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Phylogeny and species delimitation in *Silene* sect. *Arenosae* (Caryophyllaceae): a new section

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Abstract

A putatively monophyletic group of annual *Silene* species is revised taxonomically and described as the new section *S.* sect. *Arenosae*. The species of this section were previously treated as a part of a widely circumscribed and polyphyletic *S.* sect. *Rigidulae*. *Silene* sect. *Arenosae* as circumscribed here consists of nine species. Members of the section show a predominantly E Mediterranean to SW Asian distribution pattern from Turkey southward to Egypt and eastward to Iran and Pakistan, although most of the species have a limited distribution range. The species of *S.* sect. *Arenosae* are characterized by narrowly lanceolate calyx teeth, which are often highly polymorphic, and lanceolate to oblanceolate (non-spathulate) basal leaves. The provided taxonomic revision is based on morphological characters and supported by phylogenetic analyses of two nuclear loci (nrITS and an intron of the *RPB2* gene) and one chloroplast locus (the intron of the *rps16* gene). The species descriptions are formalized using a novel implementation of the Prometheus Description Model.

Keywords

Caryophyllaceae, integrative taxonomy, phylogenetics, Plant taxonomy, *Silene*, systematics, taxonomic description models

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[*] The authors contributed equally to this work.

Introduction

Silene L. is a large genus of the family Caryophyllaceae, with around 870 currently (Jafari et al. 2020) recognized species that are mainly distributed in the northern hemisphere, South Africa and South America, in temperate to arctic regions and a wide range of habitats (Manning and Goldblatt 2012, Frajman et al. 2018, Jafari et al. 2020). Chowdhuri (1957) delimited 44 sections and his taxonomy has been applied by authors of local floras in the Mediterranean region and SW Asia, including Palestine (Zohary 1966), Turkey (Coode and Cullen 1967), the Iranian Highlands (Melzheimer 1988), the Flora Europaea (Chater et al. 1993), and Iraq (Townsend et al. 2016). There have been several regionally focused studies (e.g., Greuter 1995, Oxelman and Greuter 1997) that amended the taxonomy of Chowdhuri (1957), and a number of molecular studies (e.g., Oxelman and Lidén 1995, Desfeux and Lejeune 1996, Oxelman et al. 1997, Popp and Oxelman 2004, Eggens 2006, Eggens et al. 2007, Popp and Oxelman 2007, Petri and Oxelman 2011, Rautenberg et al. 2012, Aydin et al. 2014a, Naciri et al. 2017) that revealed the artificial nature of many sections as defined by Chowdhuri (1957). Jafari et al. (2020) outlined a new, revised system taking the phylogenetic information into account.

Silene sect. *Rigidulae* (Boiss.) Schischk. as traditionally circumscribed is superficially coherent morphologically (Eggens 2006). Boissier (1867) first introduced *Rigidulae* as an unranked group (indicated as '§') with 13 species. In a monograph, Rohrbach (1868) accepted this group as a series and classified 20 species in *S.* ser. *Rigidulae* (Boiss.) Rohrb. Schischkin (1936) was the first to apply the rank of section for these species. Chowdhuri (1957) subsequently assigned 14 species from the Mediterranean area and SW Asia, Russia and India, to *S.* sect. *Rigidulae*, following a similar circumscription to that of Boissier (1867). Greuter (1995) included four Greek species in *S.* sect. *Rigidulae* and made a correction on the section's typification. Molecular phylogenetic data from three putatively unlinked genes revealed that the widely circumscribed *S.* sect. *Rigidulae* sensu Chowdhuri (1957) is not monophyletic, but rather consists of at least six independent lineages, each with a fairly good correlation with geography (Eggens 2006). One of the clades recognized in Eggens (2006) comprises taxa found in SW Asia including Turkey, Armenia, Egypt and the Arabian Peninsula, and extending eastwards to Pakistan. This clade, referred to as the "Middle East Clade" in Eggens (2006), is a strongly supported monophyletic group with associated morphological characters (often densely ciliate and lanceolate calyx teeth, and often oblanceolate rather than spathulate basal leaves) that distinguish them from other taxa earlier assigned to *S.* sect. *Rigidulae* sensu Chowdhuri (1957). In the present study we refer to this clade as the "SW Asian Clade".

In this paper, we present morphological, phylogenetic and geographical data on the "SW Asian Clade" that accumulated since Eggens (2006). We integrate all the available evidence and formally describe the "SW Asian Clade" as *Silene* sect. *Arenosae* Eggens, F. Jafari & Oxelman, sect. nov., which we consider as one out of several lineages of a polyphyletic *S.* sect. *Rigidulae* sensu lato. We provide an identification key and taxonomic revision of all species of the new section, and also place it in a wider phylogenetic context.

Materials and methods

Taxon sampling and molecular data

The specimens from the following herbaria: B, BM, BSB, C, E, G, GB, K, LD, LE, S, TUB, UPS, W, WAG and WU (abbreviations according to Thiers 2019+) were used for morphological studies and DNA extraction.

We generated a species tree phylogeny based on three putatively unlinked loci and used the species tree as a framework for our taxonomic revision. The advantage of using monophyletic groups as a starting point for taxonomic revisions in complex genera such as *Silene* is that parallelism and character reversals can be better understood in the search for diagnostic morphological characters. The species tree is based on sequences from three regions: the nuclear ribosomal internal transcribed spacers (nrITS, with the intervening 5.8S gene), the second last intron of the nuclear *RPB2* gene (Popp and Oxelman 2004), and the intron of the chloroplast gene *rps16* (Oxelman et al. 1997).

The phylogenetic study is based on 84 sequences from 55 species representing two subgenera of *Silene*, *Behenantha* (Otth) Torr. & A.Gray and *Silene* with 39 sequences of *RPB2* region being generated for the purpose of this paper. Material used for the phylogenetic analyses are presented in Suppl. material 1. The procedures for extraction of total genomic DNA, amplification of the DNA regions by the polymerase chain reaction, sequencing reactions and their visualization were described in Eggens et al. (2007). All sequences were edited using Sequencher 3.1.1 (Gene Codes Corporation) and aligned manually with Aliview (Larsson 2014) following criteria presented in Eggens et al. (2007).

Phylogenetic analyses

Maximum Parsimony (MP) analyses of individual multiple alignments were performed with PAUP* v.4.0a162 (Swofford 2018). Heuristic searches employed 100 random addition sequences, TBR (tree-bisection-reconnection) branch-swapping algorithm. Maximum parsimony bootstrap (MPB) percentages were calculated with the parameters: hsearch addseq = random, nchuck = 2, chuckscore = 600, nreps = 1, bootstrap nreps = 1000 (summarized in a 50% majority-rule consensus tree). PAUP* 4.0a162 (Swofford 2018) was used to select the best-fitted model of nucleotide substitution based on the Akaike information criteria corrected (AICc), and the General Time Reversible model with Gamma shaped rate variation (GTR+G) model was selected for all three regions. Maximum likelihood (ML) analyses were conducted in RAxML HPC v.8.2.10 (Stamatakis 2014) using GTRGAMMA model with 1000 pseudo-replicates to evaluate bootstrap support for each node. Bayesian gene tree inference was performed using MrBayes v.3.2.6 (Ronquist et al. 2012) with 20 million generations for each of the three datasets. Four Metropolis-coupled chains were run with trees and parameter values saved every 1000th generations in two parallel runs. The first 25% of total trees were discarded as burn-in.

Species tree analyses were performed with STACEY (Species Tree And Classification Estimation, Yarely) v.1.2.5 (Jones 2016) as implemented in BEAST v.2.5.1 (Bouckaert et al. 2014, 2019). All specimens where we had access to sequences from at least two of the regions were included in the species tree analysis. An input file was created with BEAUTi v.2.5.1 in which substitution models, clock models and gene trees for all loci were unlinked. The General Time Reversible (GTR) substitution model with rate variation following a gamma distribution with four rate categories, a relaxed lognormal clock and fixed average clock rate for one arbitrary locus set to 1 were chosen. The ploidy level was set to 1 for ITS and *rps16* partitions, and 2 for the nuclear *RPB2* locus. The prior growth rate was set to a lognormal distribution with mean 4.6 and standard deviation 2. The popPriorScale was set to a lognormal with mean –7 and standard deviation 2. The prior for ucldMean was set to a log normal distribution with mean 0 and standard deviation 1, otherwise the default priors were applied. The CollapseHeight, which is an approximation of zero node height in the species tree (see Jones et al. 2015) was set to 1E-4. The input file was run for 250 million iterations by logging every 25000th iterations, with two replicates. Convergence and effective sample size (ESS) values were considered sufficient when each parameter was higher than 200 as verified in Tracer v.1.7 (Rambaut et al. 2018). LogCombiner v.2.5.1 was used to discard the 1000 first trees of each of the two separate runs and then combine the rest of the trees as an estimate of the posterior. Finally, trees were summarized in TreeAnnoatator v.2.5.1. All phylogenetic analyses were carried out on the CIPRES science gateway (Miller et al. 2010).

A similarity matrix representing posterior frequencies of clusters of individuals was produced from the second replicate set of species trees generated with STACEY, using the program SpeciesDelimationAnalyser v.1.2.5 (speciesDA.jar, http://www.indriid.com/software.html) with 10% burn-in and CollapseHeight of 1E-4. The CollapseHeight is an approximation of zero node height (Jones et al. 2015) and individuals clustering together below this height can therefore be considered as belonging to the same ideal population according to the multispecies coalescent model. The estimated similarity matrix was then visualized using the R script plot.simmatrix.R (https://github.com/scrameri/smtools/tree/master/SpeciesDelimitation), which plots a heatmap of the similarity matrix after automatic sorting of rows and columns according to the summary species tree topology.

Plant descriptions

The species descriptions in this paper are extracted from a database and application (X303) developed based on "Prometheus Description Model" (Pullan et al. 2005) which is a system for handling descriptive data in a digital form. The idea behind this model is to present and store taxonomic information in a way that makes it comparable and exchangeable between different projects. This makes it different from other digitalized description systems, such as DELTA (Dallwitz 1980).

A description in the Prometheus model is built up by descriptive elements (DE) that have three parts – a structure, a property and one or more scores (states for a qualitative property, values for a quantitative property). Additionally, a DE can have modifiers such as frequency (e.g., 'usually', 'sometimes'), relative (e.g., 'less-than', 'equal-to'), spatial (e.g., 'above', 'below'), or temporal (e.g., 'after', 'during') modifiers. An important component in the Prometheus Model, to make different descriptions exchangeable, is the use of an ontology, i.e. a defined terminology, specifying the different structure and property designations that are allowed in a description. This is applied in two steps: the base ontology, and a description template (pro-forma ontology), which is a derived version of the ontology used for a specific context. For the purpose of this study we started with the published Prometheus basal angiosperm ontology (http://www.dcs.napier.ac.uk/~prometheus/prometheus_2/Resources/Ontology.xml). We found, however, that we needed to both extend the vocabulary, and to make a conceptual extension to the models to enable us to describe the *Silene* taxa adequately. After extracting the preliminary descriptions, we modified them manually for each species, and also provided a general description for *S.* sect. *Arenosae* (see "Discussion" under description of the section) that includes all constant features among the species assigned to this section. Using this method, we avoided redundancy.

Some terms missing from the ontology were such structures that are more taxon specific, e.g. 'anthophore', used in the sense proposed by Greuter (1995), i.e. a structure that separates the attachment of calyx and corolla. Other (sub-) structures could be described using the available ontology, but only very awkwardly, and we considered it justified to include them as well (e.g., the flower structures 'limb' and 'claw', the former being the upper part of the petals and the latter the lower part; see also Lawrence 1951, for definition). Some states (e.g., 'unicellular' and 'multicellular') were also added, although some could have been introduced as structures (e.g., 'cell') and used with existing properties.

A more conceptually interesting issue, where we have extended the Prometheus model, is the need to single out a specific structure (e.g., the 'uppermost') from a collection of such structures (e.g., 'internodes'). Pullan et al. (2005) briefly discussed this issue (by using a state of a property to identify a specific structure in a DE), but in our data we found the problem to be more general. Our solution is essentially to use properties and modifiers available in the ontology, but placing them in a specific context, the Specifier Element. The specifier element is a part of the description template associated with a specific instance of the ontology (structure) in question. An example for this case can be represented by the first flower. In a dichasium, there is always a first flower developing before the other flowers. Later flowers and inflorescence branches appear adjacent to the bracts of the first flower. The pedicel of the first flower (in some literature called the alar flower) is longer than the pedicels of later flowers, and as the pedicels continue to grow as long as the plant is alive, "length of pedicel of the first flower (or fruit)" is given as opposed to "length of pedicel" which could apply to any pedicel length.

Links to the descriptions, as well as details on specimens, can be found at the *Sileneae* website available at http://www.sileneae.info (Oxelman et al. 2013). The database itself is stored at http://www.sileneae.info/x303/ and can be viewed by logging in with "guest" as both username and password.

Information on localities was obtained from herbarium labels. When coordinates were not noted on the labels, coordinates were assigned to the locations using the GPS Coordinates network (https://www.gps-coordinates.net), GeoNames (https://www.geonames.org), or FallingRain (http://www.fallingrain.com) servers from information on localities (region, nearby town, etc.) on the labels. Coordinates have been assigned to a representative subset of the material studied, in attempt to provide the geographical distribution maps of the taxa studied.

Results

The results of our morphological studies are performed in the form of descriptions of the section, species and subspecies under "Discussion". The phylogenetic results, including alignment characteristics and tree topologies, are presented here.

Some features of the sequence alignments and matrices as well as statistics of the resulting phylogenetic trees are summarized in Table 1.

Silene sect. *Arenosae* was recovered as monophyletic in the species tree (PP = 1.00, Fig. 1). A clade including some members of *S.* sect. *Rigidulae* sensu Chowdhuri (1957), circumscribed as *S.* sect. *Muscipula* (Tzvelev) Oxelman, F.Jafari & Gholipour (Jafari et al. 2020), is sister to *S.* sect. *Arenosae* in the species tree (PP = 0.88, Fig. 1). *Silene arenosa* K.Koch and *S. leyseroides* Boiss. are poorly resolved at the base of the section in the species tree (Fig. 1). *Silene linearis* Decne. and *S. austroiranica* Rech.f., Aellen & Esfand. form successive sisters with respect to the rest of *S.* sect. *Arenosae* (PP = 0.86 and PP = 0.86, Fig. 1).

The similarity matrix (Fig. 2) depicts pairwise posterior probabilities that different accessions cluster at approximately zero node heights. In other words, the different accessions of *S. arenosa*, *S. austroiranica*, *S. chaetodonta* Boiss., *S. leyseroides*, and *S. linearis* form distinct clusters with high support. The different accessions of *S. microsperma* Fenzl are supported moderately. The monophyly of each of the aforementioned species is also supported by the gene trees (Figs 3–5). The two accessions of *S. georgievskyi* Lazkov do not form a clade (Fig. 2): one specimen with ID 41 groups with high posterior support with the two accessions of *S. chaetodonta* in contrast to another specimen with ID 42 which with low posterior support groups with *S. microsperma*.

Silene sect. *Arenosae* is supported as monophyletic in the gene trees of the separate regions (PP = 1.00, *rps16*, Fig. 4; PP = 1.00, MLB = 86%, *RPB2*, Fig. 5) except in the ITS tree (Fig. 3) where the section is unresolved in relation to sect. *Portenses* F.Jafari & Oxelman.

Table 1. Characteristics of the matrices and the resulting trees. (MPT = Most Parsimonious Trees, CI = Consistency Index excluding uninformative characters; RI = Retention Index).

	Terminals	Positions	No of MPT trees found	Tree length	CI	RI
ITS	76	737	115	561	0.4902	0.7925
rps16	71	1053	375	408	0.7598	0.8818
RPB2	76	1385	320	608	0.6617	0.8533

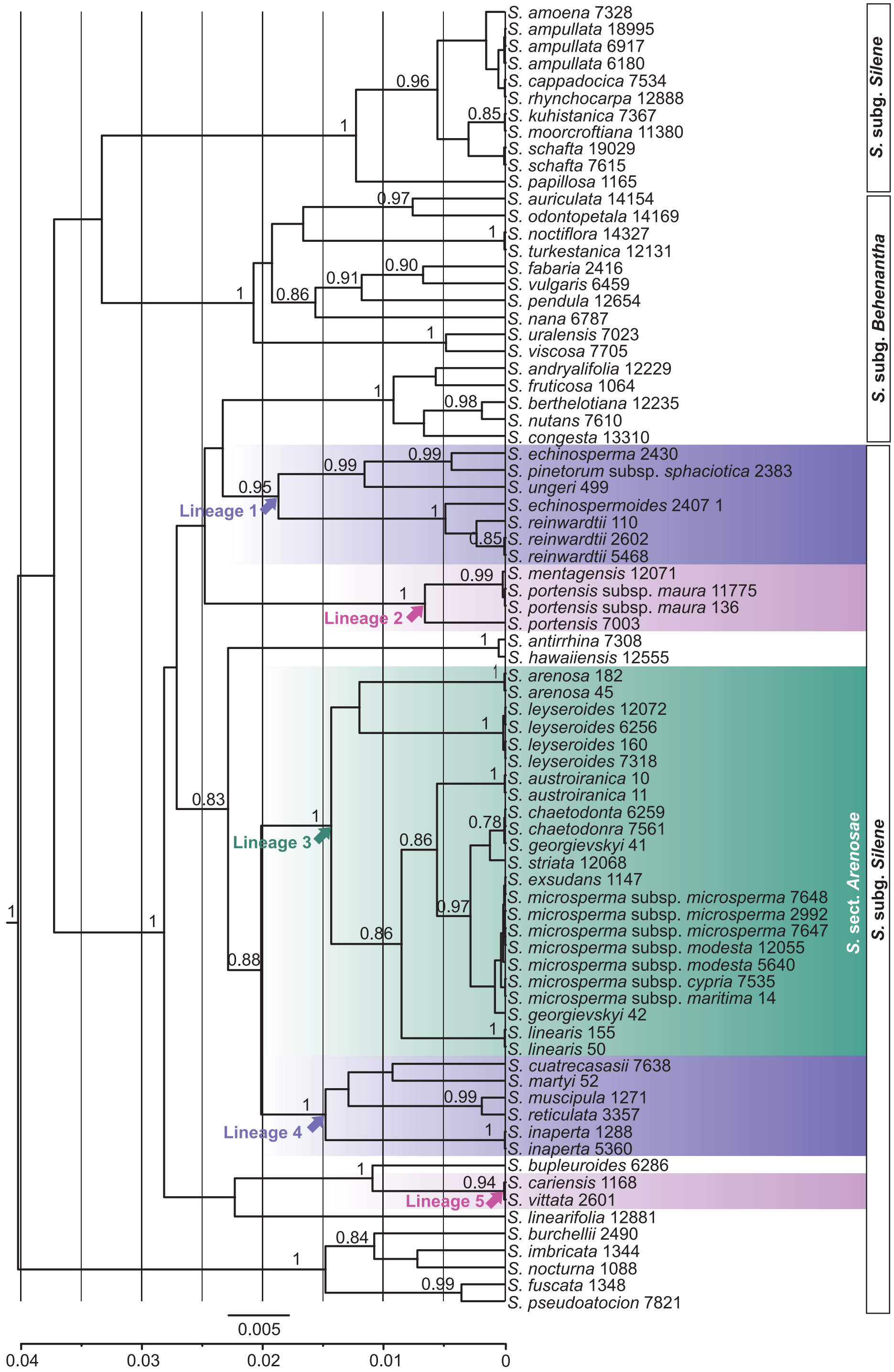

Figure 1. Species tree from two STACEY runs and three unlinked regions (ITS, *RPB2*, *rps16*). Posterior probabilities >0.75 are shown above branches. The number following the taxonomic name is the specimen ID (Suppl. material 1). Scale bar reflects the number of substitutions per site.

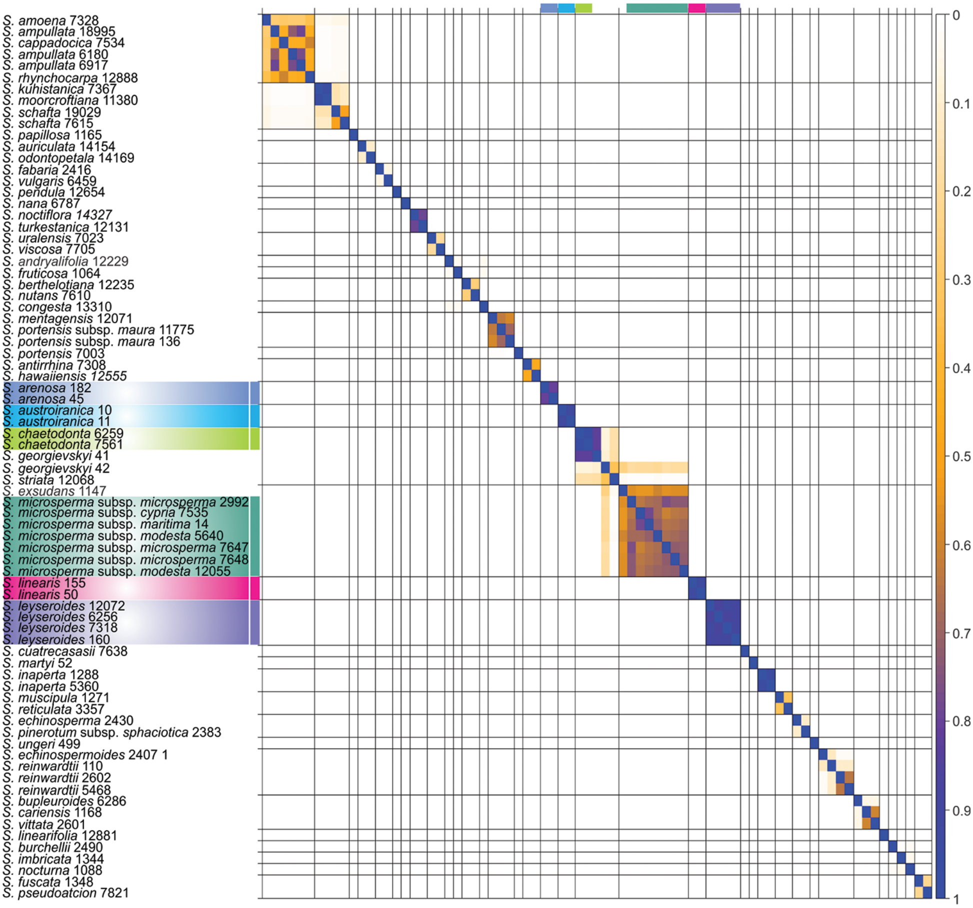

Figure 2. Similarity matrix calculated using SpeciesDelimationAnalyser v.1.2.5 (speciesDA.jar, http://www.indriid.com/software.html).

Discussion

Consistent with previous studies (Oxelman and Lidén 1995, Oxelman 1996, Eggens et al. 2007, Jafari et al. 2020), our results reveal that *S.* sect. *Rigidulae* s.l. as circumscribed by previous taxonomists from Boissier (1867) to Chater et al. (1993) is not a natural group. This broad circumscription is currently divided into five lineages (Jafari et al. 2020). Here, we concentrate on *S.* sect. *Arenosae*, which we formally describe as a new section. A taxonomic treatment and discussion of other components of *S.* sect. *Rigidulae* s.l. can be found in Jafari et al. (2020) in which lineages 1–5 refer to S. sects. *Rigidulae* s.l., *Portenses* F.Jafari & Oxelman, *Arenosae*, *Muscipula* and *Sclerocalycinae* s.l., respectively.

The use of narrow delimitations of sections has the potential to better account for the levels and patterns of diversity observed in large genera such as *Silene*, since smaller and more homogeneous groups can be circumscribed more readily, are more often geo-

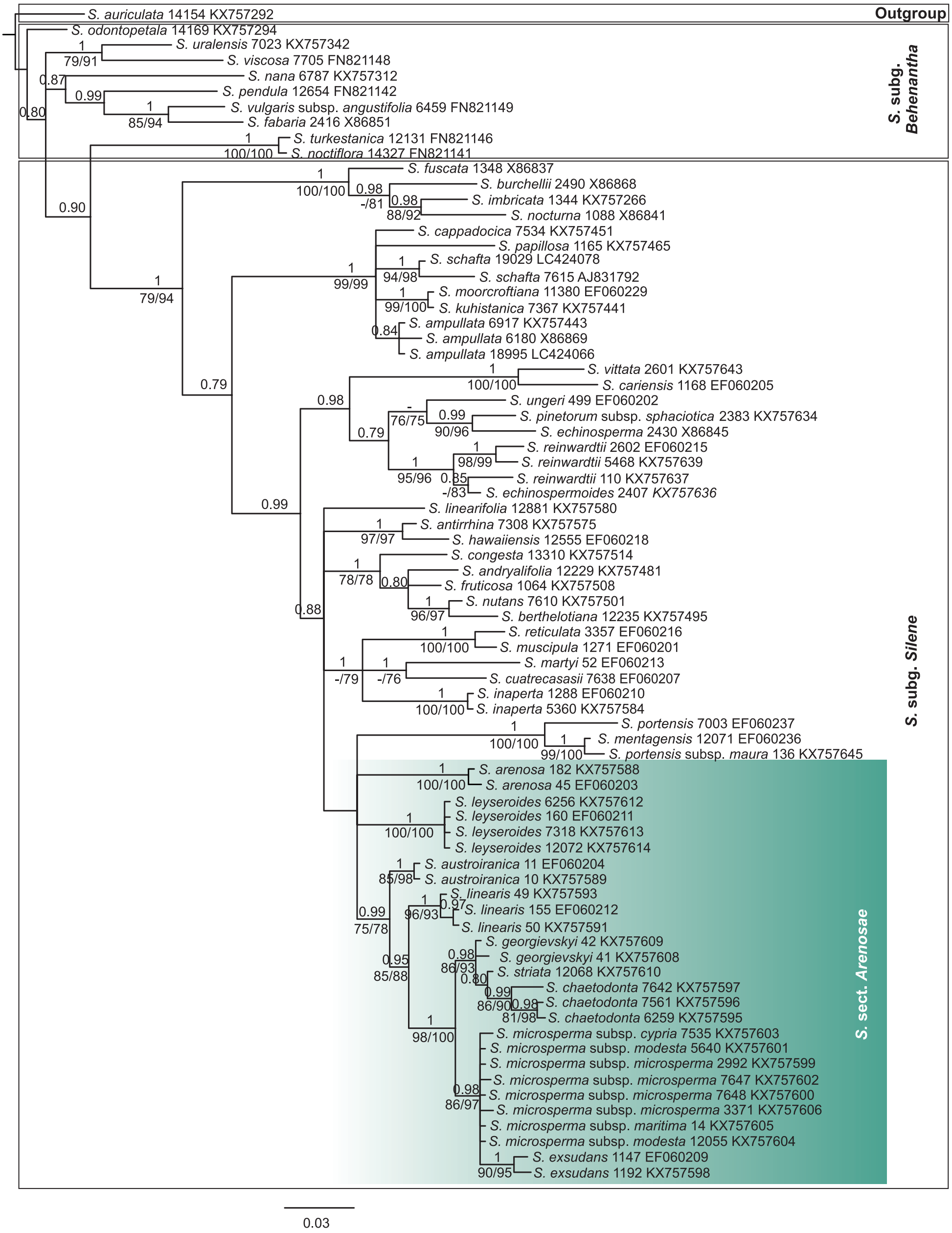

Figure 3. Phylogenetic tree resulting from Bayesian analysis of the ITS sequences including 76 taxa. The trees were summarized in a 50% majority-rule consensus tree with the posterior probabilities (PP) indicated above branches. Bootstrap support values (>75%) based on MP and ML are noted below branches, respectively. The numbers following the taxonomic name indicate the specimen ID and Genbank numbers (Suppl. material 1), respectively.

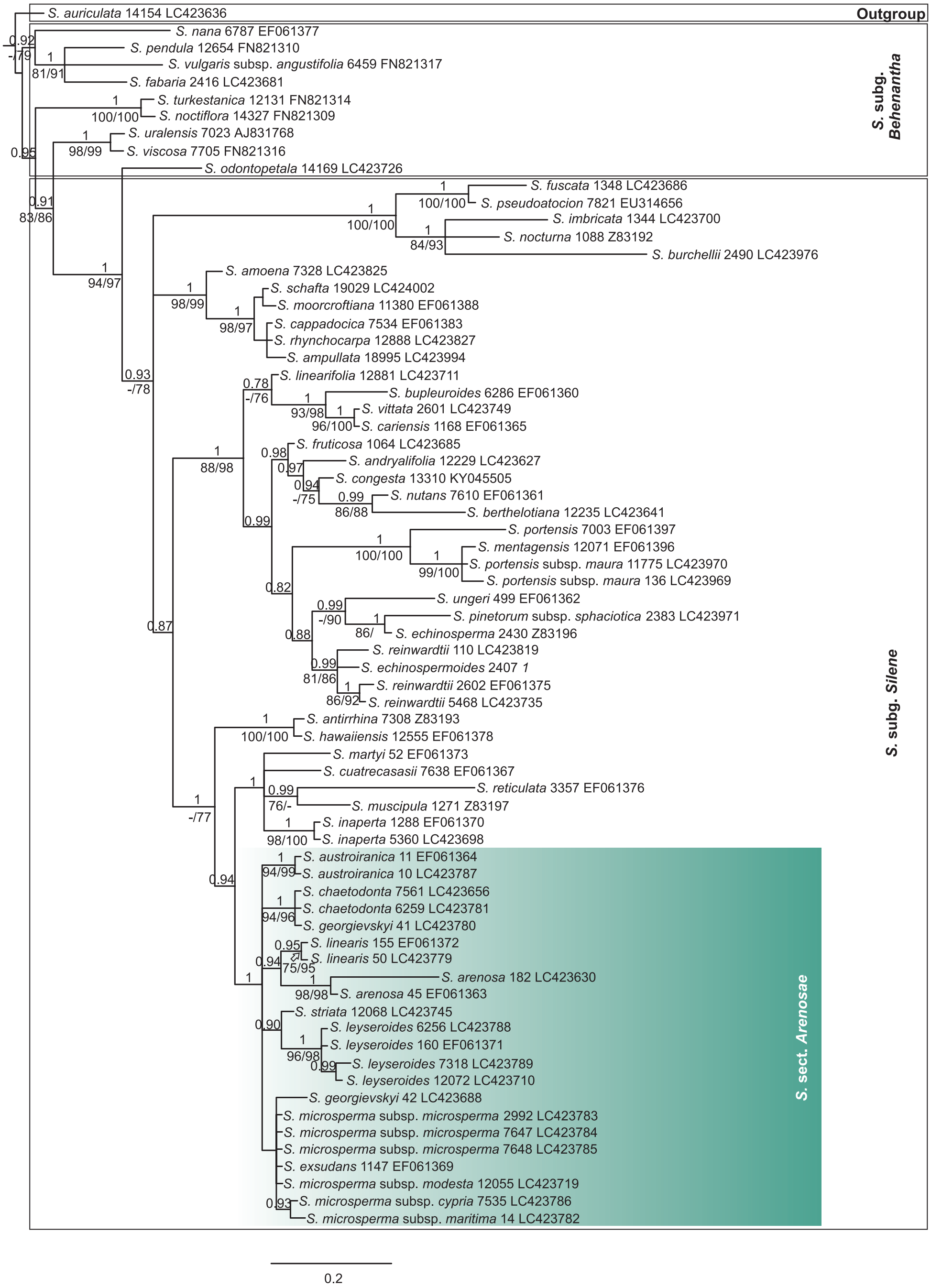

Figure 4. Phylogenetic tree resulting from Bayesian analysis of the *rps16* sequences including 71 taxa. The trees were summarized in a 50% majority-rule consensus tree with the posterior probabilities (PP) indicated above branches. Bootstrap support values (>75%) based on MP and ML are noted below branches, respectively. The numbers following the taxonomic name indicate the specimen ID and Genbank numbers (Suppl. material 1), respectively.

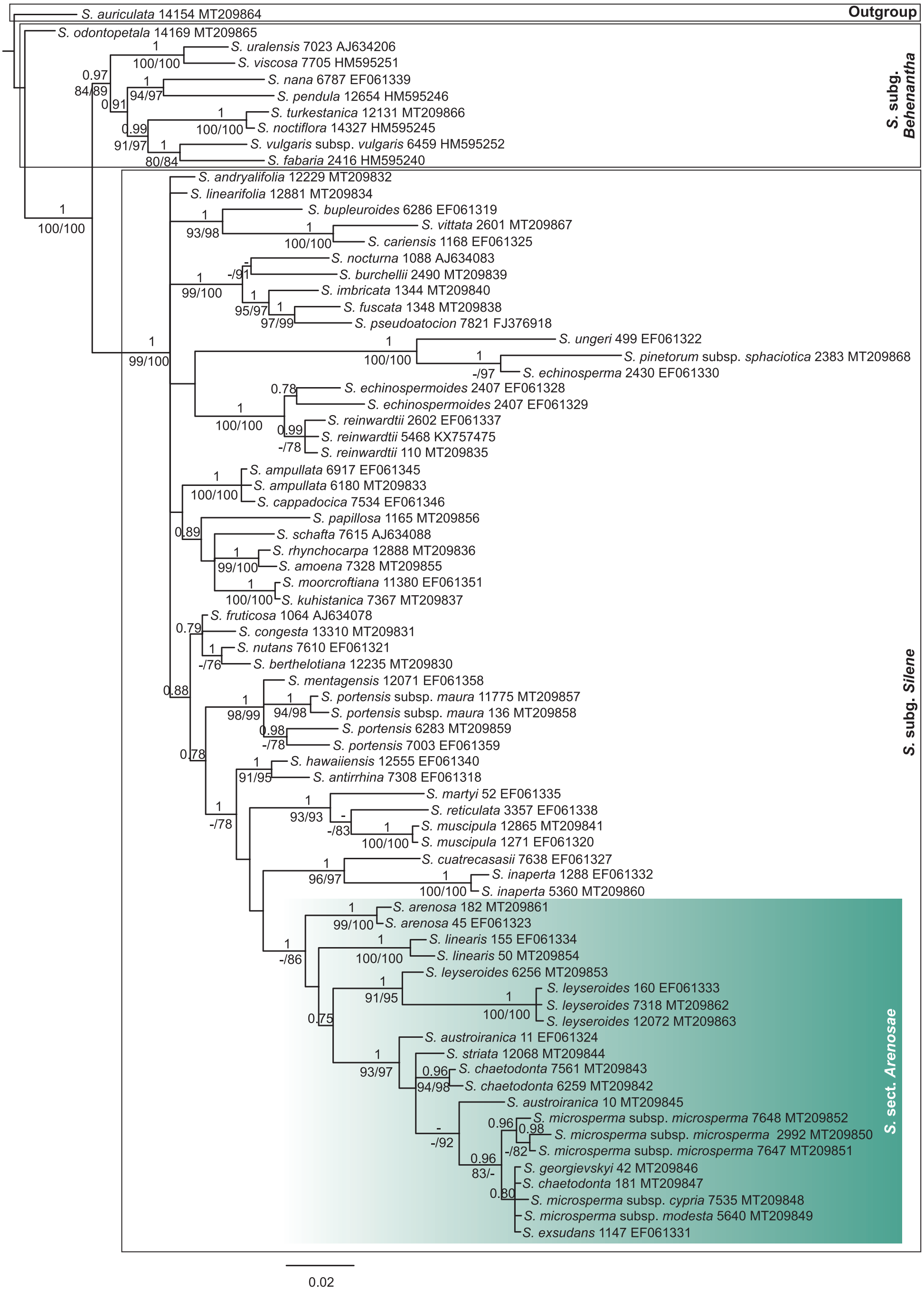

Figure 5. Phylogenetic tree resulting from Bayesian analysis of the *RPB2* sequences including 76 taxa. The trees were summarized in a 50% majority-rule consensus tree with the posterior probabilities (PP) indicated above branches. Bootstrap support values (>75%) based on MP and ML are noted below branches, respectively. The numbers following the taxonomic name indicate the specimen ID and Genbank numbers (Suppl. material 1), respectively.

graphically coherent, and are more likely monophyletic compared to larger and more heterogeneous groups. In addition, such an approach facilitates adequate or complete taxon sampling for global infrageneric studies as well as for more in-depth investigations within sections. Such an approach was successfully applied by Oxelman (1995) when he described *S.* sect. *Sedoides* Oxelman & Greuter. However, as noted by Jafari et al. (2020) the recognition of narrow groups depends on a solid understanding of the associated morphological variation, as well as on phylogenetic data from more than a couple of genetic loci (i.e., the widely used ITS and cpDNA regions).

Morphological remarks

Although it is difficult to ultimately diagnose *S.* section *Arenosae* morphologically, some characters can be used to separate these species from other species of *Silene*. Contrary to its closest relatives, the basal leaves in *S.* section *Arenosae* are not spathulate, but instead oblanceolate or lanceolate. The calyx teeth in this section are usually narrowly lanceolate, terminate in a mucro and have a narrow, often densely ciliate margin. *Silene austroiranica* and *S. georgievskyi* are typical examples of species with this kind of teeth (Fig. 6B, D). By contrast, *S. corinthiaca* Boiss. (Fig. 6C), the type species of *S.* sect. *Rigidulae* (Greuter 1995), is similar to most other *Silene* spp. that have a broad transparent margin at their rounded, broadly ovate or almost deltoid calyx teeth which are narrower (at base almost as wide as long) in other components of the former *S.* sect. *Rigidulae*. *Silene linearis* (Fig. 6A) has a broad transparent calyx tooth margin, which is unique in the section, and distinct mucro, at least on three out of five calyx teeth.

The calyx teeth in *Silene* are more or less heteromorphic, with three of the five teeth different from the remaining two. They may differ in length, width, outline of the membranous margin, and ciliation (see Fig. 6). This heteromorphism is often not taken into account and only one type of tooth is described, which of course is unfortunate, especially when the heteromorphism is prominent. A few Floras (e.g. Oxelman and Greuter 1997, Chamberlain 1996) make some occasional notes on calyx tooth heteromorphism, but Maire (1963) is an exception in having clear references to three teeth having one appearance and two teeth showing another feature. In *S.* sect. *Arenosae*, the heteromorphism is primarily seen as length difference, which is easiest to spot in flower buds. We chose to use the term lanceolate (or ovate when the teeth are broad) to describe the calyx teeth instead of triangular (or broadly triangular), to emphasise the fact that the teeth are widening slightly above the base and then tapering to the apex. The green, middle part of the teeth is always triangular in outline, with slightly concave sides.

“Cauline leaves” refer to the mostly linear or lanceolate leaves on the stem, placed at least a few (3–5) cm up on the stem, as opposed to the rosulate leaves found on the lowermost parts of the stem. Coronal scales are small structures on the petals placed at the junction of the claw and limb. In most cases there are two scales that may be dentate, crenate or lacerate.

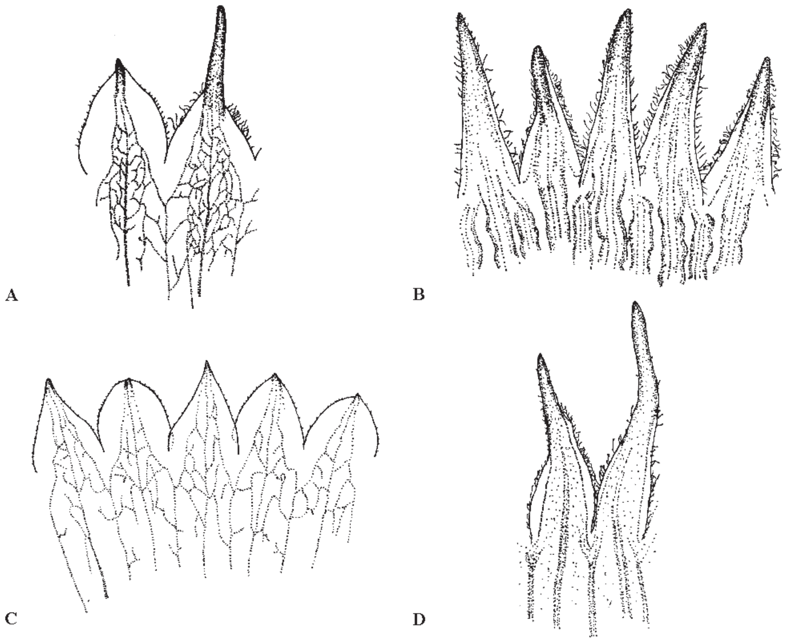

Figure 6. Different types of calyx teeth. **A** *Silene linearis* (M. Bierkamp & P. Zinth 177 BSB) **B** *Silene austroiranica* (Rechinger 10772 B) **C** *Silene corinthiaca* (B. Oxelman 1934 GB) **D** *Silene georgievskyi* (Rechinger 9828 B). **A**, **B** and **D** are representatives of *S.* section *Arenosae*. Illustrations by F. Eggens.

Information about the flower colors was extracted from the notes on herbarium labels or based on field or cultivation experience. *Silene* flowers in general are of two types depending on what time of the day the flowers are open to pollinators. The night-flowering flowers usually have petal limb upper surfaces being white or pale pink often with purple or greenish dorsal side with long, narrowly linear petal lobes that are typically curled up in daytime. The day-flowering flowers usually have pinkish petal limbs with entire or emarginate apices or, if the limb is bilobed, with obovate, elliptic, oblong or linear lobes. "lobes ovate" refers to petal limbs cleft less than the middle, while "lobes oblong or lobes linear" refer to petal limbs cleft to the middle or more. The day-flowering species in *S.* sect. *Arenosae* all have bilobed petal limbs. However, the majority of species are most likely night-flowering.

Many species of *Silene* may have both hermaphroditic and female flowers. The female flowers have shorter anthophores and shorter calyces, and the male organs are missing or present as rudimentary structures. The gynoecium is instead often larger. The measurements in the key and the descriptions are all based on hermaphroditic flowers.

The inflorescence in members of *S.* sect. *Arenosae*, as in many other Caryophyllaceae, is a terminal, compound dichasium accompanied by one to several axillary compound dichasia produced later. In *S.* sect. *Arenosae*, like in most species previously classified in *S.* sect. *Rigidulae*, it is often difficult to distinguish the terminal inflorescences from the lateral ones, because the axillary inflorescences from upper leaf axils are often produced almost simultaneously with the terminal ones. Pedicel length is a useful character, but has to be treated with caution, as pedicels grow through the lifespan of the inflorescence, and becomes smaller the higher up in the compound dichasium the flower is. Therefore, we only give measurements for the first flower in the terminal inforescence, both in flower and in fruit. If it is difficult to locate; one may simply look for the longest pedicel on the plant.

The species included in our study are most often puberulous or sometimes tomentose, with unicellular trichomes just barely visible with the naked eye (making the plant look greyish), or rarely villous. For all species, both leaves and stem tend to be more pubescent towards the base of the plant. Leaves are also more pubescent towards the base of each leaf, often with longer cilia at the basal leaf margin, while the leaves are often glabrous towards the apex and sometimes at the upper side. Calyces are often puberulous or tomentose when flowers are in bud, but can become almost glabrous when the fruits have developed, except on the calyx teeth. The pubescence of the calyx is often concentrated to the upper part.

Silene **section** ***Arenosae*** **Eggens, F.Jafari & Oxelman, sect. nov.**

urn:lsid:ipni.org:names:77211376-1

Type. *Silene arenosa* K. Koch.

Description. Annuals. Stems erect or ascending, 5–70 cm, often pubescent at least below, internodes often with sessile glands on upper part. Basal leaves lanceolate to oblanceolate, ± covered with unicellular trichomes; cauline leaves linear, lanceolate or oblanceolate, pubescent. Inflorescence an apical, uneven dichasium with long internodes, several later axillary inflorescences from upper stem nodes usually present. Flowers usually nocturnal (e.g. *S. austroiranica*, *S. linearis*), rarely diurnal (*S. exsudans* Boiss. & Heldr., *S. leyseroides*, *S. microsperma* subsp. *cypria* Eggens, F.Jafari & Oxelman, nom nov.). Calyx teeth often with distinct mucro, heteromorphic with three longer, often acute, narrowly lanceolate teeth with a narrow transparent margin, the other two teeth shorter, slightly broader, rounded and with a broad transparent margin; margin usually densely ciliate. Primary calyx veins mostly green (or reddish when exposed), often raised; secondary veins obscure; area between veins whitish. Styles 3. Petal limb upper surfaces white or pink. Capsule ellipsoid, oblong or obovate. Seeds reniform, hilum sunken, side flat, with a dorsal groove, testa smooth or papillate.

Distribution and habitat. SW Asian, from South Mediterranean Turkey to Armenia southward to Egypt and the Arabian Peninsula and eastward to Pakistan (Fig. 7). Most taxa have rather limited distributions, except *S. chaetodonta* and *S. leyseroides* that are found from South-Central Turkey to Afghanistan and from Iraq to Pakistan, respectively. All species grow in dry sandy or gravelly habitats.

Notes. Melzheimer (1988) considers *S. rhadinocalyx* Stapf [in Akad. Wiss. Wien, Math.-Naturwiss. Kl., Denkschr. 51: 352 (1886)] to belong to this group, but examination of the type led us to conclude that this taxon is closer to either of the SW Anatolian species *S. cariensis* Boiss. or *S. vittata* Stapf.

Key to species of Arenosae

This key is most applicable to adult plants in full flower or in fruiting stage.

1 Flowers diurnal; petal limbs cleft less than the middle, pink on upper surface; calyx < 10 mm; distribution: Coastal Southern Turkey .... **9. *S. exsudans***
– Flowers usually nocturnal; petal limbs cleft to the middle or more, white or pale pink on upper-surface; calyx usually >10 mm **2**
2 Anthophore > 6 mm **3**
– Anthophore < 6 mm (if more, then pedicel geniculate at apex in fruit) **5**
3 Calyx > 20 mm, longer teeth lanceolate; anthophore 13–16 mm, petal limbs 7–9 mm .... **5. *S. georgievskyi***
– Calyx < 20 mm, longer teeth ovate or lanceolate; anthophore 6.5–11 mm, petal limbs 5–8 mm **4**
4 Calyx teeth with narrow transparent margin (cf. Fig. 6B); anthophore densely tomentose; capsule oblong .... **4. *S. austroiranica***
– Calyx teeth with broad, rounded transparent margin (cf. Fig. 6A); anthophore densely puberulent; capsule ovoid .... **3. *S. linearis***
5 Calyx teeth clearly dimorphic, longer ones > 4 mm, calyx > 13 mm .... **6. *S. chaetodonta***
– Calyx teeth obscurely dimorphic, longer ones < 4 mm, calyx usually < 13 mm **6**
6 Anthophore < 4 mm, much shorter (3 times shorter) than capsule .... **8d. *S. microsperma* subsp. *modesta***
– Anthophore > 4 mm, slightly shorter than the capsule 7
7 Distinct stem internodes > 8 .... **8**
– Distinct stem internodes < 8 .... **9**
8 Uppermost stem internode equal to the next upper one; calyx teeth 1.5–2 mm; anthophore 5–6 mm .... **8b. *S. microsperma* subsp. *cypria***
– Uppermost stem internode clearly longer than the next upper one; calyx teeth 2–4 mm; anthophore 3–5 mm .... **8a. *S. microsperma* subsp. *microsperma***
9 Distinct stem internodes > 5; leaves fleshy .... **8c. *S. microsperma* subsp. *maritima***
– Distinct stem internodes < 5; leaves not fleshy **10**
10 Calyx with small papillae, the teeth ovate; anthophore glabrous; distribution: Armenia, Azerbaijan (Nachitchevan), NW Iran .... **1. *S. arenosa***
– Calyx glabrous or pubescent, but not papillate, the teeth lanceolate; anthophore puberulent to densely puberulent **11**
11 Inflorescence divaricate, branch axile usually > 90°, pedicel geniculate, rarely erect at apex in fruit. Widespread in SW Asia .... **2. *S. leyseroides***
– Inflorescence non-divaricate, branch axile (much) less than 90°, pedicel non-geniculate at apex in fruit. Syria, Lebanon .... **7. *S. striata***

1. ***Silene arenosa*** **K.Koch, Linnaea 15: 711. 1841.**

= *Silene kowalenskyi* Stschegl., Bull. Soc. Nat. Mosc. 26: 322. 1853. – Type: Tab. V.f.1. (neotype designated here: [Azerbaijan] Inter Nachitschevan et Ordubad, Kowalensky s.n. G-BOIS! [G00544651])

Type. [Azerbaijan], Prope flumen Araxin in arena frequenter, [1837, 1838], *K.Koch 873* (lectotype, designated by Lazkov in Caucasian Flora conspectus 3(2): 208. 2012, LE! [LE01051368]; syntypes: [Azerbaijan], Araxon, annu 1838, LE! [LE01051369]; B destroyed?).

Description. (5.0–)10.0–30.0 cm tall, spreading or rarely erect. Stem papillate throughout, pubescent in lower part, glabrous but with sessile glands in upper part; with 2–3 distinct internodes, the uppermost internode1.5–4.0 cm long and obviously longer than the next upper internode. Basal leaves oblanceolate, glabrous. Cauline leaves linear or lanceolate 10.0–40.0 × 2.0–4.0 mm, glabrous or slightly papillate. Calyx 10.0–14.0 mm long, cylindrical at anthesis and clavate in fruit, glabrous, slightly papillate; teeth unequal; shorter ones 1.0–1.5 mm long, ovate, mucronate; longer ones 1.5–2.0 mm, ovate, acuminate; marginal hairs short (up to 0.5 mm), sparse. Inflorescence non-divaricate, branch axile (much) less than 90°. Petal claws 6.0–7.5 mm long, glabrous; limbs 2.0–3.0 mm long, emarginate or bifid, upper-surface pink, lobes linear, petal limbs cleft to middle or more; coronal scales 0.4–0.5 mm long, ovate, apex entire. Anthophore 4.0–5.0 mm long, glabrous. Anthers exserted; filaments 7.0–8.0 mm long, glabrous. Styles exserted. First pedicel 1.0–3.0 cm in flower, 2.0–3.5 cm in fruit, spreading, glabrous, apex mostly geniculate or antrorse. Capsule 6.0–8.0 mm long, oblong or ellipsoid, fragile, opaque. Seeds 0.5–0.8 mm wide, 0.5–0.7 mm high, testa smooth.

