317064, P005317070]), Vauthier s.n. (P [P005317061]).

Putative hybrid (*M. laniflora* × *M. pentagona*). BRAZIL. Minas Gerais: Santana do Riacho Municipality ["Santa Luzia"], Serra do Cipó, Barreto 7026 (BHCB).

6. Microlicia parviflora (D.Don) Versiane & R.Romero, Bot. J. Linn. Soc. 197: 54. 2021.

Fig. 24

- *Meriania parviflora* D.Don, Mem. Wern. Nat. Hist. Soc. 4: 323. 1823. **basionym**. Type: Brazil. *F. Sellow s.n.* (lectotype, designated here: G [G00396696]!; probable isolectotype: P [P05317745]!).
- Trembleya heterostemon Mart. & Schrank ex DC., Prod. 3: 126. 1828. syn. nov. Type: Brazil. "In Brasiliae subalpinis ad fontes in prov. Minarum Generalium" [Minas Gerais], C.F.P. Martius 961 (lectotype, designated here: M [M0165884]!; isolectotypes: G [G00310210]!, M [M0165883]!).
- Trembleya triflora Mart. & Schrank ex DC., Prod. 3: 126. 1828. syn. nov. Type: Brazil.
 "In sylvis caeduis prope Villam-Riceam prov. Minarum generalium" [Minas Gerais, Ouro Preto], 1827, C.F.P. Martius s.n. (lectotype, designated here: M [M0165882]!; isolectotypes: G [G00310209]!, P [P00723390]!; image of isolectotype at P is available at http://coldb.mnhn.fr/catalognumber/mnhn/p/p00723390).

- Trembleya paniculata Naudin, Ann. Sci. Nat., Bot. Sér. 3, 2: 154. 1844. Type: Brazil. "In campis circa Juruoca in prov. Minas Geraës" [Minas Gerais], 1816–1821, [catal. D, n° 462] *A. Saint-Hilaire s.n* (lectotype, first-step designated by Martin and Cremers (2007), second-step designated here: P [P00723414]!; isolectotype: P [P00723415]!; image of lectotype is available at http://coldb.mnhn.fr/catalog-number/mnhn/p/p00723414).
- *Trembleya parviflora* (D.Don) Cogn. in Martius et al., Fl. Bras. 14(3): 127. 1883. Type: Based on *Meriania parviflora* D.Don.
- *Trembleya parviflora* subsp. *heterostemon* (Mart. & Schrank ex DC.) Cogn. in Martius et al., Fl. Bras. 14(3): 128. 1883. **syn. nov.** Type: Based on *Trembleya heterostemon* Mart. & Schrank ex DC.
- *Trembleya parviflora* subsp. *triflora* (Mart. & Schrank ex DC.) Cogn. in Martius et al., Fl. Bras. 14(3): 129. 1883. **syn. nov.** Type: Based on *Trembleya triflora* Mart. & Schrank ex DC.
- Trembleya parviflora var. angustifolia Cogn. in Martius et al., Fl. Bras. 14(3): 128. 1883. syn. nov. Type: Brazil. "In prov. Rio de Janeiro ad Serra dos Orgâos" [Rio de Janeiro], 1838, G. Gardner 379 (lectotype, designated here: P [P005317041]!; isolectotypes: BR [BR0000005520404]!, NY [NY00245857-online image]!, US [US00623960]!; image of lectotype is available at http://coldb.mnhn.fr/catalognumber/mnhn/p/p05317041).
- Trembleya parviflora var. denticulata Cogn. in Martius et al., Fl. Bras. 14(3): 129. 1883.
 syn. nov. Type: Brazil. "In prov. S. Paulo ad Paitura" [São Paulo], 1846, Prates s.n. (lectotype, designated here: P [P00723407]!; isolectotypes: P [P00723406]!, P [P00723408]!; image of lectotype is available at http://coldb.mnhn.fr/catalog-number/mnhn/p/p00723407).
- Trembleya parviflora var. farinacea Cogn. in Martius et al., Fl. Bras. 14(3): 128. 1883. syn. nov. Type: Brazil. "In campo sicco apricot vel umbroso ad Caldas prov. Minas Geraës" [Minas Gerais, Caldas], H. Mosen 1971 (lectotype, designated here: R [R000166846]!; isolectotypes: C [C10015104]!, P [P005317106]!; image of isolectotype at P is available at http://coldb.mnhn.fr/catalognumber/mnhn/p/p05317106].
- Trembleya parviflora var. latifolia Cogn. in Martius et al., Fl. Bras. 14(3): 128. 1883.
 syn. nov. Type: Brazil. "In prov. Rio de Janeiro ad Serra dos Orgâos", 1838, G. Gardner 380 (lectotype, designated here: P [P00723401]!; isolectotypes: BR [BR0000005225798]!, F [F0064040F]!, G [G00359408]!, G [G00368014-on-line image]!, NY [NY00217747]!, NY [NY00245859]!, P [P00723402]!, S [S05-3227]]!, US [US00623963]!; image of lectotype is available at http://coldb.mnhn. fr/catalognumber/mnhn/p/p00723401).
- Trembleya parviflora var. martii Cogn. in Martius et al., Fl. Bras. 14(3): 129. 1883. syn. nov. Type: Brazil. "In prov. Minas Geraës ad Serra do Ouro Preto" [Minas Gerais, Ouro Preto], *C.F.P. Martius 931* (lectotype, designated here: P [P005317103]!; isolectotypes: BM, G [G00368009]!, G [G00318575]!, M [M0165879]!, M [M0165880]!, MO [MO-2267366]!, P [P005317750]!, P [P005317751]!; image of lectotype is available at http://coldb.mnhn.fr/catalognumber/mnhn/p/p05317103).

- Trembleya parviflora var. multiflora Cogn. in Martius et al., Fl. Bras. 14(3): 129.
 1883. syn. nov. Type: Brazil. "Ayuruoca, Minas Gerais", 17 April 1878, A.F.M.
 Glaziou 9454 (lectotype, designated here: R [R000009197]!; isolectotypes: BR
 [BR0000005226733]!, BR [BR0000005226405]!, BR [BR0000005227068]!, C
 [C10015105-online image]!, G [G00368008]!, G [G00318573-online image]!, S
 [S-0912956-online image]!, P [P005317099]!, P [P005317057]!; image of isolectotype at P is available at http://coldb.mnhn.fr/catalognumber/mnhn/p/p05317099).
- Trembleya parviflora var. parvifolia Cogn. in Martius et al., Fl. Bras. 14(3): 129. 1883. syn. nov. Type: Brazil. "In prov. Minas Geraës ad Rio das Pedras" [Minas Gerais], F. Sellow 1154 (lectotype, designated here: US [US00623966-online image]!; image of lectotype is available at http://n2t.net/ark:/65665/392812a8c-782b-431cb2fc-3644dcfad16e).
- Trembleya parviflora var. selloana Cogn. in Martius et al., Fl. Bras. 14(3): 128. 1883. syn. nov. Type: Brazil. "In prov. Minas Gerais" [Minas Gerais], F. Sellow 5278 (lectotype, designated here: P [P00723410]!; image of lecotype is available at http://coldb.mnhn.fr/catalognumber/mnhn/p/p00723410).
- Trembleya parviflora var. tomentosa Cogn. in Martius et al., Fl. Bras. 14(3): 128). syn. nov. Type: Brazil. "In prov. Rio de Janeiro ad Serra dos Orgâos" [Rio de Janeiro], J.B.A. Guillemin 946 (lectotype, designated here: P [P005317767]!; isolectotypes: G [G00368013]!, P [P00723409]!; image of lectotype is available at http://coldb. mnhn.fr/catalognumber/mnhn/p/p05317767).
- *Trembleya parviflora* var. *triflora* (Mart. & Schrank ex DC.) Cogn. in Martius et al., Fl. Bras. 14(3): 129. 1883. **syn. nov.** Type: Based on *Trembleya triflora* Mart. & Schrank ex DC.
- Trembleya parviflora var. valtheri Cogn. in Martius et al., Fl. Bras. 14(3): 128.
 1883. syn. nov. Type: Brazil. "In prov. Minas Geraës" [Minas Gerais], 1833,
 M. Vauthier 43 (lectotype, designated here: P [P00723403]!; isolectotypes: BR [BR0000005226375]!, G [G00368012]!, G [G00318569]!, P [P00723404]!, P [P00723405]!; image of lectotype is available at http://coldb.mnhn.fr/catalog-number/mnhn/p/p00723405).
- Trembleya parviflora var. vulgaris Cogn. in Martius et al., Fl. Bras. 14(3): 128. 1883. syn. nov. Type: Brazil. "In prov. Minas Geraës" [Minas Gerais], 1840, G. Gardner 4602 (lectotype, designated here: R [R000168427]!, isolectotypes: NY [NY00245860]!, NY [NY00245861]!, US; image of isolectotype at NY is available at http://sweet-gum.nybg.org/science/vh/specimen_details.php?irn=535234).
- Trembleya parviflora var. warmingii Cogn. in Martius et al., Fl. Bras. 14(3): 128. 1883.
 syn. nov. Type: Brazil. "In prov. Minas Gerais ad Lagoa Santa" [Minas Gerais, Lagoa Santa], *E. Warming s.n.* (lectotype, designated here: P [P005317116]!; isolectotypes: BR [BR0000005520732]!; C [C10015107-online image]!; image of lectotype is available at http://coldb.mnhn.fr/catalognumber/mnhn/p/p05317116].
- Trembleya parviflora var. widgrenii Cogn. in Martius et al., Fl. Bras. 14(3): 128. 1883. syn. nov. Type: Brazil. "In prov. Rio de Janeiro" [Rio de Janeiro], Widgren s.n. (lectotype, designated here: P [P005317115]!; isolectotypes: BR [BR0000005227044]!, PH

[PH00027744]!, S [S-053231]!; image of lectotype is available at http://coldb. mnhn.fr/catalognumber/mnhn/p/p05317115).

Trembleya parviflora var. heterophylla Cogn. in de Candolle & de Candolle [A.D.C. & C.DC.], Monogr. Phan. 7: 75. 1891. syn. nov. Type: Brazil. "In prov. Rio de Janeiro, Nova Friburgo" [Rio de Janeiro, Nova Friburgo], 31 July 1877, A.F.M. Glaziou 16778 (lectotype, designated here: R [R000009196]!; isolecto-types: C [C10015106]!, G [G00368010]!, G [G00368011]!, L [L0056325]! P [P00723411]!, P [P00723412]!, P [P00723413]!; image of isolectotype at P is available at http://coldb.mnhn.fr/catalognumber/mnhn/p/p00723411].

Description. Erect shrubs or treelets 0.7-4.0 m tall. Branchlets quadrangular, always glandular-punctate and usually pruinose-granulose, eventually sparsely to densely covered with gland-tipped trichomes 0.1-0.9 mm long, rarely covered with rigid hyaline eglandular trichomes 0.1–0.5 mm long, light green (when fresh). Internodes 0.6–3.8 cm long, angles unwinged. Petioles 1–15 mm long. Leaf blades 12–117 mm long, 3–38 mm wide, papyraceous (when dry), elliptic to narrowly elliptic or lanceolate, rarely obovate, adaxial surface green and partially covered by a thin layer of whitish indumentum, abaxial surface totally concealed by the white lanose indumentum (when fresh), adaxial surface blackened and abaxial surface pale green to pale brown (when dry), discoloured (when dry), base attenuate, apex acute to obtuse, margin flat or slightly revolute, entire to slightly serrulate and glabrescent, granulose or granular-punctate or ciliate with gland-tipped trichomes 0.1–0.9 mm long, 5-nerved from the base, one pair of acrodromous veins and one pair of tenuous veins close to the margin, tertiaries evident on the abaxial surface, nearly perpendicular to the mid-vein, reticulate and randomly branching, adaxial surface glandular-punctate, usually pruinose and becoming glabrescent with age, abaxial surface glandular-punctate and usually pruinose, eventually sparsely to densely covered with gland-tipped or eglanduar trichomes 0.1-0.9 mm long. Inflorescences simple or compound dichasia consisting of with biparous cymes, not congested. Bracts (including petioles) 0.7–1.6 cm long, 0.1–0.6 cm wide, 3-nerved, elliptic to narrowly elliptic, indumentum like that of the principal leaves. Bracteoles (at anthesis) with petioles 0.9-1.9 mm long, blades 2.2-3.8 mm long, 0.5-1.0 mm wide, narrowly elliptic to oblanceolate, base attenuate, apex acute to obtuse, margin entire, 1-3-nerved, indumentum like that of the principal leaves. Flowers 5(-6)-merous, pedicels (at anthesis) 1.1-2.0 mm long. Hypanthia (at anthesis) 1.9–2.8 mm long, 1.5–2.2 mm wide at the torus, campanulate to urceolate, light green, sometimes with reddish stains (when fresh), externally always glandular-punctate and usually pruinose, eventually sparsely to densely covered with gland-tipped trichomes 0.1-0.9 mm long, rarely covered with rigid hyaline eglandular trichomes 0.1-0.5 mm long. Calyx tubes 0.2-0.7 mm long. Calyx lobes (at anthesis) 0.7–2.5(–3.0) mm long, 0.9–1.5 mm wide at the base, triangular, apex acute, acuminate or apiculate, margin entire, (when fresh) light green or reddish, externally like the hypanthia. Petals 4.5-8.1 mm long, 3.0-4.9 mm wide, white, usually flushed with pink at the base and around the veins, rarely entirely pink, obovate, apex emarginate, rounded or acute, margin entire, glabrous or ciliate with eglandular or gland-tipped trichomes



Figure 24. *Microlicia parviflora* **A** habit **B** leaf abaxial surface **C** bracteole abaxial surface **D** flower in lateral view **E** flowering hypanthium and pedicel **F** petal adaxial surface **G** detail of indumentum on the apex of the petal **H** antepetalous (left) and antesepalous (right) stamens **I** gynoecium **J** ovary in crosssection **K** capsule enveloped by the hypathium. Drawn from Souza-Buturi 328 (UEC) and Matsumoto et al. 428 (UEC).

0.1–0.4 mm long at the apical region, both surfaces glabrous. Stamens 10(–12), strongly dimorphic. Larger (antesepalous) stamens 5(–6), filaments 3.5–4.0 mm long, white or pink, pedoconnectives 3.0–4.0 mm long, white or pink, appendages 0.7–1.5 mm long, yellow, apex emarginate to bilobate, thecae (excluding rostra) 0.8–1.3 mm long, red to vinaceous, oblong, rostra 0.2–0.4 mm long, the circular pores 0.1–0.2 mm wide. Smaller (antepetalous) stamens 5(6), filaments 2.0–3.1 mm long, white or pink, pedoconnectives 0.2–0.5 mm long, white or pink, inconspicuous appendages ca. 0.1 mm long, yellow or pink, apex emarginate, thecae (excluding rostra) 0.8–1.3 mm long, yellow, oblong, rostra 0.2–0.4 mm long, the circular pores ca. 0.2 mm wide. Ovary 1.8–2.2 mm long, 1.6–1.8 mm wide, globose, 5-locular. Style 3.0–3.6 mm long, white or pink. Capsules (at maturity) 2.9–5.0 mm long, 2.5–4.0 mm wide, globose, initially enveloped by the hypanthium, torus constricted at the apex, fruiting calyx tubes 0.2–1.0 mm long, fruiting calyx lobes 1.2–2.9(–3.5) mm long, not thickened. Seeds 0.3–0.6 mm long, reniform.

Representative specimens (one specimen selected for each municipality of occurrence). Bahia: Abaíra, Ganev 879 (HUEFS, NY, SPF); Andaraí, Orlandi et al. 778 (MBM); Lençóis, Carvalho 1086 (CEPEC, RB, SPF); Miguel Calmon, Guedes et al. 12092 (ALCB); Morro do Chapéu, Hage et al. 2317 (CEPEC, MBM, RB); Mucugê, Roque 2869 (ALCB); Palmeiras, Bautista 1347 (CEPEC); Piatá, Ganev 965 (HUEFS, SPF); Ribeirão do Largo, Carvalho 6986 (CEPEC, NY); Rio de Contas, Carvalho et al. 6651 (CEPEC); Seabra, Irwin et al. 31141 (NY); Utinga, Samento & Bautista 859 (RB); Wenceslau Guimaráes, Goldenberg & Michelangeli 2093 (UPCB). Distrito Federal: Brasília, Azevedo et al. 675 (CAS); Taguatinga, Irwin et al. 8149 (SP). Espírito Santo: Domingos Martins, Pereira 309 (CEPEC, SP); Dores do Rio Preto, Monge et al. 2595 (UEC); Fundão, Kollmann 231 (RB, UPCB); Itaguaçu, Brade et al. 18205 (RB); Iúna, Fontana et al. 7678 (UPCB); Marechal Floriano, Hatschbach et al. 74974 (FURB, HCF, MBM); Santa Rita de Jacutinga, Krieger 8857 (MBM); Santa Teresa, Martinelli et al. 10932 (RB). Goiás: Alto Paraiso de Goiás, Marquete et al. 2332 (RB, US); Cocalzinho de Goiás, Versiane et al. 305 (HUFU, RB); Corumbá de Goiás, Irwin et al. 34521 (NY); Cristalina, Monteiro 78 (RB, SPF, UPCB); Pirenópolis, Delprete 9205 (RB). Minas Gerais: Aiuruoca, Glaziou 9454 (P); Alagoa, Guiamarães 333 (RB); Alto Caparaó, Hatschbach & Guimarães 55455 (MBM); Baependi, Souza et al. 1013 (CESJ, MBM); Barão de Cocais, Fontana 2309 (RB, UPCB); Barbacena, Barreto 4621 (SP); Barroso, Assis et al. 520 (MBM); Belo Horizonte, Vidal s.n. (CEN [46402]); Boa Esperança, Silva s.n. (UPCB [52391]); Bom Jardim de Minas, Krieger et al. 24423 (SPF); Brumadinho, Martens 524 (SPF); Buenópolis, Davis et al. 2298 (UEC); Buritizeiro, Hatschbach et al. 75995 (MBM); Caeté, Paula & Grandi s.n. (BHCB [7956], MBM [178326]); Carandaí, Costa 451 (RB); Carangola, Leoni 1 (SPF); Carmésia, Stehmann 2532 (ESA); Carrancas, Sobral et al. 14085 (RB); Catas Altas, Oliveira et al. 508 (BHCB, RB); Conceição do Ibitipoca, Oliveira 25197 (CESJ, RB); Conceição do Mato Dentro, Guarçoni & Sartori 1367 (HUFU); Coromandel, Brandão 14509 (HUFU); Cristália, Hatschbach 41498 (MBM, US); Delfinópolis, Romero & Nakajima 3432 (HUFU); Diamantina, Hatschbach & Pelanda 28014 (MBM); Espera Feliz, Foster & Leoni 64 (ESA); Estrela do Sul, Costa et al. 60 (HUFU); Extrema,

Yamamoto 1549 (UEC); Gouveia, Hatschbach 27277 (MBM); Grão Mogol, Cavalcanti CFCR8314 (SPF); Itabira, Faria et al. 1332 (HUFU); Itabirito, Brandão 22298 (HUFU); Itamonte, Batista & Naves 405 (UEC); João Pinheiro, Heringer 8544/736 (UB, US); Joaquim Felício, Cavalcanti et al. CFCR8035 (SPF, UEC); Lagoa Santa, Warming s.n. (BR [BR0000005520732], C [C10015107], P [P005317116]); Lavras, Avezum & Almeida 10 (SPF); Lima Duarte, Heluey & Castro 108 (RB); Manhuacu, Hatschbach & Silva 49393 (HUEM, MBM); Mariana, Lombardi 4045 (BHCB, ESA); Moeda, Silva & Grandi 6627 (HUFU); Nova Lima, Williams & Assis 7274 (SP); Ouro Branco, Delfini et al. 97 (ESA, RB); Ouro Preto, Colletta 161 (SPF), Martius 931 (BM, G, M, MO, P); Paracatu, Bovini & Barros 3235 (RB); Passa Quatro, Meireles et al. 1766 (RB, UEC); Patrocínio, Farah et al. 580 (ESA, HUEM); Perdizes, Mendes & Araújo 970 (SPF); Piuhmhi, Emygdio 3613 (NY, R); Poços de Caldas, Oliveira 1013 (US); Prados, Sobral et al. 12797 (UPCB); Presidente Soares, Hatschbach et al. 55434 (MBM); Rio Acima [Gandarela], Emygdio 3312 (NY, R); Rio Pardo de Minas, Sevilha et al. 7075 (CEN); Rio Preto, Barros & Feteira 1625 (RB); Rio Vermelho, Mello-Silva et al. CFCR7836 (SPF); Rosário de Limeira, Marcolino 222 (RB); Sabará, Barreto 6759 (BHCB, SP); Sacramento, Romero et al. 2155 (MBM); Santa Bárbara, Barreto 6757 (BHCB, SP); Santa Bárbara do Monte Verde, Pivari 15 (MBM); Santana de Pirapama, Zappi et al. 2504 (SPF); Santana do Riacho, Pacifico 191 (HUEM); Santos Dumont, Mello-Silva et al. 1217 (SPF); São Gonçalo do Rio Preto, Foresto et al. 59 (SPF); São Gonçalo do Sapucaí, Hatschbach 26964 (MBM); São João Batista da Glória, Kinoshita et al. 43767 (HUEM); São João del Rei, Barreto 4654 (SP, US); São Roque de Minas, Pacifico 413 (CAS, HUEM); São Tomé das Letras, Valente & Azevedo 57 (RB); Serro, Almeda et al. 9076 (CAS, UEC); Tapira, Salgado 167 (RB); Tiradentes, Alves 600 (R); Tombos, Fraga & Saddi 1786 (CEPEC, RB); Uberlândia, Romero & Nakajima 3021 (HUFU); Unknown municipality in Minas Gerais State, Gardner 4602 (NY, R, US), Martius 961 (G, M), Mosen 1971 (C, P, R), Saint-Hilaire s.n. [D462] (P [P00723414], P [P00723415]), Sellow 1154 (US), Sellow 5278 (P), Vauthier 43 [part] (BR, G, P), Widgren 967 (BR). Paraná: Adrianópolis, Camargo et al. 109 (UPCB); Antonina, Hatschbach & Guimarães 56167 (MBM); Araponga, Caiafa & Umbelino 172 (UPCB, VIC); Arapoti, Hatschbach 6908 (MBM); Balsa Nova, Hatschbach et al. 42967 (MBM); Bocaiúva do Sul, Ribas et al. 6769 (MBM, UPCB); Campina Grande do Sul, Brotto & Vieira 1921 (MBM); Colombo, Hatschbach 647 (MBM, RB); Jaguariaíva, Ribas et al. 8528 (MBM); Ortigueira, Silva et al. 6478 (MBMB, UNOP); Palmeira, Hatschbach 2775 (MBM); Piraí do Sul, Goldenberg et al. 1652 (NY, UPCB); Ponta Grossa, Silva & Koch 7610 (MBM); Rio Branco do Sul, Silva & Abe 2310 (MBM); Sengés, Hatschbach 39954 (MBM); Tibagi, Kirizawa 3665 (SP); Tunas do Paraná, Brotto 2600 (MBM, RB); Ventania, Estevan et al. 617 (UPCB). Rio de Janeiro: Bom Jardim, Hottz et al. 302 (MBM, RB); Duque de Caxias, Lima et al. 8445 (RB); Itatiaia, Baumgratz et al. 1127 (MBM, SPF); Miguel Pereira, Wängler & Ferreira 1352 (RB); Nova Friburgo, Forzza et al. 3427 (RB); Petrópolis, Vieira & Yamamoto 26186 (FUEL, RB, UEC); Resende, Eiten & Eiten 7305 (NY, P, RB, SP, US); Rio Claro, Moutinho et al. 76 (RB); Santa Maria Madalena, Lima 400 (US); Teresópolis, Duarte & Brade