Distribution. Armenia, Azerbaijan (Nachitchevan), NW Iran (Fig. 7).

Notes. The two accessions form a strongly supported clade in all trees (PP = 1.00, Fig. 1; PP = 1.00 MPB = 100% MLB = 100%, Fig. 3; PP = 1.00 MPB = 98% MLB = 98%, Fig. 4; PP = 1.00 MPB = 99% MLB = 100%, Fig. 5). Despite its geographical, morphological and phylogenetic distinctiveness, this taxon has been confused with *S. leyseroides* (Melzheimer 1988: as synonym, Schischkin 1936). The two species are superficially similar; both have spreading stems and pedicels that are upturned (or geniculate) at apex in fruit, so that all capsules are vertical although the pedicel may be almost horizontal. However, *S. arenosa* is readily distinguished by the shorter, mucronate and sparsely ciliate (not acuminate and densely ciliate) calyx teeth and the glabrous anthophore from *S. leyseroides*. It also has smaller petals that are almost completely included within the calyx, and the petal limb is sometimes emarginate rather than bilobed. We have not seen any material of *S. arenosa* from any other area than Armenia, Azerbaijan (more specifically the region Nachitchevan), and Iran (close to the borders to Armenia, Turkey, and Nachitchevan), whereas *S. leyseroides* appears to be allopatric and grows mainly in the Zagros Mountain range and in E Afghanistan/NW Pakistan (see Fig. 7).

The seeds of *S. arenosa* are possibly more shining on the surface, instead of the greyish, dull surface that is the common condition for *Silene* seeds, but we have seen

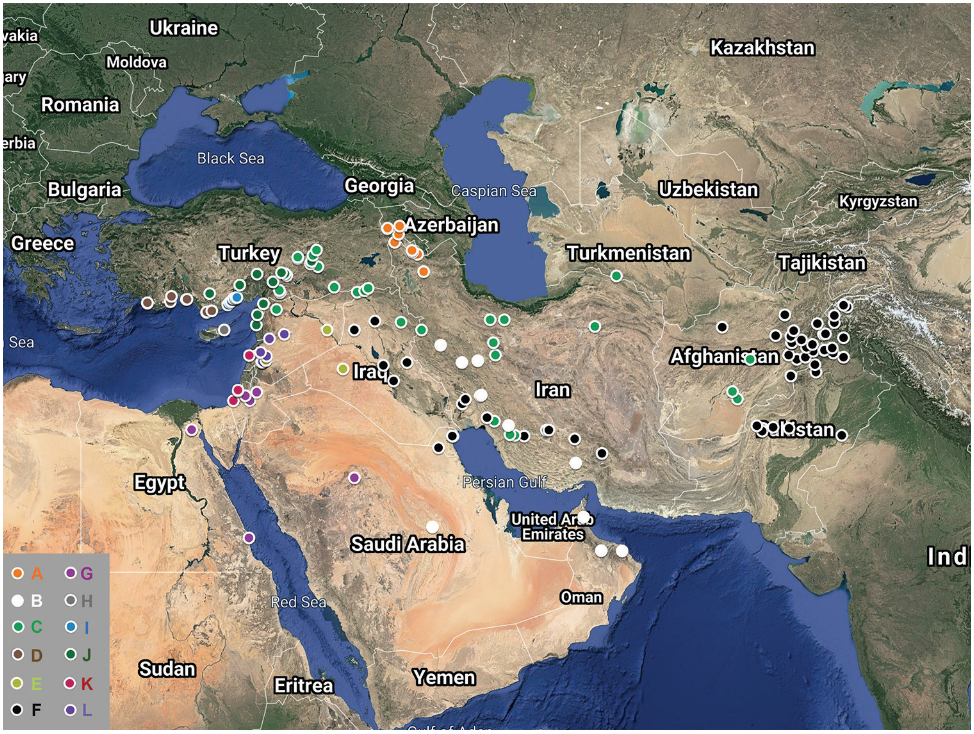

Figure 7. Distribution map of *S.* sect. *Arenosae*. Each color code corresponds to one taxon: A) *S. arenosa*; B) *S. austroiranica*; C) *S. chaetodonta*; D) *S. exsudans*; E) *S. georgievskyi*; F) *S. leyseroides*; G) *S. linearis*; H) *S. microsperma* subsp. *cypria*; I) *S. microsperma* subsp. *maritima*; J) *S. microsperma* subsp. *microsperma*; K) *S. microsperma* subsp. *modesta*; L) *S. striata*.

too few specimens with seeds to draw definitive conclusions. The green midpart of the calyx teeth is narrow, which can make the teeth look lanceolate rather than ovate. Collections from near the border between Iran and Turkey have calyces which are densely papillose in upper parts.

2. *Silene leyseroides* Boiss., Diagn. Pl. Orient. 1:41. 1843.

= *Silene salsa* Boiss., Diagn. Pl. Orient. 8:77. 1849. – Type: [Iran], Hab. in solo salso ad lacum Nemek Derja prope Schiras, 1 April 1842, *K.G.T. Kotschy*, *pl. Pers. austr. 453* (lectotype, designated here: G-BOIS! [G00544649], isolectotypes: G! [G00226818, G00226819, G00226820], C! [C10009174, C10009175], K! [K000728456], WAG! [WAG0191878])

Type. [Iraq], Hab. ad Babylonem [in deserto Babylonia], *Aucher Eloy*, *pl. exs. 448* (lectotype, designated here: G-BOIS! [G00544647]; isolectotypes: G! [G00226728, G00226729], K! [K000728455]).

Description. 5.0–35.0 cm tall, spreading or rarely erect. Stem pubescent in lower part, more or less glabrous with sessile glands in upper part; with 3–5 distinct internodes, the uppermost internode (1.0–)2.0–3.0(–4.0) cm long and obviously longer than the next upper internode. Basal leaves oblanceolate or lanceolate 10.0–30.0 × 1.0–3.0 mm, pubescent, scabrous. Cauline leaves linear or lanceolate 20.0–35.0 × 2.0–3.0 mm, pubescent, scabrous. Calyx (8.0–)9.0–13.0(–14.0) mm long, cylindrical at anthesis and clavate in fruit, rarely glabrous, or pubescent; teeth unequal; shorter ones 1.0–2.0 mm, lanceolate, acuminate; longer ones 2.0–3.0(–4.0) mm, lanceolate, acuminate; marginal hairs long (longer than 0.5 mm), dense. Inflorescence divaricate, branch axile usually > 90°. Petal claws 6.0–7.0 mm long, glabrous; limbs 4.0–7.0 mm long, bifid, upper-surface pink, lobes linear, divergent, petal limbs cleft to middle or more, lower-surface carmine or green; coronal scales 0.8–1.1 mm long, ovate, apex entire or slightly dentate. Anthophore (4.0–)5.0–7.0 mm long, densely puberulent. Anthers exserted; filaments 7.0–8.0 mm long, glabrous. Styles exserted. First pedicel 1.0–3.0 cm in flower, 2.0–4.0 cm in fruit, spreading, glabrous, apex usually geniculate, or antrorse. Capsule 6.0–8.0 mm long, oblong or ellipsoid, fragile, opaque. Seeds 0.6–0.9 mm wide, 0.4–0.6 mm high, testa smooth.

Distribution. Iraq, Iran, Kuwait, Afghanistan and Pakistan (mainly in the Zagros range of Iran and in E Afganistan/NW Pakistan) (Fig. 7).

Notes. This species is recognized by a spreading growth form with many branches from the base, upturned (or geniculate) pedicels at apex in fruit and narrowly lanceolate calyx teeth. The calyx veins are often reddish or purplish in dried material (probably green in fresh state). The petal lobes are linear and divergent.

The specimens from the eastern parts of the distribution area tend to have less pubescent calyces (sparsely puberulous or almost glabrous) and are less pubescent on stem and leaves. However, a specimen from NE Saudi Arabia (Mandaville 1645 BM) is almost glabrous on calyces and puberulous on stem and leaves.

From the original description, *S. cabulica* Bornm. [in Engl. Jahrb. 46, 221–222 (1934), type from around Kabul) seems to be very similar to *S. leyseroides*. We have, however, not been able to trace any type material and propose that the type was destroyed in B. Both Ghazanfar and Nasir (1986) and Melzheimer (1988) mention *S. cabulica* as dubious.

The *S. leyseroides* clade is strongly supported (PP = 1.00, Fig. 1; PP = 1.00 MPB = 100%, MLB = 100%, Fig. 3; PP = 1.00 MPB = 96% MLB = 98%, Fig. 4; PP = 1.00 MPB = 91% MLB = 95%, Fig. 5). Three of the *S. leyseroides RPB2* sequences (from Iran, Iraq and Kuwait) share a unique 252 bp insertion. Interestingly, this insertion is not found in the specimen from Afghanistan. The accessions from Iran, Iraq and Kuwait form a strongly supported clade (PP = 1.00 MPB = 100%, MLB = 100% Fig. 5).

3. *Silene linearis* Decne., Ann. Sci. Nat. Bot. sér. 2, 3: 276. 1835, nom. cons. prop. (in press) [non Sweet].

Type. [Egypt], Hab. le désert du Sinaï, [1.6.1832], *N. Bové 178* (lectotype, designated here: G! [G00226732]; isolectotypes: K! [K000728452], G! [G00226733]).

Description. 15.0–60.0 cm tall, erect or spreading. Stem pubescent in lower part, scabrous, glabrous but with sessile glands in upper part; with 6–10 distinct internodes, the uppermost internode length 3.0–6.0 cm long and obviously longer than the next upper internode. Basal leaves oblanceolate 30.0–60.0 × 2.0–4.0 mm, pubescent. Cauline leaves linear or lanceolate 10.0–55.0 × 1.0–4.0 mm, pubescent. Calyx 11.0–19.0 mm long, campanulate at anthesis and clavate in fruit, pubescent; teeth unequal; shorter ones 1.5–2.0 mm, ovate, mucronate; longer ones 2.0–2.5 mm, ovate, acuminate; marginal hairs short (up to 0.5 mm), dense. Inflorescence non-divaricate, branch axile (much) less than 90°. Petal claws 6.0–7.0 mm long, glabrous; limbs 6.0–8.0 mm long, divided, upper-surface white, lobes linear or oblong, divergent, petal limbs cleft to middle or more, lower-surface green; coronal scales 1.0–2.5 mm long, obovate, apex dentate. Anthophore 8.0–11.0 mm long, densely puberulent. Anthers exserted; filaments 8.0–9.0 mm long, glabrous . Styles exserted. First pedicel 1.0–3.0 cm in flower, 2.0–4.0 cm in fruit, erect, glabrous, apex antrorse. Capsule 5.0–7.0 mm long, ovoid or ellipsoid, fragile, opaque. Seeds 0.7–0.9 mm wide, 0.6–0.7 mm high, testa smooth.

Distribution. E Egypt (Red Sea area, Sinai), N Arabian Peninsula, W Jordan and Palestine (Fig. 7).

Notes. *Silene linearis* has some superficial similarity to *S. austroiranica*, which has narrowly lanceolate calyx teeth with narrow transparent margin, and not the broad rounded margin of *S. linearis* (see Fig. 6). *Silene austroiranica* is allopatric and found further south and east on the Arabian Peninsula, and in eastern Iraq and western/southern Iran.

The ranges of the calyx, anthophore and capsule lengths are unusually large in *S. linearis*. The large-flowered individuals are all found in Egypt (although not all specimens from Egypt are large-flowered), with calyx length of 17–19 mm (and proportional anthophores and capsules). The specimens are in all other respects similar (or perhaps with slightly shorter mucro on calyx teeth) to the *S. linearis* specimens with smaller flowers, and we do not think the difference is sufficient to merit taxonomic recognition. The Egyptian specimens are in general (independent of flower size) tomentose to villous while the specimens from Palestine and Jordan are often slightly puberulous, although at least one specimen from Palestine is densely tomentose.

One sequence for a specimen from Egypt (*S. linearis*, ID 49, KX757593) is included in the ITS tree. It forms a strongly supported clade together with the other two *S. linearis* accessions (PP = 1.00 MPB = 96% MLB = 93%, Fig. 3). The *S. linearis* clade (with the two Palestine accessions) is strongly supported in all trees (PP = 1.00, Fig. 1; PP = 0.95 MPB = 75% MLB = 95%, Fig. 4; PP = 1.00 MPB = 100% MLB = 100%, Fig. 5).

Nomenclatural notes. The name *Silene linearis* Decne. has been used for a long time, but the delimitation of the taxon has varied. A number of authors have used the name in our sense, e.g. Boissier (1867), Rohrbach (1868), Williams (1896), Post (1932), Chowdhuri (1957), Mouterde (1966), Zohary (1966), Chamberlain (1996) and Boulos (1999). Other authors use this name for a more inclusive taxon, e.g. Rechinger (1964) and Blakelock (1957), including *S. leyseroides*, *S. arenosa*, *S. chaetodonta* and *S. kotschyi* Boiss. (= *S. microsperma*). Sweet (1830) used the epithet "*linearis*" in Hortus Britannicus 2nd ed., in a completely different context, five years earlier than Decaisne's description was published. The name *Silene linearis* Sweet has been cited by few authors. Rohrbach (1868) referred to the name as a synonym for *Silene cucubalus* Wib. (= *Silene vulgaris* (Moench) Garcke) and Marsden-Jones and Turrill (1957) recognized the name as a part of the *Silene vulgaris*-assemblage but used the name in a highly informal way. The name is not mentioned in Chater et al. (1993), Aeschimann (1985), Pignatti (1982) or Greuter et al. (1984). *Silene linearis* Decne. has been suggested to be conserved against *Silene linearis* Sweet (Eggens & al., in press).

4. *S. austroiranica* Rech.f., Aell. & Esfand., Bot. Jahrb. Syst. 75: 349. 1951.

Type. [Iran], Lar. [Hormozgan] Hadjiabad prope Tarum, ca. 900 m, 29 April 1948, *K.H. Rechinger*, *P. Aellen & E. Esfandiari 3386* (holotype: W! [W19800014919]; isotypes: G! [G00006016, G00006017], S! [S-G-8718]).

Description. 15.0–50.0 cm tall, erect. Stem pubescent in lower part, pubescent in upper part; with 3–5 distinct internodes, the uppermost internode 1.0–10.0 cm long and obviously longer than the next upper internode. Basal leaves oblanceolate 10.0–30.0 × 1.0–6.0 mm, pubescent. Cauline leaves oblanceolate 5.0–40.0 × 2.0–6.0 mm, pubescent. Calyx 12.0–16.0 mm long, campanulate at anthesis and clavate in fruit, glabrous or pubescent; teeth unequal; shorter ones 2.0–3.0 mm, ovate, acuminate; longer ones 2.0–4.0 mm, lanceolate, acuminate; marginal hairs long (longer than 0.5 mm). Inflorescence non-divaricate, branch axile (much) less than 90°. Petal claws 7.0–10.0 mm long, glabrous; limbs 5.0–6.0 mm long, divided, upper-surface white or pink, lobes linear, divergent, petal limbs cleft to middle or more; coronal scales 1.3–2.0 mm long, elliptic or obovate, apex slightly dentate. Anthophore 6.5–9.0 mm long, densely tomentose. Anthers exserted; filaments 8.0–12.0 mm long, glabrous. Styles exserted. First pedicel 1.0–3.0 cm in flower, 2.0–5.0 cm in fruit, erect, glabrous, apex antrorse. Capsule 5.5–8.0 mm long, oblong or ellipsoid, fragile, translucent. Seeds 0.5–0.8 mm wide, 0.5–0.7 mm high, testa smooth.

Distribution. Arabian Peninsula, Kuwait, Iraq and Iran (Fig. 7).

Notes. This species has rather long internodes, two to ten times the length of the subtending leaves (rarely of the same length). In particular, the uppermost internode is long, sometimes as long as 10 cm. Plants from the Riyadh area tend to have shorter upper internodes. The internodes are often viscid. The long internodes together with the relatively long coronal scales are the best characters for recognizing this species.

The specimens from Iran tend to have broader leaves than the other specimens, in particular the ones from the Arabian Peninsula.

The clade with the two *S. austroiranica* accessions is strongly supported in the species (PP = 1.00, Fig. 1), ITS (PP = 1.00 MPB = 85% MLB = 98%, Fig. 3) and *rps16* trees (PP = 1.00 MPB = 94% MLB = 99%, Fig. 4). The two accessions of *S. austroiranica* do not form a clade in *RPB2* tree, probably due to difference in sequence length (one accession was 490 bp and another 140 bp: due to incomplete sequence read). In the *RPB2* tree the *S. austroiranica* clade is nested within a clade including *S. microsperma*, *S. exsudans*, *S. chaetodonta*, *S. striata* Ehrenb. ex Rohrb. and *S. georgievskyi* (PP = 1.00 MPB = 93% MLB = 97%, Fig. 5), but in the ITS phylogeny *S. austroiranica* and *S. linearis* are successive sisters to this clade (PP = 0.99 MPB = 75% MLB = 78% and PP = 0.95 MPB = 85% MLB = 88%, Fig. 3).

5. *S. georgievskyi* Lazkov, Bot. Zhurn. (Moscow & Leningrad). 84 (9): 123. 1999.

Type. [Syria], Desertum Syriacum. 30 km ad austro-orient. Ab urb. Deir-Ez-Zor, vallis undulata, ass. Ephem.-car. Frequens, 15 May 1985, *A. Georgievsky s.n.* (Holotype: LE! [LE01051363]).

Description. 20.0–50.0 cm tall, erect. Stem pubescent in lower part, scabrous, pubescent with sessile glands in upper part; with 8–12 distinct internodes, the uppermost internode obviously longer than the next upper internode. Basal leaves linear or oblanceolate, pubescent. Cauline leaves linear 10.0–40.0× 1.0–3.0 mm, pubescent. Calyx 25.0–30.0 mm long, ovoid at anthesis and clavate in fruit, pubescent; teeth unequal; shorter ones 2.0–4.0 mm, ovate, acuminate; longer ones 4.0–6.0 mm, lanceolate, acuminate; marginal hairs long (longer than 0.5 mm), dense. Inflorescence non-divaricate, branch axile (much) less than 90°. Petal claws 10.0–12.0 mm long, glabrous; limbs 7.0–9.0 mm long, bifid, upper-surface pink, lobes oblong, petal limbs cleft to middle or more; coronal scales 2.0–2.2 mm long. Anthophore 13.0–16.0 mm long, glabrous or puberulent. Anthers exserted; filaments 12.0–15.0 mm long, glabrous. Styles exserted. First pedicel 1.0–4.0 cm in flower, 2.0–6.0 cm in fruit, erect, glabrous, apex antrorse. Capsule 12.0 mm long, oblong or ellipsoid. Seeds 0.8–1.0 mm wide.

Distribution. Syria, N Iraq (Fig. 7).

Notes. At the molecular level, we have two sequences for each ITS and *rps16* and only one for *RPB2*. All the three markers were sequenced for the specimen from Syria (*S. georgievskyi* ID. 42), but for the specimen from Iraq, the ITS and *rps16* regions were sequenced from two duplicate specimens from different herbaria. The two accessions of *S. georgievskyi* from Iraq and Syria do not form a monophyletic group in the species, ITS and *rps16* trees (Figs 1, 3, 4). The accession from Iraq (*S. georgievskyi* ID. 41) is found together with the accessions of *S. chaetodonta* in a moderately to strongly supported clades in the species (PP = 0.78, Fig. 1) and *rps16* (PP = 1.00 MPB = 94% MLB = 96%, Fig. 4) trees, respectively. The accession from Syria is nested within a clade including *S. microsperma* in the species tree (Fig. 1) and weakly supported in *rps16* tree (Fig. 4, PP<0.75). In the ITS tree, the accessions of *S. georgievskyi* do not form a monophyletic group, but they are included in a strongly supported clade together with *S. chaetodonta* and *S. striata* (PP = 0.98 MPB = 86% MLB = 93%, Fig. 3). The morphological distinctiveness (much longer calyx, long anthophore and larger petals) speaks in favour of recognition of the species, and although chromosome numbers are unknown, we hypothesize that the incongruent pattern seen in the Syrian specimen may be explained by polyploid hybridization. Allopolyploids often grow larger than their parents (Chen 2010). *Silene georgievskyi* is morphologically larger in floral and general habit aspects compared to both *S. chaetodonta* and *S. microsperma*. There may be a small overlap in the distributions of *S. chaetodonta* and *S. georgievskyi*, in the border area between Iraq and Syria.

6. *Silene chaetodonta* Boiss., Diagn. Pl. Orient. 1: 39. 1843.

= *Silene chaetodonta* Boiss. var. *pittodes* Boiss., Fl. Or. 1: 606. 1867. – Type: [Iran], Hab. In Persiâ ad Schurab inter Ispahan et Teheran, May 1859, *Bunge s.n.* (holotype: G-BOIS! [G00544221])

= *S. debilis* Stapf, Akad. Wiss. Wien, Math.-Naturwiss. Kl., Denkschr. 51: 282. 1886. – Type: [Iran], [In agro Ecbatanensi], In colle prope Hamadan, 8 June 1882, *Th. Pichler s.n. in D.J.E. Polak Iter Persicum* (lectotype, designated here: K! [K000728462]; isolectotype: G! [G00378634])

Type. [Iran], Hab. In Persia australis, *Aucher Eloy Pl. Exs. 4223* (lectotype, designated by Lazkov in Bot. Zhurn. (Moscow & Leningrad). 87 (5): 130. 2002) G! [G00378632]; isolectotypes: G-BOIS! [G00544217], LE! [LE01051365], BM! [BM000990893], K! [K000728461], MO! [MO-149678]).

Description. 15.0–60.0 cm tall, erect or rarely spreading. Stem pubescent in lower part, scabrous, glabrous but with sessile glands in upper part; with 4–12 distinct internodes, the uppermost internode (2.0–)3.0–8.0(–10.0) cm long and obviously longer than the next upper internode. Basal leaves oblanceolate, pubescent. Cauline leaves linear or oblanceolate 10.0–50.0 × 2.0–6.0 mm, pubescent, scabrous. Calyx 13.0–17.0 mm long, ovoid at anthesis and clavate in fruit, scabrous; teeth unequal; shorter ones 2.0–4.0 mm, lanceolate, acuminate; longer ones 4.0–7.0 mm, lanceolate, acuminate; marginal hairs long (longer than 0.5 mm), dense. Inflorescence non-divaricate, branch axile (much) less than 90°. Petal claws 7.0–8.0 mm long, glabrous; limbs 5.0–8.0 mm long, bifid, upper-surface pink, lobes oblong, petal limbs cleft to middle or more; coronal scales 1.0–1.5 mm long, ovate, apex dentate. Anthophore 4.0–6.0 mm long, densely puberulent. Anthers included; filaments 8.0–9.0 mm long, glabrous. Styles exserted or included. First pedicel 1.0–4.0 cm in flower, 2.0–6.0 cm in fruit, erect, glabrous, apex antrorse. Capsule 7.0–11.0 mm long, oblong or ellipsoid, robust. Seeds ca 1.1 mm wide, ca. 0.7 mm high, testa smooth.

Distribution. Iran, SE Turkey, Syria, Iraq, S Turkmenistan, Afghanistan, and NW Pakistan (Fig. 7).

Notes. Usually, this species is readily distinguished by its whitish stems, pink and broad lobed petal limbs, long calyx teeth, total calyx length less than 20 mm, prominent calyx vein and thick, robust capsule wall. *Silene georgievskyi* differs from it by having a much longer calyx and anthophore. It seems that the length of the calyx teeth is a more important character than calyx total length for species delimitation in this group.

We have sequenced all selected markers for two specimens from the same geographical region (W Iraq). The *RPB2* sequences generated for two accessions of *S. chaetodonta* (ID 6259 and ID 7561) and one for *S. striata* shared a unique 261 bp insertion, but one accession of *S. chaetodonta* from Turkey (ID 181) and one of *S. georgievskyi* (ID 42: probably a hybrid between *S. chaetodonta* and *S. microsperma*, see above) lack this insertion. The two accessions of *S. chaetodonta* from W Iraq form a clade in the *RPB2* tree (PP = 0.96 MPB = 94% MLB = 98%, Fig. 5), but the accession from Turkey is not sister to this clade and is nested within a clade including *S. microsperma*, *S. exsudans* and *S. georgievskyi* ID 42 (PP = 0.96 MPB = 83%). The accession of *S. chaetodonta* from Turkey could be a hybrid between *S. chaetodonta* and *S. microsperma* according to *RPB2* sequence analysis. An accession from NE Iran (*S. chaetodonta* ID 7642) form a clade with the other two *S. chaetodonta* sequences in the ITS tree (PP = 0.99 MPB 86% MLB = 90%, Fig. 3). The accession from NE Iran generated only an ITS sequence in our analyses.

7. ***Silene striata*** **Ehrenb. ex Rohrb., Bot. Zeitung (Berlin) 25: 83. 1867.**

Type. [Syria], In der Ebene von Baalbek in Syrien, *C.G. Ehrenberg* (no specimen traced); (neotype, designated here: [Syria] Antiliban, entre la Sahara et Dimas (Al-Dimas), 9 June 1868, *C. Gaillardot 1643* as *S. kotschyi* G-BOIS! [G00544635]).

Description. 10.0–20.0 cm tall, erect. Stem with sessile glands in central and upper parts; with 3–5 distinct internodes. Cauline leaves linear 20.0 × 2.0 mm. Calyx 12.0–13.0 mm long, campanulate at anthesis and clavate in fruit, glabrous or sparsely pubescent; teeth unequal; shorter ones 1.0–1.5 mm, lanceolate, acuminate; longer ones 2.0–3.5 mm, lanceolate, acuminate; marginal hairs long (longer than 0.5 mm), dense. Inflorescence non-divaricate, branch axile (much) less than 90°. Petal claws 6.0–6.5 mm long, ciliate; limbs 6.0 mm long, bifid to less than half, upper-surface pink, lobes oblong, petal limbs cleft to middle or more, divergent; coronal scales 2.0 mm long, ovate, apex entire. Anthophore ca 5.5 mm long, puberulent. Anthers exserted; filaments glabrous. Styles exserted. First pedicel 1–2 cm in flower, 2–3 cm in fruit, erect or spreading, apex antrorse. Capsule 6.0–8.0 mm, oblong, fragile, opaque. Seeds unknown.

Distribution. Syria, Lebanon (Fig. 7).

Notes. This species is distinguished by its small size, rather short calyx (12–13 mm) and calyx teeth (2–3.5 mm), oblong or slightly obovate petal lobes and ciliate petal claws, and strongly exserted anthers and styles.

The sequences from the three different markers analyzed here are incongruently positioned in the phylogenies. In the ITS tree, this species is found in a clade including *S. georgievskyi* and *S. chaetodonta*, as sister to the latter but with moderate support (PP = 0.80, Fig. 3). It is unresolved in a relatively large clade in the *RPB2* tree, although shares a 261 bp insertion with the *S. chaetodonta* accessions (*S. georgievskyi* sequence is missing for this marker). In the *rps16* tree, *S. striata* is sister to the *S. leyseroides* clade

(PP = 0.90, Fig. 4). Morphology, geographical distribution and other molecular characteristics (e.g. the long insertion shared by *S. striata* and *S. chaetodonta*) suggest that *S. striata* is more closely related to *S. chaetodonta* than *S. leyseroides*.

8. *Silene microsperma* Fenzl, Pug. Pl. Nov. Syr. 9. 1842.

Type. See below subspecies.

Distribution. Turkey, Syria, N Iraq, Cyprus, Palestine and Lebanon (Fig. 7).

Notes. This species is the most variable in the section and is here divided into four subspecies. We have chosen not to treat these taxa as species because they are obviously closely related, as seen by low variation in the DNA sequences. The taxon "*S. modesta*" has sometimes been treated as a species (e.g. Zohary 1966, Mouterde 1966), but has also previously been treated as a variety of *S. chaetodonta* (Post 1932). Here, we accept it as a subspecies of *S. microsperma*.

The *S. microsperma* accessions with *S. exsudans* and one accession of *S. georgievskyi* ID. 42 form a weakly supported clade in the species (Fig. 1) and *rps16* (PP < 0.75) trees. The *RPB2* tree shows almost the same pattern, but *S. chaetodonta* ID 181 from Turkey is included in this clade (PP = 0.96 MPB = 83%, Fig. 5). The ITS phylogeny supports a close relationship between *S. microsperma* and *S. exsudans* (PP = 0.98 MPB = 86% MLB = 97%, Fig. 3). There is very little resolution within the *S. microsperma* clade.

8a. *Silene microsperma* subsp. *microsperma*.

= *Silene kotschyi* Boiss., Diagn. Pl. Orient. 1: 40. 1843. – Type: [Turkey], In monte Tauro, [1836], *K.G.T. Kotschy 85* (lectotype, designated here: G-BOIS! [G00544619]; isolectotypes: W! [W19580022871], BM! [BM000990903], LE! [LE01051362], TUB! [No Barcode], G! [G00226928, G00226929, G00226930], KFTA [KFTA0001153]); syntypes: [Syria], Syria prope Aintab, *Aucher Eloy 425* (G! [G00226812, G00226931], G-BOIS! [G00544620], BM! [BM000990904], E! [E00286983])

= *Silene kotschyi* var. *effusissima* Boiss., Fl. Or. Suppl. 85. 1888. – Type: [Turkey], Hab. Syriæ Marasch in agris, [15.7.1865], *H.K. Haussknecht s.n.* (lectotype, designated here: G-BOIS! [G00544631]; isolectotypes: JE! [JE00013446, JE00013447]; [Iran/Iraq] In apricis calcaries m. Schahu et Avroman Kurdistaniæ, 6000', *H.K. Haussknecht 192* (syntypes: JE! [JE00013444, JE00013445]).

= *Silene cassia* Boiss., Diagn. Pl. Orient. 8: 78. 1849. – Type: [Syria], Hab. in sylvaticis jugi Cassii ubi exemplaria pauca, [May-July] 1846, *P.E. Boissier s.n.* (lectotype, designated here: G-BOIS! [G00544654]; isolectotypes: G! [G00226837], LE! [LE01051366])

Type. [Turkey] Prope Süveydiye, ad Orontis, *K.G.T. Kotschy s.n.* (no specimen cited).

Description. 15.0–70.0 cm tall, erect or spreading. Stem pubescent in lower part, scabrous, glabrous but with sessile glands in upper part; with 8–12(–20) distinct internodes, the uppermost internode (3.0–)4.0–6.0(–7.0) cm long and obviously longer than the next upper internode. Basal leaves linear or oblanceolate 1.0–4.0 × 1.0–4.0 mm, pubescent. Cauline leaves linear 10.0–30.0× 1.0–3.0 mm, pubescent. Calyx 9.0–14.0 mm long, campanulate at anthesis and clavate in fruit, pubescent; teeth unequal; shorter ones 2.0–3.0 mm, lanceolate, acuminate; longer ones 2.0–4.0 mm, lanceolate, acuminate; marginal hairs long (longer than 0.5 mm), dense. Inflorescence non-divaricate, branch axile (much) less than 90°. Petal claws 4.0–7.5 mm long, ciliate; limbs 5.0–6.5 mm long, bifid, upper-surface white or pink, lobes oblong, petal limbs cleft to middle or more; coronal scales 0.8–1.4 mm long, ovate, apex dentate or erose. Anthophore 3.0–5.0 mm long, densely puberulent. Anthers exserted; filaments 6.0–9.0 mm long, sometimes pubescent. Styles exserted. First pedicel 1.0–3.0 cm in flower, 1.0–4.0 cm in fruit, erect, glabrous, apex antrorse. Capsule 6.0–7.0 mm long, oblong, fragile, opaque. Seeds 0.6–1.0 mm wide, 0.4–0.8 mm high, testa smooth or papillate.

Distribution. South Central Turkey, W and N Syria (Fig. 7). Specimens from near the border between Iraq and Iran with ciliate petal claws but in other characteristics resembling *S. chaetodonta* have been suggested to be of hybrid origin (Melzheimer 1988) and deserve closer investigation.

Notes. The stem often has a larger number of internodes than other taxa in the section, sometimes as many as 20, although more often up to 12 clearly separated, distinct stem internodes. The middle internodes are shorter than or up to two (three) times the length of the subtending pair of leaves (the basalmost nodes are very short for all species). This gives this taxon a "leafy" appearance, reinforced by many branches and leafy shoots in leaf axils. The uppermost axillary branches are often opposite. This taxon is very variable, but is recognized by the many internodes, the ciliate petal claws and the small mamillae on the seeds.

Silene cassia is the name used for white flowered variants according to Coode and Cullen (1967). It is possible that the name *S. ehrenbergiana* Rohrb. [in Bot. Zeitung (Berlin) 25: 83. 1867. – Type: "Bei Fakra (?) in Syrien im Juni" Ehrenberg, B destroyed?] is associated with this taxon, but we have not been able to confirm this.

Nomenclatural notes. Many authors have used the name *S. kotschyi* Boiss. for this species (e.g. Boissier 1867, Williams 1896, Post 1932, Chowdhuri 1957, Mouterde 1966, Coode and Cullen 1967, Meikle 1977). Melzheimer (1988) treated *S. kotschyi* Boiss. as a synonym of *S. microsperma* Fenzl. We have not been able to find any type specimen of *S. microsperma*. Fenzl noted *specimen unicum* in the protologue, so it is possible that the only type material has been destroyed during the Second World War bombings of Berlin. The description made by Fenzl is short and unspecific and fits any species in *S.* sect. *Arenosae*. However, Rohrbach (1868) used the name *S. microsperma* Fenzl and listed *S. kotschyi* Boiss. as a synonym, and it is likely that he had seen the specimen cited by Fenzl. Burtt and Lewis (1952) use the name *S. kotschyi* Boiss., but they cited the publication year as 1842, the same as for *S. microsperma* Fenzl. Stafleu and Cowan (1976) stated 1843 as the true publication year for the first part of Boissier's *Diagnoses* *plantarum Orientalum novarum*. Burtt and Lewis (1952) pointed out that Rohrbach described *S. microsperma* as having glabrous petal claws, not ciliate as the taxon dealt with here. The type specimen for *S. microsperma* Fenzl was collected in an area that nowadays belongs to Turkey, at the mouth of the river Nahr al-Asi (also known as Orontis/Orontes), probably near Samandagi (old name Süveydiye, probably the same as Svedie). There are collections from this area (*Haradjian 3069* in G, *Pabot s.n.* in G, *Mouterde V 58* in G, *Haradjian 1480* in E, *Davis*, *Dodds & Cetik 19551* in C) that clearly belong to this taxon. The type locality for *S. cassia* Boiss. is also found in this area. We therefore follow Melzheimer (1988) and use the name *S. microsperma* Fenzl for this taxon.

The *S. microsperma* subsp. *microsperma* accessions form a subclade in the *S. microsperma* clade in the *RPB2* phylogeny (PP = 0.96, Fig. 5).

8b. *Silene microsperma* subsp. *cypria* Eggens, F.Jafari & Oxelman, nom. nov.

urn:lsid:ipni.org:names:77211377-1

≡ *Silene stenocalyx* H.Lindb., Acta Soc. Sci. Fenn., Ser. B, Opera Biol. 2(7): 15. 1946. nom. illeg. [non Rouy & Foucaud]. Type: [Cyprus], Famagusta, in colle arenoso juxta mare, 8 July 1939, *H. Lindberg s.n.* (lectotype, designated by G. Lazkov in H. Väre (2012: 82): H! [H-1339014]; isolectotypes: LE! [LE01051367], H! [H-1339012, H1339013, H1339014, H1339015, H1339017], K! [K000728453, K000728454], CAI! [CAI000023])

≡ *Silene kotschyi* Boiss. var. *stenocalyx* (H. Lindb.) Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 276. 1957. Type: Based on *S. stenocalyx*

Description. 20.0–40.0 cm tall, erect or spreading. Stem pubescent in lower part, more or less glabrous but with sessile glands in upper part; with 10–20 distinct internodes, the uppermost internode 2.0–4.0 cm long and equal to the next upper internode. Cauline leaves oblanceolate 10.0–30.0 × 1.0–2.0 mm, pubescent. Calyx 12.0–13.0 mm long, campanulate at anthesis and clavate in fruit, pubescent, scabrous; teeth unequal; shorter ones 1.5–2.0 mm, lanceolate, acuminate; longer ones 2.0–2.5 mm, lanceolate, acuminate; marginal hairs long (longer than 0.5 mm), dense. Inflorescence non-divaricate, branch axile (much) less than 90°. Petal claws 6.0–7.0 mm long, ciliate; limbs 4.0–5.0 mm long, bifid, upper-surface white or pink, lobes oblong, petal limbs cleft to middle or more; coronal scales ovate, apex dentate or erose. Anthophore 5.0–6.0 mm long, densely puberulent. Anthers included; filaments 6.0–7.0 mm long, glabrous or pubescent. Styles included. First pedicel 0.5–1.0 cm in flower, and 1.0 cm in fruit, erect, glabrous, apex antrorse. Capsule 7.0 mm long, oblong, fragile, opaque. Seeds 0.7–0.9 mm wide, 0.7 mm high, testa smooth.

Distribution. Cyprus (Famagusta) (Fig. 7).

Notes. Distinguished by its rather "leafy" appearance (even more than subsp. *microsperma*), due to the many short internodes (of about half to the same length as the subtending pair of leaves), the short pedicels and the short calyx teeth in comparison with the calyx tube length. Restricted to the area around Salamis and Famagusta, on the north coast of Cyprus. This subspecies is very similar to *S. microsperma* subsp. *maritima* (Boiss.) Eggens, F.Jafari & Oxelman, comb. & stat. nov. Despite the existence of morphological overlaps, *S. microsperma* subsp. *cypria* is taller and has shorter calyx.

This subspecies is nested within a clade including *S. microsperma* subsp. *modesta* (Boiss. & C.I. Blanche) Eggens, F.Jafari & Oxelman, comb. & stat. nov., *S. exsudans*, *S. chaetodonta* ID. 181 and *S. georgievskyi* ID. 42 in *RPB2* tree (PP = 0.80, Fig. 5). This subspecies is closely related to *S. microsperma* subsp. *maritima* in the chloroplast phylogeny (PP = 0.93, Fig. 4), however, the ITS phylogeny does not have enough resolution to show the closest relative of this subspecies. All subspecies of *S. microsperma* except *S. microsperma* subsp. *cypria* share a 6 bp insertion in *rps16*. The absence of this insertion, subtle morphological differences, and geographical distinction lead us to treat it as a subspecies.

8c. *Silene microsperma* subsp. *maritima* (Boiss.) Eggens, F.Jafari & Oxelman, comb. et stat. nov.

urn:lsid:ipni.org:names:77211378-1

≡ *Silene kotschyi* Boiss. var. *maritima* Boiss., Flora Orientalis, 1: 1867. Type: [Turkey], in arenosis maritimis Ciliciae ad Mersina, 2 June 1855, *B. Balansa 801* (lectotypes, designated here: G-BOIS! [G00544628]; isolectotypes: G! [G00378630, G00378631], K! [K000728449], JE! [JE00016142, JE00016143], L [L.1713650], WAG! [WAG0004032])

Description. 5.0–20.0 cm tall, spreading. Stem pubescent in lower part, scabrous, pubescent with sessile glands in upper part; with 5–8 distinct internodes, the uppermost internode (0.5–)1.0–3.0 cm long and obviously longer than the next upper internode. Basal leaves oblanceolate 10.0–30.0× 1.0–3.0 mm, pubescent. Cauline leaves oblanceolate 10.0–30.0 × 1.0–3.0 mm, pubescent. Calyx 13.0–15.0 mm long, campanulate at anthesis and clavate in fruit, pubescent; teeth unequal; shorter ones 2.0–3.0 mm, lanceolate, acuminate; longer ones 2.0–4.0 mm, lanceolate, acuminate marginal hairs long (longer than 0.5 mm), dense. Inflorescence non-divaricate, branch axile (much) less than 90°. Petal claws 6.0–7.5 mm long, ciliate; limbs 5.0–6.5 mm long, bifid, upper-surface white, lobes oblong, petal limbs cleft to middle or more, lower-surface white; coronal scales 0.9–1.5 mm long, ovate, apex laciniate or dentate. Anthophore 5.0–6.0 mm long, tomentose or puberulent. Anthers exserted; filaments 6.0–9.0 mm long, sparsely pubescent . Styles slightly exserted. First pedicel 1.0–2.0 cm early flower, 1.0–2.0 cm in fruit, erect, glabrous, apex antrorse. Capsule 6.0–8.0 mm long, oblong, fragile, opaque. Seeds 0.7–0.9 mm wide, 0.4–0.7 mm high, testa smooth.

Distribution and habitat. Mediterranean coasts of the Içel, Adana, and Hatay provinces (Turkey) and N Syria (Fig. 7). Growing on seashores.

Notes. This taxon is readily recognized by its small size, oblanceolate leaves, and relatively long calyx. It is also characteristically tomentose. The exposed habitat (seashores) results in the calyx primary veins often to be reddish. Even though it resembles *S. exsudans* in size, habitat, leaf shape and indumentum, it is readily distinguished from this taxon by its longer (13–15 mm) calyx with longer lanceolate teeth (see also notes about *S. exsudans*). The two taxa are allopatric.

The ITS and *rps16* sequences of this subspecies are included in phylogenetic analyses, where this taxon is unresolved among others subspecies in the species and ITS trees except for the *rps16* phylogeny.

8d. *Silene microsperma* subsp. *modesta* (Boiss. & C.I.Blanche) Eggens, F.Jafari & Oxelman, comb. et stat. nov.

urn:lsid:ipni.org:names:77211379-1

≡ *Silene modesta* Boiss. & C.I.Blanche, Diagn. Pl. Orient. ser. 2, 6: 33. 1859. Type: [Lebanon], in Syriâ ad via circà Beyrout ubi detexit, *C.I. Blanche 319* (holotype: G-BOIS! [G00544238])
≡ *Silene chaetodonta* var. *modesta* (Boiss. & C.I.Blanche) Boiss., Fl. Orientalis, 1: 1867. Type: Based on *S. modesta*

Description. 20.0–50.0 cm tall, erect or sometimes spreading. Stem scabrous, pubescent in lower part, scabrous, glabrous with sessile glands in upper part; with 4–10 distinct internodes, the uppermost internode 3.0–6.0 cm long and obviously longer than the next upper internode. Cauline leaves oblanceolate 10.0–40.0 × 1.0–4.0 mm, pubescent. Calyx 13.0–15.0 mm long, campanulate at anthesis and clavate in fruit, pubescent, scabrous; teeth unequal; shorter ones 2.0–3.0 mm, ovate, acuminate; longer ones 2.0–4.0 mm, lanceolate, acuminate; marginal hairs long (longer than 0.5 mm), dense. Inflorescence non-divaricate, branch axile (much) less than 90°. Petal claws 8.0–9.0 mm long, ciliate; limbs 3.0 mm long, bifid, white to pink, lobes oblong, petal limbs cleft to middle or more; coronal scales ca 1.0 mm long, ovate, apex entire or slightly erose. Anthophore 2.5–3.5 mm long, densely puberulent. Anthers included; filaments 6.0–9.0 mm long, glabrous or sparsely pubescent. Styles included. First pedicel 1.0–3.0 cm in flower, 2.0–4.0 cm in fruit, erect, glabrous, apex antrorse. Capsule 9.0–11.0 mm long, oblong or ellipsoid, robust. Seeds 0.6–0.8 mm wide, 0.6–0.7 mm high, testa smooth.

Distribution. Palestine, Lebanon (Fig. 7).

Notes. Distinguished by the short anthophore and long capsule that is unusually thick-walled and robust. This taxon has all the characteristics of a self-pollinating *Silene*, e.g. short anthophore, large capsule, small petal limbs, and anthers and styles included in the corolla mouth (Aydin et al. 2014b). This taxon used to be considered as closely related to *S. chaetodonta*, but the molecular phylogenies (Figs 1, 3, 5) show that "*S. modesta*" belongs in the *S. microsperma*-group. In order to emphasize this information, we have therefore decided to treat this taxon as a subspecies of *S. microsperma* rather than recognizing it as a species.

9. ***Silene exsudans*** **Boiss. & Heldr., Diagn. Pl. Orient. 8: 76. 1849.**

Type. [Turkey, Antalya] in arenosis maritimis portûs Tchinova Lyciae, [12.5.1845], *T.H.H. v. Heldreich s.n.* (lectotype, designated here: G-BOIS! [G00544614]; isolectotypes: G! [G00226916], BM! [BM000990900], E! [E00286972], LE! [LE01051364], WAG! [WAG0191880]).

Description. 5.0–20.0 cm tall, spreading. Stem pubescent in lower part, scabrous, pubescent with sessile glands in upper part; with 4–7 distinct internodes, the uppermost internode obviously longer than the next upper internode. Basal leaves oblanceolate or spathulate, pubescent. Cauline leaves oblanceolate 10.0–25.0 × 1.0–5.0 mm, pubescent, scabrous. Calyx 7.5–8.5 mm long, campanulate at anthesis and clavate in fruit, pubescent, scabrous; teeth unequal; shorter ones 2.0–3.0 mm, deltoid, acuminate; longer ones 2.0–4.0 mm, deltoid, mucronate; marginal hairs long (longer than 0.5 mm). Inflorescence non-divaricate, branch axile (much) less than 90°. Petal claws 5.0–6.0 mm long, ciliate; limbs 3.0–4.5 mm long, bifid, upper-surface pink, lobes ovate, petal limbs cleft to less than middle, lower-surface pink; coronal scales ca 0.5 mm long, ovate, apex dentate or erose. Anthophore 3.0–5.0 mm long, densely puberulent. Anthers included; filaments 5.0–6.0 mm long, glabrous or pubescent. Styles exserted. First pedicel 1.0–2.0 cm in flower, 1.0–3.0 cm in fruit,erect, glabrous, apex antrorse. Capsule 5.0–7.0 mm, ellipsoid, fragile, opaque. Seeds 0.7–0.8 mm wide, 0.8–1.0 mm high, testa smooth.

Distribution and habitat. S Mediterranean, Turkey (Lycia) (Fig. 7). On sandy beaches near the sea.

Notes. Readily distinguished by its short calyx and short, deltoid (or broadly ovate) calyx teeth from *S. microsperma* subsp. *maritima* (see also notes about that taxon), its oblanceolate leaves, ascending habit and short size of the plant. Coode and Cullen (1967) considered "*S. exsudans*" as a synonym of *S. kotschyi* var. *maritima*. Our phylogenies (Figs 1, 3, 5) verify it as belonging to the *S. microsperma*-group but as a distinct species.

We generated two ITS sequences for *S. exsudans*, which form a strongly supported clade (PP = 1.00 MPB = 90% MLB = 95%, Fig. 3) in the phylogeny. This species is nested within the unresolved *S. microsperma* clade in the ITS tree and the *RPB2* phylogeny (PP = 0.98 MPB = 86% MLB = 97%, Fig. 3, PP = 0.96 MPB = 83%, Fig. 5). The significant morphological differences lead us to treat *S. exsudans* as a distinct species instead of merging it as subspecies of *S. microsperma*.

Conclusion

According to the current chloroplast and nuclear phylogenies, *S.* sect. *Arenosae* is a monophyletic group, and distinct from other lineages of *S.* sect. *Rigidulae* s.l. Although our ITS phylogeny does not provide sufficient resolution for the monophyly and closest relatives of *S.* sect. *Arenosae*, the ITS phylogeny based on a comprehensive sampling from the species-rich genus *Silene* supports the monophyly of the section. Our species tree recovers one lineage (lineage 4 in Fig. 1 which is called *S.* sect. *Muscipula*) of *S.* sect. *Rigidulae* s.l. centered in N Africa and the W Mediterranean as the closest relative of *S.* sect. *Arenosae*.

Despite the affinity between *S. chaetodonta* and one accession of *S. georgievskyi* based on the similarity matrix and phylogenies, some morphological differences lead us to retain these taxa as distinct species. The close relationship of *S. georgievskyi* ID. 42 to the clade of *S. microsperma* rather than *S. chaetodonta* and another accession of *S. georgievskyi* in the *rps16* and *RPB2* phylogenies suggests a possible hybrid origin of *S. georgievskyi*.

We propose two new combinations and status (*S. microsperma* subsp. *maritima* and *S. microsperma* subsp. *modesta*) and one new name (*S. microsperma* subsp. *cypria*).

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Supplementary material 1

Material used for phylogenetic analyses

Authors: Frida Eggens, Farzaneh Jafari, Mikael Thollesson, Simon Crameri, Shahin Zarre, Bengt Oxelman

Data type: Table including vouchers

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RESEARCH ARTICLE

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Didymocarpus phuquocensis, a new species of Gesneriaceae from Phu Quoc Island, South-western Vietnam

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Abstract

A new species of Gesneriaceae, *Didymocarpus phuquocensis*, is described and illustrated from Phu Quoc National Park, Kien Giang Province, South-western Vietnam. It is most similar to *D. pulcher*, *D. hookeri* and *D. punduanus* in having 3-verticillate petiolate leaves, morphologically similar calyx, corolla, stamens, pistil and fruit, but differs from all in the glandular-pubescent stems, petioles and leaf blades, 1(–2)-flowered cymes, longer corolla and fruit and longer and densely glandular-puberulent ovary. Data on distribution, ecology, phenology and provisional conservation assessment of the new species are given along with an illustration and a colour plate.

Keywords

Didymocarpus, Kien Giang, new species, taxonomy, Vietnam

Introduction

The genus *Didymocarpus* Wallich was established in 1819, based on the species *D. primulifolius* D.Don from Nepal. The genus has previously been considered to comprise about 180 species distributed in tropical Asia with a few scattered in Africa and Australia (Wallich 1819; Don 1825; Wang et al. 1998; Weber and Burtt 1998; Weber et al. 2000). The taxonomic delimitation of the genus *Didymocarpus* has varied considerably over time (e.g. Burtt 1998; Weber et al. 2000; Möller et al. 2011; Möller and Clark 2013; Li et al. 2015). By combining molecular phylogenetic data and morphological revision of *Didymocarpus*, recent studies have remodelled and reduced this number (Vitek et al. 2000; Weber et al. 2000, 2011a, b; Möller et al. 2011; Li et l. 2015; Möller et al. 2017), with some species being placed in other genera, particularly to *Henckelia* Spreng. (ca. 60 species (Weber et al. 2011b, Middleton et al. 2013)), *Petrocodon* Hance (more than 20 species (Weber et al. 2011a)) and *Tribounia* D.J.Middleton (2 species (Middleton and Möller 2012)). The genus, as currently recognised, has around 98 species (Möller et al. 2017). Species of *Didymocarpus* are distinguished from other genera of Gesneriaceae by having: lithophyte perennial habit, ovate to ovate-cordate lamina which is mostly glandular-hairy, tubular corolla with an oblique limb (rarely trumpet-shaped or bell-shaped), two fertile stamens, three staminodes, a capitate stigma, an orthocarpic ovary and a bivalve capsule which dehisces loculicidally (Weber et al. 2000). As currently circumscribed, *Didymocarpus* ranges from northwest India, eastwards through Nepal, Bhutan, northeast India, Burma (Myanmar), southern China, Vietnam, Laos, Cambodia, Thailand and the Malay Peninsula, with the highest species diversity being found in China and Thailand (Weber and Burtt 1998; Weber et al. 2000; Nangngam and Maxwell 2013; Nangngam and Middleton 2014; Möller et al. 2016). In Vietnam, five species of *Didymocarpus* have been reported, namely *D. bonii* Pellegr., *D. kerrii* Craib, *D. poilanei* Pellegr., *D. pulcher* C.B.Clarke and *D. purpureobracteatus* W.W.Sm. (Pellegrin 1930; Pham 2000; Phuong and Xuyen 2012; Phuong et al. 2014), but *D. bonii* Pellegr. [= *Calcareoboea bonii* (Pellegr.) Burtt] has been recognised as *Petrocodon bonii* (Pellegr.) A.Weber & Mich.Möller (Weber et al. 2011a). Recently, *Didymocarpus puhoatensis* X.Hong & F.Wen was described from Central Vietnam (Hong et al. 2018).

During medicinal plant investigations in Phu Quoc National Park (NP), Kien Giang Province, south-western Vietnam, several interesting plants of a small species of Gesneriaceae were collected by the authors in 2018–2019. The flowers of these plants have a capitate stigma and other features characterising this plant as *Didymocarpus* (Wang et al. 1998, Weber et al. 2000). A critical examination of living flowers, herbarium specimens of these plants and comparison with type material and protologues of all closely-related species in Vietnam and neighbouring countries (e.g. Clarke 1874, 1883, 1884; Wallich 1829; Wang et al. 1998; Pham 2000; Nangngam and Maxwell 2013; Phuong et al. 2014; Nangngam and Middleton 2014; Sinha and Datta 2016; Roy 2017), suggested that these specimens were different from the other known *Didymocarpus* species. These plants with 3-verticillate, petiolate leaves, campanulate calyx, funnelform corolla found in Phu Quoc NP show similarities in these characters with *D. pulcher*, *D. hookeri* C.B.Clarke and *D. punduanus* Wall. ex R.Br. However, it shows significant differences in its vegetative and floral structures (see Table 1) and we describe it here as a species new to science (see also Taxonomic Notes).

Materials and methods

The descriptions are mainly based on measurements from flowering material of living plants in the field, supplemented by measurements from herbarium specimens. Type specimens of the most closely-related species were examined from the herbaria material from the following herbaria: E, K, HN, IBK, P, VNM, VNMN and W (herbarium codes follow Thiers (2020)), as well as digitised specimen images of *Didymocarpus* species also being accessed from botanical websites (e.g. https://science.mnhn.fr/, http://www.cvh.org.cn/, https://plants.jstor.org/). All morphological characters were studied under a dissection microscope and are described using the general terminology and

Table 1. Morphological comparison of *C. puhoatensis* with its most closely-related taxa (based on Wallich 1829; Clarke 1874, 1883, 1484; Sinha and Datta 2016; Roy 2017).

Characters	*D. phuquocensis*	*D. pulcher*	*D. hookeri*	*D. punduanus*
Plant height	(8–)10–19 cm	ca. 30.5 cm	ca. 40 cm	20.3–25.4 cm
Stem	glandular-pubescent	puberulous, eglandular	villous, eglandular	pubescent, eglandular
Petiole	glandular-pubescent	puberulous, eglandular	villous, eglandular	pubescent, eglandular
Leaves	3-verticillate petiolate leaves, terminal whorl of smaller sessile leaves	3–4- verticillate petiolate leaves, terminal whorl of smaller sessile or subsessile leaves	usually 3–4- verticillate petiolate leaves, uppermost leaves sessile	3- verticillate petiolate leaves, 2 sessile leaves at the apex
Leaf blade				
Margins	serrate	crenulate to serrate	crenulate	shallowly crenulate
Base	attenuate or cuneate	auriculate cordate	cordate	cordate
Apex	attenuate to acute	short acute	subobtuse	subobtuse
Indumentum	glandular-pubescent	pubescent, eglandular	somewhat villous eglandular	puberulous, eglandular
Inflorescence	axillary or terminal 1(–2)-flowered cyme	axial and terminal many-flowered cyme	terminal many-flowered cyme	terminal many-flowered cyme
Bracts	oblong-lanceolate, abaxially densely multicellular glandular-pubescent	rounded/suborbic-ular, sparsely viscous pilose	rounded, glabrescent	ovate, nearly glabrous
Corolla	4.8–5.3 cm long, light purple, glabrous	2.5–3 cm, violet-purple, glabrous or outside sparsely multicellular-villous	ca. 1.4 cm long, pale yellow with rose marks or nearly white, outside pilose	ca. 2.2 cm long, purple, nearly glabrous
Ovary	ca. 3 cm long, densely multicellular glandular-puberulent	1.1–1.8 cm, glabrous	1.1–1.7 cm long, pubescent	0.7–1.3 cm long, glabrous
Style	sparsely glandular-puberulent	glabrous	glabrous	glabrous
Capsule	4.4–5.5 cm long	ca. 4 cm long	1.3–3.5 cm long	ca. 4 cm long

standard work of Wang et al. (1998) and Harris and Harris (2001). A distribution map was created using SimpleMappr (http://www.simplemappr.net/) (Shorthouse 2010). Conservation status was assessed using the IUCN Red List Categories and Criteria version 3.1 (IUCN 2019) and inferring from the GeoCAT website (http://geocat.kew.org/editor) (Bachman et al. 2011).

Taxonomic treatment

Didymocarpus phuquocensis **N.S.Lý, T.L.Tran & N.G.Cao, sp. nov.**

urn:lsid:ipni.org:names:77211380-1
Figures 1, 2

Diagnosis. *Didymocarpus phuquocensis* is most similar morphologically to *D. pulcher, D. hookeri* and *D. punduanus* in the 3-verticilate, petiolate leaves, the morphologically-similar calyx, corolla, stamens, pistil and fruit, but differs from all in the glandular-pubescent stems and petioles (vs. puberulous, villous, pubescent and eglandular of the latter three, respectively), glandular-pubescent leaf blades (vs. pubescent, somewhat villous, puberulous and eglandular, respectively), 1(–2)-flowered cymes (vs. many-flowered cymes of the latter three), longer corolla 4.8–5.3 cm long (vs. 2.5–3 cm in *D. pulcher,* ca. 1.4 cm in *D. hookeri* and ca. 2.2 cm in *D. punduanus*), longer and densely multicellular glandular-puberulent ovary ca. 3 cm long (vs. 1.1–1.8 cm and glabrous in *D. pulcher*, 1.1–1.7 cm and pubescent in *D. hookeri* and 0.7–1.3 cm and glabrous in *D. punduanus*) and longer fruits 4.4–5.5 cm long (vs. ca. 4 cm long in *D. pulcher*, 1.3–3.5 cm long of *D. hookeri* and ca. 4 cm long in *D. punduanus*).

Type. Vietnam. Kien Giang Province: Phu Quoc District, Phu Quoc NP, Suoi Mo, 18 September 2018, 10°14'40.90"N, 104°2'14.15"E, 82 m elev., *Lý Ngọc Sâm, Cao Ngọc Giang, Nguyễn Thị Liên, Ngô Minh Huyền, Hùng, Hà Văn Long, TNB-305* (Holotype: VNM, isotype: P, NIMM).

Description. Deciduous, perennial, epilithic herb, (8–)10–19 cm tall, stems 2.5–3.5 mm in diameter. ***Dry season*****:** new vegetative buds produced from the rhizome which then develops during the rainy season. ***Rainy season*****:** stem erect, (3–)4 nodes, pale greenish, densely white multicellular glandular-pubescent; the longest node separated from the base of stem 5.7–12.2 cm long, the medium nodes at the middle stem 1.5–4.5 cm long, the shortest nodes very shortly distanced (0.2–0.5 cm long) at the apex. **Leaves** 3- verticillate, petiolate in the 2nd and 3rd whorls, other whorls with smaller and sessile or subsessile leaves; blades coriaceous, adaxially light greenish, abaxially whitish-green, asymmetrically narrowly elliptic to elliptic-ovate, the largest ones 7.2–10 × 2.4–3.7, the smaller ones 1–4.6 × 0.5–2.1 cm, adaxially densely white multicellular glandular-pubescent, abaxially sparsely white multicellular glandular-pubescent, apex attenuate to acute, base lightly oblique, attenuate to cuneate, margin serrate; venation pinnate, with 5–6 of ascending secondary veins on each side of midrib, somewhat opposite, adaxially obscure, abaxially prominent, densely covered with indumentum as

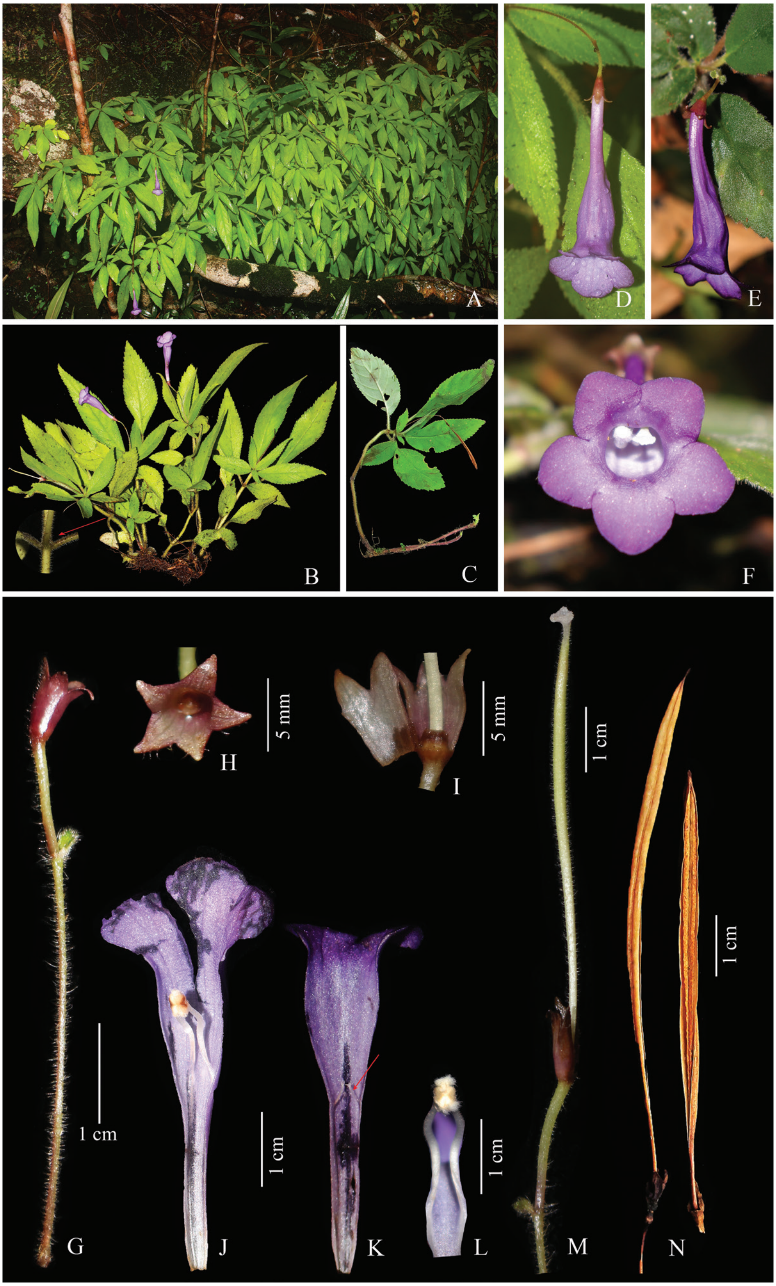

Figure 1. *Didymocarpus phuquocensis* **A** flowering plants in natural habit **B** flowering plants showing 3-verticillate leaves (red arrow) **C** mature plant with dried fruit and new stems **D** flower (top view) **E** flower (side view) **F** flower (front view) **G** inflorescence with peduncle, bract and calyx **H** calyx (top view) **I** longitudinal section of calyx showing disc **J** longitudinal section of corolla showing anterior (lower) lip with fertile stamens **K** longitudinal section of corolla showing posterior (upper) lips and staminodes (red arrow) **L** close-up of fertile stamens **M** ovary and calyx **N** dried fruits. The coloured plate prepared by Ngọc-Sâm Lý.

the stem; petioles terete, unequal in length, 0.5–3.2 cm long [the longest ones 3–3.2 cm, the shortest ones 0.5–1 cm], 2–2.5 mm in diam., whitish-green, sometimes tinted greenish-purple above, with indumentum as the stem. **Inflorescences** terminal or subterminal, cyme 1(–2) flowered, pendent; **peduncle** slender, (1.3–)3.1–4.5 cm long, ca. 0.5 mm in diam., tinted reddish-green, covered with white multicellular glandular and glandular-pubescent; **pedicels** 5–11 mm long, ca. 0.7 mm in diam., pale green, with indumentum as the peduncle, but more sparse; **bracts** paired; lanceolate to oblong-lanceolate, 4–5 × 1–1.5 mm, apex round to acute, margin entire, green, adaxially sparsely multicellular glandular-pubescent, abaxially densely white multicellular glandular-pubescent. **Calyx** campanulate, 5–6.5 mm long, dull reddish, outside sparsely multicellular glandular-puberulent; tube 3–4 mm long, 2–2.5 mm in diam.; lobes triangular, (sub)equal, 5-lobed, symmetrical, 2–2.5 mm long, ca. 1.5–1.8 mm wide at base, apices acute. **Corolla** funnelform, 4.8–5.3 cm long, glabrous, light purple, paler at base; tube 3.8–4.1 cm long, base narrow, 2–3 mm in diameter, widening abruptly at 1.9–2.1 cm from the base, widest at throat, 1–1.1 cm in diam.; lobes (sub)orbicular; anterior (lower or abaxial) lip 3-lobed, unequal, the middle one 5–7 × 7–10 mm, the lateral ones 5–7 × 4.5–5 mm, apices rounded; posterior (upper or adaxial) lip 2-lobed, slightly equal, 5–6 × 7.5–8.5 mm, apices rounded. **Stamens** 2, inserted at 2.2–2.4 cm above the base of the corolla; filaments slender, white, glabrous, 7–8 mm long, glandular-puberulent on the connective; anthers brownish, oblong, 2–2.2 × ca. 1 mm, tips and bases rounded, white-bearded; **staminodes** 3, inserted ca. 3 mm below the stamens, reduced to filaments, equal in length, 2.5–3.5 mm long, glabrous, tips with few glandular-puberulent. **Disc** cupular, ca. 1 mm high, margin irregular sinuate. **Pistil** ca. 3.2 cm long; **ovary** cylindrical, greenish with white towards the base, ca. 3 cm long, 1–1.5 mm in diam., densely glandular-puberulent; **style** continuous with the top of the ovary, ca. 2 × 1 mm, whitish, sparsely glandular-puberulent; **stigma** irregular capitate, ca. 1 × 1 mm, concave, white, papillose. **Capsules** straight to slightly curved, linear, glabrous, 2-valved, loculicidal dehiscent, 4.4–55 cm long, 1–1.5 mm in diam., turning brown when ripe, calyx and style persistent. **Pollen** and **Seeds** not studied.

Distribution and habitat. This species grows in moist places and shaded areas in primary tropical evergreen forests, on granite bedrock along streams or on moist and mossy cliffs in Phu Quoc NP, at 80–530 m elev. (Fig. 2).

Phenology. Flowering and fruiting from May to October.

Etymology. The specific epithet "*phuquocensis*" was named after the type locality.

Provisional conservation status. At present, four relatively-large subpopulations consisting of about 2000 mature individuals/mature clumps have been observed in Phu Quoc NP. The extent of occurrence (EOO) and the area of occupancy (AOO) were estimated using the web Geospatial Conservation Assessment Tool or GeoCAT (Bachman et al. 2011) and the auto-value cells width 2 km were calculated to be 53.7 km^2 and 16 km^2, respectively. These two values meet the criteria B1 (EOO < 100 km^2) for Critically Endangered and B2 (AOO < 500 km^2) for Endangered, following the IUCN Red List Categories and Criteria Version 3.1 (IUCN 2019). Although the known habitat of the new species is protected as part of the National Park, its habitat is fragmented and still faces some risk due to loss of the habitat within some parts

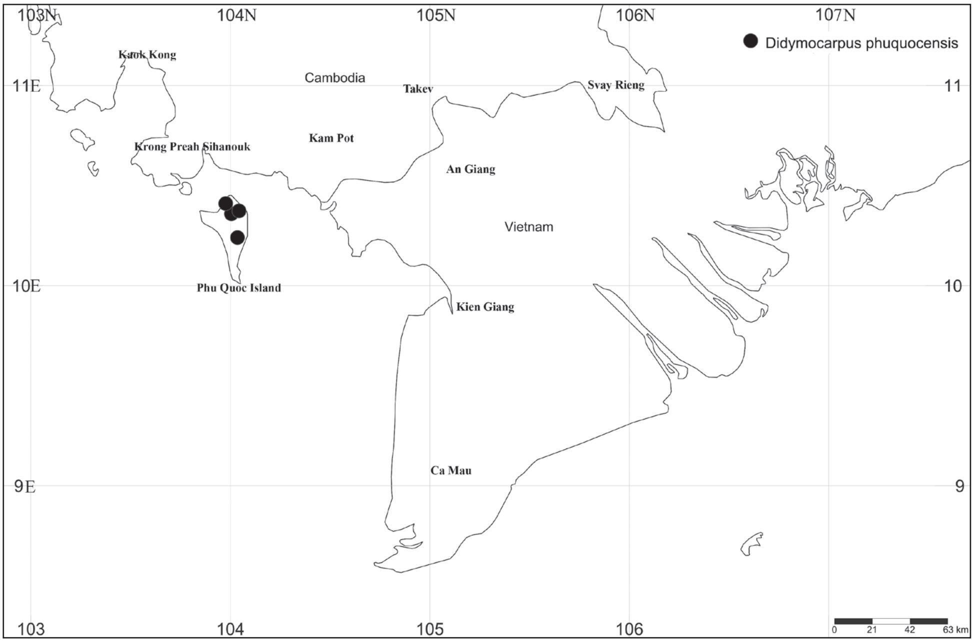

Figure 2. Distribution map of *Didymocarpus phuquocensis* in Phu Quoc National Park, Phu Quoc Island, Kien Giang Province.

of its range (in particular the clearing of forest land for agricultural fields and building of numerous roads and tourism areas). Based on the IUCN Red List Criteria (IUCN 2019), we therefore provisionally assess this species as Endangered (EN B2ab(iii), C).

Other specimens examined (*Paratypes*). VIETNAM. Kien Giang Province: Phu Quoc Island, Phu Quoc NP, K7 peak, 10°21'53.42"N, 104°0'31.22"E, 356 m elev., 21 May 2019, *Lý Ngọc Sâm*, *Hà Văn Long*, *TNB-430* (VNM); the same locality, Nui Chua peak, 10°22'40.09"N, 104°2'6.24"E, 532 m elev., 22 July 2019, *Cao Ngọc Giang*, *Ngô Minh Huyền*, *Hà Văn Long*, *TNB-502* (VNM); the same locality, Ham Rong Mount, 10°24'6.34"N, 103°58'6.47"E, 351 m elev., 10 July 2019, *Cao Ngọc Giang*, *Ngô Minh Huyền*, *Hà Văn Long*, *TNB-508* (VNM).

Vernacular name. Vietnamese language: Song bế phú quốc.

Taxonomic notes. Morphologically, the 3-verticillate petiolate leaves of *D. phuquocensis* are shared with several species of *Didymocarpus*, such as *D. insulsus* Craib (north-eastern, Thailand), *D. tristis* Craib (Chanthaburi Province, south-eastern Thailand), *D. dongrakensis* B.L.Burtt (northeast Thailand) *D. newmanii* B.L.Burtt (Chanthaburi Province, south-eastern Thailand), *D. pulcher* (from India, Buhtan, Nepal, China to Vietnam), *D. hookeri* (Assam, Arunachal Pradesh, Meghalaya and Sikkim, India), *D. punduanus* (Assam, Meghalaya and Nagaland, India) (Wang et al. 1998; Nangngam and Maxwell 2013; Phuong et al. 2014; Sinha and Datta 2016; Roy 2017). Of these, the campanulate calyx of the new species is similar to *D. pulcher*, *D. hookeri* and *D. punduanus*, but distinguished from *D. insulsus*, *D. newmanii* and *D. tristis* which have the calyx 5-lobed to the base. *Dydimocarpus phuquocensis* is most similar to *D. pulcher*, *D. hookeri* and *D. punduanus* in the morphological characters of 3-verticillate petiole leaves, the same shape of calyx, corolla, stamens, pistil and fruit. The major differences between the new species and the three latter are outlined above in the diagnosis. Moreover, the shorter plant height ((8–)10–19 cm), the narrowly elliptic to elliptic-ovate leaf blades that have serrate leaf margins, attenuate to cuneate leaf base and attenuate to acute leaf apex, the oblong-lanceolate bracts being abaxially densely multicellular glandular-pubescent, the light purple corolla and sparsely glandular-puberulent styles of *D. phuquocensis* also distinguish it from *D. pulcher*, *D. hookeri* and *D. punduanus*. A detailed morphological comparison between *D. phuquocensis*, *D. pulcher*, *D. hookeri* and *D. punduanus* is provided in Table 1.

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RESEARCH ARTICLE

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Distribution pattern and habitat preference for *Lobelia* species (Campanulaceae) in five countries of East Africa

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Abstract

East Africa is one of the centres of distribution and diversity for *Lobelia* L. (Campanulaceae, sub-family Lobelioideae). *Lobelia* habitats in East Africa have been facing habitat fragmentation and loss, which are recognised as a major threat to biodiversity. However, previous plant conservation studies in East Africa only focused on protected areas and ignored unprotected areas. Future conservation strategies of plants, such as *Lobelia*, will depend on knowledge of their distribution patterns and habitat preference in East Africa. To understand the distribution pattern and the habitat preference of *Lobelia* in five countries (Kenya, Uganda, Tanzania, Rwanda and Burundi) of East Africa, we conducted a literature review in the seven major vegetation regions (afro-alpine, afro-montane forest, drier savannah, grasslands, wetter savannah, Zambezian woodland and semi-desert and desert). We also employed meander and patterned searches, which allowed greater opportunities for recording *Lobelia* species. Our results showed that the genus is distributed in all of the seven regions of the five countries with 54 taxa. The afro-montane forest region, with 41 taxa, is the richest in species diversity, followed by the Zambezian woodland region with 18 taxa. The semi-desert and desert region has the lowest number with only four taxa. The afro-alpine region has 15 taxa, although the region is the smallest by area. The herbaceous type was found in all regions, while the giant type has a clear preference for the afro-alpine and afro-montane forest regions. Future conservation for *Lobelia* should consider its habitat preference by, for example, focusing on the afro-alpine and afro-montane forest regions. This study will facilitate the setting of future conservation strategies for *Lobelia*.

Keywords

East Africa, *Flora of Tropical East Africa*, habitat preferences, *Lobelia*, vegetation region

Introduction

Understanding species richness, habitat preferences and geographical distribution patterns is imperative in formulating conservation strategies. Assessment of species habitat and distribution patterns dates back to the late 18th century (Forster et al. 1778). Johann Reinhold Forster, a naturalist, observed that there were species diversity and distribution gradients from the Equator to the Pole (Forster et al. 1778). Later, in 1805, Alexander von Humboldt (Humboldt 2005) suggested that there may be drivers that influenced the localisation, distribution and migration of plant species on Earth. Plants may demonstrate habitat preferences due to lower survival rates outside their preferred habitats (Comita et al. 2007). Consequently, plants are not uniformly distributed in a region (Brown 2014).

East Africa (EA) includes Kenya, Uganda, Tanzania, Rwanda, Burundi, Ethiopia, Somalia and South Sudan (Kalisa et al. 2019) and is a crucial biodiversity hotspot that is characterised by elevated plateaus and isolated mountains (Wang et al. 2020). The biomes in these EA countries were divided into altitudinal zones (Hedberg 1970), which have individual species microhabitats. The biomes were also divided into different regions including afro-alpine, afro-montane forest, drier savannah, grasslands, wetter savannah, zambezian woodland and semi-desert and desert regions (Kiage and Liu 2006). The distribution pattern for the EA species mainly depended on several factors, including geological events, elevation, edaphic factors (Stuart et al. 1990; Herron 2006), distance from the Equator, presence or absence of gene flow barriers, recent quaternary epoch, habitat preferences and anthropogenic activities (Hedberg 1954; Abdi 2013). For example, *Arabis alpina* L. (Brassicaceae) and *Turritis glabra* L. (Brassicaceae) have different habitat preferences. *Arabis alpina* has a preference for stream-banks and cliffs in an altitude of 2800–4800 m, while *T. glabra* has a preference for grasslands in an altitude of 920–2650 m (Agnew and Agnew 1994).

Lobelia L. (Campanulaceae, sub-family Lobelioideae) includes about 437 species. The genus is cosmopolitan, distributed in both temperate and tropical regions of Africa, America, Australia, New Zealand, Hawaii, Asia and other regions (Ruas et al. 2001; Lammers 2011; Antonelli 2008; Kokubugata et al. 2012). Africa is a species diversity centre for *Lobelia* species (lobelias), with 37% of all lobelias distributed in Africa (Kokubugata et al. 2012). *Lobelia* is well represented in EA, particularly in the early administrative divisions of Kenya (K1–7), Tanzania (T1–8), Uganda (U1–4), Rwanda and Burundi (Thulin 1984), where it inhabits most of the mountains and surrounding lowlands. The giant lobelias that are native to the higher altitude zones of the mountain groups in the EA form a conspicuous element of the flora.

Habitat loss and fragmentation are the major causes of biodiversity loss worldwide (Sukumaran and Jeeva 2008; Laurance 2010). *Lobelia* habitats in East Africa have been facing habitat fragmentation and loss (Kebede et al. 2007). Future conservation strategies of *Lobelia* in EA will depend on knowledge of their distribution patterns, habitat threats and habitat preferences. However, plant conservation studies in the EA only focused on protected areas and ignored unprotected areas (Eilu et al. 2007).

The distribution pattern of lobelias across different vegetations in the EA and the habitat preference remain unknown. As far as we know, lobelias are non-uniformly distributed in EA (Knox 1993; Kebede et al. 2007). For example, *Lobelia telekii* Schweinf. was only found on three mountains, Mt. Elgon, Aberdare Ranges and Mt. Kenya. *Lobelia deckenii* subsp. *burtii* (E.A.Bruce) Mabb., *Lobelia burtii* subsp. *telmaticola* E.B.Knox and *Lobelia burtii* subsp. *meruensis* E.B.Knox were only found in areas within the T2 region, specifically on Mt. Meru, Mt. Hanang and Mt. Loolmalassin in Tanzania (Thulin 1984). *Lobelia aberdarica* R.E.Fr. & T.C.E.Fr. inhabits the Cherangani Hills, Mau Ranges, Aberdare Ranges, Mt Elgon and Mt. Kenya. The upland afro-montane forest species *Lobelia giberroa* Hemsl. is widely spread within an altitude of 1200–3000 m in ten African countries including Kenya, Uganda, Tanzania, Sudan, Ethiopia, DR Congo, Rwanda, Burundi, Malawi and Zambia. The growth forms in this genus include annual or perennial herbs, shrubs or sub-shrub rosettes and small trees (Thulin 1984; Ruas et al. 2001). Amongst these growth forms, the most conspicuous are the branched inflorescence vs. unbranched inflorescence forms and giant vs. herbaceous forms (Fig. 1). Several studies have investigated the adaptation to afro-alpine environments, systematics and biogeography of lobelias (Knox and Palmer 1998; Kebede et al. 2007; Chen et al. 2016). For example, phylogeographic analyses indicated that *L. giberroa* could have migrated throughout different afro-mountains via the afro-montane forest bridge in previous interglacial periods (Kebede et al. 2007).

In this study, we reviewed previous literature and extracted data from our field survey. We aimed to identify the distribution pattern and habitat preference of *Lobelia* in five countries in the EA region (Fig. 1). This knowledge will facilitate the setting of future conservation strategies of the genus in EA.

Materials and methods

Study area

This study covered five of the eight East African countries, i.e. within and amongst the early administrative divisions of Kenya (K1–7), Uganda (U1–4), Tanzania (T1–8), Rwanda and Burundi. The other three countries (Ethiopia, Somalia and South Sudan) in EA have limited data from both herbaria and the *Flora of Tropical East Africa* (FTEA) on the distribution of the lobelias. Therefore, they were not included in this study. The study area ranged from coastal regions to the alpine zones of high mountains with changes in the elevation gradient. To obtain a clear understanding of the *Lobelia* habitats and distribution patterns, seven vegetation regions (afro-alpine, afro-montane forest, drier savannah, grasslands, wetter savannah, Zambezian woodland and semi-desert and desert) were used (Fig. 1; Kiage and Liu 2006). The vegetation regions in Rwanda and Burundi were not shown in the map of Fig. 1 (Kiage and Liu 2006). However, we recorded the distribution pattern of lobelias in the two countries by checking specimens and literature. Each lobelia in the two countries was assigned to the vegetation region, which is similar to the species' habitat(s).

Figure 1. The major vegetation regions in East Africa, modified from Kiage and Liu (2006). Two pictures were used as examples of giant lobelias and herbaceous lobelias. The left picture is the giant *Lobelia deckenii* Hemsl. from Mt Kenya, while the right picture is the herbaceous *Lobelia lindblomii* Mildbr. from Mt Elgon (pictures by Ling-Yun Chen).

Methods

All lobelias described in the *Flora of Tropical East Africa* (Thulin 1984), Knox and Pócs (1992) and Knox and Palmer (1998) were included in this study. The distribution and habitat for each species were explored using data from previous studies (Mabberley 1975; Thulin 1984; Knox and Pócs 1992; Agnew and Agnew 1994; Beentje et al. 1994; Knox and Palmer 1998; Knox et al. 2004; Zhou et al. 2017; Zhou et al. 2018), voucher specimens in the East African Herbarium of the National Museum of Kenya (NMK) and voucher specimens in the herbarium of Wuhan Botanical Garden (HIB) that had been collected from 2009 to 2019.

To maximise recording lobelias in traversed habitats, meander and patterned searches (Lancaster 2000) were used. The meander search was employed on difficult terrains, such as in mountains, deep river valleys and rocky hills. On the other hand, the systematic transect was employed on flat grounds, such as grassland and shrublands. Lobelias were identified to species or subspecies level.

Results

The lobelias in the seven regions of the five countries are represented by 54 taxa including herbs, shrubs and sub-shrubs (Table 1).

(1) Afro-alpine region. In this study, the afro-alpine region includes the sub-alpine ericaceous zone and the afro-alpine zone. The sub-alpine ericaceous zone ranges from about 3000 m to 3800 m (Wesche et al. 2000) and is dominated by *Helichrysum* Mill., *Hypericum* L. and *Erica* Boehm. The afro-alpine region extends to over 4900 m and is dominated by giant species of *Dendrosenecio* (Hauman ex Hedberg) B.Nord. and *Lobelia*. The giant lobelias include *Lobelia stuhlmannii* Schweinf. & E.A.Bruce, *Lobelia deckenii* Hemsl., *Lobelia gregoriana* Baker f., *Lobelia gregoriana* subsp. *sattimae* (R.E.Fr. & T.C.E.Fr.) E.B.Knox, *Lobelia burtii* E.A.Bruce, *L. burtii* subsp. *telmaticola* E.B.Knox, *L. burtii* subsp. *meruensis* E.B.Knox, *Lobelia bequaertii* (De Wild.) Mabb., *Lobelia wollastonii* Baker f. and *L. telekii.* These species are mainly distributed in the upper alpine zone (Tables 1, 2). Besides these, a few herbaceous species, including *Lobelia minutula* Engl., *Lobelia cheranganiensis* Thulin, *Lobelia holstii* Engl. and *Lobelia lindblomii* Mildbr. (Table 1; Thulin 1984), inhabit altitudes above 3000 m. Amongst the herbaceous species, *L. lindblomii* grows at the highest elevation (3000–4300 m), particularly in the upland grassland and moorland on Mt. Elgon (Kenya/Uganda), Aberdare Ranges and Mt. Kenya. Recurring fires on the ericaceous belt created a buffer zone between the lower afro-alpine and the upper afro-montane forest regions. This buffer zone was observed to provide regeneration habitats for the herbaceous species *L. minutula*, *L. lindblomii* and *L. holstii* (see Suppl. material 1: Table S1 for species details).

(2) Afro-montane forest region. The afro-montane forest region currently occurs in anthropogenically-fragmented patches in East Africa and has an altitudinal range of

0–3000 m (Thulin 1984). The lowlands of the montane (< 1500 m) include deciduous trees and shrubs species, such as *Celtis africana* Burm.f., *Senegalia* Raf. spps., *Vachellia* (wight & Arn.) Kuntze spps., *Ilex* L. spps., *Haplocoelum foliolosum* (Hiern) Bullock and *Ficus* L. spp., amongst others. These lowlands were well inhabited by nine herbaceous lobelias, which include *Lobelia erinus* L., *Lobelia trullifolia* subsp. *minor* Thulin, *Lobelia welwitschii* Engl. & Diels ex Diels, *Lobelia sapinii* De Wild., *Lobelia fervens* subsp. *recurvata* (E.Wimm.) Thulin, *Lobelia chireensis* A.Rich., *Lobelia inconspicua* A.Rich, *Lobelia adnexa* E.Wimm. and *Lobelia hartlaubi* Buchenau. The giant lobelias distributed in this vegetation include *Lobelia morogoroensis* E. B. Knox & Pócs, *Lobelia longisepala* Engl. and *L. giberroa* (Tables 1, 2) at altitudes ranging from 1200–1500 m (Thulin 1984). An interesting exception in this category is *L. giberroa*, which is widespread in Africa and has a distribution range that extends to about 3000 m (Table 1). This species inhabits a transition zone between the lowland and upland giant species. Interestingly, the lowland range of *L. giberroa* is found in understoreys of closed forest and riparian ecosystems, a similar habitat to its upland range. This provides insight into understanding the habitat preference of the species. The highlands of the afro-montane forest region extend from 1500 m to 3000 m. These forests have recently been highly fragmented. They are similar in species composition across the East African countries. Dominant native species from other families found in this region include *Olea europaea* subsp. *africana* (Mill.) P.S. Green., *Juniperus procera* Hockst ex Endl., *Prunus africana* (Hook.) Kalkman., *Oldeania alpina* (K. Schum.) Stapleton and *Hagenia abyssinica* (Faber-Langendoen) J.F.Gmel. However, non-native species have become fully naturalised in disturbed areas for timber production. The species include *Grevillea robusta* A.Cunn. ex R.Br., *Casuarina equisetifolia* L., *Cupressus lusitanica* Lindl. Ex Parl., *Pinus patula* Schiede & Deppe ex Schltdl., *Eucalyptus globulus* Labill., *Eucalyptus saligna* Sm., *Corymbia citriodora* (Hook.) K.D.Hill & Johnson, *Corymbia maculata* (Hook.) K.D.Hill & Johnson, *Fraxinus pennsylvanica* f.colorata B.Boivin, *Araucaria cunninghamii* Sweet ex Courtois and *Acrocarpus fraxinifolius* Arn.

The afro-montane forest region above 1600 m is rich in lobelias. Most species at this altitude are herbaceous and include *Lobelia gilgii* Engl., *Lobelia graniticola* E.Wimm., *Lobelia trullifolia* Hemsl., *Lobelia uliginosa* E.Wimm., *Lobelia dissecta* M.B.Moss, *Lobelia neumannii* T.C.E.Fr., *Lobelia flaccida* subsp. *granvikii* (T.C.E.Fr.) Thulin, *Lobelia molleri* Henriques., *Lobelia rubescens* De Wild., *Lobelia heyniana* Spreng., *L. minutula*, *Lobelia cymbalarioides* Engl., *Lobelia duriprati* T.C.E.Fr., *L. holstii*, *Lobelia goetzei* Diels, *Lobelia ovina* E.Wimm., *Lobelia baumannii* Engl., *Lobelia fervens* Thunb. and *Lobelia angolensis* Engl. & Diels (Table 1).

The giant lobelias in this zone include *Lobelia mildbraedii* Engl., *Lobelia sancta* Thulin, *Lobelia stricklandae* Gilliland, *Lobelia lukwangulensis* Engl., *Lobelia ritabeaniana* E.B.Knox, *Lobelia deckenii* subsp. *incipiens* E.B.Knox, *Lobelia petiolata* Hauman, *Lobelia udzungwensis* Thulin, *L. aberdarica* and *L. bambuseti* (Thulin 1984; see Suppl. materials 1: Table S2 for species details).

(3) Drier savannah region. The drier savannah region is found in Kenya, Ethiopia and Somalia, where *Senegalia* Raf. spp., *Vachellia* Wight & Arn. spp. and *Commiphora*

Jacq. spp. dominate the area. The region ranges from 10 m to 1000 m (or up to 1500 m in some habitats; Thulin 1984). Herbaceous lobelias are found in muddy ditches, river or marshy edges and seasonally-flooding grasslands. These species include *L. fervens* subsp. *recurvata*, *L. goetzei*, *L. duriprati*, *L. inconspicua*, *L. flaccida* subsp. *granvikii*, *L. trullifolia* subsp. *minor*, *L. chireensis*, *L. holstii* and *L. welwitschii* (Table 1). No giant lobelias were found in this region (see Suppl. material 1: Table S3 for species details).

(4) Grassland region. Grassland region is the most common habitat in the EA, and is dominated by alternating grasses with thorny bush-land and thicket. Although habitats in this region are different from others, some lobelias in this region are the same as in the areas of highland, wet and dry savannah and some even from the woodland. However, lobelias in this region are mostly restricted to the wet ground after rainfall (waterlogged grassland and seasonal river banks) and at the edges of wetlands in the marshy areas, streams and river banks, as well as tops of grass hills. The species include *L. fervens*, *L. molleri*, *L. holstii*, *L. flaccida* subsp. *granvikii*, *L. baumannii*, *L. goetzei*, *L. erinus* and *L. welwitschii* (Table 1). No giant lobelias were found in this region (see Suppl. material 1: Table S4 for species details).

(5) Wetter savannah region. This region is widely distributed in Kenya, Tanzania and Uganda with altitudes from 0 m to 1250 m. Both Combretaceae R.Br., and Fabaceae Lindl. families dominate this region. Lobelias in this region include the herbaceous *L. fervens* subsp. *fervens*, *L. baumannii*, *L. goetzei*, *L. inconspicua*, *L. molleri*, *L. holstii*, *L. flaccida* subsp. *granvikii*, *L. sapinii*, *L. chireensis*, *L. erinus* and *L. welwitschii* (Table 1). No giant lobelias were found in this region (see Suppl. material 1: Table S5 for species details).

(6) Zambezian woodland region. This region occurs in the southern part of Tanzania at altitudes ranging from 700 m to 1500 m. It is dominated by members of the family Fabaceae, such as species of the genera *Brachystegia* Benth., *Julbernardia* Pellegr., *Isoberlinia* Craib & Stapf ex Holland and *Uapaca* Baill. *Lobelia* inhabits wet deciduous woodland habitats in this region. Herbaceous lobelias include *L. fervens* subsp. *fervens*, *L. chireensis*, *L. trullifolia* subsp. *trullifolia*, *L. gilgii*, *L. sapinii*, *L. duriprati*, *L. goetzei*, *L. inconspicua*, *L. uliginosa*, *L. rubescens*, *Lobelia heyneana* Schult., *L. adnexa*, *L. cymbalarioides*, *L. baumannii*, *L. erinus*, *L. angolensis* and *L. welwitschii* (Table 1). The only giant lobelia is *L. morogoroensis* (Knox and Pócs 1992), which is distributed near Morogoro, Tanzania at altitudes from 725–1400 m and may extend up to 2000 m (see Suppl. material 1: Table S6 for species details).

(7) Semi-desert and desert region. The hostile climate of this region forms semi-desert and desert vegetations in northern Kenya and southern Ethiopia. This region is characterised by thorny scattered trees and shrubs. Lobelias are distributed in muddy ditches edges and seasonal river banks. However, they are exceedingly rare and only appear in the seasonally-flooded ground or marshy edges of the freshwater wetlands. Species that are distributed in this region include *L. fervens* subsp. *recurvata*, *L. trullifolia* subsp. *minor*, *L. welwitschii* and *L. chireensis* (Table 1) (see Suppl. material 1: Table S7 for species details).

Table 1. Lobelias diversity and distribution in Kenya, Uganda, Tanzania, Rwanda and Burundi of East Africa.

Species/subspecies name	Growth height	Elevation (m)	Habitat	Vegetation region	Data sources
Lobelia aberdarica R.E.Fr. & T.C.E.Fr.	Erect subshrub 3.5 m	1700–3550	Upland swamp	Amfr	SR, HS
L. adnexa E.Wimm.	Erect herb ca. 40 cm	1000–1600	Shady or rocky areas	Amfr, Zwr	FTEA
L. angolensis Engl. & Diels	Procumbent 25 cm	1600–2200	Moist wetland banks	Amfr, Zwr	SR, *FTEA*
L. bambuseti R.E.Fr. & T.C.E.Fr.	Erect subshrub 8 m	1800–3300	Forest, bamboo zone	Amfr	SR
L. baumannii Engl.	Procumbent herb 80 cm	700–2450	Stream banks in shade	Amfr, Gr, Wsr, Zwr	HS, *FTEA*
L. bequaertii De Wild.	Erect subshrub 4–5 m	3250–4100	Moorland and bog	A-ar	HS, *FTEA*
L. burttii subsp. *meruensis* E.B.Knox	Erect subshrub 3 m	3150–3900	Wet alpine or ravine	A-ar	SR, HS
L. burttii subsp. *telmaticola* E.B.Knox	Erect subshrub 3 m	3000–3900	Wet alpine and moorland	A-ar	SR, HS
L. cheranganiensis Thulin	Decumbent herb 0.6 m	2500–3400	Moorland	A-ar	SR
L. chireensis A.Rich.	Herb ca. 25 cm	500 –1250	Marshy muddy areas	Amfr, Dsr, Wsr, Zwr, S-ddr	*FTEA*
L. cymbalarioides Engl.	Prostrate herb ca. 70 cm	1500–3000	Moist forest and woodland floor	Amfr, Zwr	*FTEA*, LR
L. deckenii Hemsl.	Erect subshrub 4 m	3000–4500	Wet moorland	A-ar	SR
L. deckenii subsp. *incipiens* E.B.Knox	Erect subshrub 5 m	2700–3000	Mist forest	Amfr	SR
L. deckenii subsp. *burtii* (E.A.Bruce) Mabb.	Erect subshrub 3 m	3150–3800	Stream bank or ravine	A-ar	SR, HS, LR (Knox and Palmer 1998)
L. dissecta M.B.Moss	Erect herb ca. 50 cm	1500–2250	Open rocky area	Amfr	*FTEA*
L. duriprati T.C.E.Fr.	Decumbent herb 32 cm	1500–3600	Swamp or river banks	Amfr, Dsr, Zwr	SR
L. erinus L.	Decumbent herb ca. 65 cm	0–2500	Wet banks, grassland	Gr, Wsr, Zwr	SR, HS, *FTEA*
L. fervens subsp. *recurvata* (E.Wimm.) Thulin	Erect herb 60 cm	400–1500	Marshy areas, Savannah, forest	Amfr, Dsr, S-ddr	SR, *FTEA*
L. fervens Thunb.	Erect herb ca. 60 cm	10–2100	Grassland, forest and woodland edge, river banks	Amfr, Wsr, Zwr	SR, HS
L. flaccida subsp. *granvikii* (T.C.E.Fr.) Thulin	Erect herb 15–60 cm	1200–3200	Upland forest edges and on wet marshy edges	Amfr, Wsr, Dsr, Gr	SR, *FTEA*
L. giberroa Hemsl.	Erect shrub 10 m	1200–3050	Upland forest edges	Amfr	SR, LR (Kebede et al. 2007; Knox and Palmer 1998)
L. gilgii Engl.	Branched prostrate herb 45 cm	1500–2500	Stream banks	Amfr, Zwr	SR, *FTEA*
L. goetzei Diels	Erect herb 75 cm	1000–3000	Grassy rocky hillside	Amfr, Dsr, Gr, Wsr, Zwr	*FTEA*
L. graniticola E.Wimm.	Decumbent herb < 50 cm	2100–2500	Rocky slopes	Amfr	SR, *FTEA*
L. gregoriana Baker f.	Erect sub shrub 3 m	3200–4500	Erica zone, wet moorland	A-ar	SR
L. gregoriana subsp. *elgonensis* (R.E.Fr. & T.C.E.Fr.) E.B.Knox	Erect subshrub 2 m	3400–4100	Swamp or stream banks	A-ar	SR, *FTEA*
L. gregoriana subsp. *sattimae* E.B.Knox	Erect subshrub 3 m	3300–4000	Wet moorland	A-ar	SR
L. hartlaubii Buchenau	Procumbent herb 90 cm	500–1300	River banks, forest	Amfr	*FTEA*
L. heyneana Schult.	Erect herb30 cm	1000–1800	Disturbed rocky area	Amfr, Zwr	*FTEA*
L. holstii Engl.	Erect/decumbent 60 cm	900–3500	Disturbed moorland, rocky and forest areas	A-ar, Amfr, Dsr, Gr, Wsr	SR

Species/subspecies name	Growth height	Elevation (m)	Habitat	Vegetation region	Data sources
L. inconspicua A.Rich.	Erect herb ca. 20 cm	1000–2400	Ditches, woodland	Amfr, Dsr, Wsr, Zwr	SR, *FTEA*
L. lindblomii Mildbr.	Prostrate herb ca. 80 cm	3000–4300	Swampy or rocky places	A-ar	SR
L. longisepala Engl.	Erect subshrub 5 m	750–1500	Along the streams	Amfr	HS, *FTEA*
L. lukwangulensis Engl.	Erect subshrub 10 m	1700–2500	Forest edges	Amfr	HS, *FTEA*
L. mildbraedii Engl.	Erect subshrub 3.5 m.	1800–3050	Upland swamp	Amfr	HS, *FTEA*
L. minutula Engl.	Prostrate herb >70 cm	200–4000	Moorland, Forest	A-ar, Amfr	SR
L. molleri Henriques.	Decumbent herb 80 cm	850–2500	Upland shady and moist places	Amfr, Wsr, Gr	FTEA
L. morogoroensis E.B.Knox & Pócs	Erect subshrub 6 m	700–1400	Dry woodland, riparian forest	Amfr, Zwr	LR (Knox and Pócs 1992)
L. neumannii T.C.E.Fr.	Decumbent herb ca. 35 cm	1800–2800	Bare or rocky ground	Amfr, Gr	SR
L. ovina E.Wimm.	Erect herb 77 cm	1800–2500	Burnt forest	Amfr	HS, *FTEA*, SR
L. petiolata Hauman	Erect shrub 5 m	1900–2100	Moist forest	Amfr	*FTEA*, LR (Knox and Palmer 1998)
L. ritabeaniana E.B.Knox	Erect subshrub 6 m	2000–2250	Moist forest	Amfr	LR (Knox and Palmer 1998)
L. rubescens De Wild.	Decumbent 60 cm	700–3000	Bamboo zone, forest, woodland in wetland banks	Amfr, Zwr	*FTEA*
L. sancta Thulin	Erect subshrub 8 m	1900–2100	Mist summit forest	Amfr	HS, *FTEA*
L. sapinii De Wild.	Erect ca. 35 cm	400–1050	Woodland, grassland	Amfr, Wsr, Zwr	FTEA
L. stricklandiae Gilliland	Erect subshrub 6 m	1700–2000	Lowland forest to bamboo	Amfr	HS, *FTEA*
L. stuhlmannii Schweinf. ex Engl.	Erect subshrub 10 m	3000–4000	Afro-alpine region, moorland	A-ar	HS, *FTEA*
L. telekii Schweinf.ex Engl	Erect subshrub 4 m	3000–5000	Lower afro-alpine to snow line	A-ar	SR
L. trullifolia Hemsl.	Decumbent herb > 60 cm	1000–2750	Forest margins, rocky areas	Amfr, Zwr	SR, *FTEA*
L. trullifolia subsp. *minor* Thulin	Erect herb 15 ca. 60 cm	1050–2200	Rocky outcrop	Amfr, Dsr, S-ddr	SR, *FTEA*
L. uliginosa E.Wimm.	Erect 45 cm	1000–1800	Rocky forest/ bog	Amfr, Zwr	*FTEA*
L. undzungwensis Thulin	Erect shrub 9 m	1500–2400	Mist forest, rock outcrop	Amfr	LR (Knox et al. 2004)
L. welwitschii Engl. & Diels ex Diels	Erect herb 45 cm	400–3200	Wet banks, bogs, swamps	Amfr, Dsr, Gr, Wsr, Zwr, S-ddr	SR, *FTEA*
L. wollastonii Baker f.	Erect subshrub 7 m	3300–4400	Erica zone, moorland	A-ar	HS, *FTEA*

A-ar = Afro-alpine region, Amfr = Afro-montane forest region, Dsr = Drier savannah region, Gr = Grassland region, Wsr = Wetter savannah region, Zwr = Zambezian woodland region and S-ddr = Semi-desert and desert region. *FTEA* = *Flora of Tropical East Africa*, SR = Sight record, HS = Herbarium specimen, LR = Literature review; only if a species were not described in *FTEA*, literature was used to check the habitat and distribution.