1155 (RB); Unknown municipality in Rio de Janeiro state, Gardner 379 (BR, NY, P, US), Gardner 380 (BR, F, G, NY, P, S, US), Guillemin 921 (P), Guillemin 946 (G, P), Widgren s.n. (BR [BR0000005227044], PH-27744, S-53231). São Paulo: Apiaí, Souza et al. 6098 (ESA, RB); Bananal, Martinelli 19464 (RB); Bom Sucesso de Itararé, Aguiar 102 (MBM); Brotas, Queiroz 2808 (CEPEC); Campos do Jordão, N. da Cruz 135 (CAS, MBM); Cunha, Mamede et al. 666 (RB, SP); Eldorado, Pastore et al. 685 (RB); Iporanga, Souza et al. 5934 (SPF); Itapeva, Baitello et al. 2136 (UPCB); Itirapina, Tannus 760 (HUFU); Lavrinhas, Caddah et al. 636 (UPCB); Mogi Mirim, Hoehne 20521 (NY, SP); Pedregulho, Polisel et al. 176 (UPCB); Pindamonhangaba, Nicolau et al. 2212 (SP); Piquete, Gonçalves et al. 172 (RB); Rio Claro, Loefgren 557 (BHCB, SP); Santo André, Kirizawa et al. 2132 (SP); São Bernardo do Campo, Kuhlmann 4381 (SP); São Carlos, Eiten et al. 3019 (SP, US); São José do Barreiro, Handro 790 (NY); São José dos Campos, Mimura 479 (SP, US); São Paulo, Beraldo & França 85 (SPF); Ubatuba, Souza et al. 1108 (UPCB); Unknown municipality in São Paulo State, Prates s.n. (P [P00723407], P [P00723406, P [P00723408]). Unknown state: Bunbury s.n. (BR [BR0000005520374]), Glaziou 12704 (BR), Glaziou 16679 (BR), Glaziou 16778 (C, L, P), Glaziou 2579 (BR, P), Glaziou 8680 (BR, P), Glaziou 9454 (BR, C, G, P, R, S), Martius 989 (BR), Raben 409 (BR), Riedel s.n. (BR [BR0000005520367]), Sellow s.n. (lectotype: G [G00396696], probable isolectotype: P [P05317745]).

Distribution, habitat and elevation range. Endemic to Brazil in the States of Bahia, Minas Gerais, Goiás, Distrito Federal, Espírito Santo, Rio de Janeiro, São Paulo and Paraná (Fig. 25A). *Trembleya parviflora* is common in gallery forests surrounding campo rupestre, Cerrado, campo sujo, campo limpo. campos de altitude, Veredas (palm swamps), and margins of roads throughout Cerrado and Atlantic forest fragments, usually exposed to full sun, at elevations between 560 and 2223 m.

Ecology. *Microlicia parviflora* is the most widely distributed species in the clade and the most studied from an ecological perspective. Giotto (2015) investigated plant occupation in palm swamps with very dense populations of *M. parviflora*, where seedlings of this species corresponded to 78% of the total seed bank. Silva (2003) reported a population density of 1.47 individuals per square metre in these areas. This elevated local dominance of *M. parviflora* negatively affects the overall plant species richness of these regions and is apparently favoured by reduction in humidity (Giotto 2015), although *M. parviflora* occurs with large populations in both wet and dry areas (Melo 2013). This species is strongly recommended for ecological restoration (Amaral et al. 2013) because it readily colonises degraded campo rupestre. Leaf extracts of *M. parviflora* proved to have allelopathic properties, inhibiting root and shoot growth of *Sesamum indicum* (Borghetti et al. 2005). According to Pereira (2011), leaves of *M. parviflora* develop increased asymmetry when damaged by insects.

Conservation. This is the most abundant species in the *Trembleya* s.s. clade, with more than 1000 collections currently housed in herbaria. The EOO is 1,152,078.308 km² and the AOO is 1,640 km². Populations of *M. parviflora* are found in all conservation units that protect the remaining species of the clade. As it occurs in large and dense populations, some have claimed that *M. parviflora* has the potential to become



Figure 25. Geographic distribution of species of the *Trembleya* s.s. clade of *Microlicia* **A** distributions of *M. parviflora* and *M. tridentata* **B** distributions of *M. pentagona*, *M. pithyoides* and *M. rosmarinoides*.

an invasive species (e.g. Silva 2003). We are not aware of records of this species occupying regions outside its natural distributional range. Based on the IUCN (2019) recommendations and criteria, we recommend that a conservation status of Least Concern (LC) be assigned to this species.

Recognition and affinities. *Microlicia parviflora* can be distinguished from its congeners by its leaves that are 5-nerved from the base, the abaxial surface glandular-punctate, sometimes covered with an indumentum of pedicellate trichomes (never dense enough to conceal the epidermis), three to many-flowered inflorescences, triangular calyx lobes 0.7–2.5(–3) mm long, petals white or pink and dimorphic stamens. *Microlicia pentagona* and *M. trembleyiformis* are somewhat similar to *M. parviflora* in leaf shape and venation and stamen morphology. *Microlicia parviflora* differs from *M. pentagona* by its leaves with tertiaries evident (vs. little evident), moderately reticulate and randomly branching (vs. parallel and/or branching apically), inflorescences (vs. solitary flowers) and triangular calyx lobes 0.7–2.5(–3) mm long (vs. subulate and 6.2–8.5 mm long) that are tenuous in fruit (vs. thickened). In turn, *M. parviflora* differs from *M. trembleyiformis* by the unwinged branchlets (vs. with narrow wings ca. 0.2 mm wide), flowers disposed in inflorescences (vs. flowers solitary), triangular calyx lobes (vs. narrowly-triangular) and consistently 5-locular ovaries (vs. 3–5-locular). For a comparison between *M. parviflora* and *M. altoparaisensis*, see notes under the latter species.

Notes. The morphological variation found in *M. parviflora* is mainly related to leaf blade shape (varying from elliptic to ovate and lanceolate), indumentum on branches

and abaxial leaf surface (always glandular-punctate, usually pruinose, eventually sparsely to densely covered with gland-tipped or eglandular trichomes 0.1-0.9 mm long) and inflorescence development (three- to many-flowered). The petals are usually white flushed with pink at the base, although some populations have entirely white petals, for example, in Serra de Carrancas (Matsumoto and Martins 2005) and Serra Negra (Justino et al. 2016) in Minas Gerais. Based on descriptions of *M. parviflora* in local floras, magenta-flowered and white-flowered variants of this species occur together in Pocos de Caldas and Paque Estadual do Ibitipoca, both in Minas Gerais. In the Serra da Canastra, Romero (2000: 283) recognised a variant of M. parviflora as a distinct entity (Trembleya sp.) characterised by tertiaries more evident, trichomes on the abaxial leaf surface with 3-4-lobed heads, inflorescence internodes 7-9 mm long and calyx lobes 2.5-3 mm long. Several other modal extremes were designated as types of infraspecific taxa by Cogniaux (1883–1888, 1891), for example, the specimen Prates s.n. (P [P00723407]; type of var. denticulata) has more conspicuous serrations on the leaf margin, whereas Guillemin 946 (P; type of var. tomentosa) has a denser indumentum on the branchlets. However, none of the mentioned variations is correlated with other characteristics in a meaningful way.

The 15 varieties of *M. parviflora* proposed by Cogniaux (1883–1888, 1891) were based exclusively on differences in leaf blade size, shape and apex and degree of inflorescence development. Based on a comprehensive sampling and analysis of representative collections from throughout the range of the species, it is clear that Cogniaux's infraspecific taxonomy is artificial and untenable. In fact, many of the specimens examined had leaf sizes that do not fit into any of the infraspecific taxa proposed by Cogniaux (1883–1888, 1891). For example, the specimen *Kinoshita et al. 10/19* (UEC) has leaves 1.5–8 cm long and could fit all varieties proposed, based on this feature. The features that Cogniaux (1883–1888) used to circumscribe the two subspecies are also imprecise and not diagnostic. After analysing several representative collections of *M. parviflora*, we did not find any specimen with clearly tetragonal and totally glabrous branches, both purported diagnostic features of *M. parviflora* subsp. *triflora*. Thus, given the highly polymorphic nature of *M. parviflora*, we do not recognise any infraspecific taxa in this species.

Like *Microlicia cataphracta* (Mart. & Schrank ex DC.) Versiane & R.Romero [= *Lavoisiera imbricata* (Thunb.) DC.], *M. parviflora* fits all the six criteria enumerated by Cronk (1998) to be considered as an ochlospecies (see Martins and Almeda 2017). Besides sharing outstanding levels of morphological variation, *M. cataphracta* and *M. parviflora* also have similar distributional ranges and usually occur in large populations. The reproductive biology, population characteristics, chemical composition and other ecological aspects of *M. parviflora* are summarised in other sections of this paper.

Martin and Cremers (2007) examined a supposed holotype of *Trembleya paniculata* at P. However, we found two duplicates of the same collection used by Naudin (1844) to describe *Trembleya paniculata* (*Saint-Hilaire* s.n., P [P00723414], P [P00723415]). Thus, we designated one of these sheets as the lectotype (P [P00723414]) and the other as an isolectotype (P [P00723415]) for *Trembleya paniculata*.

7. *Microlicia pentagona* (Naudin) Versiane & R.Romero, Bot. J. Linn. Soc. 197: 54. 2021.

Fig. 26

Trembleya pentagona Naudin, Ann. Sci. Nat., Bot. Sér. 3, 2: 154. 1844. **basionym**. Type: Brazil. "In montibus vulgo Serra d'Ouro Branco, provincia Minas-Geraes" [Minas Gerais, Ouro Branco], *A. Saint-Hilaire s.n.* (lectotype, first-step designated by Martin and Cremers (2007), second-step designated here: P [P00723399]!; isolectotype: P [P00723398]!; image of lectotype is available at http://coldb.mnhn. fr/catalognumber/mnhn/p/p00723399).

Description. Erect shrubs or treelets 0.5–1.5 m tall. Branchlets quadrangular, appearing glabrous, vernicose and minutely granulose, vinaceous (when fresh). Internodes 0.4-2.5 cm long, angles unwinged. Petioles 1.8-2.4 mm long. Leaf blades 12-40 mm long, 3-15 mm wide, chartaceous to coriaceous (when dry), elliptic, ovate, narrowly elliptic or linear, both surfaces green (when fresh), adaxial surface blackened and abaxial surface pale green to pale brown (when dry), discoloured (when dry), base cuneate to attenuate, apex rounded to acute, margin flat, entire along the basal half, serrulate on the upper half and minutely granulose and becoming glabrescent with age, 5-nerved from the base, one pair of acrodromous veins and one pair of tenuous veins close to the margin, tertiaries little evident on the abaxial surface, nearly perpendicular to the mid-vein, parallel or little reticulate and branching apically, adaxial surface glabrous to minutely granulose, vernicose, abaxial surface glabrous to minutely granulose, vernicose. Inflorescences reduced to solitary flowers apically on the branches. Bracts absent. Bracteoles (at anthesis) with petioles 1.8-3.0 mm long, blades 3.0-6.5 mm long, 1.1-3.6 mm wide, elliptic, ovate or lanceolate, base attenuate to cuneate, apex acute to obtuse, margin entire, 3-nerved, indumentum like that of the principal leaves. Flowers (4-)5-merous, pedicels (at anthesis) 0.8-2.0 mm long. Hypanthia (at anthesis) 2.5-3.5 mm long, 2.7–3.0 mm wide at the torus, campanulate to urceolate, light green or reddish (when fresh), externally glabrous, minutely granulose, vernicose. Calyx tubes 0.2–0.4 mm long. Calyx lobes (at anthesis) 6.2–8.5 mm long, 1.8–2.2 mm wide at the base, subulate, apex acute, margin entire, (when fresh) light green or reddish, externally like the hypanthia. Petals 11.8–13.8 mm long, 7.1–9.5 mm wide, magenta, obovate, apex shortly acuminate, margin entire and glabrous, both surfaces glabrous. Stamens (8)10, strongly dimorphic. Larger (antesepalous) stamens (4)5, filaments 4.0-5.0 mm long, pink, pedoconnectives 5.3-5.8 mm long, pink, appendages 1.2-1.6 mm long, yellow, apex emarginate to bilobate, thecae (excluding rostra) 1.2-2.0 mm long, vinaceous, oblong, rostra 0.5-0.7 mm long, the circular pores ca. 0.2 mm wide. Smaller (antepetalous) stamens (4)5, filaments 3.9-4.4 mm long, pink, pedoconnectives 1.0-1.6 mm long, yellow, inconspicuous appendages ca. 0.1 mm long, yellow, apex emarginate, thecae (excluding rostra) 1.6–2.0 mm long, yellow, oblong, rostra 0.5–0.6 mm long, the circular pores ca. 0.2 mm wide. Ovary 2.5-2.7 mm long, 2.4-2.6 mm wide, globose, 5-locular. Style 6.0-6.6 mm long, magenta. Capsules (at maturity)



Figure 26. *Microlicia pentagona* **A** habit **B** leaf abaxial surface **C** bracteole abaxial surface **D** floral bud **E** flower in lateral view **F** flowering hypanthium **G** petal adaxial surface **H** antesepalous (left) and antepetalous (right) stamens **I** gynoecium **J** capsule enveloped by the hypanthium. Drawn from Sazima CFSC4259 (UEC) and Almeda et al. 9203 (UEC).

4.5–5.5 mm long, 5.0–6.0 mm wide, globose, initially enveloped by the hypanthium, torus constricted at the apex, fruiting calyx tubes 0.2–0.4 mm long, fruiting calyx lobes 6.5–11.0 mm long, stout, thickened. Seeds 0.5–0.7 mm long, reniform.

Distribution, habitat and elevation range. Endemic to Minas Gerais State (Fig. 25B) in Serra do Caraça, Serra do Cipó, Serra de Ouro Preto, Serra de Ouro Branco, Serra do Itabirito, Mariana and Barão de Cocais. It occurs on quartzitic and ferruginous campo rupestre, exposed to full sun, at elevations of about 1000–1830 m.

Conservation. *Microlicia pentagona* is known from about 70 collections. The EOO is 2,667.623 km² and the AOO is 56 km². Several populations are protected within the following conservation units: Parque Estadual do Itacolomi, Parque Estadual Serra do Intendente, Parque Estadual Serra do Ouro Branco, Parque Nacional da Serra do Cipó and RPPN Serra do Caraça (Natural Heritage Private Reserve). Following the IUCN (2019) recommendations and criteria, we recommend an Endangered (EN): B1ab(iii) status for this species.

Recognition and affinities. *Microlicia pentagona* can be recognised by its branches, leaves and hypanthia that are glandular-punctate and vernicose, leaves 5-nerved from the base with one pair of acrodromous veins and one pair of tenuous veins close to the margin, inflorescences reduced to solitary terminal flowers and calyx lobes 6.2–8.5 mm long that become thickened in fruit. The elongate calyx lobes of *M. pentagona* are comparable in length only to those of *M. laniflora* (7.9–9.7 mm long) and are consistently longer than those of all remaining congeners. In fruit, the thickened calyx lobes of *M. pentagona* are unique in the clade. Overall, *M. pentagona* is morphologically similar to *M. calycina, M. chamissoana, M. laniflora* and *M. parviflora*. For comparisons, see comments under these species.

Notes. *Microlicia pentagona* is remarkably variable in leaf shape and size. The leaf blades vary from almost linear (e.g. *Irwin et al. 20537, Barreto 10734*) to narrowly elliptic (e.g. *Barreto 7025, Joly et al. CFSC 3196*) and elliptic (e.g. *Silva 1043*). Examples of variation in leaf size are *Almeda et al. 9203* (1.7–2.1 cm long) and *Silva 1043* (2.3–3.1 cm long). Some modal extremes were informally recognised as distinct taxa by Mello Barreto on herbaria labels. As no character varies in a meaningful way, we agree with Martins (1997) and treat all these extremes within the variation here attributed to *M. pentagona*.

Specimens examined. BRAZIL. Minas Gerais: Barão de Cocais Municipality, Brandão 20838 (HUFU); Catas Altas Municipality, Serra do Caraça, Hatschbach et al. s.n. (HUFU [25601]), Irwin et al. 29213 (NY), Oliveira et al. 478 (BHCB), Oliveira et al. 480 (BHCB, RB), Oliveira et al. 518 (BHCB), Silva et al. 1043 (HUFU), Sobral et al. 14508 (HUFSJ, RB); Santa Bárbara Municipality ["Capanema"], Claussen 296 (W), Vainio 33501 (US); Jaboticatubas Municipality ["Caeté"], Serra do Cipó, Magalhães 2278 (BHCB, US); Mariana Municipality, Pivari et al. 2512 (BHCB); Ouro Branco Municipality, Saint-Hilaire s.n. (lectotype: P [P00723399]; isolectotype: P [P00723398]); Ouro Preto Municipality, Antônio-Silva et al. 315 (HUFU, OUPR), Bortoluzzi et al. 678 (RB, VIC), Damazio s.n. (RB [48352], NY [NY00942037]), Michelangeli et al. 1580 (NY, UPCB), Pacifico & Bressan 294 (HUEM, SPF), Peron 256 (RB), Peron 260 (RB), Rezende 507 (HUFU), Rolim et al. 353 (UPCB, VIC), Rolim et al. 361 (NY, RB, VIC), Rolim et al. 370 (HUFU, NY, RB, VIC), Schwacke 10814 (W), Schwacke 9325 (RB, W); Santa Bárbara Municipality, Serra do Caraca, Almeda et al. 7751 (CAS, HUFU, UEC), Damazio s.n. (RB [48392]), Ordones et al. 213 (BHZB, HUFU), Pirani & Yano 692 (RB, SP, SPF), Rapini et al. 296 (HUEM, SP, SPF), Romero et al. 5303 (CAS, UEC); Santana do Riacho Municipality, Serra do Cipó, Almeda et al. 8555 (CAS, UEC), Almeda et al. 8911 (CAS, UEC), Almeda et al. 9203 (CAS, HUEM, UEC), Barreto 1182 (RB), Contro & Marques 21 (HUEM, HUFU), Duarte 2004 (FLOR, MBM, RB), Fernandes s.n. (HUFU [56535]), Irwin et al. 20178 (CAS, MO, NY, UEC, US), Irwin et al. 20486 (CAS, MO, NY, US), Irwin et al. 20537 (CAS, NY, UEC, US), Pacifico & Bressan 531 (CAS, HUEM, RB). Romero & Nakajima 5998 (HUEM, HUFU, UEC), Semir CFSC5608 (SP, SPF), Semir & Sazima CFSC3395 (UEC); Santana do Riacho Municipality ["Conceição do Mato Dentro"], Serra do Cipó, Barreto 7025 (BHCB, HB, UEC); Santana do Riacho Municipality ["Jaboticatubas"], Serra do Cipó, Giulietti & Menezes 4017 (SP, SPF, UEC), Hatschbach et al. 28759 (MBM, SPF, US), Hatschbach et al. 29958 (MBM), Joly & Semir CFSC2957 (UEC), Joly & Semir CFSC3196 (SPF, UEC), Sazima CFSC4259 (RB, SP, UEC), Semir & Joly CFSC3743 (UEC); Santana do Riacho Municipality ["Santa Luzia"], Serra do Cipó, Barreto 10734 (HB, UEC), Barreto 7023 (BHCB), Barreto 7024 (UEC), Brade 14756 (R), Duarte 2692 (R, RB, US); Unknown municipality in Minas Gerais State, Casaretto s.n. (G [G00318565]), Claussen 1617 (P), Claussen 1637 (P), Claussen 22 (P, US), Claussen 350 (W), Claussen s.n. (P [P005317034], P [P005317035]), Glaziou 14742 (K, NY, P, R), Ule 2543 (US), Schüch s.n. (W [70510]).

8. *Microlicia pithyoides* (Cham.) Versiane & R.Romero, Bot. J. Linn. Soc. 197: 54. 2021.

Fig. 27

- Trembleya pithyoides Cham., Linnaea 9(4): 428. 1835. basionym. Type: Brazil. "Caraça" [Minas Gerais, Serra do Caraça], 20 December 1830, F. Sellow 1316 (lectotype, designated here: K [K00530665]!; isolectotypes: F-BN016638-photo]!, P [P00723396]!, P [P00723397]!; image of isolectotype at P is available at http:// coldb.mnhn.fr/catalognumber/mnhn/p/p00723396).
- Trembleya pithyoides var. major Cogn. in Martius et al., Fl. Bras. 14(4): 594. 1888. syn. nov. Type: Brazil. "Minas, Serra de Capanema" [Minas Gerais, Santa Bárbara], 21
 February 1884, A.F.M. Glaziou 14746 (lectotype, designated here: P [P00723395]!; isolectotypes: BR [BR0000005223930]!, BR [BR0000005520169]!, C [C10015114-online image]!, C [C10015113-online image]!, K [K00530666]!, P [P00723394]!, P [P00723393]!; image of lectotype is available at http://coldb. mnhn.fr/catalognumber/mnhn/p/p00723395).

Description. Erect, densely-branched shrubs 0.3–0.6 m tall. Branchlets quadrangular, glandular-punctate, vinaceous (when fresh). Internodes 0.2–0.5 cm long, angles with

narrow wings ca. 0.2 mm wide. Petioles 0.7–1.5 mm long. Leaf blades 4–15 mm long, 0.5-1.4 mm wide, chartaceous (when dry), linear, both surfaces green (when fresh), adaxial surface blackened and abaxial surface pale green to pale brown (when dry), discoloured (when dry), base cuneate, apex rounded to acute, margin flat, entire and glandular-punctate, 1-nerved from the base, tertiaries not evident on the abaxial surface, adaxial surface glandular-punctate, abaxial surface glandular-punctate. Inflorescences reduced to solitary flowers apically on the branches. Bracts absent. Bracteoles (at anthesis) with petioles 0.6–0.9 mm long, blades 3.0–3.9 mm long, 0.3–0.5 mm wide, lanceolate, base cuneate, apex acute to obtuse, margin entire, 1-nerved, indumentum like that of the principal leaves. Flowers 5-merous, pedicels (at anthesis) 0.3-0.6 mm long. Hypanthia (at anthesis) 1.7–2.0 mm long, 1.9–2.1 mm wide at the torus, campanulate, light green or reddish (when fresh), externally glandular-punctate. Calyx tubes 0.3–0.4 mm long. Calyx lobes (at anthesis) 2.5-3.0 mm long, 0.4-0.7 mm wide at the base, subulate, apex acute, margin entire, (when fresh) light green or reddish externally like the hypanthia. Petals 5.0-5.7 mm long, 3.7-4.2 mm wide, magenta, obovate, apex acuminate, margin entire and glabrous, adaxial surface glabrous or sparsely glandular-punctate, abaxial surface glabrous. Stamens 10, strongly dimorphic. Larger (antesepalous) stamens 5, filaments 2.6–2.9 mm long, pink, pedoconnectives 2.9–3.2 mm long, pink, appendages 0.7-0.9 mm long, yellow, apex emarginate to bilobate, thecae (excluding rostra) 1.8–2.0 mm long, vinaceous, oblong, rostra 0.2–0.4 mm long, the circular pores ca. 0.2 mm wide. Smaller (antepetalous) stamens 5, filaments 1.9–2.1 mm long, pink, pedoconnectives 0.6–0.9 mm long, yellow, inconspicuous appendages ca. 0.1 mm long, yellow, apex emarginate, thecae (excluding rostra) 1.4-1.6 mm long, yellow, oblong, rostra 0.2–0.3 mm long, the circular pores ca. 0.2 mm wide. Ovary 1.3–1.5 mm long, 1.0-1.2 mm wide, globose, (4-)5-locular. Style 4.0-4.5 mm long, pink. Capsules (at maturity) 2.7-3.1 mm long, 2.9-3.3 mm wide, globose, initially enveloped by the hypanthium, torus constricted at the apex, fruiting calyx tubes 0.4–0.6 mm long, fruiting calyx lobes 3.2-3.7 mm long, not thickened. Seeds 0.7-0.8 mm long, reniform.

Specimens examined. BRAZIL. Minas Gerais: Catas Altas Municipality, Serra do Caraça, Oliveira 382 (BHCB, RB), Pacifico 295 (CAS, HUEM, SPF); Unknown municipality in Minas Gerais State, Serra do Caraça. Glaziou 14746 (BR, C, K, P, R), Glaziou 19239 (K, P), Sellow 1316 (lectotype: K [K00530665; isolectotypes: F-BN016638-photo, P [P00723396], P [P00723397]), Sellow s.n. (K [K00957781, K [K00957783]), Weddell s.n. (P [P005317975]).

Distribution, habitat and elevation range. Known only from Minas Gerais State (Fig. 25B), where it is probably endemic to the Serra do Caraça. *Microlicia pithyoides* grows on quartzitic campo rupestre exposed to full sun at elevations between 1827 and 2072 m. It is the only species in the clade that reaches the highest peak in Cadeia do Espinhaço, the Pico do Sol in Catas Altas Municipality (elev. 2,072 m) (personal observation by R. Pacifico).

Conservation. *Microlicia pithyoides* species is the least collected species of the *Trembleya* s.s. clade and apparently has the narrowest distribution. Less than 10 collections of this species are housed in herbaria. It had not been collected for more than a hundred years until it was re-discovered in 2009 (Oliveira 382). As all coordinates


Figure 27. *Microlicia pithyoides* **A** habit **B** detail of nodes and internodes **C** leaf abaxial surface **D** bracteole abaxial surface **E** floral bud **F** flower in lateral view **G** petal adaxial surface **H** antesepalous stamen **J** antepetalous stamen **J** capsule enveloped by the hypanthium **K** capsule in cross section. Drawn from Pacifico 295 (CAS).

available for *M. pithyoides* refer to the same population, we were unable to calculate its EOO. The AOO is 4 km². The only population known of this species occurs inside a private protected area, the RPPN Serra do Caraça (Natural Heritage Private Reserve). The type material was probably collected at the Serra de Capanema in Santa Bárbara

Municipality. Currently, this locality is also part of a private property. We are not aware of recent collections of *M. pithyoides* from the Serra de Capanema. Overall, the vegetation of Serra do Caraça is largely intact and affords a good measure of protection for the populations of *M. pithyoides*. This species is considered Critically Endangered by the Brazilian Government (Brasília 2014). Based on criterion B of the IUCN (2019), we concur with this assessment: (CR): B1ab(iii).

Recognition and affinities. *Microlicia pithyoides* can be recognised by its narrow leaves that are 0.5–1.4 mm wide, 1-nerved from the base, inflorescences reduced to solitary flowers, magenta petals and stamens with bicoloured anthers. In morphology, it is most like *M. rosmarinoides*, the only congener with leaves that are 1-nerved from the base. *Microlicia rosmarinoides* also shares with *M. pithyoides* the solitary flowers with subulate calyx lobes and the overall shape of its stamens. *Microlicia pithyoides* differs from *M. rosmarinoides* by the leaves with the mid-vein thickened (vs. not thickened), magenta petals (vs. yellow) and stamens with anthers vinaceous and yellow (vs. all anthers yellow to orange). Both species occur in central Minas Gerais State, but their distributions do not overlap; *M. rosmarinoides* has never been collected on the Serra do Caraça.

Microlicia calycina is also morphologically similar. It shares with *M. pithyoides* the narrow leaves, solitary flowers (sometimes simple dichasia only in *M. calycina*), magenta petals and stamens with bicoloured anthers. *Microlicia pithyoides* may be differentiated by its leaf blades (oblong to lanceolate) 0.5–1.4 mm wide (vs. 2–9 mm wide), 1-nerved from the base (vs. 3-nerved) with tertiaries not evident (vs. evident) and shorter calyx lobes 2.5–3.0 mm long (vs. 3.5–4.2 mm long). Both *M. calycina* and *M. pithyoides* occur sympatrically on the Serra do Caraça, but only *M. pithyoides* occurs on the highest peak in that mountain range. In fact, *M. pithyoides* apparently prefers slightly higher elevations since it has only been collected between 1827 and 2072 m (vs. 1692–1920 m for *M. calycina*).

Notes. Recent collections of *M. pithyoides* (*Oliveira 382, Pacifico 295*) have leaves with blades that are 8–12 mm long. These measurements bridge those given in the protologues of varieties *pithyoides* (8–10 mm long) and *major* (12–20 mm long). We consider these size differences to represent a continuum and here relegate var. *major* to synonymy.

9. *Microlicia rosmarinoides* (Mart. & Schrank ex DC.) Versiane & R.Romero, Bot. J. Linn. Soc. 197: 54. 2021.

Fig. 28

Trembleya rosmarinoides Mart. & Schrank ex DC., Prodr. 3: 125. 1828. basionym. Type: Brazil. "Habitat in summo Monte de V. Rica et in Itacolumi 5000 ped. alt. Provinciae Min. Gen." [Minas Gerais, Ouro Preto], C.F.P. Martius 808 (lectotype, designated here: M [M0165886]!; isolectotype: G [G00310213-online image]!).

Description. Erect, densely branched shrubs 0.3–0.6 m tall. Branchlets quadrangular, glandular-punctate, light green (when fresh). Internodes 0.1–0.4 cm long, angles with



Figure 28. *Microlicia rosmarinoides* **A** habit **B** detail of nodes and internodes **C** leaf abaxial surface **D** bracteole abaxial surface **E** floral bud **F** flower in lateral view **G** petal adaxial surface **H** antesepalous stamen **J** antepetalous stamen **J** capsule enveloped by the hypanthium **K** capsule in cross section **L** seed in lateral view. Drawn from Occhioni et al. s.n. (US [US001900109]).

narrow wings 0.2–0.3 mm wide. Petioles 0.5–1.2 mm long. Leaf blades 4–10 mm long, 1.0-1.9 mm wide, chartaceous (when dry), narrowly-lanceolate to narrowly-elliptic, both surfaces green (when fresh), adaxial surface blackened and abaxial surface pale green to pale brown (when dry), discoloured (when dry), base cuneate, apex rounded to acute, margin flat, entire and glandular-punctate, 1-nerved from the base, tertiaries little evident on the abaxial surface, adaxial surface glandular-punctate, abaxial surface glandular-punctate. Inflorescences reduced to solitary flowers on apical branches. Bracts absent. Bracteoles (at anthesis) with petioles 0.5-1.0 mm long, blades 2.5-3.3 mm long, 0.5–0.9 mm wide, lanceolate, base cuneate, apex acute to obtuse, margin entire, 1-nerved, indumentum like that of the principal leaves. Flowers 5-merous, pedicels (at anthesis) 0.4-0.6 mm long. Hypanthia (at anthesis) 2.2-3.5 mm long, 1.5-2.0 mm wide at the torus, campanulate to urceolate, light green (when fresh), externally glandular-punctate. Calyx tubes 0.3–0.5 mm long. Calyx lobes (at anthesis) 2.2–2.8 mm long, 0.5-0.8 mm wide at the base, subulate, apex acute, margin entire, (when fresh) light green, externally like the hypanthia. Petals 5.0–5.3 mm long, 2.4–3.0 mm wide, yellow, obovate, apex acute or rounded, margin entire and glabrous, both surfaces glabrous. Stamens 10, strongly dimorphic. Larger (antesepalous) stamens 5, filaments 2.2–3.0 mm long, yellow, pedoconnectives 3.2–3.8 mm long, yellow, appendages 0.8–1.0 mm long, yellow, apex emarginate to bilobate, thecae (excluding rostra) 1.4-1.7 mm long, yellow to orange, oblong, rostra 0.2-0.3 mm long, the circular pores ca. 0.2 mm wide. Smaller (antepetalous) stamens 5, filaments 1.5-2.0 mm long, yellow, pedoconnectives 0.8-1.0 mm long, yellow, inconspicuous appendages ca. 0.1 mm long, yellow, apex emarginate, thecae (excluding rostra) 1.4–1.6 mm long, yellow to orange, oblong, rostra 0.2–0.3 mm long, the circular pores ca. 0.2 mm wide. Ovary 0.9–1.1 mm long, 0.7–0.9 mm wide, ovoid, 5-locular. Style ca. 3 mm long, yellow. Capsules (at maturity) 2.5-3.5 mm long, 2.0-3.0 mm wide, globose, initially enveloped by the hypanthium, torus constricted at the apex, fruiting calyx tubes 0.3–0.6 mm long, fruiting calyx lobes 2.5-3.2 mm long, not thickened. Seeds 0.5-0.9 mm long, reniform.

Distribution, habitat, and elevation range. Restricted to central Minas Gerais State (Fig. 25B), where it is known only from Serra do Gandarela, Serra de Capanema, Serra de Ouro Preto, Serra de Itabirito, Belo Vale and Barão de Cocais. *Microlicia rosmarinoides* occurs in campo rupestre and canga, on ferruginous or quartzitic soils, exposed to full sun, at elevations between 1609 and 1807 m.

Conservation. *Microlicia rosmarinoides* is a little-collected species, known from about 15 specimens. The EOO is 298.172 km² and the AOO is 28 km². Populations of *M. rosmarinoides* are protected in the Parque Nacional da Serra do Gandarela and probably in Parque Estadual do Itacolomi. Following IUCN (2019) criteria, we recommend an assessment of Endangered (EN): B1ab(iii) for this species.

Recognition and affinities. *Microlicia rosmarinoides* can be readily recognised amongst congeners by its narrow leaves (1–1.9 mm wide) and flowers with yellow petals. The narrow leaves of *M. rosmarinoides* are more similar to those of the closely related *M. pithyoides*, while the yellow petals are shared only with the distantly related *M. flaviflora*. For comparisons, see notes under *M. flaviflora* and *M. pithyoides*.

Specimens examined. BRAZIL. Minas Gerais: Barão de Cocais, Mina do Baú, Souza et al. 2584 (BHCB); Belo Vale, Occhioni et al. s.n. (RFA, US [US001900109]); Itabirito, Serra de Capanema, Carmo 192 (BHCB), Carmo 377 (BHCB); Ouro Preto municipality, Serra do Itacolomi, Martius 808 (lectotype: M [M0165886]; isolectotype: G [G00310213]), Pedrosa 110 (HUFU, OUPR), Schwacke 9184 (BHCB, RB, US, W); Rio Acima Municipality, Serra do Gandarela, Carmo 2262 (BHCB), Versiane & Castello 677 (HUFU, UEC), Vidal s.n. (BHCB [191426]); Santa Bárbara Municipality, Serra do Gandarela, Vidal s.n. (BHCB [181346]); Unknown municipality in Minas Gerais State, Glaziou 14747 (IAN, K, RB, US), Glaziou 19242 (K), Ule 2528 (US).

10. *Microlicia trembleyiformis* Naudin, Ann. Sci. Nat., Bot. Sér. 3, 3: 172. 1845. Fig. 29

Type. BRAZIL. "Minas Geraes, in campis circa urbem Villa Ricca frequens" [Minas Gerais, Ouro Preto], 1816–1821, [catal. B1, n° 160] *A. Saint-Hilaire s.n.* (lectotype, first-step designated by Martin and Cremers (2007), second-step designated here: P [P002297746]!; isolectotype: F [F0360366]!; image of lectotype is available at http:// coldb.mnhn.fr/catalognumber/mnhn/p/p02297746).

Description. Erect shrubs 0.5-1.0 m tall. Branchlets quadrangular, glandularpunctate and sparsely covered with eglandular trichomes 0.1-0.5, light green (when fresh). Internodes 0.2–1.1 cm long, angles with narrow wings ca. 0.2 mm wide. Petioles 0.3-1.4 mm long. Leaf blades 4-25 mm long, 1.5-12 mm wide, papyraceous (when dry), ovate or elliptic, both surfaces green (when fresh), adaxial surface blackened and abaxial surface pale green to pale brown (when dry), discoloured (when dry), base rounded or attenuate, apex acute or obtuse, margin flat, slighly serrulate and ciliate with eglandular trichomes 0.1–0.4 mm long, 5-nerved from the base, one pair of acrodromous veins and one pair of tenuous veins close to the margin, tertiaries evident on the abaxial surface, nearly perpendicular to the mid-vein, little reticulate and branching apically, adaxial surface glandular-punctate, abaxial surface densely glandular-punctate and sparsely covered with eglandular trichomes 0.1-0.5 mm long around the veins. Inflorescences reduced to solitary flowers on the aplical region of the branches. Bracts absent. Bracteoles (at anthesis) with petioles 0.3-0.5 mm long, blades 2.4-6.1 mm long, 1.0-3.2 mm wide, ovate or elliptic, base cuneate, apex acute to obtuse, margin slightly serrulate and ciliate with eglandular trichomes 0.1-0.4 mm long, 3-nerved, indumentum like that of the principal leaves. Flowers 5-merous, pedicels (at anthesis) 0.7–1.9 mm long. Hypanthia (at anthesis) 2.2–2.6 mm long, 1.8–2.2 mm wide at the torus, campanulate to urceolate, light green (when fresh), externally glandular-punctate and sparsely covered with eglandular trichomes 0.1–0.5. Calyx tubes 0.2–0.4 mm long. Calyx lobes (at anthesis) 1.5–2.1 mm long, 0.5–0.7 mm wide at the base, narrowly triangular, apex acute, margin entire, (when fresh) light green, externally like the hypanthia. Petals 6.1–7.9 mm long, 3.0–3.5 mm wide, magenta, obovate, apex acute, margin entire and glabrous, both surfaces glabrous. Stamens 10, strongly dimorphic.



Figure 29. *Microlicia trembleyiformis* **A** habit **B** detail of nodes and internodes **C** leaf abaxial surface **D** leaf adaxial surface **E** bracteole abaxial surface **F** floral bud **G** flower in lateral view **H** petal adaxial surface **I** antesepalous stamen **J** antepetalous stamen **K** gynoecium **L** capsule enveloped by the hypanthium. Drawn from Duarte 2767 (US).

Larger (antesepalous) stamens 5, filaments 1.5–3.0 mm long, pink, pedoconnectives 1.9–2.9 mm long, pink, appendages 1.0–1.5 mm long, yellow, apex bilobate, thecae (excluding rostra) 1.0–1.5 mm long, purple, oblong, rostra 0.2–0.3 mm long, the circular pores ca. 0.2 mm wide. Smaller (antepetalous) stamens 5, filaments 1.5–2.0 mm

long, pink, pedoconnectives 0.8–1.2 mm long, yellow, inconspicuous appendages ca. 0.1 mm long, yellow, apex emarginate, thecae (excluding rostra) 0.7–1.1 mm long, yellow, oblong, rostra 0.2–0.3 mm long, the circular pores ca. 0.2 mm wide. Ovary 1.8–2.0 mm long, 1.9–2.1 mm wide, globose, 3–5-locular. Style 3.7–4.2 mm long, pink. Capsules (at maturity) 2.5–3.4 mm long, 2.4–3.0 mm wide, globose, initially enveloped by the hypanthium, torus constricted at the apex, fruiting calyx tubes 0.3–0.4 mm long, fruiting calyx lobes 2.4–2.9 mm long, not thickened. Seeds not seen.

Distribution, habitat and elevation range. *Microlicia trembleyiformis* is known from quartzitic campo rupestre, Cerrado and veredas (palm swamps) at Ouro Preto, Serra da Canastra, Uberlândia and Patrocínio (in Minas Gerais State) and campos de altitude in Serra Negra (Itatiaia), Rio de Janeiro State (Fig. 19B). On Serra da Canastra, it was collected on sandy soils near streams, exposed to full sun, at elevations between 786 and 1300 m. Collections from Ouro Preto and Serra Negra lack additional habitat information.

Conservation. This species is known from about 10 specimens. It is a little-collected species that, however, has a comparatively wide distributional range. The EOO is 92,214.048 km², a value that would indicate a Least Concern conservation status if criterion B of IUCN (2019) was applied. However, the AOO of 24 km² matches a status of Endangered in accordance with the same criterion. Both EOO and AOO requirements have to be fulfilled for the correct use of criterion B. Thus, we recommend a status of Least Concern (LC) for *M. trembleyiformis*. We suspect that this species occurs in low population densities. Some populations of *M. trembleyiformis* are protected in the Parque Nacional da Serra da Canastra.

Recognition and affinities. *Microlicia trembleyiformis* can be recognised by its elliptic to ovate leaves that are 5-nerved from the base and solitary flowers with narrowly-triangular calyx lobes 1.5–2.1 mm long. In morphology, it is closest to *M. parviflora* and more distantly to *M. altoparaisensis* (see notes under these species for comparisons). *Microlicia pentagona* is the only congener that shares with *M. trembleyiformis* both the leaves 5-nerved from the base and solitary flowers. *Microlicia trembleyiformis* differs in having leaves that are papyraceous when dry (vs. chartaceous to coriaceous in *M. pentagona*), the margin is ciliate with eglandular trichomes 0.1–0.4 mm long (vs. glabrous to minutely granulose) and the shorter calyx lobes are 1.5–2.1 mm long (vs. 6.2–8.5 mm long) and tenuous in fruit (vs. thickened). Amongst the compared species, only *M. parviflora* occurs in Ouro Preto, Serra da Canastra and Serra Negra, where sympatry with *M. trembleyiformis* is possible.

Notes. According to Naudin (1845), this species was frequent in Ouro Preto Municipality, although we are not aware of any recent collections from that region. Naudin (1845) justified the placement of *M. trembleyiformis* in *Microlicia* because the type had 3-locular ovaries. Recent collections of *M. trembleyiformis* have 3–5-locular ovaries (e.g. *Porto 2834*). In the Parque Nacional da Serra da Canastra, *M. trembleyiformis* is known from only a few individuals that consistently have 3-locular ovaries (Romero 2000).

Specimens examined. BRAZIL. Minas Gerais: Capitólio Municipality, estrada para Cachoeira Fecho da Serra, Romero et al. 7550 (HUFU, US); Ouro Preto Municipality, [catal. B1, n° 160] *Saint-Hilaire s.n.* (lectotype: P [P002297746]!; isolectotype:

F [F0360366]); São Roque de Minas Municipality, Serra da Canastra, Nakajima et al. 1476 (HUFU, US), Romero & Nakajima 3593 (HUFU, K, UEC), Romero 4157 (BHCB, F, HUFU), Santos 411 (HUFU, K); Serra do Salitre Municipality, Serra de Catiara, Duarte 2767 (BHCB, US); Uberlândia Municipality, Clube Caça e Pesca Itororó, Romero et al. 8689 (HUFU), Romero et. al. 8694 (HUFU); unknown municipality in Minas Gerais State, Glaziou 19221 (K, P). **Rio de Janeiro:** Itatiaia Municipality, Serra Negra, Porto 2834 (NY, RB, US).

11. *Microlicia tridentata* (Naudin) Versiane & R.Romero, Bot. J. Linn. Soc. 197: 55. 2021.