Table 2. Summary for the distribution of lobelias in the seven vegetation regions.

Vegetation region	Altitude (m)	Number of taxa	Number of giant taxa	Number of herbaceous taxa
Afro-alpine	3000–4900	15	11	4
Afro-montane forest	0–3000	41	13	28
Lowland montane forest	0–1500	12	3	9
Upland montane forest	1500–3000	29	10	19
Drier savannah	10–1000	9	0	9
Grassland	1200–3000	9	0	9
Wetter savannah	0–1250	11	0	11
Zambezian woodland	700–1500	18	1	17
Semi-desert and desert	400–1500	4	0	4

Discussion

Distribution patterns for lobelias in five countries of East Africa

We employed a map (Fig. 1) with seven vegetation regions to cover the distribution of lobelias in Kenya, Uganda, Tanzania, Rwanda and Burundi (Kiage and Liu 2006). The seven regions are mainly dominated by stepped plateaus, flat land savannah, highlands, mountains and wetland ecosystems. The lobelias in the seven regions are represented by 47 species and seven subspecies including herbs, shrubs and sub-shrubs (Table 1). The most elevated habitat was inhabited by a giant species *L. telekii* on Mt. Kenya, while the lowest habitat was inhabited by herbaceous species, such as *L. fervens* and *L. erinus*. The altitudinal distribution of lobelias could have been shaped by their habitat preferences and by the adaptive evolution (Hedberg 1964; Chen et al. 2015). For example, *L. telekii* was confined to the afro-alpine belt characterised by an extreme climate with "summer every day and winter every night" (Hedberg 1964).

The EA Mountains form altitudinal island-like habitats. Most of these mountains, which are known as sky-islands, are of volcanic origin (Hedberg 1969) and lie within the Latitudes 2°N and 4°S. The mountain vegetation is completely different from that of the surrounding lowland. For example, the savannah and the highland forest are different from those of the upper alpine in both species richness and growth habits (Tables 1, 2). Amongst the five sub-floras of EA, Tanzania with 38 taxa is the richest in lobelias followed by Kenya (21), Uganda (19), Burundi (9) and Rwanda (8) (Suppl. material 1: Tables S8–S12).

East African Mountains are a centre of endemism for giant lobelias

The East African Mountains embrace a wide range of altitudinal habitats and ecosystems, from surrounding environs at the foot of the mountains to the alpine zone (Zhou et al. 2018). The diversity and richness of lobelias can thus seem to be dependent on existing diverse habitats. In general, the diversity of giant lobelias varies greatly within habitats. The diversity is higher in the afro-montane forest region (13 taxa, Table 2), followed by the afro-alpine region (11 taxa). The giant lobelias demonstrated a clear preference for afro-montane forest and afro-alpine regions. On the other hand, the number of herbaceous lobelias is higher in the afro-montane forest (28 taxa) and Zambezian woodland regions (17 taxa). The herbaceous type demonstrates a clear preference for a habitat characterised by trees in both afro-montane forest and Zambezian woodland regions.

East African Mountain biomes were differentiated into two major categories, the mountains that reach the alpine (upland) and those without the alpine regions (lowlands and Eastern Arc Mountains). The upland giant lobelias, except *L. petiolata*, normally have a single aerial stem that is unbranched. The branched *L. petiolata* inhabits Nyungwe in Rwanda and extends its range to Kahuzi in DR Congo in very wet afro-montane forest region. These species have a clear preference for a wet forest habitat (Knox and Palmer 1998).

The Eastern Arc Mountains (lowlands) form the easternmost blocks of East Africa (Burgess et al. 2007). Although they do not extend to the afro-alpine region, their location creates a Massenerbung effect, therefore generating variable and unique habitats (Knox and Palmer 1998). The lowland biomes form habitats characterised by the branched lobelias (Knox and Palmer 1998). These species include *L. undzungwensis*, *L. morogoroensis*, *L. stricklandiae*, *L. ritabeaniana*, *L. sancta*, *L. lukwangulensis* and *L. longisepala.* The Arc Mountains have evolved their distinctive lobelias, which are different from those of the upland mountains. The Arc Mountain biome, therefore, is a hotspot for the East Africa branched lobelias. The regions inhabited by lobelias have moist and warm habitats somewhat differentiated from the regions occupied by the inland giant lobelias. The Arc Mountain giant lobelias demonstrated a clear preference for moist and warm conditions within the mountains along the East Africa Coast, which is known as one of the world's biodiversity hotspots (Stuart et al. 1990).

The Eastern Arc Mountains are separated from each other by lowland woodlands and savannah (Conte 2010). The Arc Mountain lobelias are distributed from open sites in seasonally-dry, semi-deciduous woodland (*L. morogoroensis*) to the sub-montane rainforests openings (*L. longisepala*) and also extend further to the cloud-forest summits (*L. ritabeaniana*, *L. stricklandiae*, *L. undzungwensis*, *L. sancta* and *L. lukwangulensis* (Table 1; Knox and Palmer 1998). Surprisingly, *L. giberroa*, which is found in the inland afro-montane forest, also grows on these Arc Mountains. *Lobelia giberroa* in the Arc Mountains occupies habitats with similar physiognomic characteristics and similar associated plant species found elsewhere in the highland afro-montane forests (Knox and Palmer 1998). The Eastern Arc and other East African mountains demonstrated an extraordinary pattern of lobelias' endemism and community preferences.

Major identified threats to afro-mountain lobelias' habitat and its lowlands environments

Land-use changes associated with deforestation and land degradation are major causes of biodiversity loss in East Africa (Maitima et al. 2009). Currently, the afro-montane forest is fragmented and remains isolated around the EA Mountains. Without the present anthropogenic activities, the afro-montane forest would probably have existed as a single connected habitat (Hedberg 1969). The habitat fragmentation threatens the distribution patterns of some native species, for example, *L. giberroa* (Kebede et al. 2007). Therefore, habitat loss and fragmentation could threaten the forest-dependent lobelias. For example, *L. bambuseti* has been reported as being under threat (Kipkoech et al. 2019).

Moreover, the afro-montane forest and its environment are also threatened by invasive plants (Obiri 2011; Hulme et al. 2013). Most of the mountains in the EA have become centres for ecotourism. To facilitate tourist activities, roads and paths within the mountain have been built. The invasive species could follow the roadsides to reach different altitudes (Pauchard et al. 2009). According to our observation, the disturbed roadsides created opportunities for disturbed habitat lobelias to dominate the roadsides. For example, *L. holstii* has expanded its range to almost 3900+ m on Mt. Kenya and dominated the roadsides in rocky disturbed places. Additionally, non-native tree species established in the forest plantation for timber production may pose a considerable threat (Pauchard et al. 2009) to native forest lobelias' ecosystems.

Mountain forests are major water towers, biodiversity hotspots, species evolution refugia, eco-tourism locations, sources of wild foods and centres of plant genetics (Viviroli and Weingartner 2008; Moelg et al. 2013; Kanui et al. 2016; Immerzeel et al. 2020). For example, they serve as a source of clean water for the drier lowlands, which are inhabited by lobelias, as observed in our extensive field survey. The afro-montane forest also provides places of cultural practices, such as religion for the native communities. Although lobelias are widely distributed in the seven vegetation regions, habitat loss is a challenge that calls for action. For example, the increasing human population has threatened the EA Mountain biomes. The habitat preference of lobelias' hotspots is also facing the risk of both anthropogenic and climate change (Chala et al. 2016). Habitat destruction and fragmentation are recognised as a major threat to biodiversity (Liao et al. 2013). Therefore, the afro-montane forest and its environs are especially in need of protection (Immerzeel et al. 2020).

Conclusions

Our results showed that lobelias are distributed in all of the seven vegetation regions in five countries of East Africa. The afro-montane forest region is the richest in species diversity, although it is not the largest by area. The herbaceous type has a preference for the lowland regions, while the giant type has a clear preference for the afro-alpine and afro-montane forest. Future conservation for the genus should consider the habitat preferences of lobelias.

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Supplementary material 1

Tables S1–S12

Authors: John K. Muchuku, Andrew W. Gichira, Shu-Ying Zhao, Jin-Ming Chen, Ling-Yun Chen, Qing-Feng Wang

Data type: data statistics

Explanation note: Data statistics for each species.

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RESEARCH ARTICLE

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Primulina flexusa sp. nov. (Gesneriaceae) from Guizhou Province, China

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Abstract

The limestone regions of Yunnan-Guangxi-Guizhou in southern and southwestern China are regarded as some of biodiversity's hotspots for China's Gesneriaceae where numerous rare new species of *Primulina* have been, or are being, described over the past two decades. *Primulina flexusa*, a new lithophytic species of Gesneriaceae from a limestone hill in a Karst area, from Guizhou, China, is described here with color photographs. It is similar to *P. curvituba*, but can be easily distinguished by a combination of characteristics, especially in the shape and length of its capsule. We found only one population with approximately 100 mature individuals at the type locality. This new species is provisionally assessed as Critically Endangered [CR C1] by using IUCN criteria.

Keywords

Cliff-dwelling, flora of Guizhou, limestone flora, lithophytic, taxonomy

Introduction

The vast majority of *Primulina* species have a straight funnelform-tubular to campanulate or cylindric corolla tube (Wang et al. 1990, 1998; Li and Wang 2005). They usu-

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[*] Contributed equally as the first authors.

ally are not swollen or gibbous abaxially. However, there are some exceptions; for example, in the past decade, some newly published species of *Primulina* have an inflated corolla tube, like *P. crassituba* (W.T. Wang) Mich. Möller and A. Weber (Wang 1989), *P. carinata* Y.G. Wei, F. Wen & H.Z. Lü (Wen et al. 2014) and *P. inflata* Li.H. Yang & M.Z. Xu (Xu et al. 2020). Another rare corolla characteristic of *Primulina* is the curved tube. So far, before this new taxon was discovered, only one species of *Primulina* had a curved tube, namely *P. curvituba* B. Pan, L.H. Yang & M. Kang (Yang et al. 2017), out of a total of about 210 species of *Primulina* in China (Wen et al. 2019, 2020).

Some studies have suggested that moss may play a positive role in affecting the survival and growth of some *Primulina* species, for instance *P. tabacum* Hance (Ren et al. 2010a, b). Hence, one of the authors (PT), as a bryologist, is also very concerned about the biodiversity of *Primulina* when he carries out the fieldwork for bryophyte biodiversity and flora. Significantly, when PT investigated bryophyta in Duyun City, southern Guizhou Province in the autumn of 2017, an unknown species of Gesneriaceae, but one without flowers, was collected. The vegetative characters of the individuals of this species, e.g. their small but conspicuous rhizome, opposite leaves, fleshy, and elliptical but fragile leaf blade, indicated that it should be classified as a member of *Primulina*. It is somewhat similar to *P. tenuituba* (W.T. Wang) Yin Z. Wang, namely former *Deltocheilos tenuitubum* W.T. Wang (Wang 1981a) and *Chirita shennungjiaensis* W.T. Wang (Wang 1981b; Wang et al. 1990) because of the leaf blade morphology and shape. Several living individuals were then introduced into the nursery and gardens at the Gesneriad Conservation Center of China (GCCC), at the Guilin Botanical Garden, Chinese Academy of Sciences. After six months, those introduced and cultivated plants blossomed in April 2018. To our surprise, the gross morphology of flowers, such as their curved corolla tube, was obviously different from all other species of *Primulina*, except for *P. curvituba*. We revisited the locality immediately to collect flowering plants in the field (Figure 1). Surprisingly, when we showed photographs to the staff of the Guangxi Institute of Botany, one of the authors (BP) told us that he had been collecting the flowering specimens and living plants of this species back in 2016. Further literature study (e.g. Wang et al. 1998; Li and Wang 2005; Wei et al. 2010 and all recent published papers for new taxa of *Primulina*) and morphological comparison convinced us that it represents a new species to science, which is described and illustrated below.

Taxonomic treatment

Primulina flexusa F. Wen, Tao Peng & B. Pan, sp. nov.

urn:lsid:ipni.org:names:77211381-1
Figures 1, 2

Type. China. Guizhou Province, Duyun City, Bamang town, Longtang village, 26.31N, 107.49E, altitude ca. 1040 m, 15 May 2016, *Bo Pan et al.*, *PB160425-01* (Holotype: IBK!; Isotype: IBK!).

Figure 1. The flowering plants of *Primulina flexusa* growing in the crevice of limestone hill (type locality): **A–D** flowering plants from different aspects.

Diagnosis. The new species resembles *Primulina curvituba* in having a curved corolla but is easily distinguished from the latter by bracts oblong (*vs.* lanceolate), filament glabrous (*vs.* glandular-pubescent), ovary ovoid (*vs.* cylindrical), stigma slightly 2-parted at the apex (*vs.* undivided at apex) and capsule ovoid (*vs.* linear).

Description. Herbs perennial, acaulescent. Leaves basal, 8–12, opposite, petiolate; petiole compressed, gradually broadened from the base to the upper, densely pilose, 5–13 × 1.5–3.5 mm; leaf blade ovate to broadly ovate, abaxial surface green to dark green, adaxial surface brownish-green to brownish-purple; 1.6–2.0 × 1.3–1.8 cm, pubescent and pilose on adaxial surface, puberulent on abaxial surface, base shallowly cordate to slightly cuneate, margin entire and ciliate, apex obtuse to nearly rounded; lateral veins ca. 3 on each side of the midrib, inconspicuous on adaxial surface, prominent on the abaxial surface. Cymes 2–4, 1–4-flowered; peduncle 1.5–2.4 cm long, ca. 1 mm in diameter, erect pubescent; bracts 2, opposite, oblong, ca. 3.8 × 0.7 mm, adaxially green and nearly glabrous, abaxially brownish-green to brownish-purple, densely pilose, the

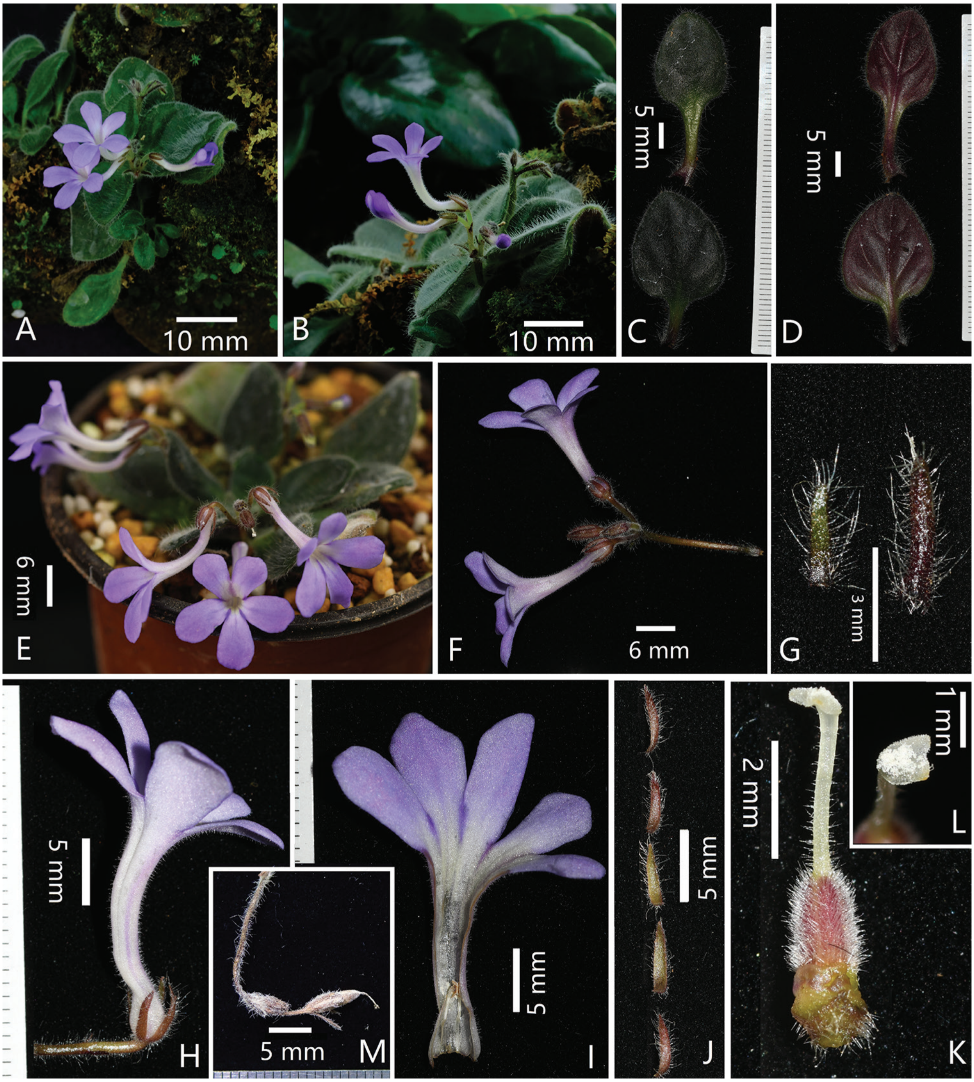

Figure 2. *Primulina flexusa* sp. nov. **A** habitat **B** habitat and flowering plant for showing curved corolla tube **C** adaxial surfaces of leaves **D** abaxial surfaces of leaves **E** cultivated potted plant in flowering **F** cyme **G** adaxial surfaces of bract (right) and bracteole **H** lateral view of corolla for showing curved corolla tube **I** opened corolla **J** calyx lobes **K** pistil **L** stigma **M** mature capsule.

pilose hairs 0.8–1.2 mm long, margin entire, apex acute, bracteole ca. 2.4 × 0.5 mm, color and indumentum same as bracts. Pedicel 6.5–8 mm long, ca. 0.9 mm in diameter, puberulent. Calyx 5-parted from the base; segments equal, pale brown to brown, lanceolate, 4–5 × 0.7–0.9 mm, outside pale brown to greenish-brown, densely pubescent, inside greenish-brown, glabrous, margin entire, apex acute. Corolla 21–25 mm long, pale purple to purple, throat with two distinctly dark purple stripes respectively between each pair of abaxial lip lobes, outside covered with extremely short glandular-puberulent hairs, inside nearly glabrous; corolla tube infundibuliform, slightly curved downwards at base (ca. 4 mm from the base), then gradually bent forwards, 16–19 mm long, ca. 6 mm in diameter at the mouth, ca. 2.5 mm in diameter at the base; limb distinctly 2-lipped, adaxial lip 2-parted over 2/3 from the top of the adaxial lip, lobes nearly equal, broadly obovate, ca. 5 × 4 mm; abaxial lip 3-parted over 4/5 from the top of the abaxial lip, lobes slightly obliquely obovate, 7.5–8 × 3.9–5 mm. Stamens 2, adnate to ca 2.5 mm above the corolla base; anthers pale yellowish-brown, elliptic, ca. 1.5 × 1.0 mm, fused by entire adaxial surfaces; filaments linear, straight, ca. 3 mm long, white, glabrous; staminodes 3, adnate to ca. 3 mm above the corolla tube base, lateral ones ca. 3.5 mm long, the middle one ca. 0.7 mm long. Disc yellowish-green, annular, margin entire or sometimes slightly erose, ca. 0.4 mm high. Pistil ca. 5 mm long; ovary brownish-red, ovoid, ca. 1.4 mm long, ca. 0.9 mm in diameter, densely puberulent and glandular-puberulent; style white, 2.2–2.5 mm long, ca. 0.2 mm in diameter, sparsely glandular-puberulent. Stigma 1, translucent to white, its upper lobe lacking, lower lobe obtrapeziform, slightly 2-parted at apex, ca. 1 mm long, ca. 0.75 mm wide. Capsule ovoid, ca. 6.5 mm long, ca. 2.2 mm in diameter, densely puberulent.

Phenology. Flowering occurs from April and fruiting from May to June.

Etymology. The specific epithet '*flexusa*' is derived from its curved corolla tube. The original epithet '*flexusa*' derived from the Latin, '*flexus*', means curved and slightly zigzagging.

Vernacular name. Qū Guǎn Bào Chūn Jù Tái (Chinese pronunciation); 曲管报春苣苔 (Chinese name).

Distribution and habitat. *Primulina flexusa* is hitherto only known from the type locality, Mangba town, Duyun City, Guizhou Province, Southwest China, growing on moist and shaded rocky crevice on the cliff in a subtropical evergreen seasonal rain forest, at an altitude of ca. 1040 m. All plants were growing in a damp and dark crevice of Karst cliff near a village.

Conservation status and IUCN RedList category. Only a single population with ca. 100 mature individuals is known to exist at the type locality. All individuals were found growing in a large horizontal crevice close to the hillside of the limestone hill. The hill is isolated by maize fields. We, therefore, assess *Primulina flexusa* as Critically Endangered (CR C1), according to IUCN RedList Categories and Criteria (IUCN 2019). The CR category assessment of this new species is based on the distributional range that extends ca. 5 km^2 around the type locality at present, as observed in the past two years.

Additional specimens examined. *Primulina curvituba* B. Pan, L.H. Yang & M. Kang, China: Guangdong Province, Guangzhou City, cultivated in South China Botanical Garden, introduced from Guangxi Zhuangzu Autonomous Region, 25°11'31.83"N, 108°14'52.41"E, growing on the moist rock surfaces of limestone hills, 29 Jul 2016 (flowering), *Li-Hua Yang*, *YLH368* (holotype: IBSC!). *Primulina tenuituba* (W.T. Wang) Y.Z. Wang, China: Hunan Province, Yongshun County, Qingtianping, growing on the limestone cliff, 14 April 2013, *Hong-Wen Huang 40826* (CSFI!);Hunan Province, Longshan County, no detailed information, 11 April 2013, *Dai-Ke Tian*, *Yan*

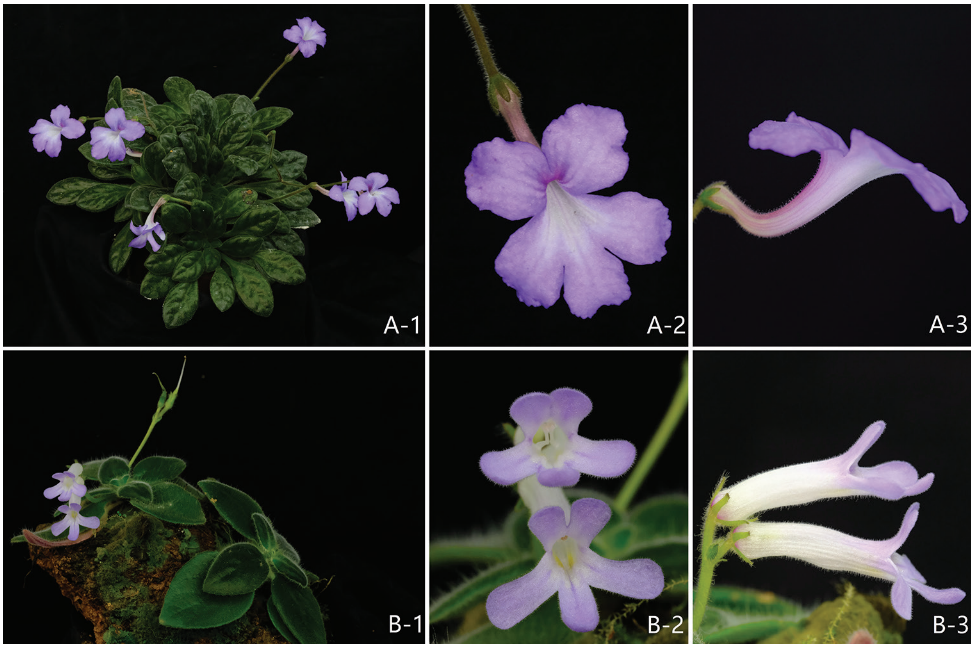

Figure 3. A *Primulina curvituba* **B** *P. tenuituba*: **1** cultivated plants in flowering **2** frontal view of corolla **3** lateral view of corolla for showing the curved and straight corolla tube.

Xiao, *Yue Chen LS-1310* (CSH!); Hunan Province, Suining County, Huangsang National Natural Reserve, Huangsang Village, Dawanpeng, 413 m a.s.l., 20 April 2014, *Jian-Jun Zhou & Zong-Ping Song 1404145* (CSFI!); Hunan Province, Suining County, Huangsang National Natural Reserve, Pingxi Village, Banchong, 894 m a.s.l., 3 May 2014, *Jian-Jun Zhou & Zong-Ping Song 1405039* (CSFI!); Hunan Province, Suining County, Huangsang National Natural Reserve, Chiban Village, Yuanyang, 461 m a.s.l., 7 April 2013, *Jian-Jun Zhou & Dian Zhou 13024* (CSFI!); Hunan Province, Suining County, Huangsang National Natural Reserve, Dawantang Village, Da, 410 m a.s.l., 11 April 2013, *Jian-Jun Zhou & Dian Zhou 13136* (CSFI!); Hunan Province, Suining County, Huangsang National Natural Reserve, Chiban Village, Yuanyang, 487 m a.s.l., 11 April 2013, *Jian-Jun Zhou & Dian Zhou 13121*(CSFI!); Guizhou Province, Tongren City, Yangtou District, Jiulongdong, growing on the surface of rocks, 8 July 1988, *Wulingshankaochadui 1577* (PE!); Guizhou Province, Guiyang City, Dongshan, growing in the crevices of limestone hill, 8 May 1991, *De-Yuan Chen & Cheng-Gang Hu*, *s.n.* (PE!); same locality, 21 May 1989, *De-Yuan Chen*, *s.n.* (PE!); Sichuan Province, Daxian County, Pingchang, Heishui, 600 m a.s.l., 1 June 1978, *Pingchangdui 212* (SM!); Sichuan Province, Bazhong City, Daluo, Shedan, 700 m a.s.l., 8 March 1979, *Bazhongpuchadui 879* (SM!); Sichuan Province, Dazhu County, Zhuqi, Sanqi, Zhongfeng, 9 September 1978, *Dazhuxian 0803* (SM!); Sichuan Province, Nanjiang County,

Table 1. Detailed comparisons among *Primulina flexusa*, *P. curvituba*, and *P. tenuituba*.

Characters	*P. flexusa*	*P. curvituba*	*P. tenuituba*
Leaf blade			
Shape	ovate to broadly ovate	elliptical to linear-elliptical	ovate to suborbicular
Size	1.6–2.0 × 1.3–1.8 cm	1.4–3.3 × 0.9–1.5 cm	1–3.2 × 0.8–2.5 cm
Indumentum	pubescent and pilose on abaxial surface, puberulent on the adaxial surface	with both surfaces densely white pubescent	appressed pubescent to appressed pilose
Margin	entire and ciliate	entire and revolute	entire to repand-crenate
Cyme			
Number / per plant	2–4	6–11	2–4
Peduncle length	1.5–2.4 cm	3–6.5 cm	0.6–1.4 cm
Bracts			
Shape	oblong	lanceolate	narrowly triangular to lanceolate
Size	ca. 3.8 × 0.7 mm	2.0–3.5 × 1.0–1.5 mm	0.8–3 × 0.3–1 mm
Indumentum	adaxially nearly glabrous, abaxially densely pilose	adaxially glabrescent, abaxially densely white pubescent	adaxially glabrescent, abaxially puberulent to pilose
Pedicel			
Length	6.5–8 mm	20–30 mm	2–5.5 mm
Indumentum	puberulent	densely pubescent	densely spreading puberulent to pilose
Calyx lobes size	4–5 × 0.7–0.9 mm	2–3 × 1.0–1.5 mm	4.5–5.5 × 0.8–1.2 mm
Corolla indumentum	outside covered extremely short glandular-puberulent hairs, inside nearly glabrous	outside pubescent, inside glabrescent	outside sparsely puberulent, inside puberulent below the abaxial lip
Corolla tube	infundibuliform, slightly curved downwards at the base (ca. 4 mm from the base), then gradually bent forwards	infundibuliform, laterally compressed at the mouth, strongly curved downwards at the base (5 – 7 mm from the base), then bent forwards	cylindric, straight
Filament			
Length	ca. 3 mm	5–6 mm	4.5–5.5 mm
Indumentum	glabrous	glandular-pubescent	Glabrous
Staminodes number and length	3, lateral ones ca. 3.5 mm, the middle one ca. 0.7 mm	3, lateral ones 1–2 mm, middle one ca. 1 mm	2, 0.5–0.8 mm
Pistil			
Length	ca. 5 mm	7–8 mm	19–22 mm
Ovary			
Length	ca. 1.4 mm	5–6 mm	3.2–6 mm
Shape	ovoid	cylindrical	Cylindrical
Stigma	slightly 2-parted at apex	undivided at apex	2-parted at apex
Capsule			
Length	ca. 6.5 mm	10–15 mm	2–2.8 mm
Shape	ovoid	linear	

Yangba, 28 August 1978, 949 (SM!); Sichuan Province, Xiushan County (Chongqing City now), Shitang, 370 m a.s.l., 17 May 1979, 0349 (SM!).

Notes. This new species is closely related to *Primulina curvituba* (Figure 3A), from which its vegetative and reproductive organs are obviously different, as stated in the diagnosis. The new species also resembles *P. tenuituba*; however, the latter has no curved corolla tube (Figure 3B). The detailed morphological differences among the three species are summarized in Table 1.

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We thank Prof. Michael LoFurno from Temple University, Philadelphia, U.S.A., for his editorial assistance. This study was financially supported by the Foundation of Guangxi Key Laboratory of Plant Conservation and Restoration Ecology in Karst Terrain (19-050-6), the Guangxi Natural Science Foundation (2017GXNSFAA198006), the National Natural Science Foundation (31860047), Basal Research Fund of GXIB (Guizhiye20009) and 21st Talent project of "Ten-Hundred-Thousand" in Guangxi.

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RESEARCH ARTICLE

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Taxonomic innovations in South American *Selaginella* (Selaginellaceae, Lycopodiophyta): description of five new species and an additional range extension

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Abstract

Five *Selaginella* species (i.e, *S. gioiae*, *S. papillosa*, *S. pubimarginata*, *S. rostrata*, and *S. xanthoneura*) from Neotropical rainforests of South America are described and illustrated as new, while *S. surucucusensis*, originally recorded only from Brazil, is redefined to account for species' morphological characters throughout its expanded distribution range and also a novel illustration is provided for it. Inferred taxonomic affinities and conservation assessment are offered for species here treated. *Selaginella gioiae* is native to Colombia, Ecuador, and Peru, and *S. xanthoneura* is so far only known in Colombia, whereas *S. surucucusensis* is now known to occur in Colombia and Venezuela in the north-central part of South America. These three species are included in the "*Selaginella flabellata* group" based on their habit, stem shape, rhizophores position, and mega- and microspores color, and ornamentation. *Selaginella papillosa*, *S. pubimarginata*, and *S. rostrata* are native to Venezuela. *Selaginella papillosa* and *S. pubimarginata* morphologically belong in the "*Selaginella deltoides* group" based on their habit, stem type, shape of lateral leaves and their indument type distributed on upper surface of the leaf lamina. On the other hand, *S. rostrata* is considered to be a member of the "*Selaginella microdonta* group," which is centered in the Guiana Highlands, based on its habit, stem type, and leaf size and shape, and for which a key to identify species is provided. Finally, all species threated here are classified in subg. *Stachygynandrum* based on their heteromorphic leaves, mostly quadrangular strobili, and monomorphic sporophylls shape (except for *S. rostrata* that has slightly dorsiventral and flattened strobili with somewhat heteromorphic sporophylls).

Resumen

Se describen e ilustran cinco nuevas especies de *Selaginella* (i.e, *S. gioiae*, *S. rostrata*, *S. papillosa*, *S. pubimarginata*, and *S. xanthoneura*) de los bosques neotropicales de Suramérica, mientras que *S. surucucusensis*, originalmente descrita de Brasil, es redefinida para incorporar los caracteres morfológicos de la especie a lo largo de su rango de distribución expandido y también una nueva ilustración se provee para ella. Además, se incorporan discusiones sobre las afinidades taxonómicas y el estado de conservación de las especies aquí tratadas. *Selaginella gioiae* es nativa de Colombia, Ecuador y Perú, y *S. xanthoneura* se conoce actualmente sólo de Colombia, mientras que *S. surucucusensis* ahora se reporta también para Colombia y Venezuela, en la región Norcentral de Suramérica. Estas tres especies se incluyen dentro del "grupo de *Selaginella flabellata*" debido a su hábito, tipo de tallo, posición de los rizóforos y color y ornamentación de las mega- y micrósporas. *Selaginella papillosa*, *S. pubimarginata* y *S. rostrata* se conocen sólo de Venezuela. *Selaginella papillosa* y *S. pubimarginata* pertenecen morfológicamente dentro del "grupo de *Selaginella deltoides*", en función de su hábito, tipo de tallo, forma de las hojas laterales y la clase y distribución de su indumento en la superficie superior de la lámina. Por otra parte, *S. rostrata* pertenece al "grupo de *Selaginella nicrodonta*", el cual se centra en el Escudo Guyanés y se caracteriza en función del hábito, tipo de tallo y forma y tamaño de las hojas de sus especies, las cuales pueden ser identificados mediante la clave que se provee. Finalmente, todas las especies aquí tratadas son clasificadas en el subg. *Stachygynandrum*, ya que poseen hojas heteromórficas, estróbilos cuadrangulares y esporofilos monomórficos (con la excepción de *S. rostrata*, la cual posee estróbilos ligeramente dorsiventrales y aplanados con esporofilos levemente heteromórficos).

Keywords

Guiana Highlands, heteromorphic, New World, non-articulate stems, South America, sporophylls, strobili

Palabras clave

Escudo Guyanés, esporófilos, estróbilos, heteromórficas, Nuevo Mundo, Sudamérica, tallos no articulados

Introduction

Selaginella, a highly diverse and species rich lycophyte genus (600–800 spp), is found in a wide variety of ecosystems almost worldwide (Valdespino 2015; Zhou and Zhang 2015; PPG I 2016; Valdespino 2016; Valdespino 2017a). *Selaginella* species can be classified using several subgeneric classification systems as discussed in Valdespino and López (2019). In the New World, there are some 350 described *Selaginella* species, most of them in Neotropical ecosystems, and the number of species described from this region has steadily increased during the last decades. The latter is the result of contemporary field studies that have yielded additional collections, critical revision of herbarium material incorporating detailed microscopic analyses, and overall reassessment of previously known taxa. This tendency will most likely continue, particularly as local and regional taxonomic monographic studies and phylogenetic analysis using molecular data of infrageneric groups are undertaken. The aim of the present contribution is to further document *Selaginella* diversity in South America by describing five new species and revising the description and distribution range of another species described not long ago from this region.

Material and methods

I studied gross morphological features of leaves and spores of *Selaginella* species using herbarium specimens from AAU, B, BM, COL, CR, F, GH, HUA, INPA, K, MG, MO, NY, PMA, R, RB, S, U, UC, US, and VEN (acronyms according to Thiers 2020) using stereomicroscopes (i.e., Olympus SZ 60-STS at the New York Botanical Garden and Olympus SZX16 at the University of Panama herbaria). I further studied fine surface details of leaves and spores using a Zeiss Model Evo 40vp Scanning Electron Microscope (SEM) at 10–15 kV at the Smithsonian Tropical Research Institute (STRI). Digitized SEM images of plant sections, leaf, and spores were taken at different magnifications, post-processed, and assembled in multipart figures using Adobe Photoshop as explained in Valdespino (2016). Terminology, measurements, and conservation status used in species descriptions follow Valdespino and López (2019) and references therein, while species classification is according to Weststrand and Korall (2016).

Results

I describe the five new *Selaginella* species *S. gioiae* Valdespino, *S. papillosa* Valdespino, *S. pubimarginata* Valdespino, *S. rostrata* Valdespino, and *S. xanthoneura* Valdespino, and provide an updated description and an extended distribution range for *S. surucucusensis* L.A. Goés & E.L.M. Assis. All these taxa are native to Neotropical rainforest ecosystems of South America where *Selaginella* is notably diverse and species rich. *Selaginella gioiae* is known to occur in Colombia, Ecuador, and Peru, whereas *S. papillosa*, *S. pubimarginata*, and *S. rostrata* are native to Venezuela, and *S. xanthoneura* is so far only known to occur in Colombia. In addition, *S. surucucusensis*, originally described based on scanty material from Brazil, is now shown to be a more widely distributed species with an extended geographical rage in the north-central part of South America, with specimens documenting its occurrence in Colombia and Venezuela.

All species here examined have heteromorphic vegetative leaves (at least on frond-like, aerial parts of erect species), non-articulate stems, and mostly quadrangular strobili comprised by monomorphic sporophylls (except for *S. rostrata* where strobili are slightly flattened and dorsiventral, composed by somewhat dimorphic sporophylls). Therefore, I consider them to belong in the broadly defined subgenus *Stachygynandrum* (P. Beauv. ex Mirb.) Baker.

Selaginella gioiae, *S. surucucusensis*, and *S. xanthoneura* are morphologically related to the Neotropical "*Selaginella flabellata* (L.) Spring group" as defined by Hieronymus (1901: 682) and Valdespino (2017a). This group comprises some thirty-five species characterized by their fern-like habit, erect stems with leaves seemingly monomorphic before branches, as well as axillary, ventral, dorsal, and occasionally, seemingly lateral rhizophores. This group is additionally defined by white to off-white megaspores with distal faces usually reticulate or rugulate-reticulate, with each reticulum open or closed, and with echinate and perforate microstructures. It also possesses orange to pale orange microspores with distal faces capitate to baculate, and with echinate to perforate microstructures (Valdespino 2017a). The dorsal position of rhizophores and overall echinate microspore microstructure are not unique characters to this group (Valdespino 2017a). Nonetheless, what is revealing about the "*Selaginella flabellata* group" is the occurrence of the three types of rhizophores on a single stem and the degree and density in which the echinate microstructure occur in capitate to baculate projections of distal faces and in the overall surface of microspores.

Selaginella papillosa and *S. pubimarginata*, in turn, are morphologically similar to taxa in the "*Selaginella deltoides* A. Braun group" (Valdespino 2016) also from South America. Most species in this group (i.e., *S. aculeatifolia* Valdespino, *S. albolineata* A.R. Sm., *S. brevifolia* Baker, *S. deltoides*, *S. papillosa*, *S. pubimarginata*, and *S. sandwithii* Alston) typically have a moss-like habit, creeping stems, lateral leaves broadly ovate to ovate-deltate with upper surfaces hispidulous, each hair short and resembling prickles, tooth-like or papilla-like projections, which are mostly found submarginally, marginally, and apically (except in *S. albolineata* and *S. papillosa*) along the basiscopic halves of the laminae, and conspicuous (less so on *S. albolineata*, *S. papillosa*, and *S. pubimarginata*), straw-colored midribs. Remarkably, in the case of *S. albolineata*, the lateral leaf upper surfaces are completely covered by elongate idioblasts, while idioblasts may also be present on lower leaf surfaces of other species in this group, as well as conspicuously hyaline median leaf margins.

Lastly, *S. rostrata* is morphologically akin to species in the "*Selaginella microdonta* A.C. Smith group", which is an alliance formed by species mainly found in the tepuis of the Guiana Highlands, particularly of Venezuela. This species group includes *S. breweriana* A.R. Sm., *S. cardiophylla* Valdespino, *S. hemicardia* Valdespino, *S. microdonta* (also found in Brazil), *S. neblinae* A.R. Sm., and *S. valdepilosa* Baker (also from Guyana). This group is characterized by its ribbon-like or leafy liverwort- to moss-like habit, creeping stems, small leaves, and usually broadly ovate-elliptic to broadly elliptic lateral leaves. Based on overall plant appearance, species of this group are commonly mistaken for bryophytes. Nonetheless, this is quickly dispelled as one observes their root-bearing rhizophores, found at branch forks throughout stems, heteromorphic leaves, which include two rows each of large, lateral and small, median leaves, as well as axillary leaves along stems. Furthermore, a key to identify species in the "*Selaginella microdonta* group" is provided.

Taxonomic treatment

Selaginella gioiae **Valdespino, sp. nov.**

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Figures 1–5

Diagnosis. *Selaginella gioiae* differs from *S. surucucusensis* by the leaves on main stems before becoming fully heteromorphic, triangular-lanceolate, triangular-ovate or deltate (vs. ovate or broadly ovate), the leaves shortly before or after fourth to sixth or even further up along (vs. above first or second) stem branches fully heteromorphic and at this point onward lateral leaves oblong or oblong-ovate (vs. ovate or ovate-oblong), median leaf inner margins straight (vs. convex), and linear-lanceolate to lanceolate (vs. ovate to ovate-lanceolate) axillary leaves.

Type. Colombia. Antioquia: Mpio. San Luis, 16 km SW de las partidas a San Luis, vía Medellín-Bogotá, Vereda La Josefina, 06°00'N, 74°50'W, 800 m, 25 Jun 1987 (fe), *R. Callejas et al. 4180* (holotype: NY!; isotypes: HUA!, MO!, PMA!).

Description. *Plants* terrestrial. *Stems* erect, stramineous, 0.6–1.2 m tall, (2.0)2.5–6.0 mm diam. on main stem before first branches, non-articulate, not flagelliform, stoloniferous, 2 or 3-branched, the terminal portion of the stem similar in shape to lateral branches (i.e., conform). *Rhizophores* axillary, ventral, dorsal, and seemingly lateral, borne on lower-most part of the stems and throughout stolons, stout, 0.3–2.0 mm diam. *Leaves* seemingly monomorphic and strongly appressed to the stem shortly before or after fourth to sixth or even further up along stem branches (depending on stem length), then heteromorphic (of three kinds of leaves: median, lateral, and axillar), coriaceous, upper surface dull to shiny green, striate or striate-corrugate, lower surface shiny yellowish green to silvery green, striate, those on main stem before fully heteromorphic triangular-lanceolate, triangular-ovate or deltate, the bases prominently raised and truncate with both edges rounded or slightly subcordate and glabrous, the margins narrowly hyaline and denticulate, the apices attenuate. *Lateral leaves* on main stems after leaves become fully heteromorphic, distant, ascending to spreading, oblong or oblong-ovate, 2.0–4.2(5.0) × 0.9–2.2(2.5) mm; bases truncate at central portion, glabrous, acroscopic bases strongly overlapping stems, rounded, entire, basiscopic bases free from stems, geniculate; margins on upper surfaces bordered by greenish, rectangular, and laevigate cells, acroscopic margins on lower surfaces narrowly bordered continuously by a hyaline band comprised of idioblasts, the band 1–3 cells wide, the idioblasts elongate, straight-walled, and papillate, the papillae in a single row over each cell lumen, basiscopic margins on lower surfaces bordered continuously by greenish, elongate, straight-walled, laevigate cells, acroscopic margins entire to sparingly denticulate along proximal ⅔, otherwise denticulate distally, basiscopic margins entire or scarcely denticulate; apices obtuse, entire or obscurely denticulate; upper surfaces consisting of irregularly shaped, somewhat rectangular, straight to sinuate-walled cells (often difficult to distinguish because of waxy deposits), with some of these sparse- and obscurely papillate, papillae in one row on each cell lumen, without stomata or with few, obscure submarginal stomata, sparsely distributed along basiscopic margins, lower surfaces consisting of elongate, sinuate-walled cells and of elongate, straight-walled, papillate idioblasts, papillae 6–22 in one rows on each cell lumen, with stomata on 3–7 rows along central most portion of midribs. *Median leaves* on main stem after leaves fully heteromorphic, distant to slightly imbricate, ascending, ovate to ovate-lanceolate, 1.4–3.4 × 0.8–1.7 mm; bases glabrous, truncate to truncate-oblique, without auricles or the outer bases with a rounded nob; margins bordered continuously by a narrow hyaline band comprised of idioblasts, the band 1–3 cells wide, the idioblasts similar to those in acroscopic, hyaline marginal

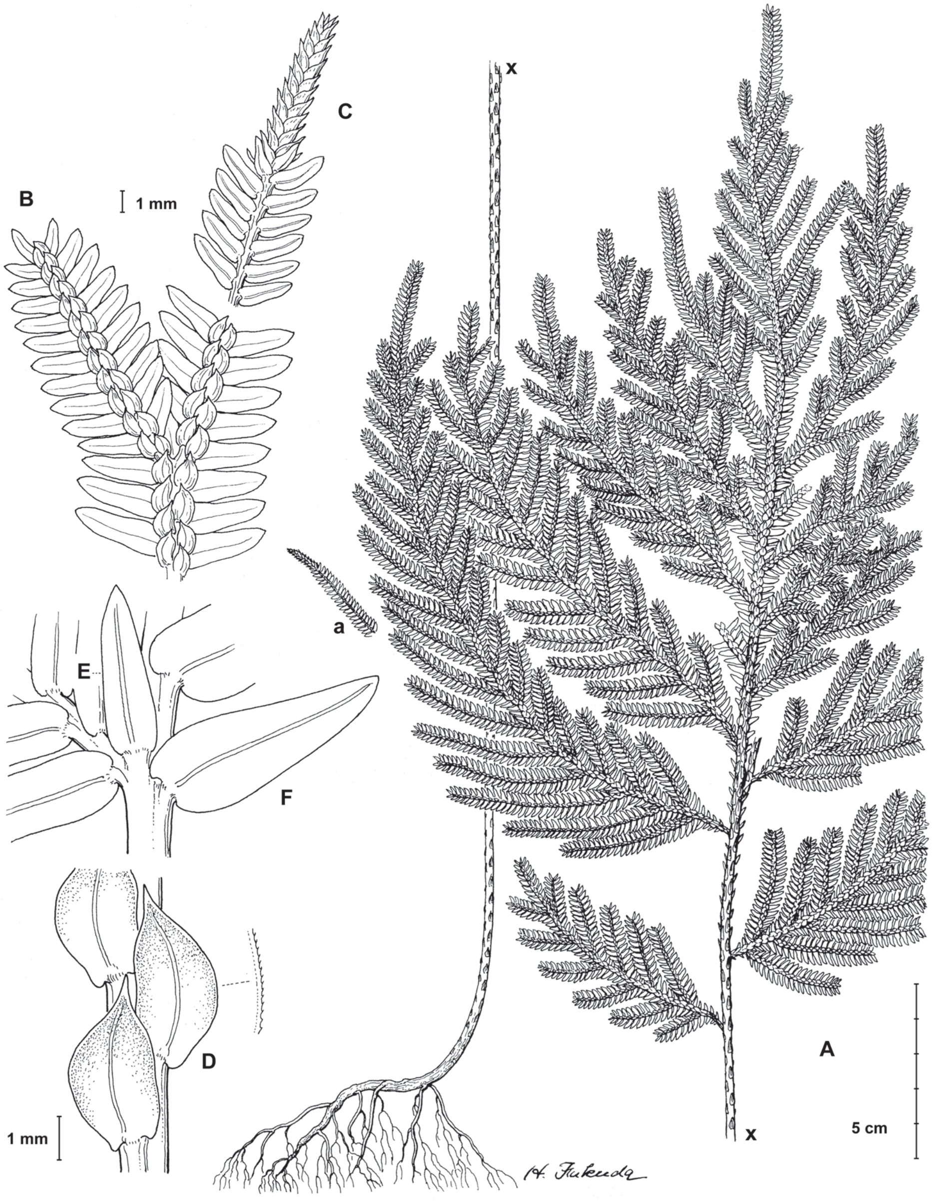

Figure 1. *Selaginella gioiae* Valdespino. **A** Habit, upper surface of stem and (a) detail of terminal strobili on branch, lower surface **B** branch section, upper surface **C** branch section showing terminal strobilus, lower surface **D** median leaves with details of a leaf margin, upper surface **E, F** branch section showing axillary leaf (**E**) and lateral leaf (**F**), lower surface. **A–F** line drawing made from the holotype. Illustration by Haruto Fukuda.

bands of lateral leaves, lower surfaces, the inner margins, straight, entire throughout or entire along proximal ½ and sparsely denticulate on distal ½, the outer margins convex, denticulate throughout; apices acute or attenuate, each 0.1–0.5 mm long, entire at tip

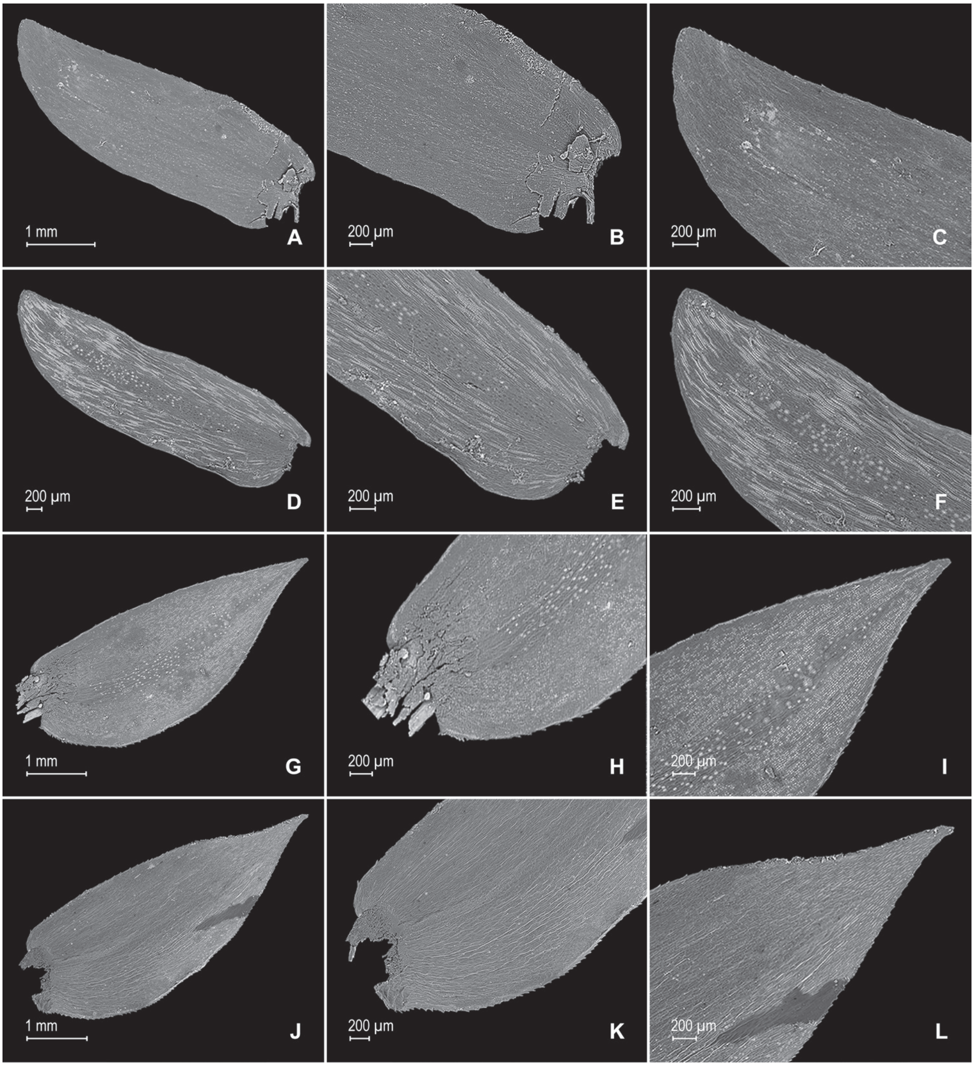

Figure 2. *Selaginella gioiae* Valdespino. **A** Lateral leaf from stem branch, upper surface **B** proximal half of lateral leaf, upper surface (same leaf shown in **A**) **C** distal half of lateral leaf, upper surface (same leaf shown in **A**) **D** lateral leaf, lower surface **E** proximal half of lateral leaf, lower surface (same leaf shown in **D**) **F** distal half of lateral leaf, lower surface (same leaf shown in **D**); note, elongate and papillate idioblasts (a) and stomata along midrib (b) **G** median leaf from stem branch, upper surface **H** proximal half of lateral leaf, upper surface (same leaf shown in **G**) **I** distal half of median leaf, upper surface (same leaf shown in **G**); note, elongate and papillate idioblasts (a) and stomata along midrib (b) **J** median leaf from stem branch, lower surface **K** proximal half of median leaf, lower surface (same leaf shown in **J**) **L** distal half of median leaf, lower surface (same leaf shown in **J**). **A–L** taken from the holotype.

or tipped by 1–3 small teeth; upper surfaces similar to those on upper surfaces of lateral leaves but more abundantly covered by irregularly arranged, papillate idioblasts, the papillae 3–14 in one row on each cell lumen, with stomata in 3–7 rows along midribs and few submarginal, along basiscopic ⅓ of outer margins, lower surfaces comprising elongate (somewhat jigsaw puzzle-like), sinuate-walled cells, without idioblasts and stomata. *Axillary leaves* on main stem after leaves fully heteromorphic linear-lanceolate to lanceolate, 2.5–4.5 × 1.0–1.7 mm; bases truncate, prominently raised, glabrous; margins as in lateral leaves, denticulate throughout; apices gradually tapering, broadly acute, tipped by 1–3 teeth; both surfaces as in lateral leaves. *Strobili* terminal on main stem and each branch tips, quadrangular, 0.5–5 cm long. *Sporophylls* monomorphic, without a laminar flap, each with a well-developed and glabrous keel along midribs, ovate-lanceolate, 1.5–2.0 × 0.6–1.0 mm; bases rounded to truncate; margins narrowly hyaline, 1 or 2 cells wide with the cells elongate, slightly sinuate-walled and glabrous, parallel to margins, denticulate throughout; apices attenuate to acuminate, the acumen 0.1–0.3 mm, tipped by 1–3 small teeth; *dorsal sporophylls* with upper and lower surfaces as in vegetative leaves; *ventral sporophylls* with both surfaces, silvery green to hyaline, comprised of elongate, papillate, sinuate-walled cells and of papillate idioblasts. *Megasporangia* intermixed with microsporangia along two ventral rows; *megaspores* white to beige colored, 325–350 µm diam., proximal faces rugulate with a strongly developed equatorial flange, the microstructure echinate to slightly granular, distal faces reticulate, the reticulae open (incomplete) to closed and the microstructure echinate and perforate. *Microsporangia* in two dorsal rows and intermixed with megasporangia along two ventral rows; *microspores* light orange, 18–20 µm diam., proximal faces rugulate-echinate on proximal faces with slightly punctate or rugulate microstructure, distal faces capitate or baculate, with each caput or bacula and the microstructure echinate or rugulate.