Fig. 30

Trembleya tridentata Naudin, Ann. Sci. Nat., Bot. Sér. 3, 2: 154: 1844. basionym. Type: Brazil. "In montibus Serra de San Jose, provinciae Minas Geraes" [Minas Gerais, Serra de São José], 1816–1821, [catal. B2, n° 2397] A. Saint-Hilaire s.n. (lectotype, first-step designated by Martin and Cremers (2007), second-step designated here: P [P00723392]!; isolectotypes: P [P00723391]!, P [P00723506]!; image of lectotype is available at http://coldb.mnhn.fr/catalognumber/mnhn/p/p00723392).

Description. Erect shrubs or treelets 1.0–1.8 m tall. Branchlets quadrangular, appearing glabrous, vernicose and minutely granulose, light green (when fresh). Internodes 0.3–1.5 cm long, angles with narrow wings 0.2–0.4 mm wide. Petioles 1.0–4.9 mm long. Leaf blades 20-49 mm long, 12-24 mm wide, coriaceous (when dry), elliptic, ovate, or rarely narrowly elliptic, both surfaces green (when fresh), adaxial surface blackened and abaxial surface pale green to pale brown (when dry), discoloured (when dry), base cuneate or attenuate, apex rounded to emarginate, margin flat, entire along the basal half, serrulate on the upper half and glandular-punctate, 5-nerved from the base, one pair of acrodromous veins and one pair of tenuous veins close to the margin, tertiaries evident on the abaxial surface, nearly perpendicular to the mid-vein, reticulate, randomly branching and surrounding stout depressions on the abaxial leaf surface, adaxial surface glandularpunctate, abaxial surface glandular-punctate. Inflorescences simple dichasia or reduced to solitary flowers, not congested. Bracts (including petioles) 1.0-1.6 cm long, 0.4-0.8 cm wide, 3- to inconspicuously 5-nerved, elliptic, indumentum like that of the principal leaves. Bracteoles (at anthesis) with petioles 2.5–5.0 mm long, blades 8.1–11.0 mm long, 4.0–5.5 mm wide, elliptic, base attenuate, apex rounded to obtuse, margin sparsely serrulate, 3-nerved, indumentum like that of the principal leaves. Flowers 5-merous, pedicels (at anthesis) 1.3-1.6 mm long. Hypanthia (at anthesis) 3.5-3.9 mm long, 2.3-2.7 mm wide at the torus, campanulate to urceolate, light green (when fresh), externally appearing glabrous, vernicose and minutely granulose. Calyx tubes 0.3-0.4 mm long. Calyx lobes (at anthesis) 4.1-4.9 mm long, 0.8-1.1 mm wide at the base, subulate, apex acute, margin entire, (when fresh) light green or reddish, externally like the hypanthia. Petals 11.5-13.0 mm long, 6.0-7.0 mm wide, magenta or rarely white, obovate, apex acute



Figure 30. *Microlicia tridentata* **A** habit **B** leaf abaxial surface **C** bracteole abaxial surface **D** floral bud **E** flower in lateral view **F** flowering hypanthium **G** petal adaxial surface **H** antesepalous (behind) and antepetalous (in front) stamens **I** gynoecium **J** capsule enveloped by the hypanthium. Drawn from Hensold et al. CFCR2880 (UEC) and Souza et al. 8015 (UEC).

or rounded, margin entire and glabrous, both surfaces glabrous. Stamens 10, strongly dimorphic. Larger (antesepalous) stamens 5, filaments 4.9–5.6 mm long, pink or rarely white, pedoconnectives 6.0–6.5 mm long, pink or rarely white with the apical region flushed with pink, appendages 1.7–1.9 mm long, yellow, apex emarginate or truncate, thecae (excluding rostra) 1.7–1.9 mm long, purple, oblong, rostra 0.3–0.5 mm long, the circular pores ca. 0.2 mm wide. Smaller (antepetalous) stamens 5, filaments 4.0–4.4 mm long, pink or rarely white, pedoconnectives 1.5–1.9 mm long, pink or rarely white with the apical region flushed with pink, inconspicuous appendages ca. 0.2 mm long, yellow, apex emarginate or truncate, thecae (excluding rostra) 1.4–1.7 mm long, yellow, oblong, rostra 0.3–0.5 mm long, the circular pores ca. 0.2 mm wide. Ovary 2.2–2.4 mm long, 2.1–2.3 mm wide, globose, 5-locular. Style 6.1–6.5 mm long, pink or rarely white. Capsules (at maturity) 3.0–4.0 mm long, 2.7–3.6 mm wide, globose, initially enveloped by the hypanthium, torus constricted at the apex, fruiting calyx tubes 0.4–0.5 mm long, fruiting calyx lobes 4.5–5.4 mm long, not thickened. Seeds not seen.

Distribution, habitat and elevation range. *Microlicia tridentata* is endemic to Minas Gerais State (Fig. 25A) at Serra de Ouro Branco, Serra de Ouro Preto, Serra de São José, Serra do Gandarela, Serra do Cipó, Serra do Lenheiro, Serra do Caraça and Barão de Cocais. It grows on quartzitic or ferruginous campo rupestre, exposed to full sun, at elevations between 1110 and 1614 m.

Conservation. *Microlicia tridentata* is known from about 40 collections. The EOO is 4,613.081 km² and the AOO is 24 km². Following IUCN (2019) recommendations, we recommend Endangered (EN): B1ab(iii) status for this species. Populations of *M. tridentata* are protected in Parque Estadual do Itacolomi, Parque Estadual Serra do Ouro Branco and RPPN Serra do Caraça (Natural Heritage Private Reserve).

Recognition and affinities. Microlicia tridentata can be recognised by its leaves that are serrulate along the upper half, 5-nerved from the base, abaxially conspicuously glandular-punctate, with tertiary veins reticulate and randomly branching and flowers with subulate calyx lobes 4.1-4.9 mm long. It shares with *M. pentagona* the shrubby to treelet habit and the serrulate leaves along the upper half that are 5-nerved from the base. Microlicia tridentata is readily differentiated by the abaxial surfaces of the leaves that are more conspicuously glandular-punctate, with tertiares reticulate and randomly branching (vs. parallel or little reticulate and branching apically) and shorter calyx lobes 4.1–4.9 mm long (vs. 6.2–8.5 mm long) that are tenuous in fruit (vs. thickened). Another close relative is *M. parviflora*, from which *M. tridentata* differs by the leaves that are not pruinose (vs. usually pruinose), inflorescences composed of simple dichasia or reduced to solitary flowers (vs. compound or simple dichasia), bracteoles longer 8.1–11.0 mm long (vs. 2.2–3.8 mm long) and longer calyx lobes 4.1–4.9 mm long [vs. 0.7–2.5(–3.0)] that are subulate (vs. triangular). The distributions of *M. parviflora* and *M. pentagona* overlap with *M. tridentata* on several mountain ranges in Minas Gerais (e.g. Serra de Ouro Branco, Serra de Ouro Preto, Serra do Cipó).

Notes. Major variation in *M. tridentata* involves inflorescence development (simple dichasia or solitary flowers) and the petals typically magenta (Fig. 8H), rarely white (Fig. 9H), which may be rounded or acute at the apex.

83

Specimens examined. BRAZIL. Minas Gerais: Barão de Cocais Municipality, Irwin et al. 29029 (IAN, NY, US), Irwin et al. 29079 (K, MO, NY, P, RB); Catas Altas Municipality, Serra do Caraça, Castro et al. 281 (HUFU); Ouro Branco Municipality, Serra de Ouro Branco, Pacifico & Bressan 290 (CAS, HUEM), Souza et al. 8015 (ESA, SPF, UEC); Ouro Preto Municipality, Serra do Itacolomi, Badini & Ferreira 9774 (HUFU), Ferreira & Helena 7844 (ESA, HUFU), Giulietti et al. CFCR13780 (K, MO, SPF), Longhi-Wagner et al. CFCR9184 (SPF, UEC, US), Magalhães 1160 (IAN, US), Michelangeli et al. 1586 (NY, RB, UPCB), Michelangeli et al. 1595 (NY, UPCB), Pedrosa 120 (OUPR), Rolim et al. 326 (HUFU, VIC), Rolim et al. 327 (UPCB, VIC), Rolim et al. 328 (HUFU, VIC), Rolim et al. 394 (HUFU, NY, RB, VIC), Roschel et al. s.n. (OUPR [1506], RB [RB01301048]), Souza et al. 8047 (ESA, SORO, SPF), Souza et al. 8061 (ESA, RB, SPF, UPCB); Rio Acima Municipality, Serra do Gandarela, Pacifico & Bressan 303 (CAS, HUEM), Versiane & Devides 682 (UEC); Santa Bárbara Municipality, Serra do Caraça, Ordones et al. 84 (BHZB, HUFU), Pereira & Pabst 2619 (RB, US); Santana do Riacho Municipality, Serra do Cipó, Duarte 8157 (G, LE, RB, US); São João del-Rei Municipality, Schwacke 10135 (BHCB, RB, W), Glaziou 17513 (P, R, US), Serra do Lenheiro, Glaziou 16781 (K, NY, P, US); Tiradentes Municipality, Serra de São José, Alves 595 (US), Alves 7359 (R), Rutter 128 (R), Rutter 150 (R), Rutter 161 (R), Rutter 186 (R), Rutter 191 (R); Unknown municipality in Minas Gerais State, Claussen 1631 (P), Glaziou 14743 (K, P, US), Glaziou 17573 (K), Mendonca 557 (US), Riedel s.n. (K [K009597799, W-18800001419, W-18890019740]), Saint-Hilaire s.n. [catal. B2, n° 2397] (lectotype: P [P00723392]; isolectotypes: P [P00723391], P [P00723506]), Sellow s.n. (US [US00292635]); Serra da Conceição (Serra B. Vista), Hensold et al. CFCR2880 (SPF, US).

A nomenclatural review on the remaining taxa previously treated in Trembleya

1. *Trembleya acuminata* **R.B.Pacifico & Fidanza, Phytotaxa 238(2): 164. 2015.** Type: Brazil. Minas Gerais, Joaquim Felício, Serra do Cabral, estrada Joaquim Felício–Várzea da Palma, ca. 24 km de Joaquim Felício, 10 July 2001, *V.C. Souza et al. 25654* (holotype: MBM!; isotypes: BHCB!, ESA!, SPF!).

Replaced with: Microlicia acuminifolia Versiane & R.Romero.

2. *Trembleya agrestis* Mart. & Schrank ex DC., Prodr. 3: 126. 1828. Type: Brazil. "In prov. Minas Geraes" [Minas Gerais], *C.F.P. Martius s.n.* (holotype: M [M0165682]!, isotype [fragment]: BR [BR0000005521203]!).

Basionym of: Microlicia agrestis (Mart. & Schrank ex DC.) Cogn.

3. *Trembleya botaensis* **R.B.Pacifico & Fidanza, Phytotaxa 238(2): 167. 2015.** Type: Brazil. Minas Gerais, Guaraciama, Cadeia do Espinhaço, Serra do Bota, 19 March 2005, *E. Guarçoni 903 & M. A. Sartori* (holotype: MBM!).

Synonym of: Microlicia curralensis Brade.

4. *Trembleya elegans* (Cogn.) Almeda & A.B.Martins, Novon 11(1): 6. 2001. Type: Based on *Lavoisiera elegans* Cogn.

Replaced with: Microlicia speciosa Versiane & R.Romero.

5. *Trembleya inversa* Fidanza, A.B.Martins & Almeda, Brittonia 65(3): 281. 2013. Type: Brazil. Minas Gerais, Joaquim Felício, Serra do Cabral, Armazém da Laje, 9 September 2003, *K. Fidanza & R. Belinello 12* (holotype: UEC!; isotype: CAS!).

Basionym of: *Microlicia inversa* (Fidanza, A.B.Martins & Almeda) Versiane & R.Romero.

6. *Trembleya neopyrenaica* Naudin, Ann. Sci. Nat., Bot. Sér. 3, 2: 154. 1844. Type: Brazil. "In montibus Pyreneos prov. Goyaz" [Goiás, Serra dos Pireneus], 1816, *A. Saint-Hilaire C1-694* (lectotype, first-step designated by Martin and Cremers (2007), second-step designated here: P [P00723416]!; isolectotypes: P [P00723417]!, P [P00723418]!, F [fragment] [F0064039F-online image]!; image of lectotype is available at http://coldb.mnhn.fr/catalognumber/mnhn/p/p00723416].

Basionym of: Microlicia neopyrenaica (Naudin) Versiane & R.Romero.

7. *Trembleya phlogiformis* Mart. & Schrank ex DC., Prodr. 3: 126. 1828. Type: Brazil. "In Brasiliae campis prov. S.-Pauli" [São Paulo State], *Martius s.n.* (holotype: M [M0165885]!, probable isotype: G [G00310212]!).

- Basionym of: Microlicia phlogiformis (Mart. & Schrank ex DC.) Versiane & R.Romero. Melastoma pumilum Vell., Fl. Flumin. 179. 1829. Type: Brazil. "Habitat campis apricis mediterraneis prope Predium Boavista inter gramina" (lectotype, designated here: Original illustration published in Vellozo, Fl. Flumin. Icones 3: t. 151. 1831; the original parchment is in the manuscript section of the Biblioteca Nacional, Rio de Janeiro; a copy of the illustration is deposited at G [G00368052]!).
- Trembleya phlogiformis var. glabra Cham., Linnaea 9: 429. 1835. syn. nov. Type: Brazil. "In Brasilia australi loco haud indicato", Sellow 2387 (lectotype, designated here: S [S09-12942-online image]!; probable isolectotype: K [K000530643]!).
- Trembleya stachyoides Naudin, Ann. Sci. Nat., Bot. Sér. 3, 2: 154. 1844. syn. nov. Type: Brazil. "In Brasilia australi, praecipue circa Tocoropa", *Laruotte s.n.* (lectotype, first-step designated by Martin and Cremers (2007), second-step designated here: P [P00723388]!; isolectotype: P [P00723389]!; image of lectotype is available at http://coldb.mnhn.fr/catalognumber/mnhn/p/p00723388).
- *Trembleya phlogiformis* var. *cuneifolia* Cogn. in Martius et al., Fl. Bras. 14(3): 132. 1883. **syn. nov.** Type: Brazil. "In prov. Minas Geraës ad Congonhas do Campo" [Minas Gerais], *Stephan s.n.* (lectotype, designated here: BR [BR0000005224203]!).
- *Trembleya phlogiformis* var. *genuina* Cogn. in Martius et al., Fl. Bras. 14(3): 132. 1883. **syn. nov.** Type: Based on *Trembleya phlogiformis* Mart. & Schrank ex DC.

Trembleya phlogiformis var. latifolia Cogn. in Martius et al., Fl. Bras. 14(3): 132. 1883. syn. nov. Type: Brazil. "In Brasilia loco haud indicato", *Raben 781* (lectotype, designated here: BR [BR0000005520855]!; isolectotype: BR [BR0000005520190]!).

- Trembleya phlogiformis var. microlicioides Cogn. in Martius et al., Fl. Bras. 14(4): 594.
 1888. syn. nov. Type: Brazil. In prov. Rio de Janeiro, *Glaziou 16046* (lectotype, designated here: R [R000009186]!; isolectotypes: BR [BR0000005223596]!, BR [BR0000005520503]!, BR [BR0000005520176]!, C [C10015111-online image]!, G [G00368051]!, P [P00723400]!; image of isolectotype at P is available at http://coldb.mnhn.fr/catalognumber/mnhn/p/p00723400).
- Trembleya phlogiformis var. parvifolia Cogn. in Martius et al., Fl. Bras. 14(3): 132. 1883. syn. nov. Type: Brazil. "In paludibus prope Lorena prov. S. Paulo", *Riedel 1418* (lectotype, designated here: P [P05317991]!; isolectotypes: K [K000530649]!, P [P05317995]!; image of lectotype is available at http://coldb.mnhn.fr/catalognumber/mnhn/p/p05317991).
- Trembleya phlogiformis var. quinquenervia Cogn. in Martius et al., Fl. Bras. 14(3): 132. 1883. syn. nov. Type: Brazil. "In prov. Goyaz" [Goiás], Gardner 4147 (lectotype, designated here: BM [BM000516951]!; isolectotypes P [P05317981]!, P [P05317982]!; image of lectotype is available at http://plants.jstor.org and http:// data.nhm.ac.uk/object/255f17a9-b371-4dd3-8eb0-9f0eafbd2e76).
- Trembleya phlogiformis var. ramosissima Cogn. in Martius et al., Fl. Bras. 14(3): 132. 1883. syn. nov. Type: Brazil. "In prov. Minas Geraës", Regnell I. 152 part (lectotype, designated here: R [R000166805]!; isolectotypes: P [P05318036]!, S [S09-12952-online image]!; images of the lectotype and an isolectotype are available at http://plants. jstor.org and http://coldb.mnhn.fr/catalognumber/mnhn/p/p05318036).
- *Trembleya phlogiformis* var. *stachyoides* (Naudin) Cogn. in Martius et al., Fl. Bras. 14(3): 132. 1883. **syn. nov.** Type: Based on *Trembleya stachyoides* Naudin.
- *Trembleya phlogiformis* var. *villosa* Cogn. in Martius et al., Fl. Bras. 14(3): 132. 1883. **syn. nov.** Type: Brazil. "In campis siccis ad Registo Velho", *Pohl & Schüch 230* (lectotype, designated here: BR [BR0000005223541]!).
- *Trembleya selloana* Cogn. in Martius et al., Fl. Bras. 14(3): 133. 1883. **syn. nov.** Type: Based on *Trembleya phlogiformis* var. *glabra* Cham.
- 8. *Trembleya pityrophylla* (Mart. ex DC.) Triana, Trans. Linn. Soc. London 28(1): 24. 1872. Type: Based on *Osbeckia pityrophylla* Mart. ex DC.
 - Synonym of: Cambessedesia pityrophylla (Mart. ex DC.) A.B.Martins.

9. *Trembleya pradosiana* Netto, Ann. Sci. Nat., Bot. Sér. **5**, **3**: **378**. **1865**. Type: Brazil. "Habitat in campis ad flumen *Rio das Velhas*, prope vivum Trahiras, in parte centrali provinciae Minas Geraes" [Minas Gerais], May 1862, *Netto s.n.* (holotype: P [P00723509]!; image of holotype is available at http://coldb.mnhn.fr/catalognumber/mnhn/p/p00723509).

Basionym of: Microlicia pradosiana (Netto) Versiane & R.Romero.

Trembleya rubra Fidanza, A.B.Martins & Almeda, Brittonia 65: 286. 2013. syn. nov. Type: Brazil. Minas Gerais, Joaquim Felício, Serra do Cabral, ca. 5 km S do Armazém da Laje, 4 December 2003, K. Fidanza & R. Belinello 112 (holotype: UEC!; isotype: CAS!). 10. Trembleya purpurascens Fidanza, A.B.Martins & Almeda, Brittonia 65(3): 284. 2013. Type: Brazil. Minas Gerais, Joaquim Felício, Serra do Cabral, estrada Joaquim Felício-Armazém, 4 May 2003, K. Fidanza & R. Belinello 56 (holotype: UEC!; isotype: CAS!).

Synonym of: Microlicia curralensis Brade.

11. Trembleya serrulata Fidanza, A.B.Martins & Almeda, Brittonia 65(3): 288.

2013. Type: Brazil. Minas Gerais, Joaquim Felício, Serra do Cabral, Pedreira, 7 December 2003, *K. Fidanza 108* (holotype: UEC!; isotype: CAS!).

Replaced with: Microlicia serratifolia Versiane & R.Romero.

12. Trembleya thomazii R.B.Pacifico & Fidanza, Phytotaxa 238(2): 171. 2015. Type: Brazil. Minas Gerais, Guaraciama, Cadeia do Espinhaço, Serra do Bota, 20 March 2005, E. Guarçoni 929 & M. A. Sartori (holotype: MBM!)

Basionym of: Microlicia thomazii (R.B.Pacifico & Fidanza) Versiane & R.Romero.

13. *Trembleya warmingii* **Cogn. in Martius et al., Fl. Bras. 14(3): 133. 1883.** Type: Brazil. "Ad Lagoa Santa" [Minas Gerais, Lagoa Santa], 9 February 1866, *E. Warming 2306* (holotype: C!).

Basionym of: Poteranthera warmingii (Cogn.) Almeda & R.B.Pacifico.

Excluded and/or dubious names

- 1. Trembleya capitata Cogn. [nom. inval.]
- 2. Trembleya canescens Schnizl. [probably = Pleroma D.Don]
- 3. Trembleya debilis Glaz. [nom. inval.]
- 4. *Trembleya santae-luziae* Glaz. [nom. inval.]
- 5. *Trembleya rhynanthera* Griff. [probably = *Melastoma* L.]
- 6. *Trembleya rosea* Sessé & Moc. [probably = *Coreopsis grandiflora* Hogg ex Sweet (Asteraceae)]

Acknowledgements

We thank: Boni Cruz and Heritiana Ranarivelo for their assistance with lab work in the Center for Comparative Genomics at the California Academy of Sciences; Sandra Knapp, Laurent Gautier, Elizabeth Woodgyer and Nicholas Hind for help in locating the type of *Meriania parviflora*; BHCB, CAS, HUEM, UEC, MBM, R, RB, SP and SPF, for herbarium-related logistical support; Mateus Reck for his help with the BI analysis; Alan Chou and Klei Souza for the line drawings; Zhi-Qiang Zhang for granting permission to reproduce the illustration of *Microlicia altoparaisensis*; V.E. Bressan, R. Gabani and P.V. Simões for their assistance during fieldwork activities; André V. Scatigna, Fabian A. Michelangeli, Fernando A.O. Silveira, Luciano Pedrosa, Orlando Graeff, Rodrigo Penati, and Vania E. Bressan for allowing us to use their photos of living specimens; Renato Goldenberg, an anonymous reviewer and the handling editor (Marcelo Reginato) for their comments and suggestions on an earlier version of this monograph. RP thanks the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for a Ph.D. degree grant and the M. Stanley Rundel Charitable Trust (U.S.A.) and the Lakeside Foundation (U.S.A.) for grants that supported his training and research visits to the California Academy of Sciences in 2017 and 2019–2020. This research was supported in part by U.S. National Science Foundation grant DEB-1146409.

References

- Aagesen L, Szumik C, Goloboff P (2013) Consensus in the search for areas of endemism. Journal of Biogeography 40(11): 2011–2021. https://doi.org/10.1111/jbi.12172
- Abadi S, Azouri D, Pupko T, Mayrose I (2019) Model selection may not be a mandatory step for phylogeny reconstruction. Nature Communications 10(1): 934. https://doi.org/10.1038/ s41467-019-08822-w
- Abrahão A, Costa PDB, Lambers H, Andrade SAL, Sawaya ACHF, Ryan MH, Oliveira RS (2019) Soil types select for plants with matching nutrient-acquisition and -use traits in hyperdiverse and severely nutrient-impoverished *campos rupestres* and *cerrado* in Central Brazil. Journal of Ecology 107: 1302–1316. https://doi.org/10.1111/1365-2745.13111
- Almeda F (1978) Systematics of the genus *Monochaetum* (Melastomataceae) in Mexico and Central America. University of California Publications in Botany 75: 1–134.
- Almeda F (2013) Systematic and phylogenetic significance of chromosome number diversity in some neotropical Melastomataceae. Memoirs of the New York Botanical Garden 108: 155–177.
- Almeda F, Martins AB (2001) New combinations and new names in some Brazilian Microlicieae (Melastomataceae), with notes on the delimitation of *Lavoisiera*, *Microlicia*, and *Trembleya*. Novon 11(1): 1–7. https://doi.org/10.2307/3393198
- Almeda F, Pacifico R (2018) Neotropical *Poteranthera* (Melastomataceae: Microlicieae) revisited. Systematic Botany 43(2): 552–556. https://doi.org/10.1600/036364418X697274
- Almeda F, Penneys DS (2022) Patterns of chromosome number diversity and evolution in the Melastomataceae. In: Goldenberg R, Michelangeli FA, Almeda F (Eds) Systematics, Evolution, and Ecology of Melastomataceae. Springer, Cham, Switzerland, 533–561. https:// doi.org/10.1007/978-3-030-99742-7_24
- Almeda F, Robinson OR (2011) Systematics and phylogeny of *Siphanthera* (Melastomataceae). Systematic Botany Monographs 93: 1–101.
- Almeda F, Michelangeli FA, Viana PL (2016) *Brasilianthus* (Melastomataceae), a new monotypic genus endemic to ironstone outcrops in the Brazilian Amazon. Phytotaxa 273(4): 269–282. https://doi.org/10.11646/phytotaxa.273.4.3
- Alvear M, Almeda F (2019) Revision of *Monochaetum* (Melastomataceae: Melastomateae) in Colombia. Systematic Botany Monographs 109: 1–153.
- Alves RJV, Silva NG, Oliveira JA, Medeiros D (2014) Circumscribing *campo rupestre* megadiverse Brazilian rocky montane savannas. Brazilian Journal of Biology 74(2): 355–362. https://doi.org/10.1590/1519-6984.23212

- Amaral WG, Pereira IM, Amaral CS, Machado ELM, Rabelo LDO (2013) Dinâmica da flora arbustivo-arbórea colonizadora em um área degradada pela extração de ouro em Diamantina, MG. Ciência Florestal 23(4): 713–725. https://doi.org/10.5902/1980509812355
- Anderson LC (1963) Studies on *Petradoria* (Compositae): Anatomy, cytology, taxonomy. Transactions of the Kansas Academy of Science 66(4): 632–684. https://doi.org/10.2307/3626813
- Antonelli AE, Verola CF, Parisod CN, Gustafsson ALS (2010) Climate cooling promoted the expansion and radiation of a threatened group of South American orchids (Epidendroideae: Laeliinae). Biological Journal of the Linnean Society 100(3): 597–607. https://doi. org/10.1111/j.1095-8312.2010.01438.x
- Bacci LF, Michelangeli FA, Goldenberg R (2019) Revisiting the classification of Melastomataceae: Implications for habit and fruit evolution. Botanical Journal of the Linnean Society 190(1): 1–24. https://doi.org/10.1093/botlinnean/boz006
- Bacci LF, Amorim AM, Michelangeli FA, Goldenberg R (2020) Flower morphology is correlated with distribution and phylogeny in *Bertolonia* (Melastomataceae), an herbaceous genus endemic to the Atlantic Forest. Molecular Phylogenetics and Evolution 149: 106844. https://doi.org/10.1016/j.ympev.2020.106844
- Bachman S, Moat J, Hill AW, 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
- Baumgratz JFA (1983) Morfologia dos frutos e sementes de Melastomataceas brasileiras. Arquivos do Jardim Botânico do Rio de Janeiro 27: 113–155.
- Baumgratz JFA, Souza MLDR, Tavares R dos AM (2007) Melastomataceae na Reserva Ecológica de Macaé de Cima, Nova Friburgo, Rio de Janeiro, Brasil: I - Tribos Bertolonieae, Merianieae e Microlicieae. Rodriguésia 58(4): 797–822. https://doi.org/10.1590/2175-7860200758406
- BFG (2022) Brazilian Flora 2020: Leveraging the power of a collaborative scientific network. Taxon 71: 178–198. https://doi.org/10.1002/tax.12640
- Bitencourt C, Rapini A, Santos Damascena L, Marco Jr P (2016) The worrying future of the endemic flora of a tropical mountain range under climate change. Flora 218: 1–10. https:// doi.org/10.1016/j.flora.2015.11.001
- Bochorny T, Michelangeli FA, Almeda F, Goldenberg R (2019) Phylogenetics, morphology and circumscription of Cambessedesieae: A new neotropical tribe of Melastomataceae. Botanical Journal of the Linnean Society 190(3): 281–302. https://doi.org/10.1093/botlinnean/boz018
- Bomfim-Patrício MC, Salatino A, Martins AB, Wurdack JJ, Salatino MLF (2001) Flavonoids of *Lavoisiera*, *Microlicia* and *Trembleya* (Melastomataceae) and their taxonomic meaning. Biochemical Systematics and Ecology 29: 711–726. https://doi.org/10.1016/S0305-1978(00)00116-2 [January 17, 2018]
- Borghetti F, Silva LCR, Pinheiro JD, Varella BB, Ferreira AG (2005) Aqueous leaf extract properties of Cerrado species in Central Brazil. In: Pratley J (Ed.) Proceedings of the Fourth World Congress on Allelopathy. Charles Sturt University, Wagga Wagga, Australia, 1–4.

Brasília (2014) DOU Diário Oficial da União. Publicado no D.O.U. de 17 de dezembro de 2014.

Briggs BG, Johnson LAS (1979) Evolution in the Myrtaceae - Evidence from inflorescence structure. Proceedings of the Linnean Society of New South Wales 102: 157–256. http:// biostor.org/reference/67846

- Brito VLG, Maia FR, Silveira FAO, Fracasso CM, Lemos-Filho JP, Fernandes GW, Goldenberg R, Morellato LPC, Sazima M, Staggemeier VG (2017) Reproductive phenology of Melastomataceae species with contrasting reproductive systems: Contemporary and historical drivers. Plant Biology 19(5): 806–817. https://doi.org/10.1111/plb.12591
- Bukatsch F (1972) Bemerkungen zur Doppelfärbung Astrablau-Safranin. Mikrokosmos 61: 255.
- Caetano APS, Oliveira PE (2022) Apomixis in Melastomataceae. In: Goldenberg R, Michelangeli FA, Almeda F (Eds) Systematics, Evolution, and Ecology of Melastomataceae. Springer, Cham, Switzerland, 563–583. https://doi.org/10.1007/978-3-030-99742-7_25
- Campos BC (2005) A família Melastomataceae nos campos rupestres e cerrados de altitude do Parque Estadual do Ibitipoca, Lima Duarte, MG, Brasil. MSc thesis, Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Brazil.
- Candolle AP (1828) Mémoire sur la famille des Mélastomacées. Treuttel et Wurtz, Paris, 1–84.
- Carmo A, Pacifico R, Gonçales-Silva R, Gonçalves Sbais P, Fidanza K, de Souza LA (2019) Epidermal micromorphology and venation patterns of Microlicieae (Melastomataceae) leaves: Looking for new characters for the taxonomy of this Neotropical tribe. Flora 261: 151494. https://doi.org/10.1016/j.flora.2019.151494
- Carmo A, Cássero LZ, Pacifico R, Fidanza K, Souza LA (2020) Leaf structure of Microlicieae (Melastomataceae): Taxonomic and adaptive implications. Systematic Botany 45(1): 142– 155. https://doi.org/10.1600/036364420X15801369352405
- Cassiano DSA, Branco A, Silva TRS, Santos AKA (2010) Caracterização morfoanatômica de folhas e caules de *Microlicia hatschbachii* Wurdack, Melastomataceae. Revista Brasileira de Farmacognosia 20(4): 529–535. https://doi.org/10.1590/S0102-695X2010000400011
- Chamisso A (1834) De plantis in expeditione speculatoria Romanzoffiana et in herbariis regiis berolinensibus observatis Melastomaceae americanae. Linnea 9: 368–402.
- Cogniaux A (1891) Mélastomacées. In: Candolle A, Candolle C (Eds) Monographiae Phanerogamarum. G. Masson, Paris, 1–1256.
- Cogniaux A (1883–1888) Melastomaceae. In: Martius CFP, Eichler AG, Urban M (Eds) Flora Brasiliensis, vol. 14(3–4). Fleischer, Monachii.
- Colli-Silva M, Vasconcelos TNC, Pirani JR (2019) Outstanding plant endemism levels strongly support the recognition of *campo rupestre* provinces in mountaintops of eastern South America. Journal of Biogeography 46(8): 1723–1733. https://doi.org/10.1111/jbi.13585
- Conceição AA, Rapini A, do Carmo FF, Brito JC, Silva GA, Neves SPS, Jacobi CM (2016) Rupestrian grassland vegetation, diversity, and origin. In: Fernandes GW (Ed.) Ecology and Conservation of Mountaintop Grasslands in Brazil, Springer International Publishing, Switzerland, 105–128. https://doi.org/10.1007/978-3-319-29808-5_6
- Cota BB, Oliveira AB, Ventura CP, Mendonça MP, Braga FC (2002) Antimicrobial activity of plant species from a Brazilian hotspot for conservation priority. Pharmaceutical Biology 40(7): 542–547. https://doi.org/10.1076/phbi.40.7.542.14682
- Cronk QCB (1998) The ochlospecies concept. In: Huxley CR, Lock JM, Cutler DF (Eds) Chorology, taxonomy and ecology of the Floras of Africa and Madagascar. Royal Botanic Gardens Kew, London, 155–170.
- Dellinger AS, Kopper C, Kagerl K, Schönenberger J (2022) Pollination in Melastomataceae: A family-wide update on the little we know and the much that remains to be discovered. In:

Goldenberg R, Michelangeli FA, Almeda F (Eds) Systematics, Evolution, and Ecology of Melastomataceae. Springer, Cham, Switzerland, 585–607. https://doi.org/10.1007/978-3-030-99742-7_26

- Doyle JJ, Doyle JL (1987) A rapid isolation procedure for small amounts of leaf tissue. Phytochemical Bulletin 28: 330–331. https://doi.org/10.2307/4119796
- Faegri K, van Der Pijl L (1979) The Principles of Pollination Ecology, 3rd edn. Pergamon Press, Oxford, 1–256. https://doi.org/10.1016/B978-0-08-023160-0.50005-0
- Farias WC, Ferreira HD, Sá S, Cunha LC, Neto JRO, Borges LL, Paula JR, Fiuza TS (2018) Evaluation of the chemical composition and variability of the volatile oils from *Trembleya parviflora* leaves. Revista Brasileira de Farmacognosia 28(4): 414–420. https://doi. org/10.1016/j.bjp.2018.04.009
- Fernandes GW (2016) Ecology and Conservation of Mountaintop Grasslands in Brazil. Springer International Publishing, Switzerland, 567 pp. https://doi.org/10.1007/978-3-319-29808-5
- Fidanza K, Martins AB, Almeda F (2013) Four new species of *Trembleya* (Melastomataceae: Microlicieae) from Serra do Cabral, Minas Gerais, Brazil. Brittonia 65(3): 280–291. https://doi.org/10.1007/s12228-012-9281-x
- Franklin GL (1945) Preparation of thin sections of synthetic resins and wood-resin composites, and a new macerating method for wood. Nature 155(3924): 51–51. https://doi. org/10.1038/155051a0
- Fritsch PW, Almeda F, Renner SS, Martins AB, Cruz BC (2004) Phylogeny and circumscription of the near-endemic Brazilian tribe Microlicieae (Melastomataceae). American Journal of Botany 91(7): 1105–1114. https://doi.org/10.3732/ajb.91.7.1105
- Giotto AC (2015) Colonização de *Trembleya parviflora* em áreas úmidas no Distrito Federal, Brasil. MSc thesis, Universidade de Brasília, Brazil.
- Giulietti AM, Pirani JR, Harley RM (1997) Espinhaço Range Region, Eastern Brazil. In: Davis SD, Heyhood VH, Herrera-Macbride O, Villa-Lobos J, Haminton AC (Eds) Centres of plant diversity - A Guide and Strategy for their Conservation. Vol. 3. The Americas. IUCN Publication Unity, Cambridge, 397–404.
- Glaziou AFM (1908) ["1905"] Liste des plantes du Brésil central. Bulletin de la Societé Botanique de France 54: 201–296. https://doi.org/10.5962/bhl.title.4336
- Goldenberg R, Amorim AM (2006) *Physeterostemon* (Melastomataceae): A new genus and two new species from the Bahian Atlantic Forest, Brazil. Taxon 55(4): 965–972. https://doi. org/10.2307/25065690
- Goldenberg R, Baumgratz JFA, Souza MLDER (2012) Taxonomia de Melastomataceae no Brasil: Retrospectiva, perspectivas e chave de identificação para os gêneros. Rodriguésia 63(1): 145–161. https://doi.org/10.1590/S2175-78602012000100011
- Goldenberg R, Almeda F, Sosa K, Ribeiro RC, Michelangeli FA (2015) *Rupestrea*: A new Brazilian genus of Melastomataceae, with anomalous seeds and dry indehiscent fruits. Systematic Botany 40(2): 561–571. https://doi.org/10.1600/036364415X688862
- Goldenberg R, Baumgratz JFA, Michelangeli FA, Guimaráes PJF, Romero R, Versiane AFA, Fidanza K, Völtz RR, Silva DN, Lima LFG, Silva-Gonçalves KC, Bacci LF, Fontelas JC, Pacifico R, Brito ES, Rocha MJR, Caddah MK, Meirelles J, Rosa P, Ferreira-Alves R,

Santos AKA, Moreira KVC, Reginato M, Oliveira LFA, Freire-Fierro A, Amorim AMA, Martins AB, Koschnitzke C, Almeda F, Jesus JC, Hinoshita LKR, Kriebel R (2020) Melastomataceae. In: Flora do Brasil 2020. Jardim Botânico do Rio de Janeiro. http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB161 [Accessed on 2 Jan 2022]

- Hijmans RJ, Guarino L, Cruz M, Rojas E (2001) Computer tools for spatial analysis of plant genetic resources data: 1. DIVA-GIS. Plant Genetic Resources Newsletter (Rome, Italy) 127: 15–19.
- Hopper SD (2009) OCBIL theory: Towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. Plant and Soil 322(1–2): 49–86. https://doi.org/10.1007/s11104-009-0068-0
- Ionta G, Judd W, Williams N, Whitten W (2007) Phylogenetic relationships in *Rhexia* (Melastomataceae): Evidence from DNA sequence data and morphology. International Journal of Plant Sciences 168(7): 1055–1066. https://doi.org/10.1086/518837
- IUCN (2019) Guidelines for using the IUCN Red List Categories and Criteria. Version 14. Prepared by the Standards and Petitions Subcommittee. http://www.iucnredlist.org/documents/RedListGuidelines.pdf [accessed May 2021]
- Jansen S, Wataname T, Smets E (2002) Aluminium accumulation in leaves of 127 species in Melastomataceae, with comments on the Order Myrtales. Annals of Botany 90(1): 53–64. https://doi.org/10.1093/aob/mcf142
- Johansen DA (1940) Plant microtechnique. McGraw-Hill Book Company Inc., New York, 523 pp.
- Justino LL, Salimena FRG, Chiavegatto B, Neto LM (2016) O clado *Merianthera* e as tribos Merianieae e Microlicieae (Melastomataceae) na Serra Negra, Minas Gerais. Rodriguésia 67(3): 823–838. https://doi.org/10.1590/2175-7860201667320
- Kirchoff BK, Claßen-Bockhoff R (2013) Inflorescences: Concepts, function, development and evolution. Annals of Botany 112(8): 1471–1476. https://doi.org/10.1093/aob/mct267
- Koschnitzke C, Martins AB (2006) Revisão taxonômica de *Chaetostoma* DC. (Melastomataceae, Microlicieae). Arquivos do Museu Nacional do Rio de Janeiro 14: 93–200.
- Kraus JE, Arduin M (1997) Manual básico de métodos em morfologia vegetal. Universidade Federal Rural do Rio de Janeiro, Seropédica, Brazil.
- Kriebel R (2012) A synopsis of the genus *Poteranthera* (Melastomeae: Melastomataceae) with the description of a new, apparently pollinator deceiving species. Brittonia 64(1): 6–14. https://doi.org/10.1007/s12228-011-9192-2
- Kriebel R, Michelangeli FA, Kelly LM (2015) Discovery of unusual anatomical and continuous characters in the evolutionary history of *Conostegia* (Miconieae: Melastomataceae). Molecular Phylogenetics and Evolution 82: 289–313. https://doi.org/10.1016/j. ympev.2014.09.021
- Kumar S, Stecher G, Tamura K (2016) MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. Molecular Biology and Evolution 33(7): 1870–1874. https://doi.org/10.1093/molbev/msw054
- Le Stradic S (2012) Composition, Phenology and Restoration of Campo Rupestre Mountain Grasslands—Brazil. PhD thesis, Universidade Federal de Minas Gerais, Brazil, and Université d'Avignon et des Pays de Vaucluse, France.

- Lughadha EN, Walker BE, Canteiro C, Chadburn H, Davis AP, Hargreaves S, Lucas EJ, Schuiteman A, Williams E, Bachman SP, Baines D, Barker A, Budden AP, Carretero J, Clarkson JJ, Roberts A, Rivers MC (2019) The use and misuse of herbarium specimens in evaluating plant extinction risks. Philosophical Transactions of the Royal Society B 374: 20170402. https://doi.org/10.1098/rstb.2017.0402
- Luo Z, Zhang D, Renner SS (2008) Why two kinds of stamens in buzz-pollinated flowers? Experimental support for Darwin's division-of-labour hypothesis. Functional Ecology 22(5): 794–800. https://doi.org/10.1111/j.1365-2435.2008.01444.x
- Maia FR, Varassin IG, Goldenberg R (2016) Apomixis does not affect visitation to flowers of Melastomataceae, but pollen sterility does. Plant Biology 18(1): 132–138. https://doi. org/10.1111/plb.12364
- Mansano VF, Pederneiras LC (2016) Proposal to add Glaziou's "Plantae Brasiliae centralis a Glaziou lectae" to the list of suppressed works in Appendix VI. Taxon 65(5): 1181–1182. https://doi.org/10.12705/655.28
- Martin CV, Cremers G (2007) Les Melastomataceae américaines décrites par C. Naudin. Le Journal de Botanique de la Société Botanique de France 37: 3–111.
- Martins E (1995) Nova espécie do gênero *Trembleya* DC. (Microlicieae Melastomataceae). Boletim de Botânica da Universidade de São Paulo 14(0): 39–42. https://doi.org/10.11606/ issn.2316-9052.v14i0p39-42
- Martins E (1997) Revisão taxonômica do gênero *Trembleya* DC. (Melastomataceae). PhD thesis, Universidade Estadual de Campinas, Brazil.
- Martins AB, Almeda F (2017) A monograph of the Brazilian endemic genus Lavoisiera (Melastomataceae: Microlicieae). Phytotaxa 315(1): 1–194. https://doi.org/10.11646/ phytotaxa.315.1.1
- Matsumoto K, Martins AB (2005) Melastomataceae nas formações campestres do município de Carrancas, Minas Gerais. Hoehnea 32: 389–420.
- Melo MD (2013) Distribuição de espécies vegetais ao longo de um gradiente de saturação hídrica em três tipos fisionômicos do Bioma Cerrado, Brasil–Distrito Federal. MSc thesis, Universidade de Brasília, Brazil.
- Mentink H, Baas P (1992) Leaf anatomy of the Melastomataceae, Memecylaceae, and Crypteroniaceae. Blumea 37: 189–225.
- Miller MA, Pfeiffer W, Schwartz T (2012) The CIPRES science gateway. In: Stewart C (Ed.) Proceedings of the 1st Conference of the Extreme Science and Engineering Discovery Environment on Bridging from the eXtreme to the campus and beyond - XSEDE '12. Association for Computing Machinery, New York, [Article 39] 1–8. https://doi. org/10.1145/2335755.2335836
- Naudin CV (1844) Additions à la flore du Brésil méridional. Annales de Sciences Naturelles, Botanique (Sér. 3), 2: 140–156.
- Naudin CV (1845) Additions à la flore du Brésil méridional. Annales de Sciences Naturelles, Botanique (Sér. 3), 3: 169–192.
- Naudin CV (1849) Melastomatacearum quae in Museo Parisiensi continentur monographieae descriptiones. Annales de Sciences Naturelles, Botanique (sér. 3), 12: 196–270.