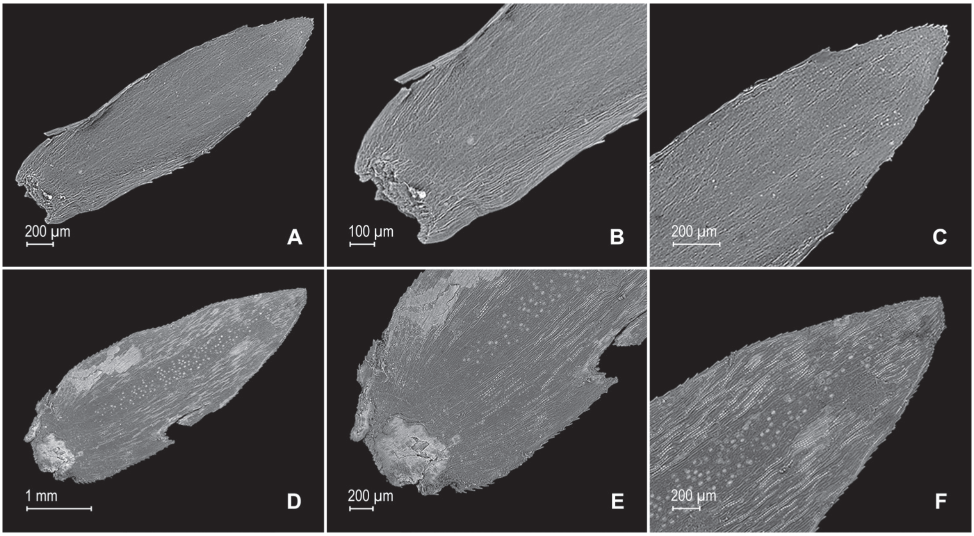

Figure 3. *Selaginella gioiae* Valdespino. **A** Axillary leaf from stem branch, upper surface **B** proximal half of axillary leaf, upper surface (same leaf shown in **A**) **C** distal half of axillary leaf, upper surface (same leaf shown in **A**) **D** axillary leaf from stem branch, lower surface **E** proximal half of axillary leaf, lower surface (same leaf shown in **D**) **F** distal half of axillary leaf, lower surface (same leaf shown in **D**); note, elongate and papillate idioblasts (a) and stomata along midrib (b). **A–F** taken from the holotype.

Habitat and distribution. *Selaginella gioiae* grows on lowland and montane rainforests at 80–1480 m. It is known from tropical rainforest ecosystems on both sides of northwestern Andes and in the Amazon basin, specifically in western Colombia and central-eastern Ecuador and northwestern Peru. It has been collected in fertile condition from February to December.

Eponomy. This unique, tall *Selaginella* species is named after Christopher Gioia (1968–), who as my longtime companion has steadfastly encouraged my work on the genus.

Conservation status. *Selaginella gioiae* is a widely distributed species that grows at low and high elevations with collections continuously made from the late nineteenth- to early in the twenty-first century over a relatively wide range in South America, which suggest it is comprised of healthy populations. Accordingly, it is here considered of Least Concern (LC) based on IUCN (2012).

Additional specimens examined (paratypes). Colombia. **Antioquia**: Mpio. San Luis, Autopista Medellín-Bogotá, Vereda La Josefina, road to Tulipán, caño La Mariola, 800 m, 18–19 Feb 1984, *Hoyos & Hernández 925* (MO); Río Guatapé, 3800 ft [ca. 1158 m], 23 Feb 1880, *Kalbreyer 1434* (B-4 sheets). **Chocó**: Mpio. Quibdó, Corr. Guayabal, Río Hugón, 14 Oct 1985, *García et al. 55* (COL). **Nariño**: Barbacoas, s.d., *Triana s.n.* (B), along road between Junín and Barbacoas, 1.9 km NE of Junín, 01°21'S, 78°06'W, 1300 m, 27 Feb 1992, *Croat 72431* (MO). **Valle de Cauca**: Costa del Pacífico, Río Raposo, 20–50 m, 26 Mar 1963, *Idrobo 5255* (COL); Cordoba, Dagua Valley, 80–100 m, 6–8 May 1922, *Killip 5092* (GH). Ecuador. **Morona-Santiago**: road between Gualaquiza and Indanza, 12 km S of Indanza along river, 03°11'47"S, 78°33'06"W, 1250 m, 8 Sep 2002, *Croat 87275* (MO-2 sheets); Ridge between ríos Ontza and Chupiasa, 02°40”S, 78°W, 4300–4700 ft [1311–1433 m], 17 Nov–5 Dec 1944, *Camp E-1194* (NY). **Napo**: El Chaco, Río Granadillo, Campamento de INECEL, Codo Alto, 00°08'S, 77°28'W, 1300 m, 13–15 Sep 1990, *Palacios 5783* (MO, UC); Reserva Biológica Jatun Sacha, Río Napo, 8 km abajo de Misahuallí, 01°04'S, 77°36'W, 450 m, 17 Jan–6 Feb 1987, *Cerón 748* (AAU, MO, UC). **Napo-Pastaza**: Mera, near Mangayacu, [ca. 01°42'27"S, 78°52'23"W], ca. 1100 m, *Asplund 19100* (S). **Pastaza**: El Porvenir, ca. 5 km N of Puyopungo, 17 Nov 1976, *Lugo 4897B* (BM); Mera, 1100 m, 25 May–6 Jun 1968, *Harling et al. 9779* (BM), *10128* (BM), between Puyo and Baños, ca. 5 km W of Mera, 01°26'S, 78°08'W, 1100 m, 7 Mar 1992, *Croat 72833* (MO); Near Napo road, 9 km N of Puyo, 18 Apr 1958, *Prescott 1361* (NY); Hacienda San Antonio de Barón von Humboldt, 2 km NE de Mera, 01°27'S, 78°06'W, 1100 m, 20 Feb–20 Mar 1985, *Palacios et al. 23A* (AAU, MO, NY), *Zaruma et al. 6* (AAU, MO, NY, UC); Vicinity of Shell, 1.6 km N of main Baños-Puyo road, along Río Claro, 40°29'39"S, 78°03'52"W, 1085 m, 9 Oct 2007, *Croat et al. 99520* (MO). **Tungurahua**: ca. 5 km E of town of Río Negro, 1350 m, 17 Jan 1973, *Humbles 6120* (MO). **Zamora-Chinchipe**: Cordillera del Condor, Chinapintza, trail to Destacamento Mayaycu Alto, 04°03'S, 78°35'W, 1350–1480 m, 6 Dec 1990, *Øllgaard 98418* (AAU); Vicinity of mining camp at Río Tundaime, along Río Quimi, 03°31'10"S, 78°25'53"W, 900–1000 m, 3 Nov 2004, *van der Werff et al. 19255* (MO, NY). Peru. **Amazonas**: Dist. El Cenepa, Tutino, Quebrada Tutino, 04°34'31"S, 78°11'34"W, 300 m, 22 Jul 1997, *Rojas et al. 136* (MO, NY).

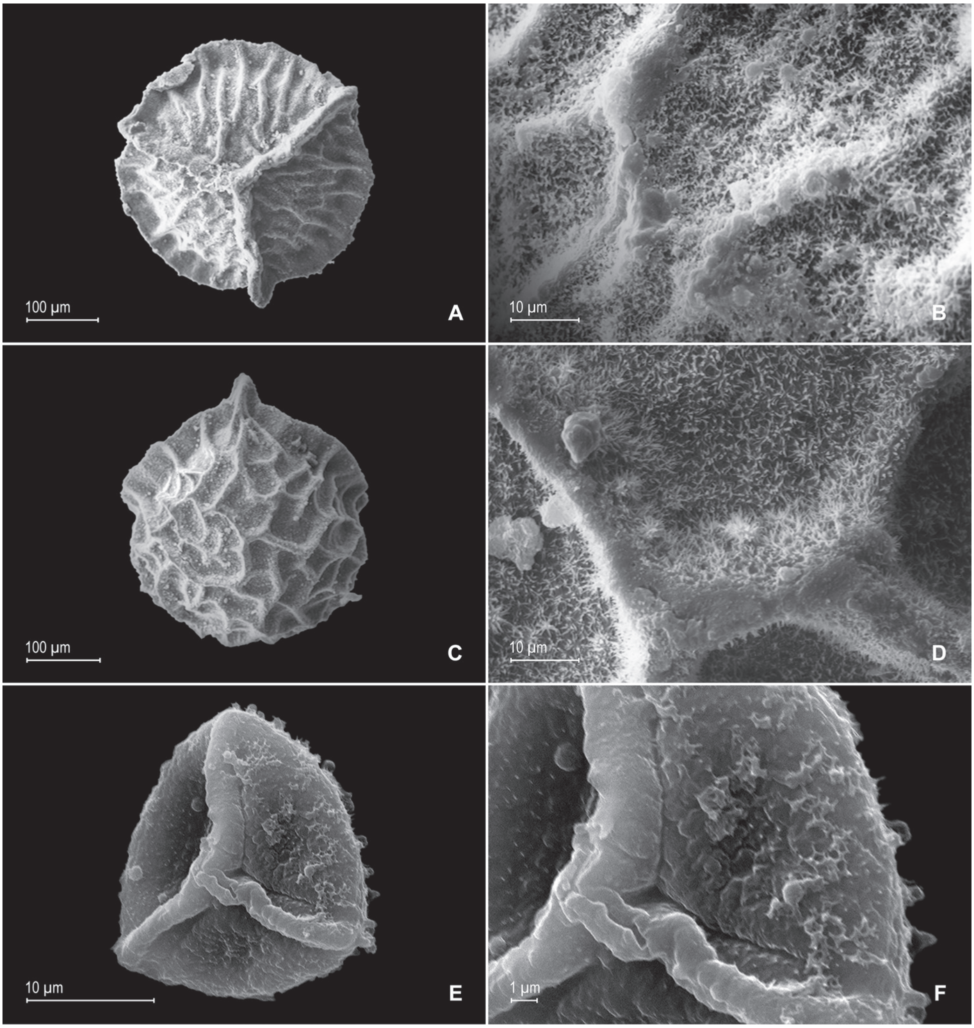

Figure 4. *Selaginella gioiae* Valdespino. **A** Megaspore, proximal face **B** detail of megaspore, proximal face **C** megaspore, distal face, equatorial view **D** detail of megaspore, distal face **E** microspore, proximal face **F** detail of microspore, proximal face. **A–F** taken from the holotype.

Discussion. *Selaginella gioiae* is characterized by its fern-like habit, erect stems, each 0.6–1.2 m tall, leaves on main stem normally fully heteromorphic shortly before or after fourth to sixth or even further shortly before or after fourth to sixth or at higher up branches depending on main stem length, with margins bordered by a narrow band of hyaline, papillate, idioblasts. On main stems it has oblong or oblong-ovate lateral leaves, median leaf bases glabrous, truncate to truncate-oblique, without auricles or the outer bases rounded or with a rounded nob, linear-lanceolate or narrowly lanceolate axillary leaves, megaspores with a prominent equatorial flange, and microspores distal faces capitate or baculate, each caput or baculum usually micro-echinate. *Selaginella gioiae* is further notable by its median

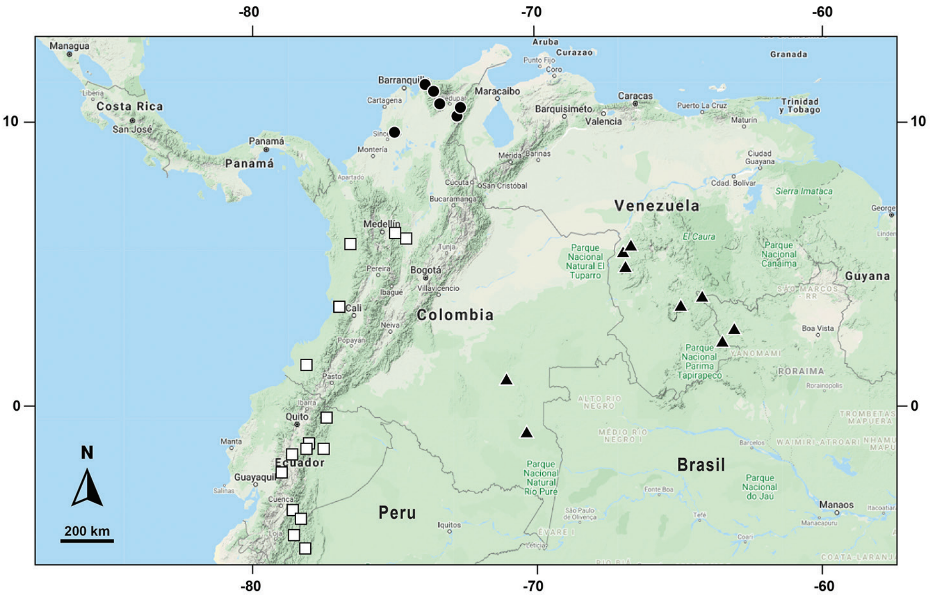

Figure 5. Distribution of *Selaginella gioiae* □, *S. surucucusensis* ▲, *S. xanthoneura* ●.

leaf lower surfaces with frequently very well defined or marked midribs and strobili tips occasionally displaying vegetative growth.

Selaginella gioiae is one of the tallest species within the "*Selaginella flabellata* group" and among these taxa it may be confused with *S. surucucusensis* because of their fairly similar median leaves with inconspicuous, short-elongate or punctate idioblasts on the upper surfaces. *Selaginella gioiae*, however, is set aside from *S. surucucusensis* by the characters listed in the diagnosis and by its median leaf with the outer bases rounded or with a rounded nob (vs. with a distinct auricle) and acute, attenuate or short-acuminate (vs. attenuate or acuminate to short-aristate) apices, each less than ¼ (vs. ¼) the length of the lamina. *Selaginella cuneata* Mickel & Beitel is another member of the "*Selaginella flabellata* group" with inconspicuous short-elongate or punctate idioblasts on the upper surface of median leaves. *Selaginella gioiae* differs from the latter by its median leaf outer half of the lamina at least ¼ to ½ wider (vs. twice as narrow) as the inner half, and hyaline (vs. greenish) bordered margins of median leaves and on acroscopic margins of lateral leaves.

Selaginella papillosa Valdespino, sp. nov.

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Figures 6–9

Diagnosis. *Selaginella papillosa* differs from *S. brevifolia* by its median leaf inner and outer halves equal in width (vs. outer halves typically wider than the inner halves), lateral leaf upper surfaces with midribs not marked and of the same color as the rest of

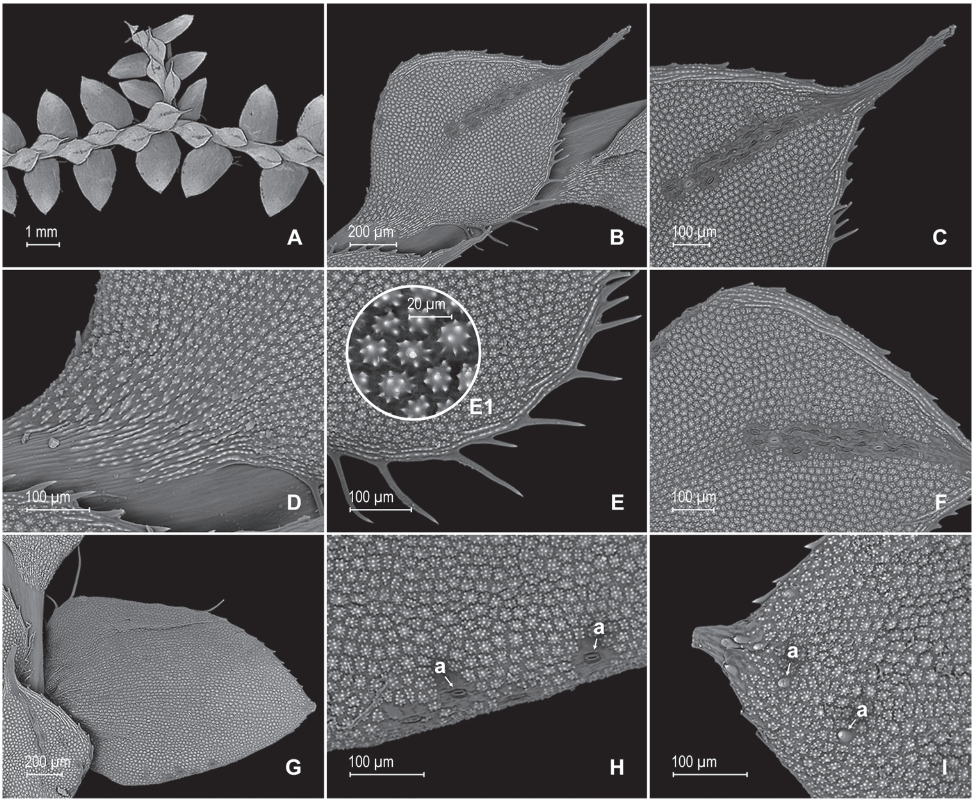

Figure 6. *Selaginella papillosa* Valdespino. **A** Section of upper surface of stem showing median and lateral leaves **B** median leaf, upper surface **C** distal half of median leaf, upper surface (same leaf shown in **B**) **D** proximal half of median leaf, upper surface (same leaf shown in **B**) **E** section median leaf inner half, upper surface; note prominent papillae on cells (E1) **F** detail of midsection of median leaf, upper surface **G** lateral leaf and sections of median leaves, upper surface **H** portion of basiscopic margin of lateral leaf, upper surface; note submarginal stomata (a) **I** distal half of lateral leaf, upper surface, note short hair on leaf surface (a). **A–I** taken from the holotype.

the laminae (vs. well-marked and straw-colored), acroscopic margins long-ciliate along proximal ¼–⅓ or occasionally proximal ½ (vs. ½–¾), and axillary leaf ovate or ovate-lanceolate (vs. ovate-deltate).

Type. Venezuela. Amazonas: Río Negro, Río Siapa near base of Cerro Aracamuni, 01°39'N, 65°40'W, 250 m, 4 Nov 1987, *R.L. Liesner & G. Carnevali 22750* (holotype: NY!; isotypes: MO!, NY!, UC!).

Description. *Plants* epipetric, moss-like. *Stems* creeping, stramineous, 5.0–15.0 cm long, 0.3–0.5 mm diam., non-articulate, not flagelliform, not stoloniferous, straw-colored, 1 or 2-branched, the branches arising at almost 90° angle. *Rhizophores* axillary, axillary-ventral or dorsal, borne throughout the stems, filiform, 0.1–0.2 mm diam. *Leaves* heteromorphic throughout, membranaceous, upper surfaces light green, lower surfaces silvery green. *Lateral leaves* distant, spreading to slightly ascending or slightly

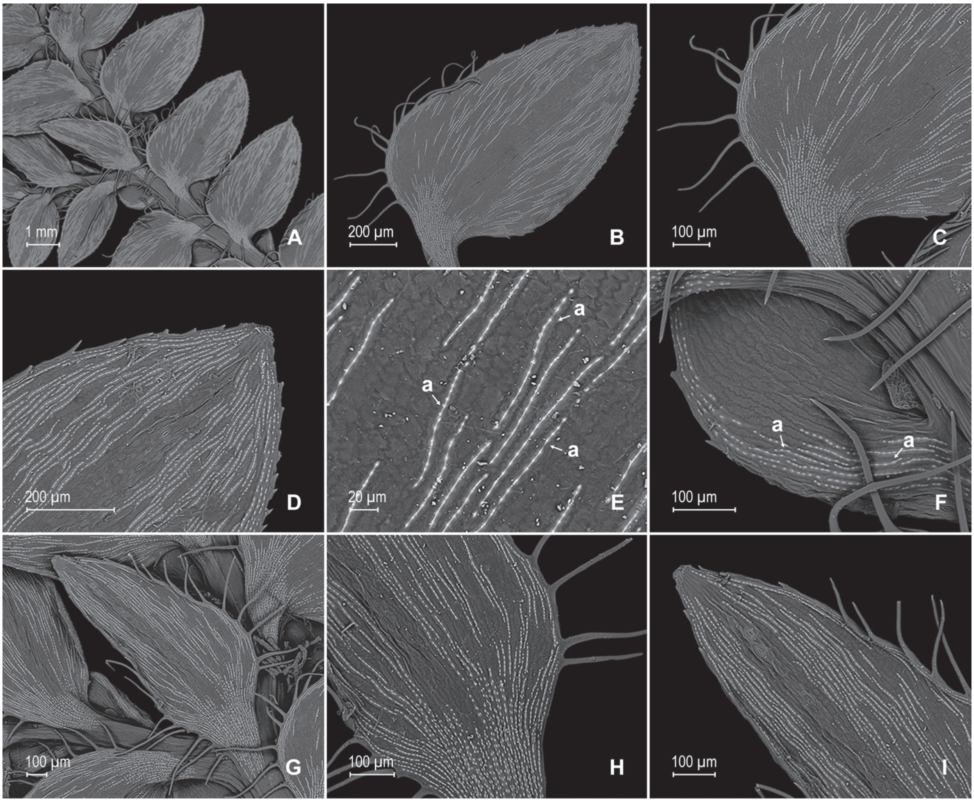

Figure 7. *Selaginella papillosa* Valdespino. **A** Section of lower surface of stem showing lateral leaves and axillar leaf **B** lateral leaf, lower surface **C** proximal half of lateral leaf, upper surface (same leaf shown in **B**) **D** distal half of lateral leaf, upper surface (same leaf shown in **B**) **E** detail of lateral leaf, lower surface; note elongate, papillate idioblasts with papillae interconnected (a) **F** detail of outer half of median leaf, lower surface; note elongate, papillate idioblasts (a) **G** axillary leaf and portion of lateral leaves, lower surface **H** portion of proximal half of axillary leaf, lower surface (same leaf shown in **G**) **I** distal half of axillary leaf, lower surface (same leaf shown in **G**). **A–I** taken from the holotype.

imbricate (at branch tips), ovate, 1.0–2.0 × 0.8–1.6 mm; bases rounded, glabrous, acroscopic bases overlapping stems, basiscopic bases free from stems; margins on upper surfaces greenish and composed of quadrangular to rounded cells, on lower surfaces bordered continuously by a hyaline band comprised of idioblasts, the band 1–3 cells wide, the idioblasts elongate, straight-walled, and papillate, the papillae in a single row over each cell lumen, acroscopic margins long-ciliate along proximal ½–⅔, otherwise dentate distally, basiscopic margins dentate along proximal ⅔, otherwise denticulate distally; apices acute, attenuate to apiculate, apiculae often falling off, tipped by 1 or 2 teeth; upper surfaces mostly glabrous, except for few, distal, teeth-like hairs near apices, comprising rounded to quadrangular, sinuate-walled, papillate cells, each cell lumen with 7–14 papillae, with few (ca. 4) submarginal to marginal stomata near central portion of basiscopic margins, lower surfaces glabrous, comprising elongate, sinuate-walled, laevigate cells and of straight-walled, papillate idioblasts, the papillae 9–15 in one row on each cell lumen, with stomata on 1–3 rows along midribs. *Median leaves* distant to slightly imbricate near branch tips, ascending, ovate to broadly ovate to ovate-orbiculate or elliptic with both inner and outer halves equal in width, 0.8–1.2 × 0.5–1.0 mm; bases glabrous, oblique and decurrent, without auricles; inner margins bordered continuously by a narrow hyaline band comprised of idioblasts, the band 1 or 2 cells wide, the idioblasts similar to those in the hyaline marginal bands of the lateral leaves on lower surfaces, except for papillae sometimes interconnecting, long-ciliate along proximal ¾, otherwise short-ciliate to dentate distally, the outer margins bordered by greenish, quadrangular to elongate, glabrous cells along proximal ½ and along distal ½ by a hyaline band comprised of idioblasts, the band 1–5 cells wide, the idioblast similar to those in the inner margins, dentate throughout; apices aristate, each arista 0.2–0.4 mm long, tipped by 1 or 2 teeth; upper surfaces glabrous, comprising rounded, sinuate-walled, papillate cells, each cell lumen with 4–15 papillae, concentrically arranged, without idioblasts, with stomata in 1 or 2 rows along midribs on distal ½ of the leaf lamina and few (1 or 2) marginal to submarginal along proximal ½ of outer margins, lower surfaces comprising elongate, sinuate-walled, glabrous cells and submedial to submarginal, sinuate-walled, papillate, idioblasts cells, the papillae similar to those in lower surfaces of lateral leaves, without stomata. *Axillary leaves* ovate to ovate-lanceolate, 1.2–1.5 × 0.6–1.0 mm; bases attenuate and covered by idioblasts

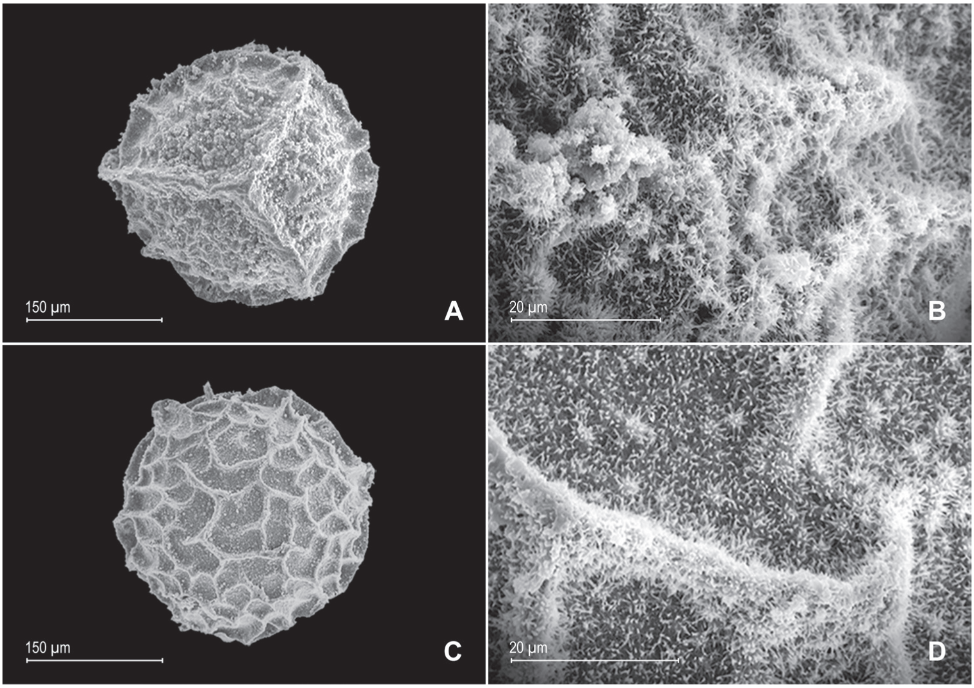

Figure 8. *Selaginella papillosa* Valdespino. **A** Megaspore, proximal face **B** detail of megaspore, proximal face **C** megaspore, distal face **D** detail of megaspore, distal face. **A–D** taken from the holotype.

similar to those in lower surfaces of lateral leaves, except for papillae in 1 or 2 rows on cell lumen; margins on upper and lower surfaces as in lateral leaves, ciliate along proximal ½–¾; apices acute, attenuate to apiculate, apiculae often falling off; both surfaces as in lateral leaves. *Strobili* terminal on branch tips, quadrangular, 0.4–5 mm long. *Sporophylls* monomorphic, without a laminar flap, each with a slightly developed keel along midribs, the keel glabrous or with few, short, tooth-like projections distally, ovate-lanceolate, 0.6–1.0 × 0.3–0.5 mm; bases rounded; margins narrowly bordered by a hyaline band, the band 1 or 2 cells wide with the cells elongate, slightly sinuate-walled and glabrous, shortly ciliate along proximal ½, denticulate on distal ½ or denticulate throughout; apices attenuate to acuminate, the acumen 0.1–0.3 mm long, tipped by 1 or 2 teeth; *dorsal sporophylls* with upper surfaces green and cells as in median leaves, except for the half that overlaps the ventral sporophylls where the surfaces are greenish hyaline to hyaline with elongate and slightly sinuate-walled cells, lower surfaces hyaline and comprising elongate, sinuate-walled cells; *ventral sporophylls* with both surfaces, hyaline, comprised of elongate, papillate, sinuate-walled cells. *Megasporangia* few and proximal, along two ventral rows; *megaspores* yellow, pale yellow to whitish, 270–310 µm diam., proximal faces rugulate-reticulate with a well-developed equatorial flange, the microstructure echinate and perforate, distal faces reticulate, the reticulae open (incomplete) to closed, the microstructure echinate and perforate. *Microsporangia* in two dorsal rows and distally along two ventral rows; *microspores* light orange, not measured or observed in detail.

Habitat and distribution. *Selaginella papillosa* grows at 250–1670 m in tropical rainforests at the base of Cerro Aracamuni and near the summit of Cerro Aratitiyope in the state of Amazonas, Venezuela.

Etymology. The specific epithet derives from the Latin "*papilla*," meaning "nipple", and refers to the abundant and distinctive papillae found on cells lumen in upper, leaf surfaces.

Conservation status. *Selaginella papillosa* is only known from two collections made at the base of Cerro Aracamuni, a Guiana Highland sandstone tepui, part of the Serranía de La Neblina National Park, and near the top of Cerro Aratitiyope, a granitic mountain designated as a Natural Monument, both in the state of Amazonas, Venezuela. Accordingly, the natural populations of this new species may not be threatened. However, as available data is scanty, it does not allow for a reliable conservation assessment. Therefore, the species is considered Data Deficient (DD) based on IUCN (2012).

Additional specimens examined (paratypes). Venezuela. **Amazonas**: Río Negro, Cerro Aratitiyope, ca. 70 km al SSW de Ocamo, 02°10'N, 65°34'W, 990–1670 m, 24–28 Feb 1984, *Steyermark et al. 130146* (MO-2 sheets, UC pp [mixed with some scraps of *S. tuberculata* Spruce ex Baker]).

Discussion. *Selaginella papillosa* is distinctive by its moss-like habit, lateral leaf with long-ciliate acroscopic margins along proximal ½–⅔ and acute, attenuate to apiculate apices, with apiculae often falling off and tipped by 1 or 2 teeth, the upper surfaces glabrous, except for few, distal, teeth-like hairs near apices, and with few

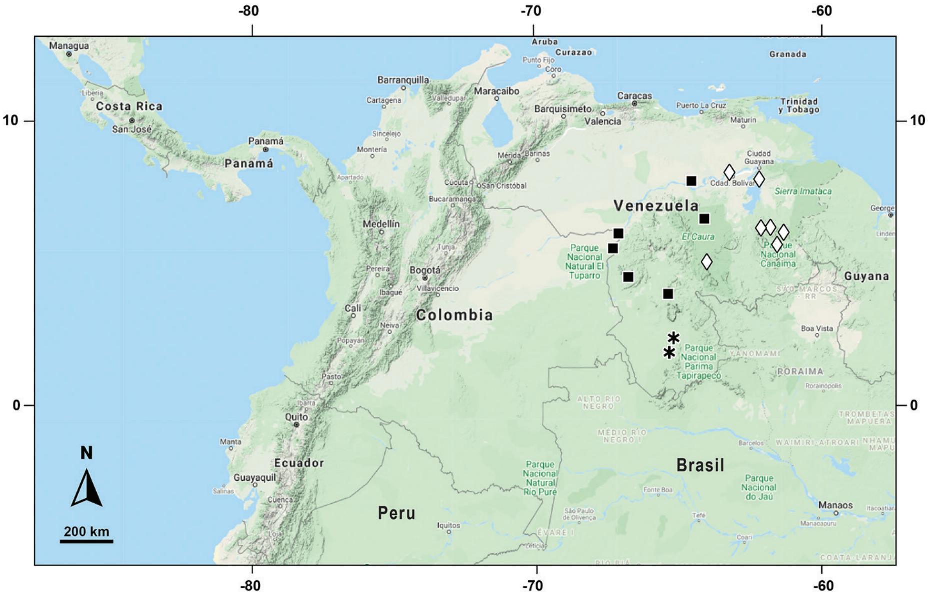

Figure 9. Distribution of *Selaginella papillosa* *, *S. pubimarginata* ◊, *S. rostrata* ■.

submarginal to marginal stomata near central portion of basiscopic margins. In addition, its leaf upper surfaces are comprised by rounded to quadrangular, sinuate-walled, papillate cells, each cell lumen with many (i.e., 7–14) papillae, and with margins bordered by elongate, straight-walled, papillate idioblasts on lower leaf surfaces. Finally, its median leaf upper surfaces have marginal to submarginal stomata along proximal ½ of outer margins.

Selaginella papillosa is a member of the "*Selaginella deltoides* group" as defined by Valdespino (2016). Among species in that alliance it is morphologically close (e.g. in habit, leaf, and overall megaspore sculpturing pattern) to *S. aculeatifolia* and the here described *S. pubimarginata* (see for discussion). These three species might, in addition, be sympatric, as they have been collected in the Guiana Highland region of Venezuela at similar low to mid elevations. *Selaginella papillosa* differs from *S. aculeatifolia* by its lateral leaf upper surfaces with few (vs. without) submarginal stomata along central, basiscopic portion of the laminae, with 3–5 (vs. many, ca. 50) short hairs or tooth-like projections near distal most portion of apices (vs. along distal ½ of basiscopic halves and apices), with midribs inconspicuous (vs. conspicuous, outlined by elongate, straight-walled and papillate idioblasts), and acute to apiculate (vs. long-acuminate) apices. It is further differentiated from the latter by its median leaves broadly ovate to ovate-orbiculate or elliptic (vs. broadly ovate to ovate-elliptic), with oblique and decurrent (vs. oblique or rounded) bases, and stomata present on upper leaf surfaces along distal ½ (vs. ¾) and with few (vs. without) stomata submarginally to marginally along proximal ½ portion of outer margins. Furthermore, its megaspores proximal and distal faces microstructure consists of long- (vs. short-) echinae.

Selaginella papillosa was confused in the past with *S. brevifolia* and, in fact, its type collection was originally identified as the latter species. *Selaginella papillosa* differs from *S. brevifolia* by the characters listed in the diagnosis and by its lateral leaf having only very few, i.e., 4–6 tooth-like short hairs near the apices, whereas the latter species has many of these hairs along the basiscopic halves of the laminae and toward the apices.

Selaginella papillosa is also set aside from the similar *S. albolineata* by its median and lateral leaves upper surfaces without (with many, elongate) idioblasts and acroscopic margins long-ciliate along proximal ½–⅔, otherwise denticulate distally (vs. entire to scarcely denticulate throughout), and median leaf inner margins long-ciliate (vs. denticulate).

The paratype specimen of *S. papillosa* (*Steyermark et al. 130146* at MO) was originally identified as *S. revoluta* Baker, vel aff., a species that is the center of a species group described by Mickel et al. (2004). *Selaginella papillosa* is a rather more slender species than *S. revoluta* and differs further from the latter by its median leaves ovate to broadly ovate to ovate-orbiculate or elliptic (vs. broadly ovate, ovate orbicular to ovate-rhombic) with oblique to decurrent (vs. subcordate) bases, and apices with rather narrow and needle-like (vs. broad and subulate) long aristae, each without (vs. with tooth-like) hairs on its surfaces. Finally, *S. papillosa* could also be compared to *S. hirtifolia* Valdespino, which is not morphologically close to it but rather is a member of the *S. revoluta* group. *Selaginella papillosa* is easily separated from the latter by its lateral leaf upper surfaces almost completely glabrous (vs. with short, teeth-like hairs along the basiscopic, submarginal region and near apices) and long-aristate (vs. acuminate) median leaf apices with the arista hyaline (vs. with the acumen green).

***Selaginella pubimarginata* Valdespino, sp. nov.**

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Figures 9–12

Diagnosis. *Selaginella pubimarginata* differs from *S. albolineata* by its ovate-deltate (vs. ovate to ovate-elliptic) lateral leaves with upper surfaces lacking (vs. with) conspicuous idioblasts, acroscopic margins long-ciliate along proximal ½, otherwise dentate to denticulate distally (vs. denticulate throughout), acute to attenuate to shortly acuminate (vs. obtuse to rounded) apices, and axillary leaves ciliate (vs. dentate) along proximal ½–⅔.

Type. Venezuela. Amazonas: Atabapo: Río Cunucunuma, entre las comunidades de Culebra y Huachamacari, entre el Cerro Duida y Huachamacari, 180–210 m, 03°40'N, 65°45'W, 28–30 Jan & 6–8 Feb 1982, *J.A. Steyermark et al. 125655* (holotype: NY!; isotypes: MO!, NY!, PMA!, UC!).

Description. *Plants* epipetric, terrestrial or epiphytic, moss-like. *Stems* creeping, stramineous, 2.0–12 cm long, 0.25–0.4 mm diam., not-articulate, not flagelliform or stoloniferous, straw-colored to brownish, 1- or 2-branched, the branches arising at ca. 45° angle. *Rhizophores* axillary, borne throughout the stems, filiform, 0.1–0.15 mm diam.

Leaves heteromorphic throughout, membranaceous, upper surfaces green, golden brown (in old leaves) or dark brown (in alcohol-preserved specimens), lower surfaces

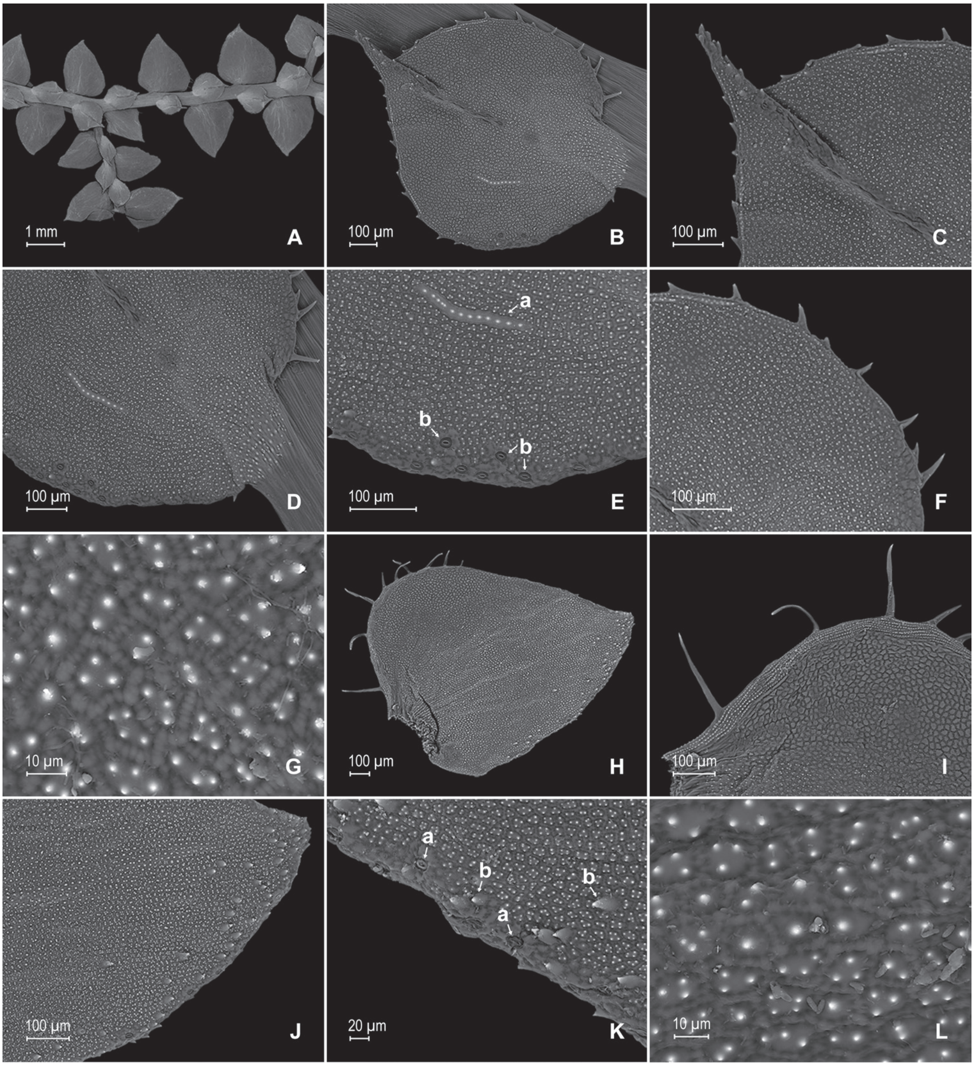

Figure 10. *Selaginella pubimarginata* Valdespino. **A** Section of upper surface of stem showing median and lateral leaves **B** median leaf, upper surface **C** distal half of median leaf, upper surface (same leaf shown in **B**) **D** proximal half of median leaf, upper surface (same leaf shown in **B**) **E** section of median leaf outer half, upper surface; note prominent elongate, papillate idioblast (a) and submarginal stomata (b) **F** detail of midsection of inner half of median leaf, upper surface **G** detail of median leaf, upper surface; note papillate cells **H** lateral leaf, upper surface **I** section of proximal, acroscopic half of lateral leaf, upper surface (same leaf shown in **H**) **J** section of distal and basiscopic half of lateral leaf, upper surface (same leaf shown in **H**) **K** detail of section of basiscopic margin of lateral leaf, upper surface (same leaf shown in **H**); note submarginal stomata (a) and teeth-like hairs (b) **L** detail of lateral leaf, upper surface; note papillate cells. **A–L** taken from the holotype.

silvery. *Lateral leaves* distant, spreading, perpendicular to stems or less often slightly ascending, broadly ovate, ovate-deltate or ovate-elliptic, 1–1.5 × 0.5–1.2 mm; bases rounded, glabrous, acroscopic bases slightly overlapping stems, basiscopic bases free from stems; acroscopic margins on both surfaces plane or sometimes revolute on upper surfaces, along proximal ½–⅔ bordered by a hyaline band comprised of idioblasts, the band 1–6 cells wide, the idioblasts elongate, straight-walled, and papillate, the papillae in a single or double row over each cell lumen, long-ciliate, otherwise on distal ⅓–½, greenish, bordered by quadrangular to rounded cells, entire or sparse- and minutely denticulate, especially along distal ⅓, basiscopic margins on both surfaces greenish, bordered by quadrangular to rounded cells, entire throughout or sparse- and minutely denticulate, along distal ⅓; apices attenuate to shortly acuminate, each acumen ca. 0.1 mm long, tipped by 1–3 teeth; upper surfaces mostly glabrous, except for many, short, teeth-like hairs marginally to submarginally along basiscopic margins and distally towards and at the apices, comprising rounded to quadrangular, slightly sinuate, and broad-walled cells on basiscopic ⅔ of the laminae, the cells papillate, the papillae 1–5 and irregularly arranged on each cell lumen, on acroscopic ⅓ of the laminae comprising strongly sinuate, thin-walled, and glabrous cells, without idioblasts, stomata present on acroscopic margins along distal ⅓ and on basiscopic margins along distal ¾, lower surfaces glabrous, comprised of elongate, sinuate-walled, laevigate cells and of straight-walled, papillate idioblasts, the papillae 7–28 in one or two rows on each cell lumen, the idioblasts evenly distributed on the laminae and strongly grouped on proximal, basal region of the laminae, with stomata on 1–5 rows along midribs. *Median leaves* distant to slightly imbricate near branch tips, ascending, broadly elliptic to orbicular or broadly ovate-elliptic with both inner and outer halves equal in width, 0.7–1.2 × 0.5–0.8 mm; bases glabrous, oblique, not decurrent, without auricles; margins plane or outer margins on proximal ¼ revolute, along proximal ½ bordered by greenish, quadrangular cells, on distal ½ bordered continuously by a narrow hyaline band comprised of idioblasts, the band 1 or 2 cells wide, the idioblasts similar to those in the hyaline marginal bands of proximal ½–⅔ of acroscopic margins of the lateral leaves, dentate on outer margins and short-ciliate along proximal ½, otherwise dentate along distal ½ on inner margins; apices short acuminate, each acumen 0.1 or 0.2 mm long and tipped by 1–3 teeth; upper surfaces glabrous, except for few, submarginal, short, teeth-like hairs on mid portion of outer margins, comprised of round to quadrangular slightly sinuate, thick-walled, papillate cells and one, papillate idioblast along mid-section of outer margins, the papilla 10–13 on a single row on each cell lumen, stomata on midrib along distal ½ and submarginally to marginally along proximal ½ of outer margins, lower surfaces glabrous, comprised of elongate, sinuate-walled, laevigate cells, without stomata. *Axillary leaves* broadly ovate, ovate-deltate or ovate-elliptic, 1.2–1.6 × 0.7–1.2 mm; bases attenuate; margins bordered continuously by a hyaline band comprised of papillate idioblasts along proximal ⅔, the band 1–6 cells wide, the papillae in a single row, on distal ⅓ bordered by greenish, quadrangular cells, long-ciliate along proximal ½–⅔, otherwise entire to denticulate distally; apices attenuate, each 0.1 mm long, tipper by 1–5 teeth. *Strobili* terminal, loosely quadrangular, 1.5–9 mm long. *Sporophylls* monomorphic, without a laminar flap, each with a slightly developed keel along midribs, the keel puberulent with short, tooth-like projections distally, ovate to ovate-lanceolate, (0.6)0.9–1.5 × (0.3)0.5–0.7 mm; bases rounded; margins obscurely hyaline bordered by 1–3(4) elongate, papillate idioblasts

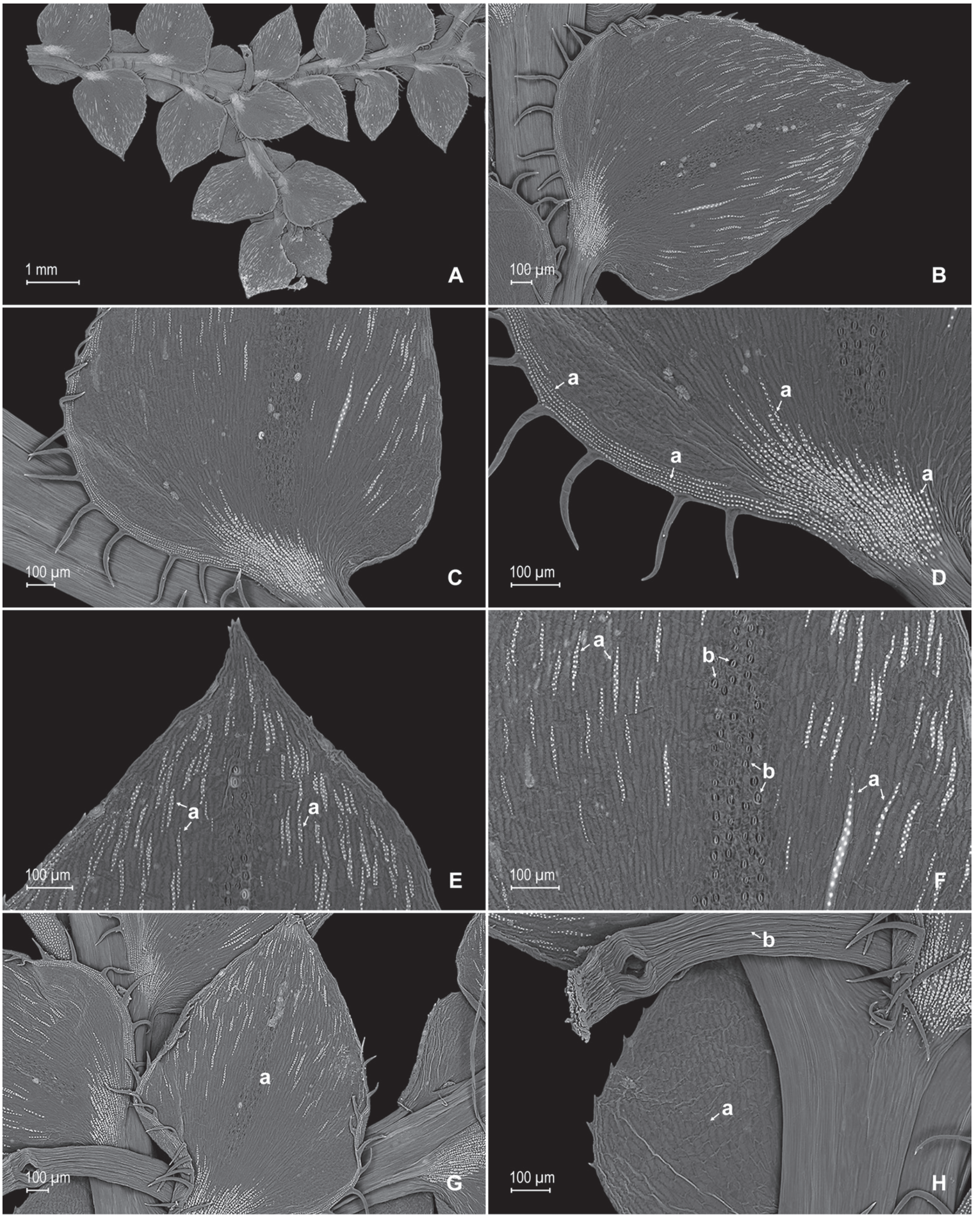

Figure 11. *Selaginella pubimarginata* Valdespino. **A** Section of lower surface of stem showing lateral and median leaves and axillar leaf **B** lateral leaf, lower surface **C** proximal half of lateral leaf, upper surface (same leaf shown in **B**) **D** section of proximal acroscopic margin and base of lateral leaf, lower surface (same leaf shown in **B**); note elongate, papillate idioblasts (a) **E** distal half of lateral leaf, lower surface (same leaf shown in **B**); note elongate, papillate idioblasts (a) **F** mid-section of lateral leaf, lower surface (same leaf shown in **B**); note elongate, papillate idioblasts (a) and stomata along midrib (b) **G** axillary leaf (a) and portions of lateral and median leaves, lower surfaces **H** detail of outer half of median leaf (a) and axillary rhizophores (b), lower surfaces (same leaf shown in **G**). **A–H** taken from the holotype.