- O'Brien TP, Feder N, McCully ME (1965) Polychromatic staining of plant cell walls by toluidine blue O. Protoplasma 59(2): 368–373. https://doi.org/10.1007/BF01248568
- Ocampo G, Almeda F (2013) Seed diversity in the Miconieae (Melastomataceae): Morphological characterization and phenetic relationships. Phytotaxa 80: 1–129. https://doi. org/10.11646/phytotaxa.141.1.1
- Ocampo G, Michelangeli FA, Almeda F (2014) Seed diversity in the tribe Miconieae (Melastomataceae): Taxonomic, systematic, and evolutionary implications. PLoS ONE 9(6): e100561. https://doi.org/10.1371/journal.pone.0100561
- Ocampo G, Michelangeli FA, Penneys DS, Handley V González-Moreno, Herrera-Dimas, Almeda F (2022) A new perspective on seed morphological features in Melastomataceae. In: Goldenberg R, Michelangeli FA, Almeda F (Eds) Systematics, Evolution, and Ecology of Melastomataceae. Springer, Cham, Switzerland, 491–531. https://doi.org/10.1007/978-3-030-99742-7_23
- Oliveira U, Soares-Filho B, Leitão RFM, Rodrigues HO (2019) BioDinamica: A toolkit for analyses of biodiversity and biogeography on the Dinamica-EGO modelling platform. PeerJ 7: e7213. https://doi.org/10.7717/peerj.7213
- Pacifico R, Almeda F (2022) Lavoisiereae: A Neotropical tribe with remarkable endemism on eastern Brazilian mountaintops. In: Goldenberg R, Michelangeli FA, Almeda F (Eds) Systematics, Evolution, and Ecology of Melastomataceae. Springer, Cham, Switzerland, 385–408. https://doi.org/10.1007/978-3-030-99742-7_19
- Pacifico R, Fidanza K (2015) Three new endangered species of *Trembleya* DC. (Melastomataceae: Microlicieae) from Minas Gerais, Brazil. Phytotaxa 238(2): 163–173. https://doi. org/10.11646/phytotaxa.238.2.4
- Pacifico R, Almeda F, Carmo AA, Fidanza K (2019) A new species of *Trembleya* (Melastomataceae: Microlicieae) with notes on leaf anatomy and generic circumscription. Phytotaxa 391(5): 289–300. https://doi.org/10.11646/phytotaxa.391.5.2
- Pacifico R, Almeda F, Frota A, Fidanza K (2020) Areas of endemism on Brazilian mountaintops revealed by taxonomically verified records of Microlicieae (Melastomataceae). Phytotaxa 450(2): 119–148. https://doi.org/10.11646/phytotaxa.450.2.1
- Patel VC, Skvarla JJ, Raven PH (1984) ["1985"] Pollen characters in relation to the delimitation of Myrtales. Annals of the Missouri Botanical Garden 71(3): 858–969. https://doi. org/10.2307/2399170
- Penneys DS, Judd WS (2013) Combined molecular and morphological phylogenetic analyses of the Blakeeae (Melastomataceae). International Journal of Plant Sciences 174(5): 802– 817. https://doi.org/10.1086/670011
- Penneys DS, Michelangeli FA, Judd WS, Almeda F (2010) Henrietteeae (Melastomataceae): A new neotropical berry-fruited tribe. Systematic Botany 35(4): 783–800. https://doi. org/10.1600/036364410X539862
- Penneys DS, Almeda F, Michelangeli FA, Goldenberg R, Martins AB, Fritsch PW (2020) Lithobieae and Eriocnemeae: Two new Neotropical tribes of Melastomataceae. Phytotaxa 453(3): 157–178. https://doi.org/10.11646/phytotaxa.453.3.1
- Penneys DS, Almeda F, Reginato M, Michelangeli FA, Goldenberg R, Fritsch PW, Stone RD (2022) A new Melastomataceae classification informed by molecular phylogenetics and

morphology. In: Goldenberg R, Michelangeli FA, Almeda F (Eds) Systematics, Evolution, and Ecology of Melastomataceae. Springer, Cham, Switzerland, 109–165. https://doi.org/10.1007/978-3-030-99742-7_5

- Pereira CTT (2011) Assimetria flutuante, herbivoria e polinização em Melastomataceae. MSc thesis, Universidade Federal de Minas Gerais, Brazil.
- Pflaum (1897) Anatomisch systematische Untersuchung des Blattes der Melastomaceen aus den Triben Microlicieen und Tibouchineen. PhD thesis, Munich University, Germany.
- Prusinkiewicz P, Erasmus Y, Lane B, Harder LD, Coen E (2007) Evolution and development of inflorescence architectures. Science 316(5830): 1452–1456. https://doi.org/10.1126/ science.1140429
- QGIS Development Team (2021) QGIS Geographic information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org [accessed 1 May 2021]
- Raffauf RF (1996) Plant Alkaloids: A guide to their discovery and distribution. The Haworth Press, Binghamton, 283 pp.
- Rapini A, Ribeiro PL, Lambert S, Pirani JR (2008) A flora dos campos rupestres da Cadeia do Espinhaço. Megadiversidade 4: 16–24.
- Rapini A, Bitencourt C, Luebert F, Cardoso D (2020) An escape-to-radiate model for explaining the high plant diversity and endemism in campos rupestres. Biological Journal of the Linnean Society 133(2): 481–498. https://doi.org/10.1093/biolinnean/blaa179
- Reginato M (2016) monographaR: An R package to facilitate the production of plant taxonomic monographs. Brittonia 68(2): 212–216. https://doi.org/10.1007/s12228-015-9407-z
- Reginato M, Michelangeli FA (2016) Untangling the phylogeny of *Leandra* s.str. (Melastomataceae, Miconieae). Molecular Phylogenetics and Evolution 96: 17–32. https://doi. org/10.1016/j.ympev.2015.11.015
- Rego MA, Moreira-Lima L, Silveira LF, Frahnert S (2013) On the ornithological collection of Friedrich Sellow in Brazil (1814–1831), with some considerations about the provenance of his specimens. Zootaxa 3616(5): 478–484. https://doi.org/10.11646/ zootaxa.3616.5.4
- Reis C, Bieras AC, Sajo MG (2005) Anatomia foliar de Melastomataceae do cerrado do Estado de São Paulo. Revista Brasileira de Botânica. Brazilian Journal of Botany 28(3): 451–466. https://doi.org/10.1590/S0100-84042005000300004
- Renner SS (1989) A survey of reproductive biology in neotropical Melastomataceae and Memecylaceae. Annals of the Missouri Botanical Garden 76(2): 496–518. https://doi. org/10.2307/2399497
- Renner SS (1990) A revision of *Rhynchanthera* (Melastomataceae). Nordic Journal of Botany 9(6): 601–630. https://doi.org/10.1111/j.1756-1051.1990.tb00551.x
- Renner SS (1993) Phylogeny and classification of the Melastomataceae and Memecylaceae. Nordic Journal of Botany 13(5): 519–540. https://doi.org/10.1111/j.1756-1051.1993. tb00096.x
- Rocha MJR, Guimarães PJF, Michelangeli FA, Romero R (2016) Phylogenetic placement and a new circumscription of *Poteranthera* (Microlicieae; Melastomataceae). Phytotaxa 263(3): 219–232. https://doi.org/10.11646/phytotaxa.263.3.3

- Rocha MJR, Guimaráes PJF, Michelangeli FA, Batista JAN (2018) Taxonomy of Marcetieae: A new neotropical tribe of Melastomataceae. International Journal of Plant Sciences 179(1): 50–74. https://doi.org/10.1086/694932
- Rodrigues ERS, Silveira FAO (2013) Seed germination requirements of *Trembleya laniflora* (Melastomataceae), an endemic species from neotropical montane rocky savannas. Plant Species Biology 28(2): 165–168. https://doi.org/10.1111/j.1442-1984.2012.00396.x
- Rolim TP (2011) Melastomataceae Juss. no campo rupestre do Parque Estadual do Itacolomi: Relações ecológicas, fitofisionômicas, padrões de distribuição geográfica e comparação florística. MSc thesis, Universidade Federal de Viçosa, Brazil.
- Romero R (2000) A família Melastomataceae no Parque Nacional da Serra da Canastra Minas Gerais Brasil. PhD thesis, Universidade Estadual de Campinas, Brazil. https://doi. org/10.1590/S0100-84041999000500006
- Romero R, Castro NM (2014) Microlicia longicalycina (Melastomataceae), a new species from the state of Minas Gerais, Brazil, with notes on leaf anatomy. Systematic Botany 39(4): 1177–1182. https://doi.org/10.1600/036364414X682607
- Ruchkys UA, Machado MMM (2013) Patrimônio geológico e mineiro do Quadrilátero Ferrífero, Minas Gerais – Caracterização e iniciativas de uso paraeducação e geoturismo. Boletim Paranaense de Geociências 70: 120–136. https://doi.org/10.5380/geo. v70i0.31541
- Salazar A, Goldstein G, Franco AC, Miralles-Wilhelm F (2011) Timing of seed dispersal and dormancy, rather than persistent soil seed-banks, control seedling recruitment of woody plants in Neotropical savannas. Seed Science Research 21(2): 103–116. https://doi. org/10.1017/S0960258510000413
- Santos CMD, Fuhlendorf M (2018) GeX: An automated tool for generating XYD files for analysis of endemicity using VNDM. Cladistics 35(1): 125–129. https://doi.org/10.1111/ cla.12236
- Santos APM, Fracasso CM, Santos ML, Romero R, Sazima M, Oliveira PE (2012) Reproductive biology and species geographical distribution in the Melastomataceae: A survey based on New World taxa. Annals of Botany 110(3): 667–679. https://doi.org/10.1093/aob/ mcs125
- Silva SCS (2001) Biologia Reprodutiva e Polinização em Melastomataceae no Parque do Sabiá, Uberlândia, MG. Acta Botanica Brasilica 15(2): 284–285. https://doi.org/10.1590/ S0102-33062001000200017
- Silva DB (2003) Distribuição espacial de duas espécies de Melastomataceae na vereda da Estação Ecológica de Águas Emendadas. MSc thesis, Centro Universitário de Brasília, Brazil.
- Silva CI, Bordon NG, Rocha Filho LC, Garófalo CA (2012) The importance of plant diversity in maintaining the pollinator bee, *Eulaema nigrita* (Hymenoptera: Apidae) in sweet passion fruit fields. Revista de Biología Tropical 60(4): 1553–1565. https://doi.org/10.15517/ rbt.v60i4.2073
- Silva KR, Romero R, Simão DG (2018) Leaf characters of *Lavoisiera*, *Microlicia* and *Trembleya* (Microlicieae, Melastomataceae) and their implications for taxonomy. Feddes Repertorium 129(2): 123–136. https://doi.org/10.1002/fedr.201700019

- Silveira FAO, Ribeiro RC, Oliveira DMT, Fernandes GW, Lemos-Filho JP (2012) Evolution of physiological dormancy multiple times in Melastomataceae from Neotropical montane vegetation. Seed Science Research 22(1):37–44. https://doi.org/10.1017/S0960258511000286
- Silveira FAO, Negreiros D, Barbosa NPU, Buisson E, Carmo FF, Carstensen DW, Conceição AA, Cornelissen TG, Echternacht L, Fernandes GW, Garcia QS, Guerra TJ, Jacobi CM, Lemos-Filho JP, Le Stradic S, Morellato LPC, Neves FS, Oliveira RS, Schaefer CE, Viana PL, Lambers H (2016) Ecology and evolution of plant diversity in the endangered campo rupestre: A neglected conservation priority. Plant and Soil 403(1–2): 129–152. https://doi. org/10.1007/s11104-015-2637-8
- Simon MF, Grether R, de Queiroz LP, Skema C, Pennington RT, Hughes CE (2009) Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by *in situ* evolution of adaptations to fire. Proceedings of the National Academy of Sciences of the United States of America 106(48): 20359–20364. https://doi.org/10.1073/pnas.0903410106
- Spix JB, Martius KFP (1824) Travels in Brazil, in the years 1817–1820: Undertaken by command of His Majesty the King of Bavaria. Volume 1. Longman, Hurst, Rees, Orme, Brown, and Green, London, 1–327. https://doi.org/10.5962/bhl.title.85332
- Soares NC, Morellato LPC (2018) Crepuscular pollination and reproductive ecology of *Trembleya laniflora* (Melastomataceae), an endemic species in mountain rupestrian grasslands. Flora 238: 138–147. https://doi.org/10.1016/j.flora.2016.12.005
- Somavilla NS, Graciano-Ribeiro D (2011) Análise comparativa da anatomia foliar de Melastomataceae em ambiente de vereda e cerrado *sensu stricto*. Acta Botanica Brasilica 25(4): 764–775. https://doi.org/10.1590/S0102-33062011000400004
- Somavilla NS, Graciano-Ribeiro D (2012) Ontogeny and characterization of aerenchymatous tissues of Melastomataceae in the flooded and well-drained soils of a Neotropical savanna. Flora 207(3): 212–222. https://doi.org/10.1016/j.flora.2012.01.007
- Stamatakis A (2014) RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30(9): 1312–1313. https://doi.org/10.1093/bioinformatics/btu033
- Szumik CA, Cuezzo F, Goloboff PA, Chalup AE (2002) An optimality criterion to determine areas of endemism. Systematic Biology 51(5):806–816. https://doi.org/10.1080/10635150290102483
- Szumik CA, Goloboff PA (2004) Areas of endemism: An improved optimality criterion. Systematic Biology 53(6): 968–977. https://doi.org/10.1080/10635150490888859
- Thiers B (2022) [continuously updated]: Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/science/ih/ [accessed 18 October 2022]
- Triana JJ (1872) ["1871"] Les Mélastomacées. Transactions of the Linnean Society of London 28(1): 1–188. https://doi.org/10.1111/j.1096-3642.1871.tb00222.x
- Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber W-H, Li D-Z, Marhold K, May TW, McNeill J, Monro AM, Prado J, Price MJ, Smith GF (2018) International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Koeltz Botanical Books, Glashütten, Germany, [Regnum Vegetabile 159] 1–254. https://doi.org/10.12705/Code.2018

- Ulloa Ulloa C, Almeda F, Goldenberg R, Kadereit G, Michelangeli FA, Penneys DS, Stone RD, Veranso-Libalah MC (2022) Melastomataceae: Global diversity, distribution, and endemism. In: Goldenberg R, Michelangeli FA, Almeda F (Eds) Systematics, Evolution, and Ecology of Melastomataceae. Springer, Cham, Switzerland, 3–28. https://doi. org/10.1007/978-3-030-99742-7_1
- Varassin IG, Penneys DS, Michelangeli FA (2008) Comparative anatomy and morphology of nectar-producing Melastomataceae. Annals of Botany 102(6): 899–909. https://doi. org/10.1093/aob/mcn180
- Vasconcelos MF (2011) O que são campos rupestres e campos de altitude nos topos de montanha do Leste do Brasil? Brazilian Journal of Botany 34(2): 241–246. https://doi. org/10.1590/S0100-84042011000200012
- Vasconcelos MF, Vasconcelos PN, Fernandes GW (2001) Observations on a nest of Hyacinth Visorbearer *Augastes scutatus*. Cotinga 16: 57–61.
- Vasconcelos TNC, Alcantara S, Andrino CO, Forest F, Reginato M, Simon MF, Pirani JR (2020) Fast diversification through a mosaic of evolutionary histories characterizes the endemic flora of ancient Neotropical mountains. Proceedings of the Royal Society B 287: 20192933. https://doi.org/10.1098/rspb.2019.2933
- Ventura CP, Oliveira AB, Braga FC (2007a) Antimicrobial activity of *Trembleya laniflora*, *Xyris platystachia* and *Xyris pterygoblephara*. Revista Brasileira de Farmacognosia 17(1): 17–22. https://doi.org/10.1590/S0102-695X2007000100005
- Ventura CP, Filho JDS, Oliveira AB, Braga FC (2007b) A flavanone and other constituents of the Brazilian endemic species *Trembleya laniflora* (D.Don) Cogn. (Melastomataceae). Biochemical Systematics and Ecology 35(1): 40–41. https://doi.org/10.1016/j. bse.2006.08.001
- Versiane AFA, Romero R, Reginato M, Welker CAD, Michelangeli FA, Goldenberg R (2021) Phylogenetic analysis of Microlicieae (Melastomataceae), with emphasis on the re-circumscription of the large genus *Microlicia*. Botanical Journal of the Linnean Society 197(1): 35–60. https://doi.org/10.1093/botlinnean/boab011
- Weberling F (1988) The architecture of inflorescences in the Myrtales. Annals of the Missouri Botanical Garden 75(1): 226–310. https://doi.org/10.2307/2399476
- Westerkamp C (1996) Pollen in bee-flower relations some considerations on melittophily. Botanica Acta 109(4): 325–332. https://doi.org/10.1111/j.1438-8677.1996.tb00580.x
- Wurdack JJ (1953) A revision of the genus *Brachyotum* (Tibouchineae-Melastomaceae). Memoirs of the New York Botanical Garden 8: 343–407.
- Wurdack JJ (1970) Erroneous data in Glaziou collections of Melastomataceae. Taxon 19(6): 911–913. https://doi.org/10.2307/1218309
- Wurdack JJ (1986) Atlas of hairs for neotropical Melastomataceae. Smithsonian Contributions to Botany 63: 1–80. https://doi.org/10.5479/si.0081024X.63
- Zappi DC, Moro MF, Meagher TR, Nic Lughadha E (2017) Plant biodiversity drivers in Brazilian *campos rupestres*: Insights from phylogenetic structure. Frontiers in Plant Science 8: 2141. https://doi.org/10.3389/fpls.2017.02141
- Zhou R, Zhou Q, Liu Y (2018) *Bredia repens* (Melastomataceae), a new species from Hunan, China. Systematic Botany 43(2): 544–551. https://doi.org/10.1600/036364418X697265

Appendix I

List of species

- 1. Microlicia altoparaisensis (R.B.Pacifico, Almeda & Fidanza) Versiane & R.Romero
- 2. Microlicia calycina (Cham.) Versiane & R.Romero
- 3. Microlicia chamissoana (Naudin) Versiane & R.Romero
- 4. Microlicia flaviflora Versiane & R.Romero
- 5. Microlicia laniflora (D.Don) Baill.
- 6. Microlicia parviflora (D.Don) Versiane & R.Romero
- 7. Microlicia pentagona (Naudin) Versiane & R.Romero
- 8. Microlicia pithyoides (Cham.) Versiane & R.Romero
- 9. Microlicia rosmarinoides (Mart. & Schrank ex DC.) Versiane & R.Romero
- 10. Microlicia trembleyiformis Naudin
- 11. Microlicia tridentata (Naudin) Versiane & R.Romero

Specimens examined

Aguiar 102 (6). Almeda et al. 7726 (5); 7751 (7); 7753 (5); 8395 (5); 8549 (5); 8555 (7); 8580 (3); 8862 (5); 8911 (7); 9076 (6); 9179 (5); 9203 (7). Alves 595 (11); 600 (6); 7359 (11). Alves & Almeida-Lafetá 5573 (5). Alves et al. 2109 (5); 6925 (5). Andrade et al. 374 (5). Antar et al. 1662 (5). Antônio-Silva et al. 315 (7). Araújo et al. 2043 (4); 323 (5); 334 (5). Arbo et al. 3906 (5); 4030 (5). Assis et al. 520 (6). Avezum 6017 & Almeida 10 (6). Azevedo et al. 675 (6). Badini & Ferreira 9774 (11). Baitello et al. 2136 (6). Barreto 10734 (7); 1182 (7); 4621 (6); 4654 (6); 6745 (3); 6757 (6); 6759 (6); 6769 (5); 6771 (5); 6772 (5); 7023 (7); 7024 (7); 7025 (7); 7026 (putative hybrid M. laniflora × M. pentagona); 706 (5); 9019 (2). Barreto & Viégas s.n. (5). Barros & Feteira 1625 (6). Batista & Naves 405 (6). Baumgratz et al. 1127 (6). Bautista 1347 (6). Beraldo & França 85 (6). Bidá et al. CFCR11951 (4). Borges et al. 153 (5). Bortoluzzi et al. 678 (7). Bovini & Barros 3235 (6). Brade 13735 (5); 14756 (7). Brade et al. 18205 (6). Brandão 14509 (6); 20838 (7); 22298 (6); 28574 (5). Brotto 2600 (6). Brotto & Vieira 1921 (6). Bruniera et al. 37 (5). Bunbury s.n. (6). Bunge s.n. (5). Caddah et al. 636 (6). Caiafa & Umbelino 172 (6). Camargo et al. 109 (6). Carmo 192 (9); 2262 (9); 377 (9); 4819 (5). Carvalho 1086 (6); 6986 (6); s.n. (5). Carvalho et al. 6651 (6). Casaretto s.n. (7). Castro et al. 281 (11). Castro et al. 283 (2); s.n. (5). Cavalcanti CFCR8314 (6). Cavalcanti et al. CFCR8035 (6). Ceccantini et al. 3914 (5). Cerati et al. 246 (4). Chuckr et al. s.n. (5). Claussen 1 (5); 1617 (7); 1631 (11); 1637 (7); 1645 (5); 22 (7); 296 (7); 332A (5); 350 (7); 554 (5); 640 (5); 923 (5); s.n. (5,7). Claussen 10 (2); 368 (2). Colletta 161 (6). Collo et al. s.n. (5). Contro & Margues 21 (7). Cordeiro et al. CFSC10504 (5). Costa 451 (6). Costa et al. 60 (6). Damazio 1025 (5); 1540 (5); 2026 (3); s.n. (277). Davis et al. 2298 (6). Delfini et al. 78 (5); 97 (6). Delprete 9205 (6). Drummond et al. 321 (1). Duarte 2004 (7); 2692 (7); 2767 (10); 8157 (11). Duarte & Brade 1155 (6). Ducke s.n. (5). Eiten & Eiten 7305 (6). Eiten et al. 3019 (6). Emygdio 3312 (6); 3314 (5); 3353 (5); 3613 (6). Escaramai et al. 52 (3); 65 (5). Estevan et al. 617 (6). Farah et al. 580 (6). Faria & Mazucato 105 (5). Faria et al. 1332 (6). Farinaccio et al. 36 (5). Fernandes s.n. (7). Fernandes et al. 1468 (5). Ferreira 5544 (5). Ferreira & Helena 7844 (11). Ferreira et al. 433 (5). Fontana 2309 (6). Fontana et al. 2288 (5); 7678 (6). Forero et al. 7700 (5); 7831 (5). Foresto et al. 59 (6). Forzza et al. 3427 (6); 4897 (4); 6344 (5); 6359 (5); 993 (5). Foster & Leoni 64 (6). Fraga & Saddi 1786 (6). Fraga et al. 3333 (5); 3341 (5). Franco et al. 1270 (5). Furlan et al. CFCR771 (4). Ganev 879 (6); 965 (6). Gardner 379 (6); 380 (6); 4601 (5); 4602 (6). Giulietti & Menezes 4017 (7). Giulietti et al. CFCR13780 (11); CFSC12492 (3); CFSC12560 (3); CFSC12564 (5). Glaziou 11953 (5); 12704 (6); 14740 (5); 14741 (5); 14742 (7); 14743 (11); 14745 (2); 14746 (8); 14747 (9); 16679 (6); 16778 (6); 16781 (11); 17513 (11); 17573 (11); 18232 (2); 19221 (10); 19239 (8); 19242 (9); 21300 (1); 2579 (6); 8680 (6); 9454 (6); s.n. (5). Goldenberg & Michelangeli 2093 (6). Goldenberg & Silveira 1573 (5). Goldenberg et al. 1652 (6). Gonçalves et al. 172 (6). Gounelle s.n. (5). Grandi et al. 6593 (2). Groppo & Ulwin 676 (5). Guarçoni & Sartori 1367 (6). Guedes et al. 12092 (6). Guiamaráes 333 (6). Guillemin 921 (6); 946 (6). Hage et al. 2317 (6). Handro 790 (6). Hatschbach 27277 (6); 2775 (6); 39954 (6); 41337 (4); 647 (6); 6908 (6). Hatschbach 26964 (6); 41498 (6). Hatschbach & Guimarães 55455 (6); 56167 (6). Hatschbach & Hatschbach 52005 (4). Hatschbach & Pelanda 28014 (6). Hatschbach & Silva 49393 (6). Hatschbach et al. 27400 (5); 28759 (7); 29958 (7); 42967 (6); 54239 (4); 55434 (6); 68067 (4); 68138 (5); 74974 (6); 75995 (6); s.n. (7). Heluey & Castro 108 (6). Hensold 778 (5). Hensold et al. CFCR2880 (11); CFCR3525 (4). Heringer 8544/736 (6). Hoehne 20521 (66). Hottz et al. 302 (6). Irwin 19974 (5). Irwin et al. 19974 (5); 20178 (7); 20486 (7); 20537 (7); 29029 (11); 29079 (11); 29213 (7); 31141 (6); 34521 (6); 8149 (6). Joly CFSC2405 (5); CFSC82 (5). Joly & Semir CFSC2957 (7); CFSC3196 (7). Kameyama et al. CFSC10403 (3). Kinoshita et al. 43767 (6). Kirizawa 3665 (6). Kirizawa et al. 2132 (6). Klein et al. 2465 (1). Kollmann 231 (6). Kral et al. 72723 (4). Kral et al. 72997 (5). Krieger 10641 (5); 8857 (6). Krieger et al. 24423 (6). Kubo et al. 109 (5); 125 (5). Kuhlmann 4381 (6). Leitão et al. 17281 (5). Leitão Filho et al. 7893 (4). Leoni 1 (6). Lima 400 (6). Lima et al. 1296 (5); 1443 (5); 49 (5); 8445 (6). Loefgren 557 (6). Lombardi 4045 (6). Longhi-Wagner et al. CFCR9184 (11). Lund 135 (5). Macedo 3758 (5). Machado et al. 153 (1). Magalhães 1160 (11); 2278 (7). Maguire et al. 49016 (5); 49140 (5). Mamede et al. 666 (6). Mantovani 99 (5). Marcolino 222 (6). Marcondes-Ferreira et al. 281 (5). Marques et al. 274 (5). Marquete et al. 2332 (6); 3817 (5). Martens 383 (5); 524 (6); 7 (5). Martinelli 19464 (6). Martinelli & Tavora 2583 (5). Martinelli et al. 10932 (6). Martius 930 (5); 931 (6); 961 (6); 989 (6); s.n. (59). Mattos & Rizzini 107 (5); 480 (5). Meireles et al 1362 (5). Meireles et al. 1124 (4); 1766 (6). Mello-Silva et al. 1217 (6); 509 (4); CFCR7836 (6). Mello et al. 61 (5). Mendes & Araújo 970 (6). Mendonça 557 (11). Messias et al. 1922 (5); 2151 (5). Meyer 1171 (1). Michelangeli et al. 1580 (7); 1586 (11); 1595 (11). Mimura 479 (6). Monge et al. 2595 (6); 384 (5). Monteiro 78 (6). Mosen 1971 (6). Moutinho et al. 76 (6). N. da Cruz 135 (6). Nakajima & Romero 3040 (5). Nakajima et al. 1476 (10); 4547 (5); 4764 (4). Netto s.n. (5). Nicolau et al. 2212 (6). Occhioni et al. s.n. (9). Oliveira 1013 (6); 25197 (6); 382 (8). Oliveira & Giacomin 47 (2); 84 (2). Oliveira et al. 478 (7); 480 (2); 508 (6); 518 (7); CFCR12997 (4). Ordones et al. 1856 (5); 213 (7); 84 (11). Orlandi et al. 778 (6). Pacifico 185 (5); 191 (6); 295 (8); 413 (6); 565 (4). Pacifico & Bressan 290 (11); 291 (2); 294 (7); 296 (2); 303 (11); 380 (1); 531 (7); 565 (4). Pacifico & Carmo 154 (3). Pacifico & Simoes 353 (4). Pastore et al. 685 (6). Paula & Grandi s.n. (6). Paula et al. 136 (5); 295 (5); 8 (5). Pedrosa 110 (9); 120 (11). Pena & Viana 365 (5); 417 (3). Pereira 309 (6). Pereira & Pabst 152 (5); 2944 (5); 3107 (5). Pereira & Pabstii 2619 (11). Peron 220 (2); 256 (7); 260 (7); 268 (2); 269 (2). Pirani & Mello-Silva CFCR10814 (4). Pirani & Yano 692 (7); 696 (5). Pirani et al. 1663 (1); 1694 (1); 5082 (5); 696 (5); CFCR11211 (5). Pires & Braga s.n. (5). Pivari 15 (6). Pivari et al. 2512 (7). Polisel et al. 176 (6). Porto 2834 (10). Prates s.n. (6). Queiroz 2808 (6). Raben 409 (6); 428 (5). Rapini et al. 296 (7). Reginato et al. 1401 (5). Rezende 507 (7). Ribas et al. 6769 (6); 8528 (6). Riedel s.n. (255611). Rocha 694 (3). Rocha et al. 497 (4); 602 (5); 672 (5). Rolim 366 (2). Rolim et al. 326 (11); 327 (11); 328 (11); 329 (5); 353 (7); 361 (7); 370 (7); 386 (5); 394 (11); 61 (5). Romero 4157 (10). Romero & Nakajima 3021 (6); 3432 (6); 3593 (10); 5998 (7). Romero et al. 2155 (6); 5303 (7); 5307 (5); 7550 (10); 8627 (3); 8694 (10); 8689 (10). Roque 2869 (6). Roschel et al. s.n. (11). Roth s.n. (5). Rutter 128 (11); 150 (11); 161 (11); 186 (11); 191 (11). Saint-Hilaire 160 [catal. B] (10); 216 (5); 2399 [catal. B2] (11); s.n. (7). Saint-Hilaire s.n. [catal. D, n° 462] (6). Sakuragui & Souza 38 (5). Salatino et al. 14 (5); 18 (5). Salgado 167 (6). Samento & Bautista 859 (6). Sampaio 7194 (5). Santos 411 (10). Saraiva et al. 85 (5). Sazima CFSC4259 (7). Scatigna & Galváo 376 (4). Schüch s.n. (7). Schwacke 10135 (11); 10814 (7); 9184 (9); 9325 (7); 9368 (2). Sellow 1154 (6); 1316 (8); 1446 (5); 1727 (5); 260 (3); 5278 (6); s.n. (3, 5). Semir CFSC2005 (5); CFSC4133 (5); CFSC5001 (5); CFSC5068 (5); CFSC5607 (3). Semir CFSC5608 (7). Semir & Joly CFSC3743 (7). Semir & Sazima CFSC3395 (7). Semir et al CFCR230 (5). Semir et al. 28809 (5). Sena s.n. (3). Sevilha et al. 7075 (6). Sheperd & Kirzenzaft 10214 (3). Silva s.n. (6). Silva & Abe 2310 (6). Silva & Grandi 6627 (6). Silva & Koch 7610 (6). Silva et al. 1043 (7); 6478 (6). Silveira s.n. (3). Sobral et al. 12797 (6); 14085 (6); 14508 (7). Souza 1606 (5). Souza & Miranda 1639 (3). Souza et al. 1013 (6); 1108 (6); 11565 (5); 25181 (5); 2584 (9); 5934 (6); 6098 (6); 8015 (11); 8047 (11); 8061 (11). Stehmann 2532 (6). Stehmann & Morais 2354 (5); 2650 (5). Tales et al. 17 (5). Tameirao Neto & Mansur 4874 (5). Tannus 760 (6). Teixeira s.n. (5); s.n. (5). Temponi & Vasconcelos s.n. (5). Torres s.n. (5). TSMG & Tales 81 (5). Ule 2528 (9); 2543 (7). Vainio 33501 (7). Valente & Azevedo 57 (6). Valente et al. 1229 (5); 1230 (5); 2574 (5); 535 (5). Vasconcelos s.n. (55). Vauthier 37 (5); 43 [part] (6); s.n. (5). Verdi et al. 6501 (5). Versiane & Devides 677 (9); 682 (11). Versiane et al. 305 (6). Vidal s.n. (9). Vieira & Yamamoto 26186 (6). Wängler & Ferreira 1352 (6). Warming s.n. (6). Weddell s.n. (8). Widgren 967 (6); s.n. (6). Williams & Assis 6352 (5); 7274 (6). Yamamoto 1549 (6). Zappi et al. 2504 (6); CFCR9903 (4); CFSC9353 (5).

Supplementary material I

List of species sampled in this study, their respective Genbank accession codes (for nrITS and nrETS), and specimen vouchers

Authors: Ricardo Pacifico, Frank Almeda, Darin S. Penneys, Karina Fidanza

Data type: table (word document)

- Explanation note: List of species sampled in this study, their respective Genbank accession codes (for nrITS and nrETS), and specimen vouchers. Codes highlighted in bold refer to sequences previously obtained from GenBank.
- Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/phytokeys.126.91032.suppl1

RESEARCH ARTICLE



Solanum scalarium (Solanaceae), a newly-described dioecious bush tomato from Judbarra/Gregory National Park, Northern Territory, Australia

Tanisha M. Williams¹, Jonathan Hayes¹, Angela J. McDonnell², Jason T. Cantley³, Peter Jobson⁴, Christopher T. Martine¹

I Department of Biology, Bucknell University, 1 Dent Drive, Lewisburg, PA, USA 2 Negaunee Institute for Plant Conservation Science and Action, Chicago Botanic Garden, 1000 Lake Cook Rd, Glencoe, IL 60022, USA 3 Department of Biology, San Francisco State University, 1600 Holloway Avenue, San Francisco, CA 96132, USA 4 Northern Territory Herbarium, Alice Springs, Department of Environment, Parks and Water Security, Alice Springs, Northern Territory, 0870, Australia

Corresponding author: Tanisha M. Williams (tmw018@bucknell.edu)

Academic editor: Sandy Knapp | Received 29 April 2022 | Accepted 15 November 2022 | Published 20 December 2022

Citation: Williams TM, Hayes J, McDonnell AJ, Cantley JT, Jobson P, Martine CT (2022) *Solanum scalarium* (Solanaceae), a newly-described dioecious bush tomato from Judbarra/Gregory National Park, Northern Territory, Australia. PhytoKeys 216: 103–116. https://doi.org/10.3897/phytokeys.216.85972

Abstract

A new species of functionally dioecious bush tomato of *Solanum* subgenus *Leptostemonum* is described. *Solanum scalarium* Martine & T.M.Williams, **sp. nov.**, is a member of the taxonomically challenging "Kimberley dioecious clade" in Australia and differs from other species in the group in its spreading decumbent habit and conspicuously prickly male floral rachis. The species is so far known from one site in Judbarra/Gregory National Park in the Northern Territory. Ex situ crosses and confirmation of inaperturate pollen grains produced in morphologically cosexual flowers indicate that these flowers are functionally female and the species is functionally dioecious. The scientific name reflects the ladder-like appearance of the inflorescence rachis armature of male individuals, the stone staircase that provides access to the type locality at the Escarpment Lookout Walk, and the importance of maintaining equitable and safe access to outdoor spaces. The common name Garrarnawun Bush Tomato is proposed in recognition of the lookout point at this site, a traditional meeting place of the Wardaman and Nungali-Ngaliwurru peoples whose lands overlap in this area.

Keywords

Australia, dioecy, inaperturate pollen, Judburra/Gregory National Park, new species, Northern Territory, Solanaceae, *Solanum dioicum*

Copyright Tanisha M.Williams et al. This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Solanum L. is the most species-rich genus in the family Solanaceae and among the largest in the angiosperms, with ca. 1400 accepted species distributed on every continent except Antarctica (Gagnon et al. 2022). Much of the richness of the genus is concentrated in circum-Amazonian tropical South America, but other hotspots include Africa and Australia (Symon 1981; Särkinen et al. 2013; Vorontsova et al. 2013; Gagnon et al. 2022). The genus is often recognized by its pentamerous flowers with fused sepals and petals, five stamens, 2-chambered superior ovary, poricidal anthers, and, in many species, branched hairs and/or prickles (Knapp 2013). Solanums exhibit great diversity both in vegetative and reproductive traits (especially in floral and fruit traits), ecology, and reproductive biology (see Hilgenhof et al. in review).

Despite decades of research on phylogenetic relationships within *Solanum*, there is still a great deal of work to be done to fully understand the evolutionary history of this hyper diverse group. This challenge arises, in part, due to the large number of species already described within the genus coupled with a large number of species still being described. In the past decade alone, there have been more than 100 newly described *Solanum* species (see McDonnell et al. 2019). One hotspot for new descriptions over that period has been northern Australia (e.g., Brennan et al. 2006; Bean and Albrecht 2008; Barrett 2013; Martine et al. 2013, 2016a, c; Bean 2016; Lacey et al. 2017; McDonnell et al. 2019). This area is home to a clade of ca. 45 currently described species of "spiny solanums" (i.e., *Solanum* subgenus *Leptostemonum* Bitter, the Leptostemonum Clade) belonging to the *S. dioicum* + *S. echinatum* Group sensu Martine et al. (2019) (see Fig. 1 for breakdown of clade names related to this group). Key morphological characteristics of Leptostemonum Clade include the presence of stellate pubescence, stems and leaves with prickles, and attenuate anthers (Whalen 1984).

Phylogenetic work has uncovered two Australian clades (Fig. 1) of functionally dioecious *Solanum* species: the "Kakadu dioecious clade" (two species [plus one forthcoming] of the upper Northern Territory) and the "Kimberley dioecious clade" (12 species occurring from the Kimberley Plateau of Western Australia to far northwestern Queensland (Bean 2004; Martine et al. 2006; Martine et al. 2009; Martine et al. 2019; McDonnell and Martine 2020; Figs 1, 2). The "Kimberley dioecious clade" is a well-supported clade of usually clonal shrub taxa that have proven to be taxonomically challenging, ostensibly due to a complex (or at least quite recent) evolutionary history (Symon 1981; Martine et al. 2006, 2009). Species boundaries are often blurred by overlapping or intermediate morphological traits, making it sometimes difficult to distinguish taxa in the field (Symon 1981; Martine et al. 2016c); the employment of molecular phylogenetic data to address this challenge has so far resulted in poorlyresolved intraclade relationships (see Gagnon et al. 2022).

Judburra/Gregory National Park, where the new species described here is found, is floristically diverse as a result of its sandstones and limestones that have been weathered to produce deep gorges and escarpments that sustain a diversity of habitats (Australian Government Department of the Environment and Energy 2015). In recent decades



Figure 1. Representational phylogeny showing hypothesized relationships among the clades included in the "*S. dioicum* + *S. echinatum* Group" sensu Martine et al. (2019), based on that study plus forthcoming work by McDonnell and Martine (in prep). *Solanum scalarium* sp. nov. is one of twelve described species in the "Kimberley dioecious clade" sensu Martine et al. (2006), a clade of functionally dioecious species (and phrase-named morphological variants of *S. dioicum*) sometimes also referred to as the "Dioicum Complex".

the Northern Territory government has funded a number of monitoring and vegetation surveys throughout the territory. These have resulted in a series of papers describing new endemic species to the region (e.g., Craven 1998; Walsh and Albrecht 1998; Jobson 2014; Martine et al. 2016a), and others recognized as phrase-name taxa — i.e., potentially-new species recognized as distinct variants by regional field botanists (e.g., Cowie et al. 2017). On a recent collecting trip to the region as part of phylogenetic and biogeographical studies on the flora of the Australian Monsoon Tropics (AMT), a *Solanum* population was recognized as a possibly new species by CTM because of its spreading decumbent habit and its unusual staminate inflorescence axis armed with relatively stout, spreading, straight prickles (Fig. 6) and is described here as *Solanum scalarium* Martine & T.M.Williams, sp. nov. This taxon is one of the many "Kimberley dioecious clade" variants found throughout north and northwestern Australia (Symon 1981; Purdie et al. 1982; Barrett 2013).

Methods

A single fertile voucher specimen collected from the type locality included mature fruits. Once back at Bucknell University, seeds from those fruits were removed and germinated in order to build a living collection of greenhouse plants to better assess the morphology of this putative new species. Seeds were germinated following a 24-hour soak in 1,000-ppm gibberellic acid and sown in a controlled growth chamber environment following Martine et al. (2016a). Mature plants were cultivated in an IPM-managed greenhouse following Hayes et al. (2019). Observations of the taxon by JTC, PJ, CTM, and AJM in Judbarra/Gregory National Park (NT) are combined here with measurements of characters by JH and TMW from plants grown in cultivation (Figs 4–6). The morphological description is based mostly on those cultivated individuals because of limited herbarium material of the species; data in the Australasian Virtual Herbarium and physical examination of "*S. dioicum*" holdings at the Northern Territory Herbaria (DNA, NT) suggest the species is not represented in collections beyond the type collections cited below. A map (Fig. 2) comparing the distributions of dioecious *Solanum* species in Australia was generated using records from the Australasian Virtual Herbarium.



Figure 2. Functionally dioecious species of the "S. dioicum + S. echinatum Group." A S. ossicruentum Martine & J.Cantley B S. carduiforme F.Muell. C S. dioicum W.Fitzg. D S. asymmetriphyllum Specht E S. cowiei Martine F S. sejunctum K.Brennan, C.Martine & Symon G S. petraeum Symon H S. leopoldense Symon and I S. tudununggae Symon. Solanum cataphractum Cunn. ex Benth., S. cunninghamii Benth., S. scalarium Martine & T.M.Williams, S. vansittartense C.Gardner, and S. zoeae R.L.Barrett not pictured here. Colors are associated with the distribution map shown in Fig. 3. (Photos by C.T. Martine except for E by K. Brennan.).

Taxonomic treatment

Solanum scalarium Martine & T.M.Williams, sp. nov.

urn:lsid:ipni.org:names:77310466-1 Figs 4–7

Diagnosis. This species is distinguished from *Solanum dioicum* W.Fitzg. (as currently delineated) and other Australian functionally dioecious *Solanum* species of the "Kimberley dioecious clade" by the combination of a spreading decumbent habit and the staminate inflorescence axis armed with relatively stout, spreading, straight prickles.

Type. AUSTRALIA. Northern Territory: Victoria River Valley, Judbarra National Park, off Victoria Highway (Highway 1), NW of Victoria River Roadhouse, Escarpment Walk, just off track above Garrarnawun Lookout on flat area between there and peak of outcrop, 15.61054°S, 131.11571°E, elev. 167 m, 2 June 2018 (fr), *C. T. Martine, J. Cantley, A. McDonnell & P. Jobson 4748* (holotype: DNA).

Description. Perennial spreading decumbent pale green shrub up to 30 cm tall. Main stem single, 4–12 cm tall, woody (not corky) branching 2–4 times with thickest lateral stems ca. 2-4 cm in diameter; younger stems yellow-green to tan-green in color and older woody stems eventually becoming dark tan or gray. Internodes 12-40 cm long in male plants, 30-46 cm long in functionally female plants. Stems with short, dense indumentum of porrect-stellate trichomes 0.5-1.3 mm, these mostly short stalked (occasionally on longer stalks up to 1 mm) with central midpoint ca. 0.2 mm. Prickles abundant and dense (8-10 per cm of internode), 1-8 mm long, straight, fine, widened at base, somewhat sharp. Leaves simple; blades 5-9 cm long, 1-3 cm wide, alternate, lanceolate; unarmed or with 1-3 straight prickles along adaxial midvein, soft yellow green above, slightly lighter beneath, both sides densely stellate-hairy, trichomes mostly short stalked, porrect-stellate with short central ray; apex acuminate; margins entire, sometimes ciliate; base oblique and tapering; petiole 0.5-14 mm long; Male *inflorescence* a scorpioid cyme 9–24 mm long with up to ca. 50 flowers (typically 1–4 flowers open at a time with previous blooms abscised); rachis densely stellate-pubescent, armed with straight prickles 5-7 mm, ca. 1 mm in diameter at the base, each subtending a flower; pedicel 3-7 mm long, sparsely armed with small prickles. Male *flowers* 5-merous; calyx with the tube 6–7 mm long, campanulate, armed with weak prickles ca. 2 mm long, the lobes 3-4 mm long, tipped with a linear acumen; corolla 16-27.4 mm in diameter, rotate to rotate-campanulate, pale violet; stamens equal; filaments 1-2 mm long; anthers ca. 4 mm long, tightly connivent, oblong-lanceolate to somewhat tapered, poricidal at the tips; ovary vestigial, non-functional. Female inflorescence of a solitary, morphologically cosexual flower (functionally female and producing inaperturate pollen); pedicel 7–8 mm long, sparsely armed with small prickles ca. 2 mm. *Female flowers* 5-merous; on; calyx with the tube campanulate, densely stellate-pubescent and armed, the prickles 5–6 mm long, straight, the lobes 5–11 mm long, unequal, long-triangular with a linear acumen, prickly; corolla 36-46 mm in diameter, rotate to rotate-campanulate, violet to pale violet; stamens equal, like those of the male flowers; filaments 1–2 mm long; anthers ca. 4 mm long, slightly spreading,

poricidal at the tips; ovary ca. 5 mm in diameter at anthesis, glabrous; style ca. 5 mm long (including stigmatic surfaces), straight; stigma yellow, bifid, the lobes 1.5-2 mm long. *Fruit* a berry, 20–25 mm diameter, globose; immature fruit green, fleshy; mature fruit light green, drying to yellow-orange or tan, becoming leathery-reticulate and bony hard and loosely retained and partly-enclosed in calyx (75% enclosed when developing; mature, hardened fruit less than 25% enclosed), apparently detaching from calyx once hard and dry. Fruiting calyx lobes 2.1–2.8 cm long, long acuminate, tapered to a long fine tip, accrescent, slightly sticky and adherent to fruit when immature, readily separating from fruit as the berry matures, hardens, and shrinks from drying, densely armed with sharp prickles ca. 6 mm long. *Seeds* up to 420–586 per fruit in cultivation (two wild-collected fruits were N = 96 and N = 162), 1.1–1.5 mm in diameter, reniform dark brown to black, conspicuously and minutely reticulate.