(especially apically), serrate; apices long-acuminate, tipped by 1–3 teeth; *dorsal sporophylls* with upper surfaces green and cells as in median leaves, except for the half that overlaps the ventral sporophylls where the surfaces are greenish hyaline to hyaline with elongate and slightly sinuate-walled cells, lower surfaces hyaline and comprising elongate, sinuate-walled cells; *ventral sporophylls* with both surfaces, hyaline, comprised of elongate, papillate, sinuate-walled cells. *Megasporangia* few and proximal, along two ventral rows; *megaspores* light to lemon-yellow, 240–250 µm diam., proximal faces rugulate with a slightly developed equatorial flange, the microstructure sparsely, short echinate and perforate, distal faces rugulate to reticulate, the rugulae or reticulae open (incomplete) to closed, each reticulum with low walls, the microstructure sparsely, short echinate and perforate. *Microsporangia* light orange in two dorsal rows and distally along two ventral rows; 22–250 µm diam., *microspores* light orange, rugulate on proximal and distal faces, with the microstructure perforate.

Habitat and distribution. *Selaginella pubimarginata* grows on shaded or exposed moist boulders, along streambeds, and waterfalls in tropical rainforests at 80–700 m; it is known at and around Cerro Huachamacari, along the rivers Sipapo and Coromoto in Amazonas state, and along Río Caura in Bolívar state, Venezuela.

Etymology. The epithet derives from the Latin "*puberulus*," slightly pubescent, and "*marginatus*," having a border. Together these refer to the presence of submarginal hairs on lateral leaves upper surfaces near the basiscopic and apical portion of leaf laminae.

Conservation status. *Selaginella pubimarginata* is known from four collections made in two states in the Guiana Highland region of Venezuela. Current available data, however, is scanty and does not allow for a reliable conservation assessment. Accordingly, this new species is considered Data Deficient (DD) based on IUCN (2012).

Additional specimens examined (paratypes). Venezuela. **Amazonas**. Atabapo: Cerro Huachamacari, E slope, 03°49'N, 65°42'W, 600–700 m, 2 Nov 1988, *Liesner 25697* (MO, UC); Río Cunucunuma, entre las comunidades de Culebra y Huachamacari, entre el Cerro Duida y Huachamacari, 03°40'N, 65°45'W, 180–210 m, 28–30 Jan & 6–8 Feb 1982, *Steyermark et al. 125639* (NY, UC), 200–400 m, 28–30 Jan & 6–9 Feb 1982, *Guariglia et al. 1676* (NY-2 sheets); Atures: 125 km de la boca (delta) del Guayapo en Sipapo, 04°22'N, 67°06'W, 130 m, May 1989, *Foldats & Velazco 9203* (NY); 40 km S of Puerto Ayacucho, Tobogán de la Selva, 05°35'N, 67°30'W, 70–100 m, 21 Jan 1985, *Beitel & Buck 85010* (NY, UC); Río Coromoto, above Tobogán de la Selva, 35 km SE of Puerto Ayacucho, 05°27'N, 67°33'W, 80 m, 7 Sep 1985, *Steyermark et al. 131528* (MO, UC). **Bolívar**: alrededor del campamento "Las Pavas", vecindad del Salto Para, Río Caura (lado derecho del río abajo), 230–280 m, 15–17 Jan 1977, *Steyermark et al. 112992* (GH, MO); Medio Caura, selva del Salto de Para, 300 m, 5 Mar 1939, *Williams 11385* (BM, F).

Discussion. *Selaginella pubimarginata* is characterized by its moss-like habit, lateral leaf ovate-deltate, with tooth-like, short hairs on the upper surfaces along basiscopic halves of leaf laminae, long-ciliate margins along proximal ½, and acute to attenuate to shortly acuminate apices, axillary leaves similar in overall shape and apices to lateral leaves and long-ciliate margins along proximal ½.

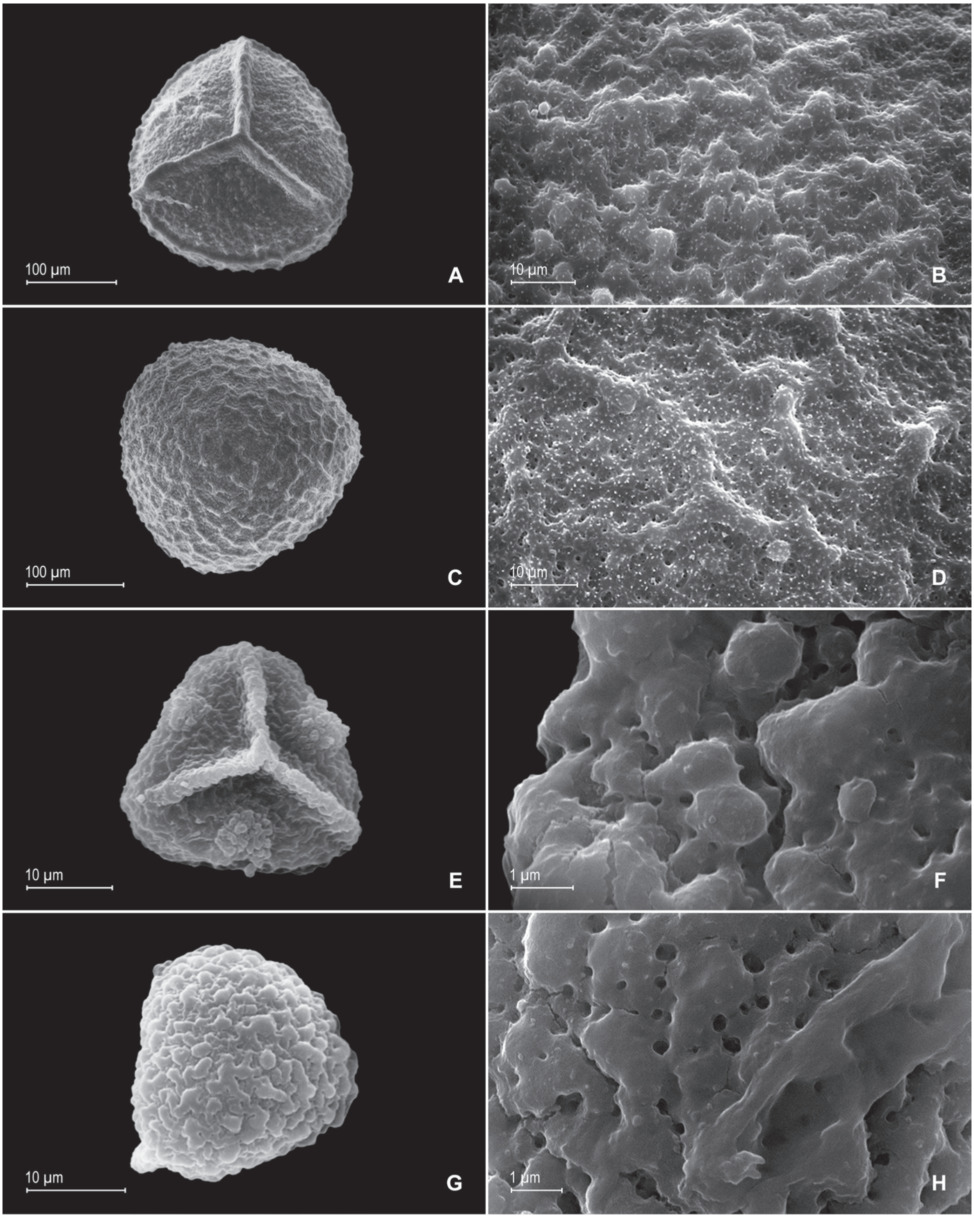

Figure 12. *Selaginella pubimarginata* Valdespino. **A** Megaspore, proximal face **B** detail of megaspore, proximal face **C** megaspore, distal face **D** detail of megaspore, distal face **E** microspore, proximal face **F** detail of microspore, proximal face **G** microspore, distal face **H** detail of microspore, distal face. **A–H** taken from the holotype.

Selaginella pubimarginata belongs in the "*Selaginella deltoides* group", and among species in this alliance it is morphologically close to *S. albolineata* and *S. papillosa*. It is set aside from *S. albolineata* by characters listed in the diagnosis. *Selaginella pubimarginata* is distinct from *S. albolineata* by its axillary leaves ovate-deltate (vs. ovate-elliptic) with acute to attenuate to shortly acuminate (vs. obtuse to rounded) apices, lateral leaf upper surfaces without (vs. with many) idioblasts, and median leaf upper surfaces with a single, elongate and papillate idioblast on either the outer or inner halves of the laminae (vs. with two or three, elongate, and papillate idioblasts on the outer and inner halves of the laminae). *Selaginella pubimarginata* differs most noticeable from the also similar *S. papillosa* by its median leaf upper surfaces with a single (vs. lacking) elongate and papillate idioblasts on either the outer or inner halves of the laminae, with (vs. lacking) one or two, teeth-like hairs on mid, submarginal portion of the outer half of the laminae, and laminae comprised of rounded, sinuate-walled cells with the cell lumina including 1–5 (vs. 4–15) rounded (vs. conical) and not protruding (vs protruding or elevated) papillae, as well as apices covered by (vs. without) teeth-like, short hairs. In addition, the lateral leaf upper surfaces of *S. pubimarginata* are covered by many (vs. few) ca. 40 (vs. 3–5) short hairs or teeth-like projections along submarginal portion of basiscopic margins and on distal, apical portion (vs. concentrate on distal most portion) of apices. Finally, *S. pubimarginata* is further distinct from *S. papillosa* by its rugulate (vs. rugulate-reticulate) megaspores on proximal faces with a slightly developed (vs. with a well-developed) equatorial flange, with microstructure sparsely (vs. abundantly) covered by short- (vs. long-) echinae and distal faces slightly (vs. strongly) reticulate with open (vs. with open and closed) reticulae delimited by low (vs. high) muri.

All specimens of *S. pubimarginata* here cited were previously identified either as *S. brevifolia* or *S. brevifolia* vel aff. *Selaginella pubimarginata* is set aside from *S. brevifolia* by its median leaf ovate-orbicular to orbicular (vs. ovate) with the laminae almost as wide as long (vs. longer than wider) with outer and inner leaf halves about the same width (vs. outer leaf half frequently wider than the inner leaf half), attenuate to shortly acuminate (vs. long-aristate) apices, each acumen ⅕–¼ (vs. ⅓–½) the length of the leaf lamina, and margins obscurely hyaline or greenish (vs. conspicuously hyaline, especially the outer margin). *Selaginella pubimarginata* differs further from *S. brevifolia* by its lateral leaf upper surfaces when viewed with a dissecting scope with midribs not marked and of the same color as the laminae (vs. well-marked and straw-colored) and laminae epidermal cells inconspicuously (vs. conspicuously) rounded, and long-ciliate along proximal ½ (vs. ½–¾) margins.

Selaginella rostrata **Valdespino, sp. nov.**

urn:lsid:ipni.org:names:77211385-1
Figures 9, 13

Diagnosis. *Selaginella rostrata* differs from *S. microdonta* by its broadly ovate to ovate-deltate (vs. ovate to ovate-lanceolate) median leaves that are wider at middle (vs. at base) of the laminae, with cordate to subcordate (vs. oblique) bases, hyaline (vs. greenish to weakly hyaline) inner margins, strongly beveled (vs. plane or weakly beveled) apices in profile that are long-aristate (vs. acute to attenuate), the arista (0.06)0.1–0.2 mm long (vs. apices less than 0.05 mm long), usually tipped by one to three teeth (vs. bluntly tipped or tipped by one teeth).

Type. Venezuela. Bolívar: Piar, Ptari-tepui, steep forested slopes at base of first line of sandstone bluff, on south-facing part, E of "Cave Rock," 2130 m, 4 Nov 1944, *J.A. Steyermark 59836* (holotype: NY!; isotypes: BM-n.v., F!, MO!, US!).

Description. *Plants* epipetric or terrestrial, ribbon-like, with leafy liverwort habit. *Stems* creeping, stramineous, 3–10 cm long, (0.1)0.18–0.34 mm diam., non-articulate, not flagelliform, non-stoloniferous, 1- or 2-branched, the lateral branches resulting from division of the main stem usually becomes arrested. *Rhizophores* axillary and subdorsal, borne throughout stems, 0.08–0.12 mm diam. *Leaves* heteromorphic throughout, chartaceous to thin-coriaceous, upper surfaces green or light-brown when old or due to dying process, lower surfaces silvery green or light-brown when old or due to dying process. *Lateral leaves* distant, ascending to slightly perpendicular to stems, broadly elliptic to broadly ovate, 0.7–2.0 × 0.4–1.4 mm; bases rounded to round-truncate, glabrous, acroscopic bases overlapping stems, basiscopic bases free from stems; acroscopic margins on upper surfaces greenish or weekly hyaline along proximal ½, otherwise greenish on distal ½, composed of quadrangular to rounded cells, basiscopic margins on upper surfaces greenish, bordered by quadrangular to rounded cells, margins on lower surfaces continuously bordered by a hyaline band comprised of idioblasts, the band 3–15 cells wide, the idioblasts elongate, straight-walled, and papillate, the papillae in a single row over each cell lumen, acroscopic margins dentate to denticulate throughout or denticulate along proximal ⅓–½ and entire distally, basiscopic margins sparsely denticulate or entire throughout; apices obtuse to rounded, occasionally tipped by a caducous short or tooth-like hair; upper surfaces glabrous, comprising rounded to irregularly, sinuate-walled, laevigate cells, without idioblasts or stomata; lower surfaces comprising elongate, slightly sinuate-walled cells, without idioblasts, with stomata in 1–3 rows along midribs. *Median leaves* slightly imbricate to distant, ascending, ovate to ovate-deltate with the inner halves of the leaf lamina ⅛–¼ wider than the outer halves, 0.6–1.5 × 0.4–1.0 mm; bases glabrous, cordate to subcordate, without auricles; margins bordered continuously by a hyaline band comprised of idioblasts, the band 2–5 cells wide, the idioblasts, elongate, straight-walled, and papillate, the papillae on one row on each cell lumen, denticulate throughout or entire along proximal ½ and denticulate along distal ½; apices keeled, long-acuminate to long-aristate, the acumen or arista denticulate, ⅓–¼ the length of the laminae, each (0.06–)0.1–0.2 mm long, usually tipped by one to three teeth; upper surfaces similar to lateral leaves upper surfaces, without idioblasts, with stomata in 1 or 2 rows restricted to distal ⅓ along the keel; lower surfaces similar to lower surfaces of lateral leaves, without idioblasts or stomata. *Axillary leaves* shape (except, occasionally oblong), size, bases, margins, apices and leaf surfaces similar to lateral leaves. *Strobili* terminal, single or dichotomous at branch tips, loosely quadrangular to slightly dorsiventral flattened, 2–12 mm long. *Sporophylls* slightly heteromorphic, broadly ovate to ovate-lanceolate (ventral sporophylls more broadly ovate and slightly shorter, dorsal sporophylls usually ovate-lanceolate and slightly larger), with a strongly developed keel along midrib, the keel glabrous, 1.0–1.3 × 0.5–0.9 mm; bases rounded; margins bordered by a hyaline band similar to that of the median leaves, dentate; *dorsal sporophylls* spreading, strongly keeled along midribs and especially near apices, the keel glabrous; apices acute to short-

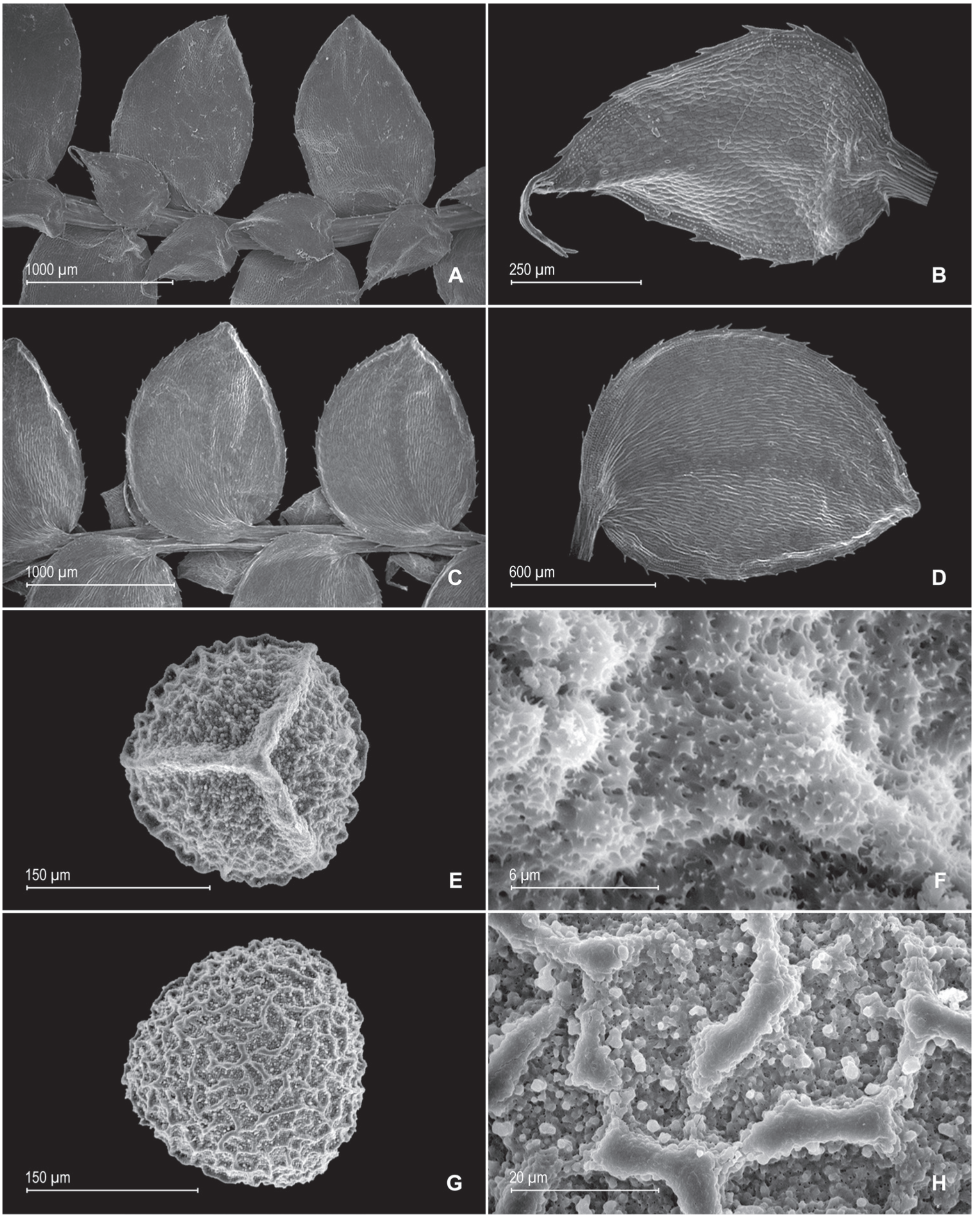

Figure 13. *Selaginella rostrata* Valdespino. **A** Section of upper surface of stem showing median and lateral leaves **B** median leaf, upper surface **C** section of lower surface of stem showing lateral and median leaves **D** lateral leaf, lower surface **E** megaspore, proximal face **F** detail of megaspore, proximal face **G** megaspore, distal face **H** detail of megaspore, distal face. **A–H** taken from the holotype.

acuminate and beveled in profile and abruptly ending in a short, tooth-like cilia, the cilia often caducous; upper surfaces green and cells as in median leaves, except for the half that overlaps the ventral sporophylls where the surfaces are hyaline composed of idioblasts similar to those of the median leaves margins, lower surfaces hyaline and comprising elongate, sinuate-walled cells; *ventral sporophylls* ascending, slightly keeled along midribs, the keel glabrous; apices acute to short-acuminate, not beveled in profile and usually ending in a short cusp; upper and lower surfaces hyaline, comprised of idioblasts similar to those of the median leaves margins. *Megasporangia* along two ventral rows; *megaspores* lemon yellow, 200–220 µm diam., proximal faces rugulate-reticulate with a well-developed equatorial flange, the microstructure echinate and perforate, distal faces reticulate, the reticulae open (incomplete) to closed, the microstructure granulose and perforate; *microsporangia* on two dorsal rows; *micropores* light-orange, 30–35 µm diam., proximal and distal faces gemmate, the microstructure granulose.

Habitat and distribution. *Selaginella rostrata* grow on wet and mossy sandstone bluffs, near damp stream banks, and at the base of waterfalls in mountainous tropical rainforests at 1000–2130 m. It has been found on several tepuis of the Guiana Highland in the state of Bolívar, Venezuela.

Etymology. The specific epithet derives from the Latin "*rostratum*," meaning beaked, and refers to the keeled/beaked median leaf and dorsal sporophyll apices.

Conservation status. *Selaginella rostrata* is known from several collections made over a time span of more than fifty years from mid-to-late twentieth century at different localities in the Guiana Highland region of Venezuela, some of which are adjacent to the neighboring country of Guyana. This suggests an overall wide distribution. Unfortunately, the paucity of more recent collections due, in part, to a decline in botanical exploration in the aforementioned areas, does not allow for an accurate conservation assessment. Consequently, this new species is considered Data Deficient (DD) based on IUCN (2012).

Additional specimens examined (paratypes). Venezuela. Bolívar: Altiplanicie of Auyan-tepui, SW sector, 05°48.02'N, 62°33.82'W, ca. 1850 m, 23–25 Apr 1996, *Anderson 13880* (MO, NY), Auyan-tepui, 1660 m, 12 May 1964, *Steyermark 93788* (US), 1820 m, 13 May 1964, *Steyermark 93871* (GH, K, NY, US), 2100 m, 17 May 1964, *Steyermark 94074* (NY, US), 1850 m, Dec 1937–Jan 1938, *Tate 1271* (NY); Cerro Venamo, 1100 m, 21 Apr 1960, *Steyermak & Nilsson 439* (NY, US-2 sheets), 1400–1450 m, 1 Jan 1964, *Steyermark et al. 92528* (GH, U, US), 1500 m, 2 Jan 1964, *Steyermark et al. 92588* (GH, U p.p., US, VEN), *Steyermark et al. 92588-A* (U p.p.), 1400–1500 m, 3 Jan 1964, *Steyermark et al. 92626* (US); Heres, Cerro Marutani, 03°50'N, 62°15'W, 1200 m, 11–14 Jan 1981, *Steyetmark et al. 123925* (GH, MO, NY), 1000–1050 m, 11–14 Jan 1981, *Steyermark et al. 124067* (GH, MO, NY); Meseta de Jáua, Cerro Jáua, 60 km NE Sanidad del Río Kanarakuni Camp, 04°45'N, 64°26'W, 1922–2100 m, 22–27 Mar 1967, *Steyermark 98018* (US), *Steyermark 98116* (US), *Steyermark 98120* (US); Piar, Amaruay-tepui, 05°54'N, 62°15'W, 700–810 m, 27 Apr 1986, *Liesner & Holst 20424 p.p.* [mixed coll. *20424a*] (MO, UC), Ptari-tepui, 2130 m, 4 Nov 1944, *Steyermark 59836* (F, MO, NY, US); Torono-tepui, Chimantá Massif, 1880–1970 m, 27 Feb 1955, *Steyermark & Wurdack 1181* (F, NY, UC, US).

Discussion. *Selaginella rostrata* is characterized by its creeping, ribbon-like, leafy liverwort habit, median leaf ovate to ovate-deltate, with inner halves of leaf laminae ⅛–¼ wider than outer halves, margins continuously bordered by a hyaline band of idioblasts, each band 2–5 cells wide, the idioblasts elongate, straight-walled, and papillate, and dentate to denticulate, and apices strongly keeled, long-acuminate to long-aristate, the acumen or arista denticulate, ¼–⅓ the length of the laminae, each (0.06)0.1–0.2 mm long, each usually tipped by one to three teeth. *Selaginella rostrata* its further defined by lateral leaf broadly elliptic to broadly ovate with obtuse to rounded apices, which occasionally are tipped by a caducous short or tooth-like hair, and sporophylls (especially dorsal sporophylls) conspicuously keeled (i.e., carinate) along midribs, and with apices acute with those of dorsal sporophylls apiculate ending on a single tooth-like, short hair, and stomata along midribs and keeled apices.

Selaginella rostrata is morphologically close to a species group that I informally call the "*S. microdonta* group," and in particular to the latter species and *S. neblinae*. *Selaginella rostrata* can be distinguished from *S. microdonta*, which may still need to be further circumscribed, by the characters listed in the diagnosis and its median leaf with inner halves of leaf laminae ⅛–¼ wider than outer haves (vs. inner and outer halves of leaf laminae about the same width or inner halves ⅛ narrower than outer halves). *Selaginella rostrata* further differs from *S. microdonta* by its acroscopic lateral leaf margins dentate to denticulate throughout or denticulate along the proximal ⅓–½, and entire distally, and basiscopic margins sparsely denticulate or entire (vs. acroscopic and basiscopic margins serrate). Furthermore, *S. rostrata* is also set aside from *S. neblinae* by its broadly elliptic to broadly ovate (vs. ovate-lanceolate) lateral leaves, with obtuse to rounded (vs. long attenuate to acuminate) apices, each occasionally tipped by a caducous short or tooth-like hair (vs. hair or teeth absent), and median leaf apices acuminate to long-aristate, each acumen or aristae ¼–⅓ (vs. ½) the length of the laminae, and margins conspicuously hyaline (vs. greenish).

Selaginella microdonta, *S. rostrata*, and *S. neblinae* along with *S. breweriana*, *S. cardiophylla*, *S. hemicardia*, and *S. valdepilosa* are part of the *S. microdonta* group. The relationship of the "*S. valdepilosa* group" still needs to be ascertained by phylogenetic methods but an initial hypothesis would suggest that *S. breweriana* and *S. neblinae* seem to be sister species, whereas *S. cardiophylla* and *S. rostrata* form another putative sister alliance that in turn is sister to a *S. microdonta* and *S. hemicardia* alliance, to which probably *S. valdepilosa* also belongs to as an offshoot that is most distinct by its leaves and sporophylls densely, long-ciliate.

Interestingly and as part of this study, it was observed that branches of *S. rostrata* can become arrested at branch forks giving the species a ribbon-like, leafy liverwort resemblance. Valdespino (1992) previously reported this condition as resting branches in *S. hemicardia*. Furthermore, as a result of the undeveloped branches, rhizophores in both species are seemingly subdorsal.

Additionally, one paratype collection here cited (i.e., *Lierner & Holsts 20424* p.p. at MO and UC) represents mixed gatherings, which I identified as *a* = *S. rostrata* and *b* = *S. tuberculata*, while two other collections (*Steyermark et al. 92588* p.p. at U, and *Steyermark et al. 92588-A* p.p at U) are also mixed gatherings, which I identified as *a* = *S. rostrata* and *b* = *S. cardiophylla*). *Selaginella tuberculata* also has a leafy, liverwort habit and creeping stems and might eventually prove to be part of the "*S. microdonta* group," but it is distinct from the rest of species here included in that alliance by its acroscopic lateral leaves margins long-ciliate along the proximal ¼–⅓ with upper surfaces puberulent along the basiscopic halves and towards the apices as well as occasionally also distally along the acroscopic halves.

Finally, to help identify species in the "*S. microdonta* group" a key is provided below, which summarizes distinguishing characters among taxa in this alliance.

Key to the *Selaginella microdonta* group

1 Apices of lateral and axillary leaves attenuate to acuminate **2**

2 Margins of lateral and median leaf long-ciliate, the cilia on the acroscopic halves of the lateral leaves and on the basiscopic halves of the median leaves ⅓ to ½ the width of the laminae .... ***S. breweriana***

2' Margins of lateral and median leaf entire, sparsely dentate or ciliolate, the teeth or cilia, when present, less than ⅛ the width of the laminae .... ***S. neblinae***

1' Apices of lateral and axillary leaves broadly acute, obtuse to rounded **3**

3 Vegetative leaves and sporophyll margins densely long-ciliate, leaf surfaces without idioblasts; median leaf apices tipped by two divergent, long hairs .... ***S. valdepilosa***

3' Vegetative leaves and sporophyll margins sparsely dentate to denticulate or entire distally or, if short-ciliate, the leaf upper surfaces with conspicuous idioblasts; median leaf apices usually tipped by one to three teeth **4**

4 Median leaf apices acute or short- to long-acuminate to long-aristate. **5**

5 Median leaves widest towards the bases of the laminae, bases subcordate to rounded; upper surfaces of median and lateral leaves dull green and strongly wrinkled. .... ***S. hemicardia***

5' Median leaves widest at the middle of the laminae, bases cordate to subcordate; upper surfaces of median and lateral leaves shiny green and smooth .... ***S. rostrata***

4' Median leaf apices acute to attenuate **5**

6 Median and lateral leaves with conspicuous idioblasts on upper surfaces of the laminae; median leaf bases cordate to infrequently rounded and not auriculate... .... ***S. cardiophylla***

6' Median and lateral leaves lacking idioblasts on upper surfaces of laminae; median leaf inner bases oblique and not auricled and outer bases with a subventricose, small lobe or auricle .... ***S. microdonta***

Selaginella xanthoneura **Valdespino, sp. nov.**

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Figures 5, 14–18

Diagnosis. *Selaginella xanthoneura* is distinct from *S. hartii* Hieron. by lacking (vs. often with) flagelliform stem and branch apices, coriaceous (vs. chartaceous) leaves, lateral leaves ovate to broadly ovate (vs. ovate-oblong) with rounded (vs. truncate) bases and shortly ciliate (vs. denticulate) acroscopic margins, and acroscopic halves near proximal ⅓ of the lamina about the same width of (vs. twice as wide as) basiscopic halves, and median leaf outer margins distinctly widely hyaline (vs. green) with acuminate to short-aristate (vs. long-aristate) apices, each acumen or arista 0.1–0.3 (vs. 1.0) mm long.

Type. Colombia. Magdalena [La Guajira]: Sierra de Perijá, 10 km ENE of Manaure, 46 km E of Valledupar, 3 km from the Venezuelan border, 2300 m, 4 Feb 1945 (fe), *M. Grant 10811* (holotype: COL!; isotypes: CR!, GH!, NY!, US-2 sheets!).

Description. *Plants* terrestrial. *Stems* erect, stramineous, 28–60 cm tall, (0.5)1.0–2.5 mm diam. on main stem before first branches, non-articulate, not flagelliform, stoloniferous, 2 or 3-branched, the terminal portion of the stem similar in shape to lateral branches (i.e., conform). *Rhizophores* axillary, ventral, dorsal, and seemingly lateral, borne on lowermost part of the stems and throughout stolons, stout, 0.2–0.5 mm diam. *Leaves* seemingly monomorphic and strongly appressed to the stems up to shortly before (ca. 3 cm below) first branch, then heteromorphic throughout, coriaceous, upper surfaces shiny greenish yellow (i.e., citrine) when dry, smooth to slightly striate, lower surfaces shiny to silvery greenish-yellow, striate submedially and smooth towards margins, those on main stems before fully heteromorphic ovate-deltate or deltate, the bases prominently raised and truncate with both edges rounded or slightly subcordate and entire or denticulate, the margins narrowly to broadly hyaline, greenish-hyaline or greenish, inner margins short-ciliate along proximal ¼, otherwise dentate to denticulate distally, outer margins dentate to denticulate distally, apices acute, tipped by 1–4 teeth or entire. *Lateral leaves* on main stem after leaves fully heteromorphic, imbricate and ascending up to proximal ½ of the stems, otherwise distant and spreading along distal ½ of the stems, ovate to broadly ovate ascending, 4.0–6.0 × (1.5)2.0–3.5 mm; bases rounded to subcordate with a truncate and prominent central portion, glabrous, acroscopic bases strongly overlapping stems, rounded, basiscopic bases free from stems, rounded; margins on upper surfaces narrowly bordered by greenish, rectangular, and laevigate cells, acroscopic margins on lower surfaces bordered continuously by a hyaline band comprised of idioblasts, the band 2–7 cells wide, the idioblasts elongate, straight-walled, and papillate, the papillae in a single row over each cell lumen, basiscopic margins on proximal ⅓ bordered by elongate, greenish, rectangular, and laevigate cells and submarginally bordered by a hyaline band comprised of idioblasts, the band 1–5 cells wide, the idioblasts elongate, straight-walled, and papillate, the papillae in a single row over each cell lumen, on distal ⅔ bordered by a hyaline band comprised of idioblasts, the band 3–10 cells wide, the idioblasts similar to those of the acroscopic margins and submarginal proximal ⅓ of basiscopic margins and often specially toward distal ⅓ intermixed with cells similar to those of basiscopic proximal ⅓; apices acute to shortly attenuate, tipped by 1–3 teeth; upper surfaces comprising irregularly shaped, somewhat rectangular to quadrangular, sinuate-walled cells, with some sparingly distributed short, quadrangular to round, papillate idioblasts, each idioblast cell lumen with 5–8 papillae, without stomata, lower surfaces comprised of elongate, sinuate-walled cells and of elongate, straight-walled, papillate idioblasts, each idioblast cell lumen with 8–45 papillae in 1–3 rows, stomata on 1–6 rows along midribs. *Median leaves* on main stem after leaves fully heteromorphic, distant, ascending, broadly ovate, ovate-elliptic or ovate-lanceolate,

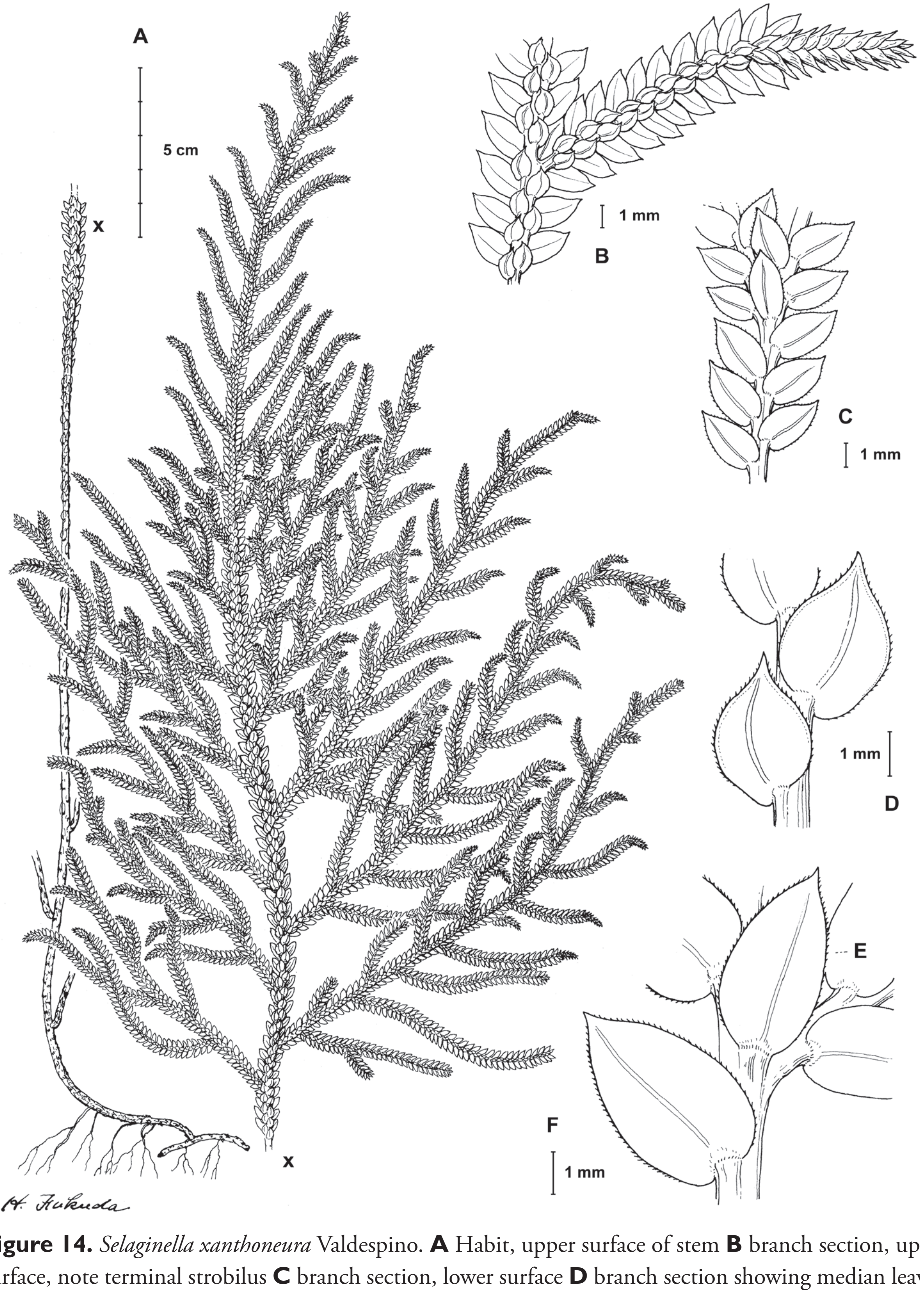

Figure 14. *Selaginella xanthoneura* Valdespino. **A** Habit, upper surface of stem **B** branch section, upper surface, note terminal strobilus **C** branch section, lower surface **D** branch section showing median leaves, upper surfaces **E, F** branch section showing axillary leaf (**E**) and lateral leaf (**F**), lower surfaces. **A–F** line drawing made from the holotype and isotypes as follow: **A, C–D**. **E, F** (holotype) and **B** (isotypes at GH & NY). Illustration by Haruto Fukuda.

2.0–4.0 × 1.3–2.0 mm; bases glabrous, subcordate with a prominent, round outer lobe, without auricles; inner margins on upper surfaces bordered continuously by a narrowly hyaline band of idioblasts along distal ¾, the band 1–4 cells wide, the idioblasts similar to

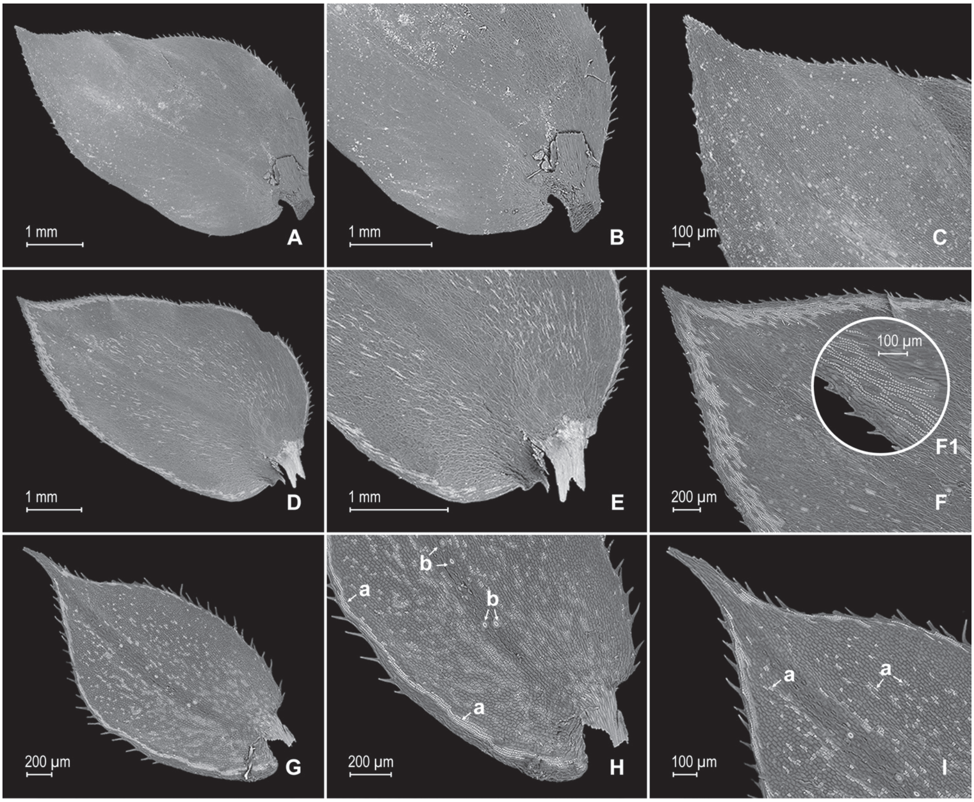

Figure 15. *Selaginella xanthoneura* Valdespino. **A** Lateral leaf from stem, upper surface. **B** proximal half of lateral leaf, upper surface (same leaf shown in **A**) **C** distal half of lateral leaf, upper surface (same leaf shown in **A**) **D** lateral leaf, lower surface **E** proximal half of lateral leaf, lower surface (same leaf shown in **D**) **F** distal half of lateral leaf, lower surface (same leaf shown in **D**); note, submarginal, elongate and papillate idioblasts (F1) **G** median leaf from stem branch, upper surface **H** proximal half of lateral leaf, upper surface (same leaf shown in **G**); note submarginal band of idioblasts (a) and stomata along midrib (b) **I** distal half of median leaf, upper surface (same leaf shown in **G**); note, short elongate and papillate idioblasts (a). **A–I** taken from the holotype.

those in the hyaline marginal bands of lateral leaves acroscopic margins on lower surfaces of lateral leaves, the outer margins on upper surfaces obscurely greenish and comprising elongate, straight-walled, glabrous cells along proximal ⅓–½, on proximal ⅓–½ submargins and distal ½–⅔ margins bordered continuously by a hyaline band of idioblasts, the idioblasts similar to those in the hyaline marginal bands of lateral leaves acroscopic margins on lower surfaces but the band 2–7 cells wide and with one or two rows of papillae on cell lumen, entire along proximal ⅓ and shortly ciliate along distal ⅔; apices acuminate to short-aristate, each acumen or arista 0.1–0.3 long, tipped by 1–3 teeth; upper surfaces comprising quadrangular, rectangular to roundish, sinuate-walled cells and many, evenly distributed papillate idioblasts, each idioblasts with 5–12 papillae, stomata in 1–4 rows on distal ⅔–¾ along the midribs and marginal to submarginal along proximal ⅓ of outer margins, lower surfaces comprising elongate, straight-walled cells, without idioblasts, ex-

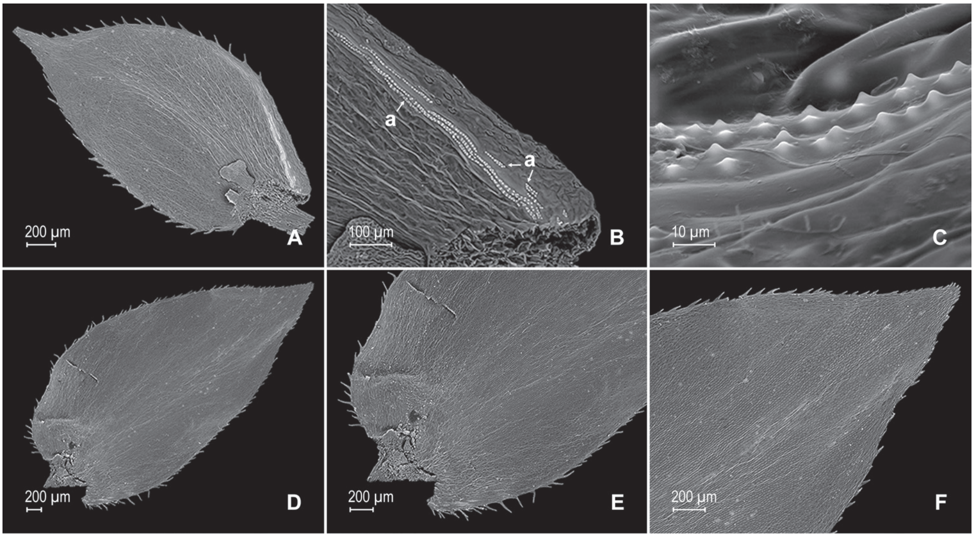

Figure 16. *Selaginella xanthoneura* Valdespino. **A** median leaf from stem, lower surface **B** proximal, inner half section of median leaf, lower surface (same leaf shown in **A**); note elongate and papillate idioblasts (a) **C** detail of papillae on idioblasts present on inner half section of median leaf, lower surface (same leaf shown in **A**) **D** axillary leaf from stem branch, upper surface **E** proximal half of axillary leaf, upper surface (same leaf shown in **D**) **F** distal half of axillary leaf, upper surface (same leaf shown in **D**). **A–F** taken from the holotype.

cept for idioblasts present along proximal submarginal portion of outer margins where the idioblast are similar to those on distal ½–⅔ of outer margin on upper surfaces, without stomata. *Axillary leaves* on main stem after leaves fully heteromorphic similar in shape to lateral leaves or narrowly ovate, 3.5–4.4 × 1.5–2.4 mm; bases similar to those of lateral leaves; margins on upper and lower surfaces as those in margins of lateral leaves; apices as those of lateral leaves; both surfaces similar to those of lateral leaves. *Strobili* terminal on branch tips, quadrangular, 0.4–1.0 cm long. *Sporophylls* monomorphic, without a laminar flap, each with a slightly developed keel along midribs, the keel glabrous or with few, short, tooth-like projections distally, ovate-lanceolate, 1.4–2.0 × 0.5–1.0 mm; bases rounded; margins narrowly hyaline, 1 or 2 cells wide with the cells elongate, slightly sinuate-walled and glabrous, parallel to margins, shortly ciliate along proximal ½, denticulate on distal ½ or denticulate throughout; apices long-attenuate to long-acuminate, the acumen 0.1 or 0.2 mm long, tipped by 1 tooth; *dorsal sporophylls* with upper surfaces green and cells as in median leaves, except for the half that overlaps the ventral sporophylls where the surfaces are greenish hyaline with elongate and slightly sinuate-walled cells, lower surfaces silvery green and comprising elongate, sinuate-walled cells; *ventral sporophylls* with both surfaces, silvery green to hyaline, comprised of elongate, papillate, sinuate-walled cells. *Megasporangia* few on two proximal ventral rows; *megaspores* yellow, 100–120 μm diam., proximal faces rugulate-reticulate with a well-developed equatorial flange, the microstructure perforate and echinate, distal faces reticulate, the reticula closed, the microstructure granulate and perforate. *Microsporangia* on two dorsal rows and along most of two ventral rows; *microspores* light orange, 25–30 µm diam., proximal faces rugulate, the microstructure echinate and perforate, distal faces capitate, with each caput microechinate, the rest of the microstructure echinate and perforate.