Distribution and ecology. Solanum scalarium is presently known from a single population (Fig. 3) of perhaps 50–100 individuals found within Judbarra/Gregory National Park. The species here occurs on skeletal pink soil, exposed sandstone pavement and dissected rock high above the Victoria River Valley (Fig. 4). The associated vegetation at this site is a low open woodland dominated by *Corymbia terminalis* (F.Muell.) K.D.Hill & L.A.S.Johnson (Myrtaceae) and *Eucalyptus miniata* (F.Muell.) A.Cunn. ex Schauer (Myrtaceae), with a sparse low mid story of *Owenia vernicosa* (F.Muell.) (Meliaceae), *Calytrix exstipulata* DC. (Myrtaceae), *Xanthostemon paradoxus* (F.Muell.) W.J.Hooker (Myrtaceae), *Hibbertia* spp. (Dilleniaceae), *Corchorus* spp. (Malvaceae), *Senna oligoclada* (F.Muell.) Randell (Fabaceae), *Acacia* sp. nov. (Fabaceae); the sparse ground layer is dominated by *Cyperus cunninghamii* (C.B.Clarke) C.A. Gardner



Figure 3. Geographic distribution of *Solanum scalarium* (black star) and other Australian dioecious *Solanum* species (source: The Australasian Virtual Herbarium).


Figure 4. *Solanum scalarium* in the field **A**, **C**, **F** type locality and habitat, Escarpment Walk, Judbarra National Park, Northern Territory **B–D** immature green fruits enclosed in prickly calyx and **E** prickly male rachis after male flowers have dropped off. (Photos by A.J. McDonnell.).

(Cyperaceae) and *Triodia pungens* R.Br. (Poaceae). Although *S. scalarium* was not conspicuous on a visit by PJ and JTC in 2017, it appeared in 2018 to have sprouted vigorously from above-ground stems after fire occurring at some point in the previous 2–3 years. At the time of the type collection, plants were robust and vigorous in areas that had been burned and only represented by a few weak ramets in unburned areas dominated by *Triodia pungens* tussocks.

Pollination biology of the species is unknown, but, like other Australian congeners, the flowers are likely buzz pollinated by bees in the genera *Xylocopa* and *Amegilla* (Apidae; see Anderson and Symon 1988; Switzer et al. 2016) and likely to present high levels of pollen nutritional reward – although with slightly differential rewards available to pollen foragers from male versus functionally female flowers (Ndem-Galbert et al. 2021). A small set (N = 10) of ex situ hand pollinations conducted for this study showed that inaperturate pollen produced by functionally female flowers does not lead to fruit set when used to pollinate other females. This suggests that reproduction in *S. scalarium* is dependent on intersexual male-to-female outcrossing via biotic pollination like in other dioecious *Solanum* species.

Seed dispersal mechanism for this species is also unknown, although young fleshy fruits are mostly enclosed in a spiny calyx that gradually reflexes to some degree as fruits become dry and bony (Fig. 6D, E), suggesting that endozoochory is less likely than

either ectozoochory (as a trample burr) or passive dispersal (see Symon 1979b; Martine et al. 2019). Peoples of the Walmajarri language area of the Kimberley region (west of this distribution) report that the fruits of *S. dioicum (kara)* are eaten by *Osphranter rufus* (Desmarest, 1822) (plains or red kangaroos; Doonday et al. 2013), and CTM has seen bustard birds (*Ardeotis australis* (Gray, 1829)) picking apart *S. dioicum* fruits near the northwest Kimberley coast (Martine et al. 2019). However, there is no published evidence that any extant animal acts as an effective seed dispersal agent of taxa within the "Kimberley dioecious clade" (see Martine et al. 2016b). Notably, seeds removed



Figure 5. Functionally male individuals of *Solanum scalarium* in cultivation: **A** leaf shape and **B**, **C** inflorescence axes of male individuals; note the distinctive spreading straight prickles that give the inflorescence axis a ladder-like appearance. (Photos by T.M. Williams.).



Figure 6. Functionally female individuals of *Solanum scalarium* in cultivation: **A** flower **B** reproductive branch **C** leaf shape **D**, **E** reflexing of calyx around brown, bony fruits and **F** overall habit. (Photos by T.M. Williams.).



Figure 7. A Holotype of *Solanum scalarium* (C.T. Martine 4748; female fruiting specimen) **B** paratype of *S. scalarium* (C.T. Martine 4796B; male specimen). (Photos by M. Sain.).

from green fruits (enclosed in calyces) of the type collection as well as seeds removed from older brown fruits (calyces reflexed) in cultivation were both germinable, suggesting that effective seed dispersal might happen at either stage.

Phenology. Plants encountered on 2 June 2018 were largely sterile, with several withered flowers and two mature fruits. The low fruit set in the population at the time of collection suggests that *S. scalarium* typically flowers earlier in the calendar year.

Etymology. Latin *scalare* from *scala*, ladder or stair, and suffix *aris*, pertaining to; the epithet *scalarium* is the genitive plural of *scalare*, indicating ladder-like appearance of staminate inflorescence rachises, which are conspicuously and unusually armed with relatively stout, spreading, straight prickles resembling ladder steps. It is also a nod to the type locality at the Escarpment Walk, Judbarra/Gregory National Park, where stone stairs lead from the car park up to the habitat of this species. By choosing this name we acknowledge the access these steps provide to the newly-described species as well as the importance of providing broad access to nature, outdoor recreation, and scientific discovery. We suggest the use of Garrarnawun Bush Tomato for the English-language common name of the species in recognition of the Garrarnawun Lookout near where the type collection was made, a traditional meeting place of the Wardaman and Nungali-Ngaliwurru peoples whose lands overlap in this area (Parks and Wildlife Commission of the Northern Territory 2021).

Preliminary conservation status. While we expect that more localities for *S. scalarium* are likely to be found given the prevalence of similar (and less accessible) outcrops in the immediate region of the type collection, at present it is known from one protected (though frequently-visited) collection site in Judbarra/Gregory National Park (Fig. 4). Based on IUCN Red List Categories (IUCN 2012), *S. scalarium* should be considered Data Deficient (DD).

Specimens examined. UNITED STATES. Pennsylvania: Cultivated in Bucknell University: (Lewisburg) Burpee Research Greenhouse (staminate flowers/inflorescences, functionally female flowers, and fruits), 9 Oct 2020*CT Martine & TM Williams 4796.* (To be distributed to AD, BM, BUPL [Fig. 7b], DNA, NY, PERTH, US).

Diagnostic couplets. A comprehensive "Kimberley dioecious clade" key, including newly-recognized species, is forthcoming (Barrett and Barrett in prep). The most complete key to date can be found in Barrett (2013), which lumps the numerous variations of *S. dioicum* sensu lato as a single taxon. The following couplets may be inserted where *S. dioicum* occurs at couplet 60 in the key in Barrett (2013) and supplants the single replacement couplet 60a [previously published in Martine et al. (2016c)].

[Barrett 2013; couplet 60]

60a	Plants less than 1 m tall, many-branched; stems moderately to densely prick-
	ly; leaf indumentum silvery/rusty/yellow, overall aspect silvery-green, yellow-
	green, or reddish-green; stigma deeply bifid, the lobes 2-5 mm long; calyx
	not fully enclosing mature fruit60b
60a	Plants more than 1 m tall, few-branched and conspicuously "Y"-shaped in
	form; stems very prickly; leaf indumentum silvery, overall aspect silvery-blue;
	stigma shallowly bifid, the lobes 0.5-1 mm long; calyx fully enclosing the
	mature fruit Solanum ossicruentum Martine & J.Cantley
60Ь	Plants many-branched; stems moderately prickly; leaf indumentum silvery or
	rusty, overall aspect silvery-green, yellowish green, or reddish green; stigma
	lobes 2–5 mm long; mature fruits green and fleshy; male floral rachis typically
	unarmed
60Ь	Plants many-branched and spreading decumbent in form; stem densely
	prickly; leaf indumentum yellow, overall aspect yellow-green; stigma lobes
	1.5–2 mm; mature fruits light green to yellow-orange and fleshy, becoming
	tan and bony hard; male floral rachis armed
	Solanum scalarium Martine & T.M.Williams

Discussion

Solanum scalarium is the latest in a series of newly-described functionally dioecious species from the "Kimberley dioecious clade" (see Martine et al. 2011, 2013, 2016c; Barrett 2013) a group that is still rife with undescribed species lumped under the umbrella of *S. dioicum* (Barrett 2013). Although some of the variation within the clade

is subtle and/or continuous, *S. scalarium* can be distinguished from all known members by the combination of spreading decumbent habit and male inflorescence rachis armed with relatively stout, spreading, straight prickles. Complex habitat and environmental characteristics, coupled with climate fluctuations over the last two million years, have been drivers of the high species diversity and speciation events throughout Australia (Bowman et al. 2010; Edwards et al. 2017; Edwards et al. 2018). There are particularly high levels of plant diversity and newly described species within the AMT (Bowman et al. 2010; Barrett 2013; Edwards et al. 2017; Edwards et al. 2018; Martine et al. 2019).

Forthcoming phylogenomic work (e.g., McDonnell and Martine in prep) should aid in resolving what has been a decades-long effort to gradually assign species names to recognizable local forms in this complex group. In the meantime, the best course of action continues to be collecting all forms of "*Solanum dioicum*" when they are encountered such that the variation within the group continues to be captured in herbarium collections (see Heberling et al. 2019; Thiers 2020).

The scientific name and English-language common name proposed here acknowledge the critical importance of maintaining equitable and safe access to outdoor spaces, the Garrarnawun Lookout being a poignant example of shared use of special places.

Acknowledgements

Thanks to Ian Cowie, Donna Lewis, and Deborah Bisa for assistance in the Northern Territory Herbarium; and to Rachel Martine, Terri Barner, and Val Cook for logistical support during fieldwork. Ariel Antoine helped with the initial morphological measurements and greenhouse maintenance. Thanks to Wanda Boop, Lori Smith, Claire Marino, Dia Zizis, Jenny Davis, Cheyenne Moore, and Maddie Wickers who also provided greenhouse support at Bucknell. Helpful comments were provided by three reviewers during manuscript preparation. Funding was provided through Bucknell via the David Burpee Endowment and the Wayne E. Manning Internship Fund (to JH). JTC received support from the College of Science and Engineering at San Francisco State University. The Department of Environment, Parks, and Water Security supplied equipment and vehicular support via PJ.

References

- Anderson GJ, Symon DE (1988) Insect foragers on *Solanum* flowers in Australia. Annals of the Missouri Botanical Garden 75(3): 842–852. https://doi.org/10.2307/2399372
- Australian Government Department of the Environment and Energy (2015) Judbarra/Gregory National Park, Northern Territory 2015: A Bush Blitz Survey Report. https://bushblitz. org.au/wp-content/uploads/2017/05/Judbarra-Report.pdf [accessed 2.02.2022]
- Barrett RL (2013) *Solanum zoeae* (Solanaceae), a new species of bush tomato from the North Kimberley, Western Australia. Nuytsia 23: 5–21.

- Bean AR (2004) The taxonomy and ecology of *Solanum* subg. *Leptostemonum* (Dunal) Bitter (Solanaceae) in Queensland and far north-eastern New South Wales, Australia. Austrobaileya 6: 639–816.
- Bean AR, Albrecht DE (2008) *Solanum succosum* A.R.Bean & Albr. (Solanaceae), a new species allied to *S. chippendalei* Symon. Austrobaileya 7: 669–675.
- Bean AR (2016) Two new species of *Solanum* (Solanaceae) from the Northern Territory, Australia. Austrobaileya 9: 524–533.
- Bowman DMJS, Brown GK, Braby MF, Brown JR, Cook LG, Crisp MD, Ford F, Haberle S, Hughes J, Isagi Y, Joseph L, McBride J, Nelson G, Ladiges PY (2010) Biogeography of the Australian monsoon tropics. Journal of Biogeography 37(2): 201–216. https://doi. org/10.1111/j.1365-2699.2009.02210.x
- Brennan K, Martine CT, Symon DE (2006) Solanum sejunctum (Solanaceae), a new functionally dioecious species from Kakadu National Park, Northern Territory, Australia. The Beagle. Records of the Museums and Art Galleries of the Northern Territory 22: 1–7.
- Cowie IC, Cuff NJ, Lewis DL, Jobson PC [Eds] (2017) Checklist of the vascular plants of the Northern Territory. Northern Territory Herbarium, Department of Environment and Natural Resources, Palmerston, Northern Territory.
- Craven LA (1998) A result of the 1996 Mueller Commemorative Expedition to northwestern Australia: *Melaleuca triumphialis* sp. nov. (Myrtaceae). Muelleria 11: 1–4. https://doi. org/10.5962/p.198402
- Doonday B, Samuels C, Clancy EM, Milner J, Chungulla R, Whisputt M, Yoomarie S, Lulu V, Johns A, Brown S, Vernes T, Richards E, Wightman G (2013) Walmajarri Plants and Animals: Aboriginal Knowledge from the Paruku Indigenous Protected Area, Southern Kimberley. Northern Territory Botanical Bulletin No 42 Department of Land Resource Management, NTG, Broome.
- Edwards RD, Crisp MD, Cook DH, Cook LG (2017) Congruent biogeographical disjunctions at a continent-wide scale: Quantifying and clarifying the role of biogeographic barriers in the Australian tropics. PLoS ONE 12(4): e0174812. https://doi.org/10.1371/journal.pone.0174812
- Edwards RD, Crisp MD, Cook LG (2018) Species limits and cryptic biogeographic structure in a widespread complex of Australian monsoon tropics trees (broad-leaf paperbarks: *Melaleuca*, Myrtaceae). Australian Systematic Botany 31: 495–503. https://doi. org/10.1071/SB18032
- Gagnon E, Hilgenhof R, Orejuela A, McDonnell AJ, Sablok G, Aubriot X, Giacomin L, Gouvêa Y, Bohs L, Dodsworth S, Martine CT, Poczai P, Knapp S, Särkinen T (2022) Phylogenomic data reveal hard polytomies across the backbone of the large genus *Solanum* (Solanaceae). American Journal of Botany 109: 1–22. https://doi.org/10.1002/ajb2.1827
- Hayes D, Jordon-Thaden IE, Cantley JT, McDonnell AJ, Martine CT (2019) Integrated pest management in the academic small greenhouse setting: A case study using *Solanum* spp. (Solanaceae). Applications in Plant Sciences 7(8): e11281. https://doi.org/10.1002/aps3.11281
- Heberling JM, Prather LA, Tonsor SJ (2019) The changing uses of herbarium data in an era of global change: An overview using automated content analysis. Bioscience 69(10): 812– 822. https://doi.org/10.1093/biosci/biz094

- Hilgenhof R, Gagnon E, Knapp S, Aubriot X, Tepe EJ, Bohs L, Giacomin LL, Gouvêa Y, Stehmann JR, Martine CT, Orejuela A, Orozco CI, Peralta IE, Särkinen T (In review) Morphological trait evolution in *Solanum* (Solanaceae): evolutionary lability of key taxonomic characters.
- IUCN (2012) IUCN Red List Categories and Criteria: Version 3.1. 2nd Edn.
- Jobson PC (2014) Two rare new species of *Isotropis* (Fabaceae: Faboideae: Mirbelieae) from tropical northern Australia. Telopea 17: 347–354. https://doi.org/10.7751/telopea20148179
- Knapp S (2013) A revision of the Dulcamaroid Clade of *Solanum* L. (Solanaceae). PhytoKeys 22(0): 1–432. https://doi.org/10.3897/phytokeys.22.4041
- Lacey LM, Cantley JT, Martine CT (2017) Solanum jobsonii, a novel andromonoecious bush tomato species from a new Australian national park. PhytoKeys 82: 1–13. https://doi. org/10.3897/phytokeys.82.12106
- Martine CT, Vanderpool D, Anderson GJ, Les DH (2006) Phylogenetic relationships of andromonoecious and dioecious Australian species of *Solanum* subgenus *Leptostemonum* section *Melongena*: Inferences from ITS sequence data. Systematic Botany 31(2): 410–420. https://doi.org/10.1600/036364406777585801
- Martine CT, Anderson GJ, Les DH (2009) Gender-bending aubergines: Molecular phylogenetics of cryptically dioecious *Solanum* in Australia. Australian Systematic Botany 22(2): 107–120. https://doi.org/10.1071/SB07039
- Martine CT, Lavoie EM, Tippery NP, Vogt FD, Les DH (2011) DNA analysis identifies Solanum from Litchfield National Park as a lineage of S. dioicum. Northern Territory Naturalist 23: 29–38. https://doi.org/10.5962/p.295491
- Martine CT, Symon DE, Capaldi Evans E (2013) A new cryptically dioecious species of bush tomato (*Solanum*) from the Northern Territory, Australia. PhytoKeys 30: 23–31. https:// doi.org/10.3897/phytokeys.30.6003
- Martine CT, Frawley ES, Cantley JT, Jordon-Thaden IE (2016a) *Solanum watneyi*, a new bush tomato species from the Northern Territory, Australia named for Mark Watney of the book and film "The Martian". PhytoKeys 61: 1–13. https://doi.org/10.3897/phytok-eys.61.6995
- Martine CT, Boni AJ, Capaldi EA, Lionheart G, Jordon-Thaden IE (2016b) Evidence of rockdwelling macropod seed dispersal in a tropical monsoon community. Northern Territory Naturalist 27: 68–77. https://doi.org/10.5962/p.295470
- Martine CT, Cantley JT, Frawley E, Butler A, Jordon-Thaden IE (2016c) New functionally dioecious bush tomato, *Solanum ossicruentum*, may utilize "trample burr" seed dispersal. PhytoKeys 63: 19–29. https://doi.org/10.3897/phytokeys.63.7743
- Martine CT, Jordon-Thaden IE, McDonnell AJ, Cantley JT, Hayes DS, Roche MD, Frawley ES, Gilman IS, Tank DC (2019) Phylogeny of the Australian *Solanum dioicum* group using seven nuclear genes, with consideration of Symon's fruit and seed dispersal hypotheses. PLoS ONE 14(4): e0207564. https://doi.org/10.1371/journal.pone.0207564
- McDonnell AJ, Martine CT (2020) Phylogenomics and breeding system evolution of Australian Solanum ("S. dioicum group", Solanaceae). Botany 2020: Virtual Annual Meeting of the Botanical Society of America. [online abstract:] http://2020.botanyconference.org/engine/search/index.php?func=detail&aid=238

- McDonnell AJ, Wetreich HB, Cantley JT, Jobson P, Martine CT (2019) *Solanum plastisexum*, an enigmatic new bush tomato from the Australian Monsoon Tropics exhibiting breeding system fluidity. PhytoKeys 124: 39–55. https://doi.org/10.3897/phytokeys.124.33526
- Ndem-Galbert JR, Hall J, McDonnell AJ, Martine CT (2021) Differential reward in "male" versus "female" pollen of functionally dioecious *Solanum* (Solanaceae). American Journal of Botany 108(11): 2282–2293. https://doi.org/10.1002/ajb2.1765
- Parks and Wildlife Commission of the Northern Territory (2021) Judbarra/Gregory National Park Fact Sheet. Katherine NT 0850. https://nt.gov.au/__data/assets/pdf_file/0009/278442/ judbarra-gregory-national-park-fact-sheet-and-map.pdf [accessed 2.02.2022]
- Purdie RW, Symon DE, Haegi L (1982) Flora of Australia. Solanaceae. Vol. 29. Australian Government Publishing Service, 1–227.
- Särkinen T, Olmstead RG, Bohs L, Knapp S (2013) A phylogenetic framework for evolutionary study of the nightshades (Solanaceae): A dated 1000-tip tree. BMC Evolutionary Biology 13(1): 214. https://doi.org/10.1186/1471-2148-13-214
- Switzer CM, Hogendoorn K, Ravi S, Combes SA (2016) Shakers and head bangers: Differences in sonication behavior between Australian *Amegilla murrayensis* (blue-banded bees) and North American *Bombus impatiens* (bumblebees). Arthropod-Plant Interactions 10(1): 1–8. https://doi.org/10.1007/s11829-015-9407-7
- Symon DE (1979b) Fruit diversity and dispersal in *Solanum* in Australia. Journal of the Adelaide Botanic Gardens 1: 321–331.
- Symon DE (1981) A revision of the genus *Solanum* in Australia. Journal of the Adelaide Botanic Gardens 4: 1–367.
- Thiers BM (2020) Herbarium: The Quest to Preserve and Classify the World's Plants. Journal of the Botanical Research Institute of Texas 15: 524.
- Vorontsova MS, Stern S, Bohs L, Knapp S (2013) African spiny Solanum (subgenus Leptostemonum, Solanaceae): A thorny phylogenetic tangle. Botanical Journal of the Linnean Society 173(2): 176–193. https://doi.org/10.1111/boj.12053
- Walsh NG, Albrecht DE (1998) A new species of *Eucalyptus* (series *Subexsertae*) from the Northern Territory. Muelleria 11: 41–44. https://doi.org/10.5962/p.198406
- Whalen MD (1984) Conspectus of species groups in *Solanum* subgenus *Leptostemonum*. Gentes Herbarum 12: 179–282.