Habitat and distribution. *Selaginella xanthoneura* grows in tropical montane rainforests at 1800–2300 m. It is known from Serranía del Perijá, an extension of the eastern Andean branch (Western Cordillera) in the state of Magdalena, and in the isolated mountain range of Sierra Nevada de Santa Marta, states of César and Magdalena, both in northern Colombia, and is expected to also occur in the neighboring state of Zulia, Venezuela. It has been collected in fertile condition from February to June.

Etymology. The specific epithet derives from the Gr. "*xanthos*," yellow, and "*neuron*," nerve, referring to the conspicuous yellow, leaf midribs on upper surfaces.

Conservation status. *Selaginella xanthoneura* is known from only six collections made in two adjacent Colombian Departments, growing at high elevations, probably in and around protected areas, which however are imperiled by human encroachments and natural adversities such as landslides. It might eventually prove to be present in adjacent areas in Venezuela, but there is no current documentation to support this. It might well be that this species is relatively well protected, but the limited number of documented occurrences and distribution, as well as possible threats enumerated above indicate that it should be considered Vulnerable (VU) based on IUCN (2012).

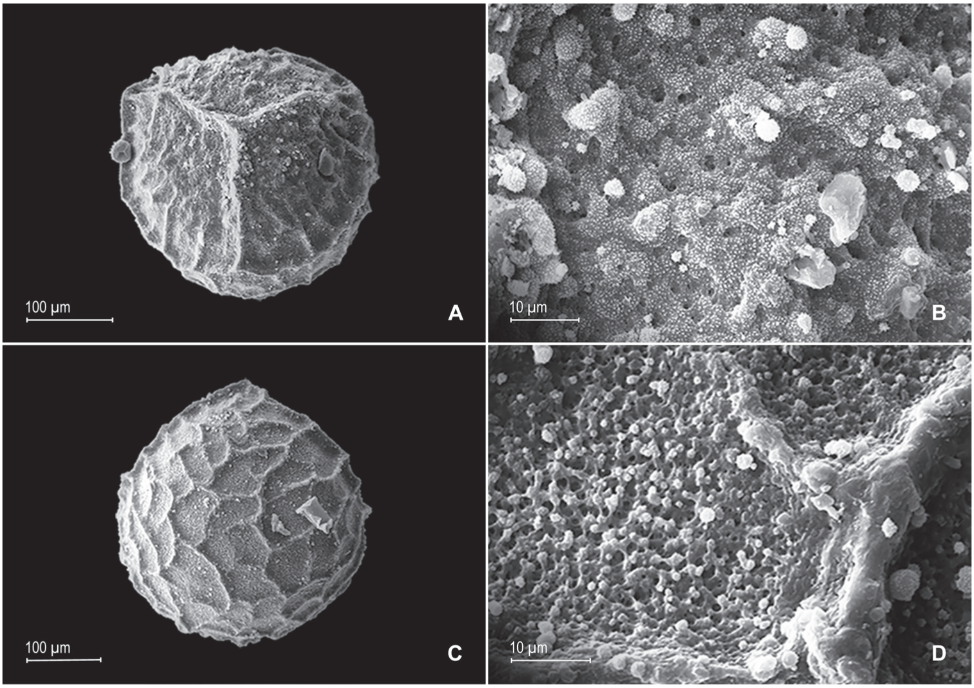

Figure 17. *Selaginella xanthoneura* Valdespino. **A** Megaspore, proximal face **B** detail of megaspore, proximal face **C** megaspore, distal face **D** detail of megaspore, distal face. **A–D** taken from the holotype.

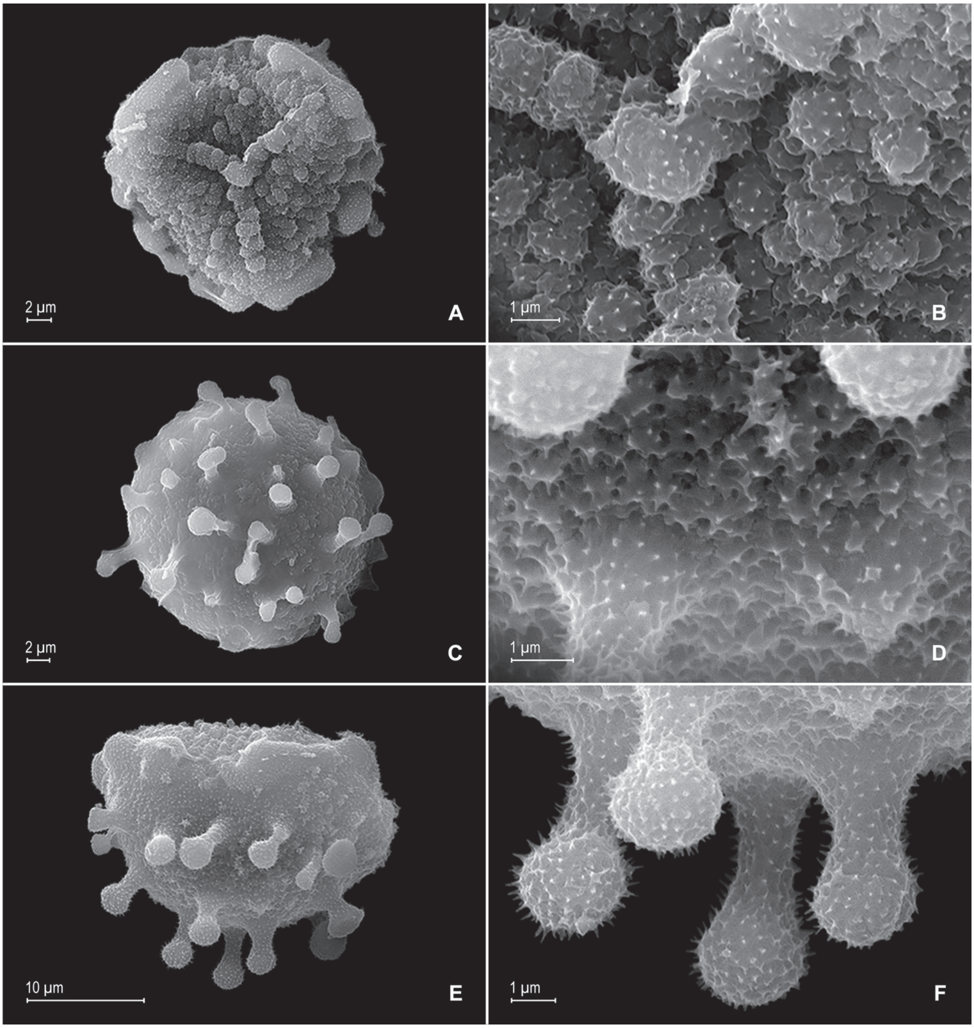

Figure 18. *Selaginella xanthoneura* Valdespino. **A** Microspore, proximal face **B** detail of microspore, proximal face **C** microspore, distal face **D** detail of microspore, distal face **E** microspore, distal face, equatorial view **F** detail of capitate projections with echinate microstructure surfaces. **A–F** taken from the holotype.

Additional specimens examined (paratypes). Colombia. **César**: Santa Marta, between Playoncito and Cuchilla Monogaca N, Pueblo Bello, 1900 m, 4 Feb 1967, *Mägdefrau 1247* (UC); Sierra Nevada de Santa Marta, Playoncito an Clisndivana? [illegible], 1800 m, Jun 1928, *Schultze 1518* (B, BM, PMA); Mpio. Manaure, Serranía del Perijá El Cinco, Finca Vistahermosa, SE de la carretera, 10°26'N, 72°57'W, 2200 m, 13 Nov 1993, *Rangel et al. 11420* (COL-image), 2235 m, 14 Nov 1993, *Pardo et al. 304* (COL-image). **Magdalena**: Sierra Neva de Santa Marta, entre San Pedro y cabeceras del Río Sevilla, slopes of La Cebolleta and Yerba Buena, ca. 2300 m and lower, 1 Feb 1959, *Barclay & Juajibioy 6808* (MO-2 sheets).

Discussion. *Selaginella xanthoneura* is characterized by its fern-like habit, erect stems, each 28–60 cm tall, leaves on main stems shortly (ca. 3 cm) before first branches seemingly monomorphic and strongly appressed, the leaves after becoming fully heteromorphic with shiny, greenish yellow (i.e., citrine) upper surfaces when dry and yellowish to stramineous midribs. It is further distinguished by its median leaf bases subcordate with a prominent, round outer lobe, outer margins along proximal, submarginal ⅓–½ and distal, marginal ½–⅔ continuously bordered by a hyaline band of idioblasts, and acuminate to short-aristate apices, the upper surfaces of median leaves and the lower surfaces of lateral leaves with papillate idioblasts, and relatively short strobili, each 0.4–1.0 cm long, and with few megasporangia restricted to proximal portion of two rows of strobili ventral sporophylls.

Interestingly, one examined duplicate specimens of *S. xanthoneura* (*Schultze 1518*, B) has vegetative growth from strobili tips. This is a feature that has been amply documented in other morphologically related members of the "*Selaginella flabellata* group," as well as on unrelated taxa from different regions of the world (Hieronymus 1901; Williams 1931; Jermy 1990; Valdespino 1993a, 1993b; Valdespino 1995; Zhang et al. 2014; Valdespino et al. 2015) and for which specific patterns were described (Valdespino et al. 2015). This same collection (*Schultze 1518*) at B and BM was originally determined by Alston as *S. hartii*, which certainly is somewhat similar to *S. xanthoneura* because of their overall fern-like habit with erect stems and leaves fully dimorphic shortly before first stem branches. *Selaginella xanthoneura* is easily set aside from the latter species by characters listed in the diagnosis. In addition, *S. xanthoneura*, at present, is only known to occur in Colombia, whereas *S. hartii* is only known from Trinidad and Tobago and the Peninsula of Paria in Sucre state, Venezuela. Furthermore, *S. xanthoneura* has a more robust plant habit with stems 2 or 3- (vs. 1 or 2 or occasionally 3-) branched.

Selaginella xanthoneura, as well as other members of the "*Selaginella flabellata* group," such as *S. cheiromorpha* Alston, *S. hartwegiana* Spring, and *S. mosorongensis* Hieron. all have similar median and lateral leaf shapes. Nevertheless, *S. xanthoneura* differs from all those species by its median leaf outer bases lacking a distinct auricle and having conspicuously yellow to yellowish lateral and median leaf midribs. *Selaginella xanthoneura* is further set aside from *S. mosorongensis* by its entire (vs ciliate) median leaf outer bases.

Emended description of *Selaginella surucucusensis*, including new distribution records and a line drawing

***Selaginella surucucusensis* L.A. Goés & E.L.M. Assis, Kew Bull. 72: 40, 1. 2017.**
Figures 5, 19

Type. Brazil. Roraima: Serra Surucucú, 26 Jan 1975, *B.G.S. Ribeiro 15.189(616)* (holotype: HRB-n.v.; isotypes: BHCB-n.v., HRB-n.v., MG!, NY!, RB!).

Description. *Plants* terrestrial. *Stems* erect, stramineous, (25)35–75 cm tall, 1.2–3.0 mm diam., non-articulate, usually not flagelliform or infrequently so, stoloniferous, 3-branched, the terminal portion of the stems similar in shape to lateral branches (i.e., conform). *Rhizophores* axillary, ventral, dorsal, dorso-axillary, and seemingly lateral, borne on lower most part of stems and throughout stolons, filiform or stout, 0.2–1.0 mm diam. *Leaves* seemingly monomorphic and strongly appressed to the stem shortly before or after the first or second branches and without distinctive auricles, then heteromorphic throughout, chartaceous to coriaceous, upper surfaces shiny dark, brown-green (dark olive) to brownish (due to drying technique), seemingly smooth, lower surfaces shiny, yellowish green, dark olive to brown (due to drying technique), smooth. *Lateral leaves* on main stem after leaves become fully heteromorphic, distant, ascending to slightly spreading, ovate or ovate-oblong, 3.0–4.8 × 1.4–2.6 mm; bases rounded to truncate, glabrous, without auricles, acroscopic bases strongly overlapping stems, basiscopic bases free from stems; margins on upper and lower surfaces bordered by a narrow band comprised of greenish cells, the band 1–3 cells wide, the cells elongate, slightly sinuate-walled, and glabrous, on acroscopic margins dentate along proximal ¼, otherwise denticulate on distal ¾, on basiscopic margins entire along proximal ¾, otherwise sparsely denticulate distally; apices broadly acute to obtuse, tipped by 3–5 teeth; upper surfaces consisting of quadrangular to rectangular (jigsaw puzzle-like), sinuate-walled cells (often difficult to distinguish because of waxy deposits), many of these consisting of papillate idioblasts, comprising some sparse, elongate and papillate idioblasts, the papillae 4–11 in 1 or 2 rows on each cell lumen, without stomata; lower surfaces consisting of elongate, irregularly sinuate-walled cells (jigsaw puzzle-like) and of many elongate, straight-walled, papillate idioblasts, papillae 4–11 in 2 rows on each cell lumen, with stomata on 2–4 rows along central portion of midribs *Median leaves* on main stem after leaves fully heteromorphic, imbricate, ascending, ovate, ovate-elliptic, ovate-lanceolate to ovate-oblong, 1.7–4.2 × 0.8–2.8 mm; bases glabrous, oblique, truncate or asymmetric, inner bases rounded to truncate, outer bases auricled, the auricles ciliate with 3–14 short hairs; margins bordered continuously by a band of glabrous cells, the band 1–3 cells wide with the cells elongate, slightly sinuate-walled, glabrous, except for those on distal ⅓ of outer margins that are composed by a narrow hyaline band of idioblasts, the band 1–3 cells wide, the idioblasts straight-walled, and papillate, the papillae in one row, margins dentate to denticulate; apices acute, acuminate or aristate, each acumen or arista 0.1–0.6 mm long, tipped by 1–3 teeth; upper surfaces similar to those on upper surfaces of lateral leaves, except abundantly covered by quadrangular and elongate and papillate idioblasts, the papillae 4–32 in 1 or 2 rows on each cell lumen, with stomata in 1–5 rows along the midribs, lower surfaces comprising by elongate, irregularly sinuate-walled cells, (jigsaw puzzle-like), without idioblast and stomata. *Axillary leaves* on main stem after leaves fully heteromorphic ovate to ovate-lanceolate, 2.0–4.0 × 0.8–2.2 mm; bases rounded to slightly truncate, entire, without auricles; inner and outer margins as acroscopic margins of lateral leaves, denticulate throughout; apices broadly acute to obtuse, tipped by 1–4 teeth; both surfaces as lateral leaves. *Strobili* terminal on main stem and each branch tip, quadrangular, 0.5–4.0 cm. *Sporophylls* monomorphic, without a laminar flap, each with a slightly developed and glabrous keel along distal ¾ of the midrib, ovate to ovate-lanceolate, 0.8–1.2 × 0.4–0.7 mm; bases rounded; margins narrowly hyaline, 1 or 2 cells

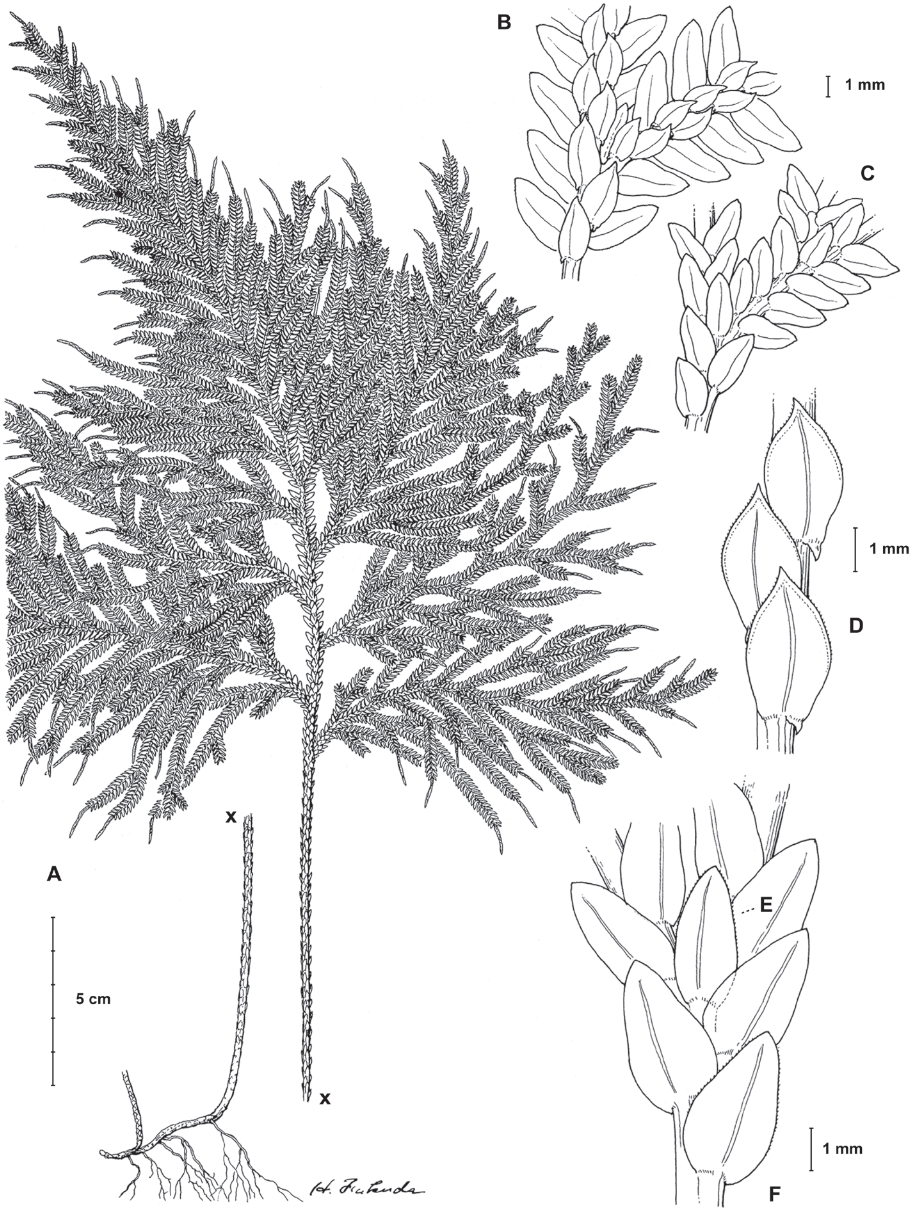

Figure 19. *Selaginella surucucusensis* **A** Habit, upper surface of stem **B** branch section, upper surface. **C** branch section, lower surface **D** branch section showing median leaves, upper surfaces **E, F** branch section showing axillary leaf (**E**) and lateral leaf (**F**), lower surfaces. **A–F** line drawing made from the isotype at NY. Illustration by Haruto Fukuda.

wide with the cells elongate, slightly sinuate-walled and glabrous, parallel to margins, denticulate throughout; apices shortly acuminate, the acumen 0.1–0.2 mm long, tipped by 1–3 teeth-like projections; *dorsal sporophylls* with upper surfaces green and cells as in median leaves, except for the half that overlaps the ventral sporophylls where the surfaces are greenish hyaline comprising elongate, slightly sinuate-walled cells, lower surfaces silvery green, comprised of elongate, sinuate-walled cells; *ventral sporophylls* with both surfaces hyaline, comprised of elongate, sinuate-walled cells and of papillate idioblasts. *Megasporangia* in two ventral rows; *megaspores* white, 240–310 µm diam., proximal faces rugulate-reticulate without an equatorial flange, the microstructure strongly echinate and perforate, distal faces reticulate the reticulae open (incomplete) to closed, each reticulum with low muri, the microstructure strongly echinate and perforate. *Microsporangia* in two dorsal rows; *microspores* orange, 23–27 µm diam., proximal faces rugulate, the microstructure echinate and granulate, distal faces capitate or baculate, the microstructure of capita or bacula and the rest of the surface echinate.

Additional specimen examined. Colombia. **Amazonas**: Río Miritiparaná, ca. 00°30'S, 70°40'W, 700 ft [213 m], 8 May 1952, *Schultes & Cabrera 16471* (US [cited by Crabbe and Jermy (1973) as a paratype of *S. palmiformis* Alston ex Crabbe & Jermy]. **Vaupés**: Mpio. Carurú, Caño Carurú, Comunidad del Palmar, Cachivera Pacú, camino entre cachivera y sabana de Kuw (Kuvai), 01°14'47.0"N, 71°19'23.5"W, 270–430 m, 10 Sep 2013, *Rodríguez et al. 7916* (NY). Venezuela. **Amazonas**: Depto. Atabapo, sector Norte de la Sierra Parima, cuenca alta del Río Matacuni, ca 20 km NNW de Shimada-Wochi, 03°59'N, 64°41'W, 1000–1500 m, 10 Nov 1983, *Huber & Colchester 8430* (NY-2 sheets); Depto. Atures, E del Cerro Cuao, Caño Piedra, 75 km SE de Puerto Ayacucho, 05°05'N, 67°19'W, 1050 m, Sep 1989, *Fernández et al. 6113* (NY), vicinity of and upstream from damsite, N side of Río Cataniapo, 45 km SE of Puerto Ayacucho, 05°35'N, 67°15'W, 100 m, 13 May 1980, *Steyermark et al. 122394* (MO, UC); Cerro Marahuaca, 1000 m, 3 May 1949, *Maguire & Maguire Jr. 29202* (NY, US); Cerro Sipapo (Paráque), 3 km SW of Base Camp, 200 m, 8 Feb 1949, *Maguire & Politi 28814* (NY, UC, US); Comision de Frontera, ca 0.5 km below Camp 3, 02°27'24"N, 63°56'W, 20 May 1972, *Steyermark 106041* (NY); Serranía Batata, 2 km NE of Salto Colorado, Caño Colorado, 55 km SE of Puerto Ayacucho, 05°33'N, 67°08'W, 550 m, Sep 1989, *Fernández et al. 6360* (MO, NY, US). Brazil. **Roraima**: Serra dos Surucucú, NE of mission station, 02°42–47'N, 63°33–36'W, 1000–1400 m, 17 Feb 1969, *Prance et al. 9979* (F, INPA-image, NY, R, UC, US).

Habitat and distribution. *Selaginella surucucusensis* grows on humid forest floors, creek- and riverbanks in lowland to montane tropical rainforests and in open scrub savanna on white sand at 200–1500 m. It was originally described from Serra dos Surucucú in the state of Roraima, Brazil. Nevertheless, its distribution range is here significantly expanded farther north- and northwestwards into the Amazon basin region to include Colombia and Venezuela. Moreover, it is here documented to be fertile from February to November.

Conservation status. This species is widely distributed at low and high elevations in tropical rainforests of South America. Accordingly, it is considered of Least Concern (LC) based on IUCN (2012).

Discussion. Despite the relatively recent publication of *S. surucucusensis*, with an originally limited, corroborated distribution range in Brazil provided by Góes-Neto et al. (2017), a number of specimens from Colombia and Venezuela are known and here newly documented. The study of these broader spectrum of specimens provides a better understanding of morphological characters (including mega- and microspores ornamentation features) of the species, expanded geographic circumscription, as well as of its presumed affinities. Consequently, an emended description for *S. surucucusensis* is provided, including a novel illustration.

Selaginella surucucusensis is characterized by its fern-like habit, non-articulate and usually not flagelliform or infrequently so, stoloniferous, 3-branched erect stems, each (25)35–75 cm tall and 1.2–3.0 mm in diam., with axillary, lateral, and dorsal to dorso-axillary rhizophores, which are borne on the lower most part of the stems and throughout stolons, each filiform or stout, 0.2–1.0 mm diam. In addition, the leaves on main stems are seemingly monomorphic and strongly appressed to stems, shortly below or above first stem branches and after this become fully heteromorphic, with median leaf upper surfaces covered with short-elongate or punctate, papillate idioblasts, and with a small or reduced, dentate outer auricle on outer bases, and lateral leaf with scattered, elongate, papillate idioblasts on lower surfaces. Furthermore, megaspores of this species are white, rugulate-reticulate on proximal faces without an equatorial flange and with strongly echinate and perforate microstructure, reticulate with open and closed reticulae formed by low muri and reticulate-granulose on distal faces with strongly echinate and perforate microstructure. Finally, microspores of this species are orange, echinate, rugulate, and granulate on proximal faces with punctate microstructure, capitate or baculate on distal faces with each caput or bacula and the rest of the surface with an echinate microstructure. In addition, the most examined specimens of *S. surucucusensis* have their leaf upper surfaces dark, brown-greenish to brownish, probably due to being fixed in alcohol.

Selaginella surucucusensis is morphologically somewhat similar to *S. gioiae*, from which it is set aside by the characters listed under the diagnosis and discussion of the latter. Furthermore, because of the fern-like habit and erect stems of *S. surucucusensis* most examined specimens were variously misidentified as *S. anceps* (C. Presl) C. Presl, *S. amazonica* Spring, *S. mazaruniensis* Jenm., *S. oaxacana* Spring or *S. palmiformis*. The short-elongate or punctate, papillate idioblasts on upper surfaces in median leaf of *S. surucucusensis* are somewhat similar to those of *S. cuneata* Mickel & Beitel from Mexico. *Selaginella surucucusensis* differs from *S. cuneata* by its ovate or ovate-oblong (vs. broadly ovate to ovate-orbicular) lateral leaves; median leaves bases (on main stems after first branches) oblique, truncate or asymmetric with the outer bases prominent (vs. slightly so) with (vs. without) an outer auricle, outer halves of leaf laminae at least ¼ to ½ wider (vs. twice as narrow) than inner halves, and margins of median and acroscopic margins of lateral leaves hyaline (vs. greenish).

Selaginella surucucusensis also appears morphologically close to *S. oaxacana* because both have median leaf with acuminate to short-aristate apices, narrowly hyaline and denticulate margins, outer basal auricles, and axillary, lateral, and dorsal rhizophores. *Selaginella surucucusensis* is set aside from *S. oaxacana* by its lateral leaf basiscopic bases rounded to adnate to the stems (vs. geniculate to auricled) and upper surfaces of the median leaves and sporophylls with short-elongate or punctate (vs. with long) idioblasts.

Selaginella surucucusensis differs from *S. amazonica* by its upper surfaces of leaf shiny, dark brown-green (vs. dark olive) to brownish (due to drying technique) and smooth (vs. dark brown and corrugate), with (vs. without) punctate or elongate idioblasts, median leaves above first branches ovate, ovate-elliptic, ovate-lanceolate to ovate-oblong (vs. broadly ovate to ovate-deltate) with (vs. lacking) an outer auricle, and lateral leaves shortly below or immediately above first branches ovate to ovate-oblong (vs. ovate-deltate). *Selaginella surucucusensis* is easily set aside from *S. anceps* by its leaf on main stems seemingly monomorphic and strongly appressed to the stem shortly before or after the first or second branches (vs. up to the third of fourth) branches, truncate and without (vs. with one or two, long, incurved, and ciliate) auricles. Likewise, *S. surucucusensis* is separated from *S. mazaruniensis* by its median leaf upper surfaces smooth (vs. corrugate), those above first branch with (vs. without) short-elongate or punctate, papillate idioblasts, with an outer (vs. lacking) auricle, and branches distinctly pinnate and conform (vs. usually flabelliform).

Crabbe and Jermy (1973: 141) cited one specimen here included in *S. surucucusensis* (*Schultes & Cabrera 16471*, US) as a paratype of *S. palmiformis* and Alston et al. (1981: 256) followed them. Both species are similar in having their median leaf bases with an outer, ciliate auricle. Nevertheless, in *S. palmiformis* the auricle is less prominent and covered only by 3–6 hairs. *Selaginella surucucusensis* further differs from *S. palmiformis* by its stems 3- (vs. 1- or 2-) branched, rounded when dry (vs. quadrangular) with the overall shape of proximal branches wider at base (vs. at middle) and rhombic-triangular to deltate-triangular (vs. elliptic or elliptic-lanceolate), leaves obviously heteromorphic above first or second (vs. usually at or above fourth) branches with upper surfaces having (vs. lacking conspicuous) short-elongate or punctate, and papillate idioblasts. It differs further from the latter by median leaf margins denticulate (vs. coarsely dentate), truncate (vs. often subcordate) axillary leaf bases, and ovate-lanceolate to ovate-oblong (vs. oblong) lateral leaves. *Selaginella surucucusensis* further differs from *S. palmiformis* by its median leaves on main stems after fully heteromorphic ovate, ovate-elliptic, ovate-lanceolate to ovate-oblong (vs. broadly ovate to ovate-deltate) with arcuate (vs. straight and almost central) midribs, outer halves of leaf laminae ca. ⅛ wider than inner halves (vs. both halves about the same width), and leaf bases evenly raised (vs. centrally ventricose).

Selaginella surucucusensis as well as *S. altheae* Valdespino are members of the "*Selaginella flabellata* group," and have similar microspore ornamentation but they diverge on their leaf shapes. *Selaginella surucucusensis* differs from *S. altheae* by its median leaf margins denticulate (vs. inner margins short ciliate along proximal ⅔, otherwise denticulate on distal ⅓ and outer margins entire along proximal ⅓, becoming short-ciliate along medial ⅓, otherwise denticulate on distal ⅓), with (vs. without) an outer basal auricle, and lacking marginal to submarginal stomata (vs. stomata present on proximal ¼ along outer margins), and lateral leaf acroscopic margins dentate along proximal ¼, otherwise denticulate on distal ¾ (vs. long-ciliate along proximal ½–¾, otherwise short-ciliate to dentate distally).

Finally, the presence of dorsal rhizophores in *S. altheae*, *S. oaxacana*, *S. surucucusensis*, and other members of the "*Selaginella flabellata* group" might eventually prove to be a morphological character that helps define this alliance. Nevertheless, dorsal rhizophores are also found in other heterophyllous *Selaginella* species such as *S. psittacorhyncha* (Valdespino 2017b) within subg. *Stachygynamdrum*, where it has not been widely reported, and is characteristic of articulate species of subg. *Gymnogynum* s.l. (Valdespino et al. 2018; Valdespino and López 2019), subg. *Lepidophyllae* (Weststrand and Korall 2016), and homophyllous species classified in subg. *Rupestrae* (Valdespino 1993a; Weststrand and Korall 2016). Consequently, it might well be that dorsal rhizophores are underreported in subg. *Stachygynandrum* and of wider occurrence in *Selaginella* or perhaps this feature has originated several times in different evolutionary lineages within the genus. Accordingly, the occurrence of dorsal rhizophores within *Selaginella* warrants further morphological, anatomical, molecular, and phylogenetic studies throughout species alliances to ascertain its evolutionary implications.

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Rhamnella intermedia (Rhamnaceae), a new evergreen species from southwest Guangxi

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Abstract

Rhamnella intermedia, a new evergreen species from southwest Guangxi, is described and illustrated in this study. This species is similar to *R. brachycarpa* by the size and ratio of length to width of dried fruit and seeds, by which it differs from *R. rubrinervis* and *R. tonkinensis*. However, it differs from *R. brachycarpa* by rarely mucronate seed apices, larger ratio of length to width of leaves, leaf apices acuminate to long acuminate, shorter leaf petioles, and longer fruiting pedicels. Principal component analysis based on phenotypic traits further recognised three separated groups. *Rhamnella rubrinervis* and *R. tonkinensis* were clustered into one group; the other two groups represented *R. brachycarpa* and two Guangxi populations, respectively. Furthermore, phylogenetic analysis of nuclear ITS sequence variations highly supported that the two Guangxi populations represented an independent evolutionary lineage and were closest to *R. rubrinervis*. Four fixed nucleotide sites were found and were different from *R. rubrinervis*. However, besides the differentiated traits in seeds and fruit, densely pilose young branches also separated them from *R. rubrinervis*. In addition, during our field investigations, none of the three closely related species were found at locations where this new species was distributed. Therefore, this new species, based on the two Guangxi populations, is named *R. intermedia*. The key to four closely related species is also presented.

Keywords

evergreen species, independent evolutionary lineage, intermediate morphology, phenotypic cluster, *Rhamnella*

Introduction

Rhamnella (Miquel, 1867) in the tribe Rhamneae Hook. f. of Rhamnaceae is a small genus (Hauenschild et al. 2016, Richardson et al. 2000). It is characterised by pedicellate flowers and fleshy fruits, 1-stoned drupes, pinnately veined leaves, serrate leaf margins, semi-inferior ovaries, stipules without thorns, and flowers in axillary cymes (Chen and Schirarend 2007). To date, 10 species have been accepted into this genus (Lu and Sun 2019). Two groups are separated based on the characters of deciduous broad-leaved and evergreen leaves respectively (Fan and Yang 1997; Chen and Schirarend 2007; Lu and Sun 2019). For all species in the latter group, including *R. rubrinervis*, *R. tonkinensis*, and *R. brachycarpa*, the length of leaf petioles, leaf apices, ratio of length to width of leaves, and size and ratio of length to width of dried fruit and seeds are their differentiated traits (Chen and Schirarend 2007; Lu and Sun 2019). However, on the basis of these traits, two *Rhamnella* populations from southwest Guangxi that belonged to the evergreen group could not be ascribed to any of the three evergreen *Rhamnella* species. We found that they had similar size and ratio of dried fruit and seeds to *R. brachycarpa*, similar leaf shapes to *R. rubrinervis*, and the same length of fruiting petioles with *R. tonkinensis*. Therefore, the two Guangxi populations may represent a new species. In order to clarify this hypothesis, we carried out field investigations on the distribution and habitat of this potential new species, and characterised its morphology based on these two populations from southeast Guangxi. Furthermore, we conducted the principal component analysis (PCA) based on phenotypic traits to show their morphological differences. Finally, we sequenced the nuclear internal transcribed spacer (ITS) fragment to clarify its genetic distinctness.

Material and methods

We collected the fruit-bearing specimens of this potential new species for morphological measurement and other analyses referring to Lu and Sun (2019). These newly collected specimens in this study were deposited as *Z.Q. Lu 2019YG2601– Z.Q. Lu 2019YG2619* (GXMI and HITBC), *Z.Q. Lu 2018LZQ108* (HITBC), and *Z.Q. Lu 2018LZQ10802* (HITBC). In order to demonstrate its morphological differences, we compared them to all closely related evergreen *Rhamnella* species that had been shown in Lu and Sun (2019), including *R. rubrinervis*, *R. tonkinensis*, and *R. brachycarpa*. In addition, 21 newly collected and 239 previous specimens were further used to perform the PCA based on 10 phenotypic traits, as described by Lu and Sun (2019). Because they were attributed to evergreen taxa closely related to *R. rubrinervis*, *R. tonkinensis*, and *R. brachycarpa*, and were distinctly different from deciduous species of *Rhamnella* by larger drupe size (Chen and Schirarend 2007; Lu and Sun 2019), we excluded all deciduous species from morphological comparison and PCA analysis. Furthermore, we investigated the population consensus and explored whether other closely related species co-occurred with this potential new species. The habitat and distribution were also characterised through our field investigations.

Table 1. Voucher number and location of populations of collected leaves used for DNA extraction and sequencing in this study.

Species	Location	Latitude (N) / Longitude (E)	Altitude (m)	No. of individuals	Voucher No.
R. intermedia Pop1	Pingxiang, Guangxi	22°07'19"N, 106°44'40"E	298	6	*Z.Q. Lu 2019YG2601– Z.Q. Lu 2019YG2614*
R. intermedia Pop2	Wude, Guangxi	22°34'15"N, 106°44'56"E	276	2	*Z.Q. Lu 201810801–Z.Q. Lu 201810802*
R. rubrinervis Pop1	Chengxiang, Guangxi	23°28'04"N, 105°54'19"E	1000	3	*Z.Q. Lu 201726501– Z.Q. Lu201726503*
R. rubrinervis Pop2	Dongying, Guangxi	23°13'23"N, 105°56'32"E	960	4	*Z.Q. Lu 201802701–Z.Q. Lu 201802704*
R. rubrinervis Pop3	Dongjing, Guangxi	23°39'8"N, 106°33'22"E	460	6	*Z.Q. Lu 201818201–Z.Q. Lu 201818206*
R. rubrinervis Pop4	Dizhou, Guangxi	22°58'38"N, 106°21'8"E	790	3	*Z.Q. Lu 201819001–Z.Q. Lu 201819003*
R. rubrinervis Pop5	Debao, Guangxi	23°26'46"N, 106°29'52"E	830	2	*Z.Q. Lu 201818601–Z.Q. Lu 201818602*
R. rubrinervis Pop6	Donggan, Yunnan	23°30'19"N, 105°11'45"E	940	3	*Z.Q. Lu 201811101–Z.Q. Lu 201811103*
R. tonkinensis	Maogan, Hainan	18°35'36"N, 109°25'48"E	620	1	*Z.Q. Lu 2018HN3001*
R. brachycarpa	Maogan, Hainan	18°35'37"N, 109°25'34"E	650	1	*Z.Q. Lu 2019HN101*

We also collected fresh leaves from several populations for DNA extraction and sequencing (Table 1). Taking habit differentiation into consideration, we marked each of the climbing trees. In total, 21 individuals (including six climbing trees and 15 erect ones) from the potential new species based on Pingxiang and Wude populations, 21 individuals from 6 populations of *R. rubrinervis*, one individual from *R. tonkinensis*, and one individual from *R. brachycarpa* were used for sequencing the nuclear ITS fragment. PCR amplification was performed according to Lu et al. (2018). In total, 5 of 21 individuals failed in the ITS sequencing, but the six climbing individuals were all sequenced successfully. Finally, we obtained 37 ITS sequences, including 7 types. All were deposited in GenBank database (Accession numbers from MT764159 to MT764165). In addition, we also downloaded some ITS sequences of deciduous species of *Rhamnella*. The aligned sequences were 630 bp in length. A maximum likelihood (ML) tree based on ITS sequences was constructed by MEGA version 5.0 (Tamura et al. 2011) using the Tamura-Nei model, and the bootstrap was set as 1000. *Berchemiella wilsonii*, *B. berchemifolia*, *Pseudoziziphus celata*, and *P. parryi* were selected as outgroups referring to the phylogenetic backbone presented by Hauenschild et al. (2016).

Results

Two Guangxi populations that are considered as new species have an intermediate morphology compared to the three closely related species *R. rubrinervis*, *R. tonkinensis*, and *R. brachycarpa* (Figures 1, 2; Table 2). Morphological comparison based on the characteristics of fruit and seeds showed that they shared maximum resemblance to *R. brachycarpa* by the similar sizes of dried fruit (6.0–7.0 × 4.7–5.3 vs. 6.5–7.5 × 4.7–6.0 mm) and seeds (5.5–6.5 × 4.5–5.0 vs. 5.0–7.0 × 4.5–5.5 mm), and ratios of length to width of dried fruit (1.3–1.5 vs. 1.3–1.5) and seeds (1.2–1.4 vs. 0.9–1.5). Meanwhile, they differed from *R. brachycarpa* by the larger ratio of length to width of leaves (2.7–3.8 vs. 1.9–2.4), smaller length of leaf petioles (3–8 vs. 7–12 mm), larger length of fruiting pedicels (5–9 vs. 4–6 mm), leaf apices acuminate to long acuminate, and seed apices rarely mucronate. Furthermore, morphological comparison showed that these two Guangxi populations were also morphologically similar to *R. rubrinervis* by the ratio of length to width of leaves (2.7–3.8 vs. 2.7–4.3), leaf apices acuminate to long acuminate, length of leaf petioles (3–8 vs. 3–9 mm) and rarely mucronate seed apices, and to *R. tonkinensis* by the length of fruiting petioles (5–9 vs. 5–9 mm). In contrast, they differed from *R. rubrinervis* and *R. tonkinensis* by smaller sizes of dried fruit (6.0–7.0 × 4.7–5.3 vs. 7.5–11.1 × 4.2–5.8 mm) and seeds (5.5–6.5 × 4.5–5.0 vs. 7.0–9.9 × 4.2–5.5 mm), and smaller ratios of length to width of dried fruit (1.3–1.5 vs. 1.6–2.2) and seeds (1.2–1.4 vs. 1.6–2.1). In addition, they were also separated from *R. rubrinervis* by densely pilose young branches, and from *R. tonkinensis* by the ratio of length to width of leaves (2.7–3.8 vs. 2.1–2.8). In total, two Guangxi populations characterised by the ratio of length to width of leaves and length of leaf petioles from *R. rubrinervis*, by the length of fruiting petioles from *R. tonkinensis*, and by the size and ratio of length to width of dried fruit and seeds from *R. brachycarpa*. Other phenotypic traits, such as leaf apices acuminate to long acuminate and rarely mucronate seed apices also showed a morphological combination from other species. PCA analysis distinguished 260 specimens into three groups, based on 10 phenotypic traits (Figure 3). One group consisted of *R. rubrinervis* and *R. tonkinensis*, while the other two groups corresponded to *R. brachycarpa* and two Guangxi populations respectively. The first principal component axis (PC1; accounting for 34.40% of the variation) significantly separated these *R. brachycarpa* specimens and those of *R. tonkinensis* and *R. rubrinervis* into two clusters, and the two Guangxi populations showed the overlap with both clusters; the second principal component axis (PC2; accounting for 24.40% of the variation) significantly separated the two Guangxi populations from the other two clusters, and failed in the separation of others (Figure 3). In addition, during our field investigations, none of the three closely related species *R. brachycarpa*, *R. tonkinensis*, and *R. rubrinervis* were found at locations where these two Guangxi populations distributed. Furthermore, phylogenetic analysis highly supported that the evergreen group was monophletic, and these two Guangxi populations represented an independent evolutionary lineage distinctly different from other species (Figure 4). They were closest to *R. rubrinervis* based on ITS sequence variations; however, four fixed nucleotide sites were found (Table 3). Sequence alignments showed that six climbing trees shared the same ITS sequence types with those of erect ones.

Taxonomic treatment

Rhamnella intermedia Z. Qiang Lu & Y. Shuai Sun, sp. nov.

urn:lsid:ipni.org:names:77211387-1
Figures 1, 2

Diagnosis. *Rhamnella intermedia* differs from *R. rubrinervis* and *R. tonkinensis* by smaller size of dried fruit (6.0–7.0 × 4.7–5.3 vs. 7.5–11.1 × 4.2–5.8 mm) and seeds (5.5–6.5 × 4.5–5.0 vs. 7.0–9.9 × 4.2–5.5 mm) and smaller ratio of length to width of dried fruit (1.3–1.5 vs. 1.6–2.2) and seeds (1.2–1.4 vs. 1.6–2.1), and from *R. brachycarpa* by the larger ratio of length to width of leaves (2.7–3.8 vs. 1.9–2.4), smaller length of leaf petioles (3–8 vs. 7–12 mm), larger length of fruiting pedicels (5–9 vs. 4–6 mm), leaf apices acuminate to long acuminate and seed apices rarely mucronate. In addition, the characters of densely pilose young branches can also significantly separate this new species from *R. rubrinervis*.

Type. China. Guangxi: Pingxiang County, 22°07'19"N, 106°44'40"E, 298 m altitude, karst limestone hill, 5 Oct 2019, *Z.Q. Lu 2019YG2601* (holotype, GXMI; isotypes, HITBC).

Description. Shrubs or small trees, rarely climbing vines, evergreen. Young branches densely pilose; older branches grey-brown or grey, sparsely pilose or glabrous. Leaves alternate; stipules subulate, persistent; petiole 0.3–0.8 cm long, densely pilose when young, late sparsely pilose, rarely glabrous, narrowly grooved on the upper surface; leaf blade abaxially dark green, shiny, adaxially pale green, oblong or ovate-oblong, 6.4–13.0 × 2.0–5.0 cm, length-width ratio 2.7–3.8, leathery, abaxially sparsely pilose or glabrous, sparsely pilose along leaf veins or glabrous, adaxially glabrous, lateral veins 6–7 pairs, slightly impressed abaxially, prominent adaxially, base commonly rounded, rarely cuneate, margin inconspicuously remotely serrate or subentire; apex acuminate to long acuminate. Flowering branches axillary 8–13 cm long, densely or sparsely pilose, rarely glabrous. Flowers bisexual, ca. 4 mm diam., 5–merous, few to 10 in axillary cymes, cymes subsessile or shortly pedunculate at bracteole leaf of flowering branches; bracteole leaf similar to leaves in vegetative branches, but smaller, 3.5–6.5 × 1.3–2.0 cm, lateral veins 3–5 pairs. Pedicel 4.0–7.0 mm long, densely or sparsely pilose. Sepals triangular, ca. 2 mm, adaxially midvein raised, rostellate at lower middle. Petals obovate, shortly clawed. Stamens involute by petals, ca. 2 mm long. Disc rounded, thick. Ovary globose, not immersed in disc. Drupe purple-red or orange at maturity, ovoid-cylindrical or globose, 8.5–10.2 × 8.2–10.1 mm, 6.0–7.0 × 4.7–5.3 mm when dried, base with persistent calyx tube; fruiting pedicel 5.0–9.0 mm, sparsely pilose, 1-loculed, 1-seeded; seed short, apex rarely mucronate, smooth on the surface, 5.5–6.5 × 4.5–5.0 mm, length-width ratio 1.2–1.4.

Etymology. Owing to its intermediate morphology compared to the other three closely related species, we provide the epithet *intermedia*.

Phenology. Flowering from June to September and fruiting from August to October.

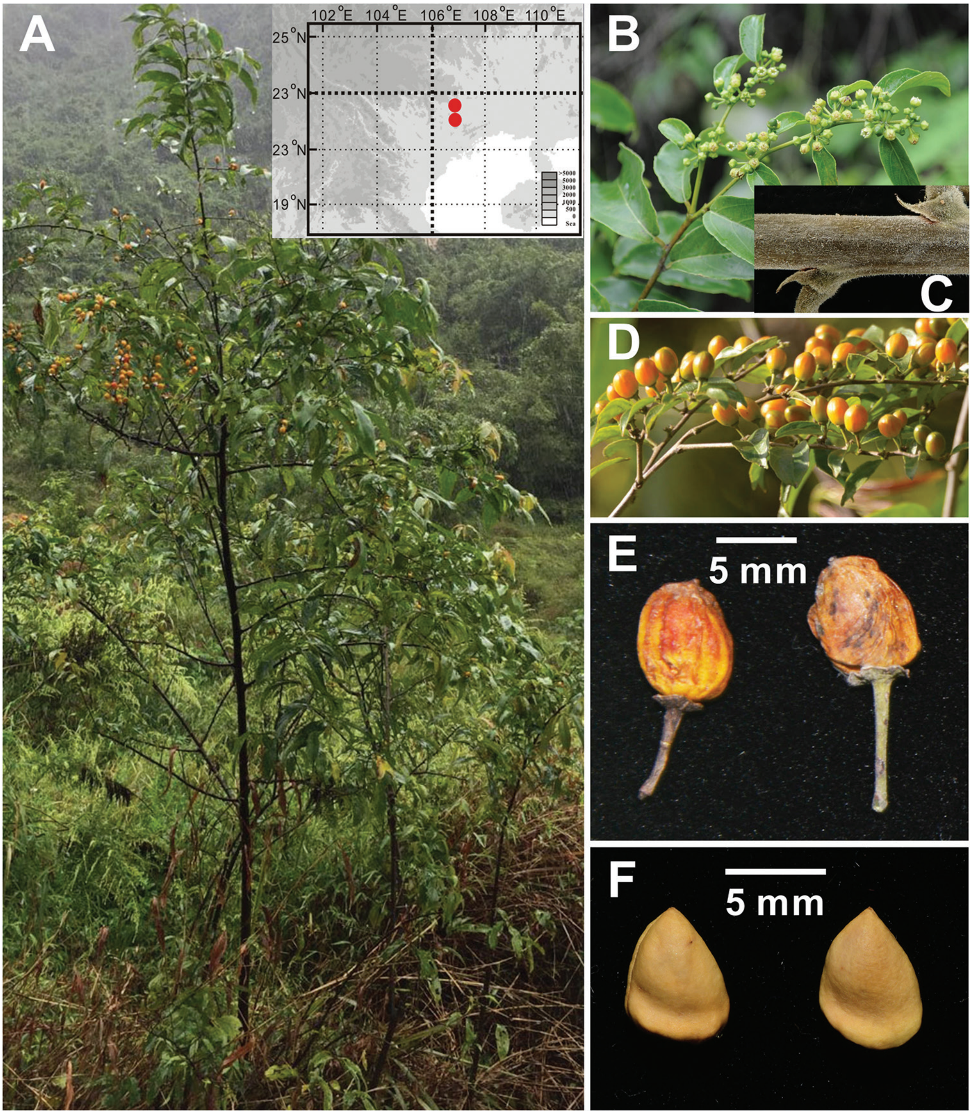

Figure 1. *Rhamnella intermedia* Z. Qiang Lu & Y. Shuai Sun. **A** The whole plant, habitat and two geographical locations **B** flowering branches **C** a young branch with the persistent stipule **D** branches with leaves and fruit **E** dried fruit **F** mature seeds.

Habitat and distribution. To date, only two *R. intermedia* populations have been collected from southwest Guangxi. For its population census, more than 20 mature trees (3–6 m in height) and a large number of seedlings grow on the karst limestone hill. We also found that six individuals present a climbing habit at locations where there is a relative high canopy; however, all others are erect. Interestingly, they shared the same ITS types between erect and climbing trees, suggesting no genetic differentiation. In addition, this new species may be also distributed in Vietnam, because it is

Figure 2. *Rhamnella intermedia* Z. Qiang Lu & Y. Shuai Sun, sp. nov., drawn from *Z.Q. Lu 2019YG2601*.

found in Pingxiang and Daxin from southwest Guangxi, which is close to Vietnam. Further field investigations on its entire distribution are recommended in the future.

Additional specimens examined. China. Guangxi: Pingxiang County, 22°07'19"N, 106°44'40"E, 298 m altitude, karst limestone hill, 5 Oct 2019, *Z.Q. Lu 2019YG2602–Z.Q. Lu 2019YG2619* (HITBC); Daxin County, Wude Township, 22°34'15"N, 106°44'56"E,

Table 2. Morphological comparision of *Rhamnella intermedia*, *R. rubrinervis*, *R. tonkinensis* and *R. brachycarpa*. Traits that differ between species are marked in bold.

Characters	*R. intermedia*	*R. rubrinervis*	*R. tonkinensis*	*R. brachycarpa*
LEAF				
Shape and size	Leaf blade oblong or ovate-oblong, 6.4–13.0 × 2.0–5.0 cm, **length-width ratio 2.7–3.8**; base commonly rounded, rarely cuneate, margin inconspicuously remotely serrate or subentire; **apex acuminate to long acuminate**; bracteole leaf similar to leaves in vegetative branches, but smaller	Leaf blade oblong or ovate-oblong, 5.4–14.4 × 1.7–5.1 cm, **length-width ratio 2.7–4.3**; base commonly rounded, rarely cuneate, margin inconspicuously remotely serrate or subentire; **apex acuminate to long acuminate**; bracteole leaf similar to leaves in vegetative branches, but smaller	Leaf blade elliptic-ovate, 6.5–11.2 × 3.1–4.5 cm, **length-width ratio 2.1–2.8**; base cuneate or nearly rounded, margin inconspicuously remotely serrate or subentire; **apex short acuminate to long acuminate or acute**; bracteole leaf similar to leaves in vegetative branches, but smaller	Leaf blade elliptic-ovate, 5.8–10.3 × 3.1–4.8 cm, **length-width ratio 1.9–2.4**; base cuneate or nearly rounded, margin inconspicuously remotely serrate or subentire; **apex short acuminate or acute**; bracteole leaf similar to leaves in vegetative branches, but smaller
Length of petiole	**3–8 mm**	**3–9 mm**	**7–11 mm**	**7–12 mm**
Lateral veins on each side of midvein	6–7	5–8	5–6	5–7
Average distance between lateral veins located in the middle of leaf	3–8 mm	3–8 mm	3–6 mm	3–6 mm
BRANCH				
Young branches densely pilose or not	Densely pilose	Sparsely pilose or glabrous	Incompletely clear	Sparsely pilose or glabrous
Stipules lanceolate or subulate	Subulate	Lanceolate or subulate	Incompletely clear	Subulate, but seemingly lanceolate when young
FLOWER				
Number of flowers for each axillary cyme	3–10	2–10	3–11	2–9
Length of pedicel	4–7 mm	2–5 mm	5–7 mm	3–5 mm
Shape and size	Flower diameter ca. 4 mm; sepals triangular, ca. 2 mm; stamens involute by petals, ca. 2 mm in length	Flower diameter ca. 4 mm; sepals triangular, ca. 2 mm; stamens involute by petals, ca. 2 mm in length	Flower diameter ca. 4 mm; sepals triangular, ca. 2 mm; stamens involute by petals, ca. 2 mm in length	Flower diameter ca. 4 mm; sepals triangular, ca. 2 mm; stamens involute by petals, ca. 2 mm in length
FRUIT				
Size of fleshy fruit	8.5–10.2 × 8.2–10.1 mm	10.2–12.1 × 10.1–12.5 mm	9.7–11.1 × 8.9–10.1 mm	8.7–10.9 × 7.5–10.6 mm
Size of dried fruit	**6.0–7.0 × 4.7–5.3 mm**	**8.2–11.1 × 4.2–5.8 mm**	**7.5–9.8 × 4.5–5.5 mm**	**6.5–7.5 × 4.7–6.0 mm**
Length-width ratio of dried fruit	**1.3–1.5**	**1.6–2.2**	**1.6–2.0**	**1.3–1.5**
Length of fruiting pedicel	**5–9 mm**	**3–6 mm**	**5–9 mm**	**4–6 mm**
SEED				
Size of seed	**5.5–6.5 × 4.5–5.0 mm**	**7.1–9.9 × 4.0–5.5 mm**	**7.0–9.0 × 4.2–5.0 mm**	**5.0–7.0 × 4.5–5.5 mm**
Length-width ratio	**1.2–1.4**	**1.6–2.1**	**1.7–2.0**	**0.9–1.5**
Seed apex	**Rarely mucronate**	**Rarely mucronate**	**Mucronate or not**	**Mucronate**

276 m altitude, along road, 27 May 2018, *Z.Q. Lu 201810801* (HITBC); the same locality: 26 August 2018, *Z.Q. Lu 201810802* (HITBC). Longzhou County, Daqingshan, hillside, July 1953, *Guangxi team 2967* (PE).

Table 3. Nuclear ITS sequences variations between the two closely related *Rhamnella* species (*R. intermedia* vs. *R. rubrinervis*). The fixed nucleotides of *R. intermedia* are shown in bold. Variable positions interpreted based on the aligned sequences where mutation sites occur.

	Variable positions						
Species (individuals)	**4**	**6**	**1**	**1**	**2**	**2**	**2**
	2	**9**	**1**	**2**	**1**	**2**	**2**
			6	**2**	**3**	**0**	**7**
R. intermedia Type1 (10)	G	G	T	**T**	**T**	**T**	**C**
R. intermedia Type2 (5)	G	–	C	**T**	**T**	**T**	**C**
R. intermedia Type3 (1)	R	–	T	**T**	**T**	**T**	**C**
R. rubrinervis Type1 (5)	G	–	C	C	C	G	A
R. rubrinervis Type2 (16)	G	–	C	C	C	G	A

R: A/G.

Notes. *R. intermedia* is morphologically similar to *R. rubrinervis* based on leaf characters, but they can be easily distinguished between each other by fruit and seed characters. However, it also can be significantly distinguished from *R. rubrinervis* by the densely pilose young branches, if the specimen has no fruit and seeds. In addition, it also needs to be mentioned that the flower of *R. brachycarpa* is 5-merous.

Key to four closely related evergreen *Rhamnella* species

1 Dried fruit size 6.0–7.5 × 4.7–6.0 mm, length-width ratio 1.3–1.5; seed size 5.0–7.0 × 4.5–5.5 mm, length-width ratio 0.9–1.5 .... **2**

– Dried fruit size 7.5–11.1 × 4.2–5.8 mm, length-width ratio 1.6–2.2; seed size 7.0–9.9 × 4.0–5.5 mm, length-width ratio 1.6–2.1 .... **3**

2 Young branch sparsely pilose or glabrous, leaf blade length-width ratio 1.9–2.4, apex short acuminate or acute, petiole 7–12 mm; fruiting pedicel 4–6 mm; seed apex mucronate.. ***R. brachycarpa***

– Young branch densely pilose, leaf blade length-width ratio 2.7–3.8, apex acuminate to long acuminate, petiole 3–8 mm; fruiting pedicel 5–9 mm; seed apex rarely mucronate .... ***R. intermedia***

3 Leaf blade length-width ratio 2.1–2.8, petiole 7–11 mm; fruiting pedicel 5–9 mm.. ***R. tonkinensis***

– Leaf blade length-width ratio 2.7–4.3, petiole 3–8 mm; fruiting pedicel 3–6 mm.. ***R. rubrinervis***

Discussion

Many differentiated phenotypic traits between the evergreen *Rhamnella* species have been demonstrated (Lu and Sun 2019), such as length of leaf petioles, ratio of length to width of leaves, leaf apices and size and ratio of length to width of dried fruit and

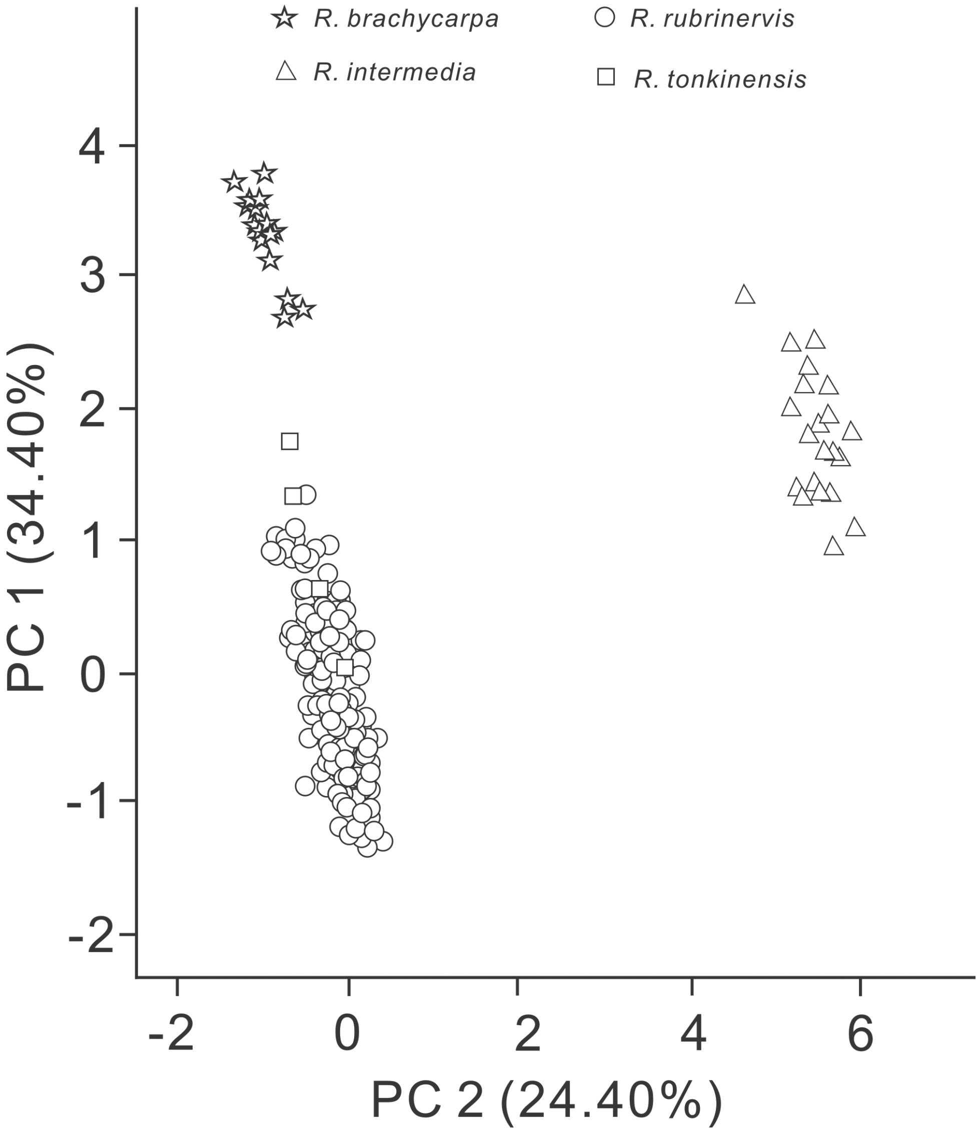

Figure 3. Phenotypic clustering based on principal component analysis.

seeds. In the present study, we proposed two Guangxi populations as a new evergreen species, based on the following evidence. First, they are ascribed to the evergreen group that are significantly different from those deciduous broad-leaved species within *Rhamnella*, at the species level (Fan and Yang 1997; Lu and Sun 2019). Other characters such as drupe and seed sizes can also separate these two groups (Table 2; Chen and Schirarend 2007; Lu and Sun 2019). Second, they have intermediate morphology and stable phenotypic differences, and could be easily distinguished from the three closely related evergreen species within *Rhamnella* (Table 2). Third, PCA analysis further sup-

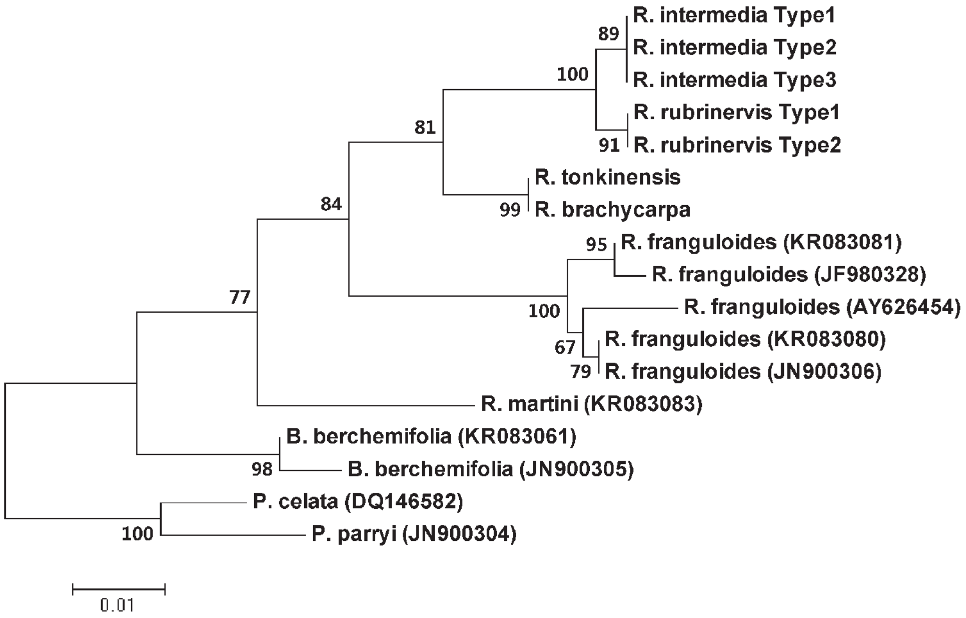

Figure 4. Phylogenetic analysis of evergreen *Rhamnella* species based on nuclear ITS sequences. *Berchemiella wilsonii*, *B. berchemifolia*, *Pseudoziziphus celata*, and *P. parryi* are outgroups.

ported that they represent a distinct phenotypic cluster different from all published relatives (Figure 3; Lu and Sun 2019). However, the intermediate morphology of these two Guangxi populations also conforms to the characteristic of hybrids (Mallet 2005), which usually co-occur with parental species (Zha et al. 2010). Nevertheless, our field investigations show that none of the three closely related species co-occurred with this assumed new species. Furthermore, phylogenetic analysis of nuclear ITS sequence variations suggested they represented a distinct genetic lineage and closest to *R. rubrinervis* (Figure 4). Four fixed nucleotide sites were found between these two Guangxi populations and *R. rubrinervis* in the present study. Therefore, they are not hybrids, but represent an independent evolutionary lineage sister to *R. rubrinervis*. This new evolutionary lineage is distinguished from *R. rubrinervis* by densely pilose young branches, smaller size of dried fruit and seeds, and smaller ratio of length to width of dried fruit and seeds (Figure 1; Chen and Schirarend 2007). In total, these two Guangxi populations are distinctly different from all the published relatives. Hence, the two Guangxi populations are proposed to be erected as a new species, named as *R. intermedia*.

Acknowledgements

This study was supported by the grants from CAS "Light of West China", "Youth Innovation Promotion Association" Programs (2019386).

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RESEARCH ARTICLE

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A new species of *Chrysosplenium* (Saxifragaceae) from Shaanxi, north-western China

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Abstract

Chrysosplenium zhouzhiense Hong Liu, a new species from Shaanxi, north-western China, is described and photographed. The new species belongs to Subgen. *Gamosplenium* Sect. *Nephrophylloides* Ser. *Macrophylla* and is most similar to *C. macrophyllum* and *C. zhangjiajieense* from which it differs by having a shorter stem, rhizome absent, basal leaf absent, sterile branch arising from the flowering stem and a light yellow flower with longer stamen. A global conservation assessment is performed and classifies *C. zhouzhiense* as Endangered (EN).

Keywords

Chrysosplenium zhouzhiense, Sect. *Nephrophylloides*, Ser. *Macrophylla*, Subgen. *Gamosplenium*, taxonomy

Introduction

Chrysosplenium L. (Saxifragaceae) is a small perennial herbaceous genus that comprises ca. 70 species (Kim et al. 2019). *Chrysosplenium* is distributed throughout the temperate regions of the Northern Hemisphere, with high species diversity in eastern Asia, America and Europe (Hara 1957; Pan 1986a, b, 1992; Pan and Ohba 2001; Soltis 2007). China is one of the diversification centres of this genus including ca. 37 species, the majority of which are distributed in south-western, northern and central China, particularly the Provinces of Yunnan, Xizang, Sichuan and Shaanxi (Pan and Ohba 2001; Liu et al. 2016; Kim et al. 2019).

Based on the morphological features of leaf arrangement, *Chrysosplenium* was classified into two groups, namely, Sect. *Alternifolia* Franch. and Sect. *Oppositifolia* Franch. (Franchet 1890–1891). However, Hara (1957) argued that this classification was not natural due to the characters of flower, capsule and seed being highly variable within each section. He proposed a classification of 17 series instead. Briefly, characters such as leaf arrangement, pedicel length, sterile branch position, capsule shape, seed surface, stem surface, ovary position, stamen length, leaf surface, leaf isomery, sepal length and basal leaf size are used to establish and distinguish the series (Hara 1957). Of these, leaf arrangement occurs as the primary character in the key to the series in his classification (Hara 1957). This character was also considered to establish subgenus by Pan (1986a, b) when he made the taxonomic revision of Chinese *Chrysosplenium*. Seed surface was also used as an important character to delimit sections in his classification (Pan 1986a, b). Using *matK* sequence data, Soltis et al. (2001) conducted the extensive phylogenetic study demonstrating that two sections/subgenera are both monophyletic and form two sister clades. Thus, they agreed with leaf arrangement as a good indicator of the relationship within the genus.

In 2019, we found an unknown species of non-flowering *Chrysosplenium* when conducting a field investigation in Shaanxi, north-western China. We revisited the same locality in 2020 and collected specimens with flowers. Morphologically, this unknown species belongs to *Chrysosplenium* Subgen. *Gamosplenium* Maxim., Sect. *Nephrophylloides* Turcz., Ser. *Macrophylla* by leaves all alternate, seed minute papillae, ovary semi-inferior and disc absent (Pan 1986a, b). A thorough literature survey (Pan 1992; Pan and Ohba 2001; Liu et al. 2016; Kim et al. 2019) and review of herbarium specimens at A, E, HNWP, HZU, IBSC, KUN, MO, NEFI, NWTC, PE, SI, WUK (herbarium acronyms according to Index Herbariorum; Thiers 2019), suggested that it is a distinct and undescribed species.

Materials and methods

Morphology examination and conservation assessments

Photographs of the plant habit and morphological characters were taken in the field. All available specimens of the new species were deposited at the herbarium of South-Central University for Nationalities (**HSN**) and the herbarium of Guangxi Institute of Botany (**IBK**). All morphological characters from three specimens were studied using a dissecting microscope (SMZ171, Motic, China). For seed morphology, we also undertook SEM observation; seed materials were collected from the field and dried by silica gel. Seeds were placed in a bath-type ultrasonic cleaner for 10 min with 70% ethanol to remove impurities. After air-drying, the seeds were mounted using double-sided adhesive tape and coated with gold in a sputter coater, then observed and photographed under a Hitachi SU8010 scanning electron microscope. At least ten seeds were used to determine the size and surface. Conservation assessment was undertaken following IUCN (2019).

Distribution map

A distribution map of *Chrysosplenium zhouzhiense*, *C. macrophyllum* Oliv. and *C. zhangjiajieense* X.L.Yu, Hui Zhou & D.S.Zhou was made using the software ArcGIS 10.2 (ESRI, Inc.). The geographical information for three species was obtained from the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/zh/), and Chinese Virtual Herbarium (CVH, http://www.cvh.ac.cn/) and specimens deposited at HSN. We retained one accession per County to display the geographical range of each species. Specimens with ambiguous or incorrect identification were not used in this study.

Taxonomic treatment

Chrysosplenium zhouzhiense **Hong Liu, sp. nov.**
urn:lsid:ipni.org:names:77211388-1
Figs 1–4

Diagnosis. Most similar to *Chrysosplenium macrophyllum* and *C. zhangjiajieense* from which it differs by having a shorter stem, rhizome absent, basal leaf absent, sterile branch arising from flowering stem, light yellow flower with longer stamen.

Type. China. Shaanxi: Niguhe Village, Zhouzhi County, Xi'an City, 34°01'44"N, 107°58'12"E, under broad-leaved forests in a mountain area at ca. 1350 m altitude, 10 May 2020, *Hong Liu, De-Qing Lan and Wen Huang HSN13356* (holotype HSN; isotypes HSN, IBK).

Description. Perennial herbs, 5–16 cm high. Root fibrous and soft. Stolons 1–3, filiform, without long creeping rhizome or bulbs. Flowering stem(s) erect, simple, 5–15 cm high, smooth and subglabrous at base, dark red, rounded. Sterile branch 1 or (2), arising from the lower part and 2–7 cm above the base of flowering stem, rounded, 5–13 cm long, upper-middle part densely covered with white villose, hairs ca. 2–3 mm long. Basal leaves absent. Cauline leaves of flowering stem 2–4, alternate, slender, petiole 10–25 mm long; blade 5–12 × 7–15 mm, flabelliform or subrounded, sparsely white villose or subglabous, apex rounded, margin obtusely dentate (10–13 teeth), base cuneate to subcordate. Leaves of sterile branches 4–8, alternate, heterophyllous, upper leaves 3–4 crowded at stem apex larger, petiole 5–15 mm long, covered with soft downy hairs; blade 10–30 × 10–30 mm, flabelliform, densely lanate at both surfaces, apex subtruncate to rounded, margin undulate-crenate (12–16 teeth), base truncate to round; lower leaves 2–4, petiole 8–25 mm long; blade 5–15 × 5–15 mm, flabelliform, sparsely pubescent or subglabrous at both surfaces, apex subtruncate to rounded, margin undulate-crenate (8–11 teeth), base decurrent. Inflorescence often 6-flowered cyme, dense, 2–5 cm wide, branches glabrous or sparsely pubescence, surrounded by leaf-like bracts; bracteal leaves green, broadly ovate or obovate, rarely rounded, smooth at both surfaces, margin or petioles sparsely villose, base slightly oblique, broadly cuneate, triangular and two-rounded arranged, unequal; mid-

中南民族大学植物标本馆采集记录
Herbarium of South-Centeal University for Nationalities(HSN)
采集号 NO. ZJ2020051013356
采集人 Collector(s) 刘虹/兰德庆/黄文
标本份数 Copy 6 日期 Date 20200510
名称 Name 周至金腰 *Chrysosplenium zhouzhiense* Hong Liu
科名 Family 虎耳草科 Saxifragaceae
产地 Location 陕西省，西安市周至县竹峪镇泥峪河村
经度 Lon. 107°58'12.67" 纬度 Lat. 34°01'44.26" 海拔 Alt.(m) 1350 m
分布 Frequency
生境 Habitat
基质 Substrate
性状 Habit 林下、沟边分布、叶互生、不育枝密被白毛. 生活型 Life f.
体高 Height(m) 5-16cm 胸径 Diam(cm)
根 Root 纤细状 茎 Stem
叶 Leaf 花 Flower 黄色
果实 Fruit
种子 Seed
引种 Introduction
分子材料 Molecular sample 已采集
附记 Additional

Holotype.
中南民族大学植物标本馆
Herbarium of South-Centeal University for Nationalities(HSN)
采集人 Collected by 刘虹/兰德庆/黄文 采集号 NO. ZJ2020051013356
周至金腰 *Chrysosplenium zhouzhiense* Hong Liu
鉴定人 Det. By 刘虹 鉴定日期 Dat. Date 2020.07.01

Figure 1. Type specimen of *Chrysosplenium zhouzhiense* Hong Liu, sp. nov. (Photo by Hong Liu).

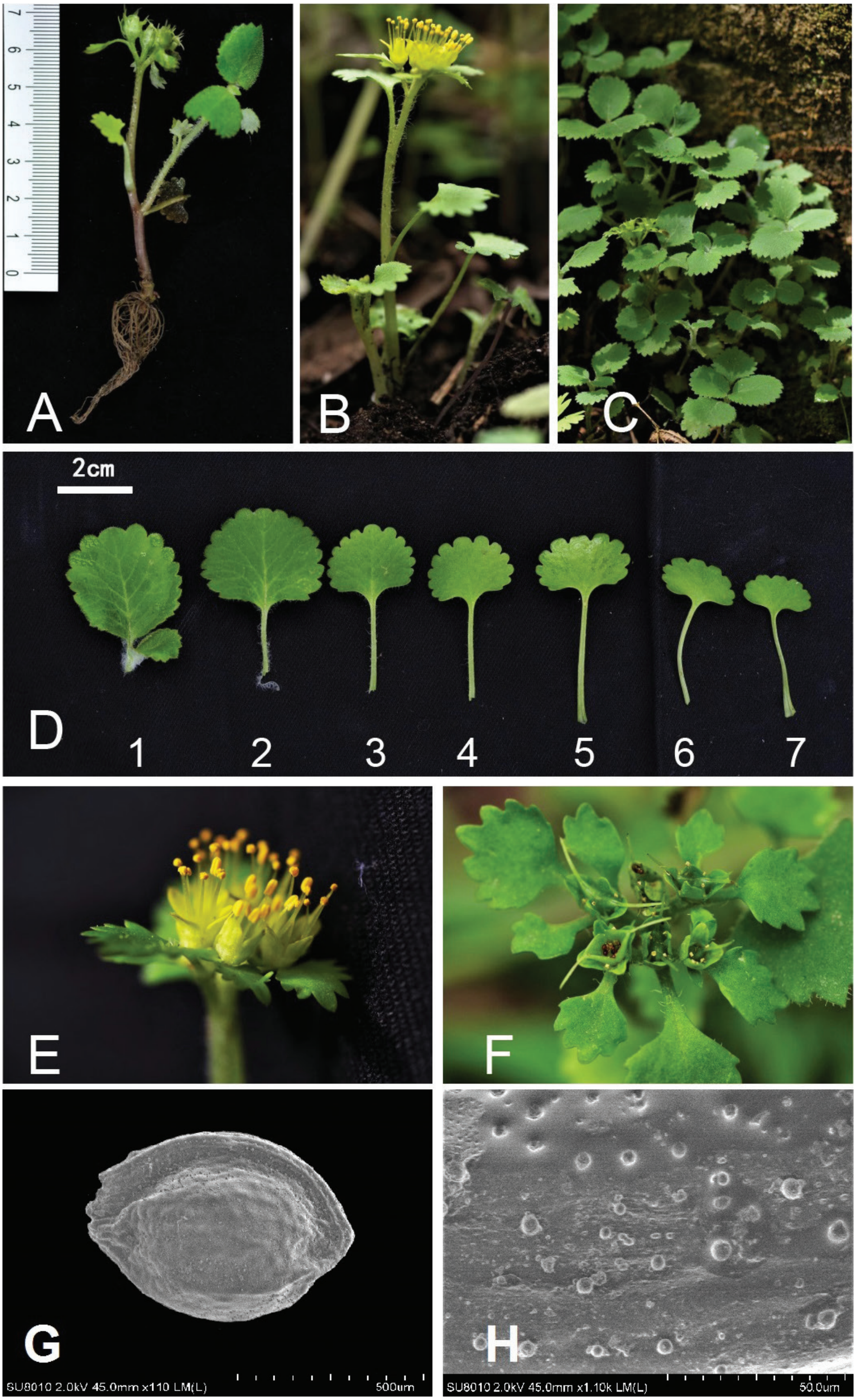

Figure 2. *Chrysosplenium zhouzhiense* Hong Liu, sp. nov. **A** fruiting plant **B** flowering plant **C** habitat **D** leaves of sterile branch **E** flowers close-up view **F** capsules **G, H** seeds, scanning electron micrograph, 110× (**G**) and 1,100× (**H**). (Photos by Hong Liu).

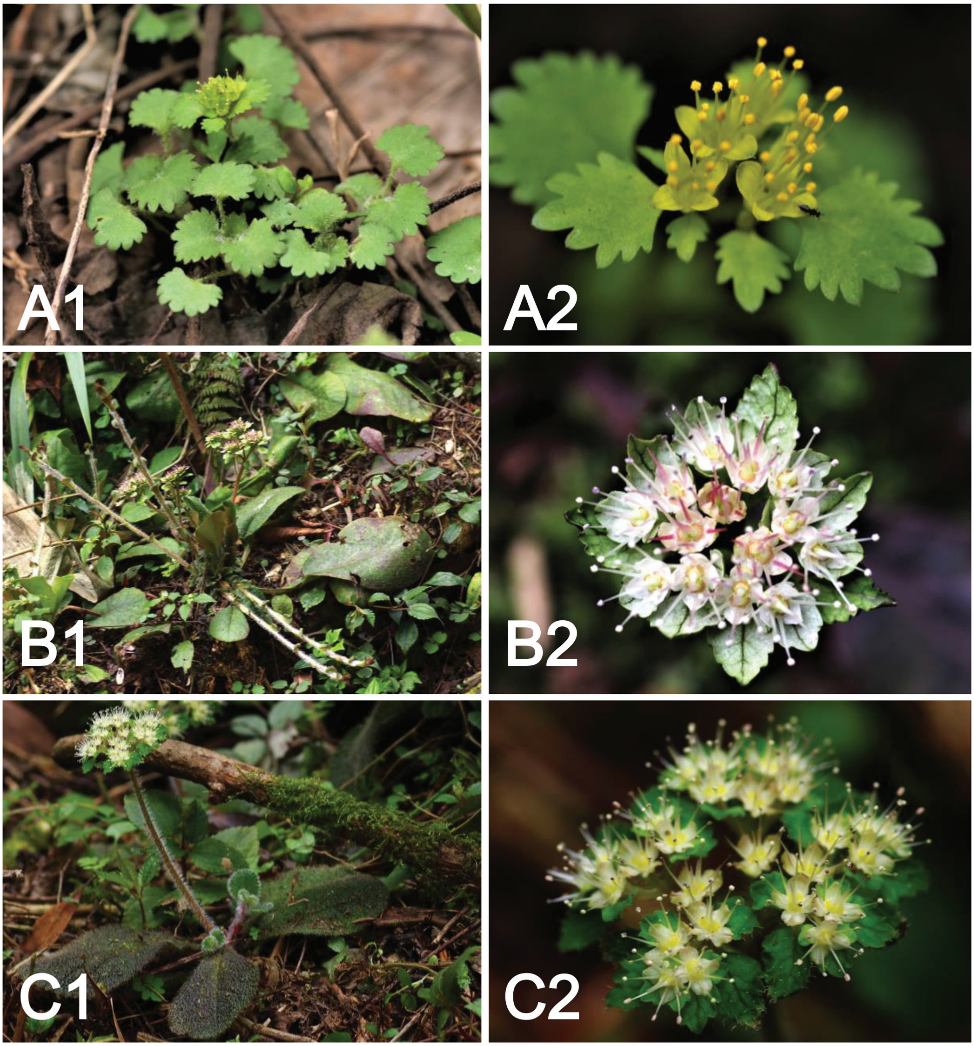

Figure 3. *Chrysosplenium* spp. habit and inflorescence **A** *C. zhouzhiense* Hong Liu, sp. nov., habit (**A1**), inflorescence with yellow flower (**A2**) **B** *C. macrophyllum*, habit (**B1**), inflorescence with white flower (**B2**) **C** *C. zhangjiajieense*, habit (**C1**), inflorescence with white flower (**C2**).

dle one major, petiole 5–8 mm long, blade 5–12 × 4–12 mm, margin obtusely dentate (7–11 teeth); two lateral ones minor, petiole 2–5 mm long, blade 3–5 × 2–4 mm, margin obtusely dentate (3–5 teeth). Flowers tetramerous, actinomorphic; sepals 4 (2 pairs), erect, yellow in flowering time, but turn green in fruiting time, 2.6–3.9 × 1.8–2.2 mm, ovate, apex acuminate; stamens 8, homostylic, 6–8 mm long, twice longer than sepals; filaments slender, 6–7 mm long; anther yellow, 2-locular, longitudinally dehiscent; ovary 2-locular, semi-inferior; stigma 2, 3–4 mm long; styles erect, shorter than stamens, 2–3 mm long. Fruit a capsule, 3–4 mm long, green, smooth, 2-lobed (horn-shaped), equal, dehiscent along the adaxial suture; seeds numerous, dark brown, ovoid, a raphe on one side, 550–640 × 350–450 µm, minute papillae.

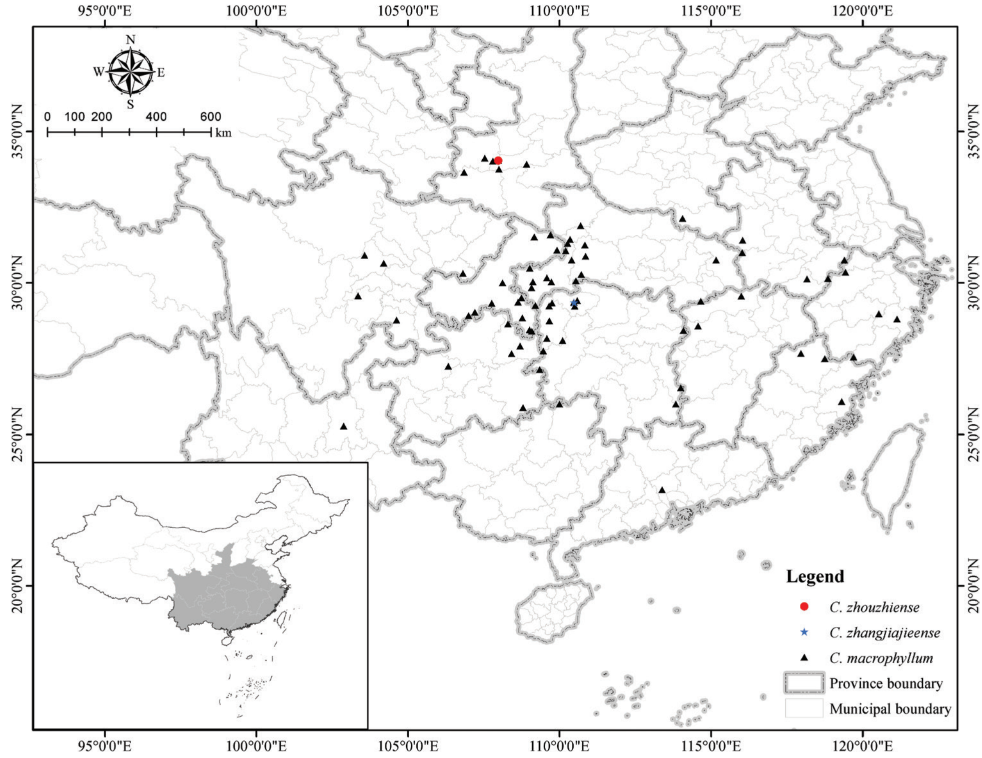

Figure 4. Distribution map of *Chrysosplenium zhouzhiense* (red circle), *C. macrophyllum* (black triangle) and *C. zhangjiajieense* (blue star).

Etymology. *Chrysosplenium zhouzhiense* is named after the type locality, Zhouzhi County, Shaanxi Province, China.

Vernacular name. zhōu zhì jīn yāo (Chinese pronunciation); 周至金腰 (Chinese name).

Discussion. *Chrysosplenium zhouzhiense* is characterised by leaves all alternate, seed minute papillae, ovary semi-inferior and disc absent. Thus, it belongs to *Chrysosplenium* Subgen. *Gamosplenium*, Sect. *Nephrophylloides*, Ser. *Macrophylla* (Pan 1986a, b). *Chrysosplenium* Ser. *Macrophylla* contains five species including *C. chinense* (Hara) J.T.Pan, *C. davidianum* Dence. ex Maxim, *C. macrophyllum* Oliv., *C. glossophyllum* Hara and a recently-described species *C. zhangjiajieense* (Pan 1986a; Liu et al. 2016). Amongst them, the new species is most similar to *C. macrophyllum* and *C. zhangjiajieense* by stamens long exserted from sepals, but can be distinguished based on plant height, rhizome, stolon, sterile branch, basal leaf, flower colour and stamen morphology as summarised in Table 1.

Conservation Status. At present, *Chrysosplenium zhouzhiense* is only known from a single locality (IUCN 2019). At this locality, the population of this species comprises ca. 100 mature individuals (< 250 mature individuals, criteria D1). Therefore, we propose that *C. zhouzhiense* should be considered as Endangered D1 (EN) according to IUCN criteria (IUCN 2019).

Table 1. Morphological comparison of *Chrysosplenium zhouzhiense*, *C. macrophyllum* and *C. zhangjiajieense*.

Characters	*C. zhouzhiense*	*C. macrophyllum*	*C. zhangjiajieense*
Plant height	5–16 cm	17–21 cm	13–19 cm
Rhizome	absent	thick	thick
Stolon	1–3	absent	absent
Flowering stem and sterile branch	sterile branch arising from flowering stem	separate	separate
Cauline leaf	2–4	1	1
Basal leaf	absent	large, 2.3–19 cm long	large, 4–10.5 cm long
Flower colour	light yellow	white	white
Stamen	6–8 mm	4–6 mm	4–6 mm

Key to species of *Chrysosplenium* Subgen. *Gamosplenium* Sect. *Nephrophylloides* Ser. *Macrophylla* modified from Pan and Ohba (2001)

1 Stamens long exserted from sepals...**2**
– Stamens subequalling or shorter than sepals...**3**
2 Stolon 1–3; basal leaf absent; flower light yellow; stamen 6–8 mm... ***C. zhouzhiense***
– Stolon absent; basal leaf large; flower white; stamen 4–6 mm......................**4**
3 Stem glabrous; basal leaves reniform to orbicular-reniform......... ***C. chinense***
– Stem brown villous; basal leaves broadly ovate to orbicular **5**
4 Basal leaves sparsely pilose; cauline leaves 12–17 × 5–7.5 mm, narrowly elliptic.. ***C. macrophylla***
– Basal leaves densely long villous; cauline leaves 3–5 × 4–6 mm, oval to circular... ***C. zhangjiajieense***
5 Sterile branches absent; basal leaf margin 20–36-crenate, sometimes obscurely so; stamens shorter than sepals; capsule rostrums ca. 0.5 mm... ***C. glossophyllum***
– Sterile branches arising from stem base; basal leaf margin (7–)13–17-crenate; stamens subequalling sepals; capsule rostrums 1–2 mm ....***C. davidianum***

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Taxonomic revision of the genus *Glochidion* (Phyllanthaceae) in Taiwan, China

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Abstract

A comprehensive taxonomic revision of the genus *Glochidion* J.R. Forst. & G. Forst. from Taiwan in China was carried out based on the examination of herbarium specimens and filed investigations. Eight species and three varieties are recognized, including a new species endemic to Taiwan, *G. lanyuense* Gang Yao & S.X. Luo, which is described and illustrated. Three names, viz. *G. chademenosocarpum* Hayata, *G. kusukusense* Hayata, and *G. ovalifolium* F.Y. Lu & Y.S. Hsu, are reduced to the new synonyms of *G. rubrum* Blume, *G. lanceolatum* Hayata, and *G. ellipticum* Wight, respectively. Two names, viz. *G. lanceolatum* Hayata and *G. suishaense* Hayata, are lectotypified here. A key to the *Glochidion* species in Taiwan is provided.

Keywords

lectotypification, new species, new synonym, Phyllantheae, taxonomy

Introduction

Glochidion J.R. Forst. & G. Forst. is the second largest genus within the tribe Phyllantheae Dumort. (Phyllanthaceae Martinov) (Govaerts et al. 2000; Webster 2014; Duocet Group 2016 onwards). It is represented by more than 300 species of shrubs or trees distributed primarily in the Indo-Pacific, east to southeast Polynesia and south into Australia (Govaerts et al. 2000; Li and Gilbert 2008), with about 30 species in China (Li and Gilbert 2008; Yao and Zhang 2015a; Yao et al. 2017). Molecular phylogenetic studies have shown that *Glochidion* and some other genera (viz. *Breynia* J.R. Forst. & G. Forst., *Phyllanthodendron* Hemsl. and *Sauropus* Blume) were nested deeply within the large and morphologically heterogeneous genus *Phyllanthus* L. s.s. (over 800 species) (Hoffmann et al. 2006; Kathriarachchi et al. 2006; Pruesapan et al. 2012; van Welzen et al. 2014). Therefore some authors suggested the inclusion of these genera in *Phyllanthus*, and accepted the concept of *Phyllanthus* s.l. (over 1200 species; including *Breynia*, *Glochidion*, *Phyllanthodendron* and *Sauropus*) (Hoffmann et al. 2006; Wagner and Lorence 2011). However, others suggested that it might be more reasonable to disintegrate *Phyllanthus* s.s. into smaller genera, and accept the generic status of *Glochidion* and other relevant genera (Pruesapan et al. 2012), which is further supported in morphological (van Welzen et al. 2014), palynological (Yao and Zhang 2016) and wood anatomical (Jangid and Gupta 2016) analyses. Thus, the generic name *Glochidion* is still accepted widely in recent taxonomic literature (e.g. van Welzen et al. 2014; Webster 2014; Ramana et al. 2015; Chia et al. 2017; Yao et al. 2017; Chakrabarty and Balakrishnan 2018; Xu et al. 2020).

Taxonomic studies of *Glochidion* have largely been conducted at the regional level, such as in China (Li 1994; Li and Gilbert 2008), Indo-Burma (Chakrabarty and Balakrishnan 2018), Indo-China (Beille 1927), Indian subcontinent (Chakrabarty and Gangopadhyay 1995), Java (Backer and Bakhuizen 1963), the Philippines (Robinson 1909), Sumatra (Airy Shaw 1981), Thailand (Airy Shaw 1972; van Welzen 2007) and Vietnam (Nguyen 2007). Thus, a comprehensive taxonomic revision of the genus is still lacking, and an acceptable infrageneric classification system of the genus has not been proposed. In *Flora Republica Popularis Sinicae*, the Chinese *Glochidion* species were classified into two sections based on the number of stamens, viz. sect. *Glochidiopsis* (Blume) Hook.f. (stamen 3) and sect. *Multandrum* P.T. Li (stamen 4–8) (Li 1994), but this classification system was not supported in molecular phylogenetic studies (Kawakita et al. 2004; Luo et al. 2017). In China, the taxonomic study of *Glochidion* in Taiwan has a long history. Forbes and Hemsley (1894) were the first authors to report *Glochidion* species from Taiwan and three species were reported then, viz. *G. arnottianum* Müell. Arg., *G. fortunei* Hance, and *G. hongkongense* Müell. Arg. Subsequently, a number of taxonomic studies of Taiwanese *Glochidion* were conducted (e.g., Hayata 1903, 1904, 1920; Kanehira 1936; Croizat and Hara 1940; Keng 1955; Li 1963; Hsieh 1977; Deng and Wang 1993; Li 1994; Hsu et al. 2006; Li and Gilbert 2008). In the latest taxonomic monograph accomplished by Hsu et al. (2006), they reviewed the taxonomic history of Taiwanese *Glochidion* and recognized nine species, viz. *G. acuminatum* Müell. Arg., *G. hirsutum* (Roxb.) Voigt, *G. kusukusense* Hayata, *G. lanceolatum* Hayata, *G. ovalifolium* F.Y. Lu & Y.S. Hsu, *G. philippicum* (Cavan.) C.B. Rob., *G. puber* (L.) Hutch., *G. rubrum* Blume, *G. zeynanicum* (Gaertn.) A. Juss. Among some of these studies, four taxa described from Taiwan [viz. *G. assamicum* (Müll. Arg.) Hook. f. var. *magnicapsulum* Croiz. & Hara., *G. chademenosocarpum*

Figure 1. A holotype of *Glochidion assamicum* var. *magnicapsulum* Croiatz & Hara (*A. Henry 117*, A) **B** holotype of *G. kusukusense* Hayata (*B. Hayata & S. Sasaki s.n.*, TI) **C** lectotype of *G. lanceolatum* Hayata (*T. Makino s.n.*, TI) **D** holotype of *G. chademenosocarpum* Hayata (*B. Hayata s.n.*, TI) **E** isotype of *G. rubrum* Blume (*C.L. von Blume s.n.*, NY) **F** isolectotype of *G. suishaense* Hayata (*B. Hayata s.n.*, TI).

Hayata, *G. kusukusense*, and *G. suishaense* Hayata] have long been treated as dubious taxa because relevant specimens, especially the types, were unavailable (Kanehira 1936; Keng 1955; Deng 1992; Deng and Wang 1993; Hsu et al. 2006). Although the latter three species were accepted in *Flora Reipublicae Popularis Sinicae* (Li 1994) and *Flora of China* (Li and Gilbert 2008), their morphological descriptions were merely derived from their protologues without further observations. Hsu et al. (2006) accepted the species *G. kusukusense* and synonymized the name *G. suishaense* under *G. rubrum*, but types of the two species were still not referred to in their study.

In our taxonomic study of the genus *Glochidion*, types of aforementioned enigmatic taxa were found in the herbaria A (*G. assamicum* var. *magnicapsulum*, Fig. 1A) and TI (*G. chademenosocarpum*, Fig. 1D; *G. kusukusense*, Fig. 1B; *G. suishaense*, Fig. 1F), and a collection of the genus from Lanyu island of Taiwan, China, was found to be very different from all of the other *Glochidion* species recorded from Taiwan and adjacent regions. Thus, a comprehensive taxonomic revision of *Glochidion* in Taiwan was conducted in this study.

Material and methods

Specimens of *Glochidion* deposited in the herbaria A, HAST, K, KUN, IBSC, LINN, MA, NAS, NCAI, NY, P, PE, PH, TAI and TI, were studied carefully in the present study. Field investigations of Taiwanese Phyllantheae species were also conducted from 2015 to 2019. Additionally, most materials of Taiwanese *Glochidion*, which were obtained by Dr. A. Kawakita from Kyoto University, Japan, in his recent field studies of the co-evolutionary system involving *Glochidion* plants and *Epicephala* moths (Kawakita et al. 2004; Kato and Kawakita 2017), were generously provided for the present study. Morphology of leaves, styles and capsules, as well as the number of ovaries and stamens, were all studied carefully. Herbarium abbreviations cited here are based on the Index Herbarium of Thiers (2013 continuously updated).

Results

In total, over 800 specimens were examined in the present study. Morphological studies based on the careful examination of herbarium specimens and extensive filed investigations revealed that eight species and three varieties of *Glochidion* should be recognized in Taiwan, China, viz. *G. acuminatum* var. *acuminatum*, *G. ellipticum* Wight, *G. lanceolatum*, *G. lanyuense* Gang Yao & S.X. Luo, *G. philippicum*, *G. puber*, *G. rubrum*, *G. zeylanicum* var. *zeylanicum*, *G. zeylanicum* var. *tomentosum* Trim., among which the species *G. lanyuense* is new to science. Additionally, the three names *G. chademenosocarpum*, *G. kusukusense* and *G. ovalifolium* should be reduced to the new synonyms of *G. rubrum*, *G. lanceolatum* and *G. ellipticum*, respectively. Because other species were morphologically described in detail by previous authors (e.g. Hsieh 1977; Deng and Wang 1993; Hsu et al. 2006; Li and Gilbert 2008), we only provide a morphological description for the new species *G. lanyuense*, but a key to all of the *Glochidion* species in Taiwan is presented.

Taxonomic treatment

1. *Glochidion acuminatum* Müll. Arg., Linnaea 32: 68. 1863

Figure 2A–C

Bradleia acuminata Wallich, Numer. List 7855. 1847, nom. nud. Basionym.

Type. Nepal. "Nepalia", *Wallich 7885* (lectotype: K-000246416, photo!, designated by Yao and Zhang 2015b).

var. *acuminatum*

Figure 2A–C

Glochidion hayatae Croiz. & Hara, in J. Jap. Bot. 16: 316. 1940. Type: China. Formosa (now Taiwan). Holisha, Giochi. 28 April 1916, *B. Hayata s.n.* (holotype: TI-01804, photo!).

Distribution and habitat. The typical variety *G. acuminatum* var. *acuminatum* is widely distributed from India, Nepal, through Indo-China Peninsula, to China and Japan. In China, it occurs widely from the southwestern area to Taiwan. It grows in evergreen broad-leaved forests, open forests, valleys, or near streams, usually from low altitude to 2600 m. The species is recorded from Ilan and Taipei Hsien, through Nantou and Taichung Hsien, to Kaosiung and Pingtung Hsien, in Taiwan.

Taxonomic discussion. Two taxa are described under the species *G. acuminatum*, the typical variety *G. acuminatum* var. *acuminatum* and the variety *G. acuminatum* var. *siamense* Airy Shaw. The species is represented in Taiwan by the typical variety, and another variety is distributed in Thailand and Yunnan province of China (Li and Gilbert 2008; Yao and Zhang 2015b). A detailed morphological comparison between the two taxa can be referenced in Yao and Zhang (2015b). The typical variety can be distinguished from all other Taiwanese *Glochidion* species by its small (5–7 mm in diameter) and deeply 6- or 8-grooved capsules (Figure 2C).

Representative specimens examined. China. Taiwan. Kaosiung Hsien, Shanping Station, at an elevation of 1000 m, 7 November 1991, *C.C. Wang 818* (HAST); Ilan Hsien, Fushan, at roadside, 26 April 1992, *S.L. Chen 927* (HAST); Nantou Hsien, at an elevation of 650 m, 5 October 2001, *C.M. Wang 04509* (IBSC, PE); Nantou Hsien, Yuchih Hsiang, Lienhuachih, 23°55'08"N, 120°52'41"E, at an elevation of 640 m, 24 April 1996, *C.N. Chen et al. 03316* (KUN); Nantou Hsien, Lienhuachi, 23°55'17"N, 120°54'20"E, 6 July 1936, *K. Mori 1527* (TAI); Nantou Hsien, Lienhuachi, 23°53'53"N, 120°52'58"E, 24 July 1955, *Y. Keng & Liu et al. s.n.* (TAI); Nantou Hsien, Jenai Hsiang, Hui-Sun Experimental Forest, 24°05'34"N, 121°01'27"E, at an elevation of 660 m, 5 October 2000, *C.M. Wang 04509* (IBSC, PE); Pingtung Hsien, Kueitsuchia, 21°57'56"N, 120°48'18"E, 1 January 1917, *E. Matuda 1177* (TAI); Taichung Hsien, forest margin, at an elevation of 900 m, 18 April 2003, *C.M. Wang 6609* (HAST); Taipei Hsien, Chutsuhu, 25°10'9"N, 121°31'54"E, 16 November 1969, *C.C. Hsu 6561* (TAI); Taipei Hsien, Neihu, Naihosyo, 25°4'32"N, 121°34'49"E, 21 July 1973, *C.M. Kuo 3640* (TAI); Taipei Hsien, Neihu, 25°05'0"N, 121°34'0"E, 16 October 1993, *S.Y. Lu 24147* (PE); Taipei Hsien, Sekitei, 24°59'21"N, 121°38'57"E, 6 July 1949, *K. Kao 1350* (TAI); Taipei Hsien, Wulai, Urai, 24°51'47"N, 121°32'34"E, 25 October 1929, *S. Suzuki 3268* (TAI).

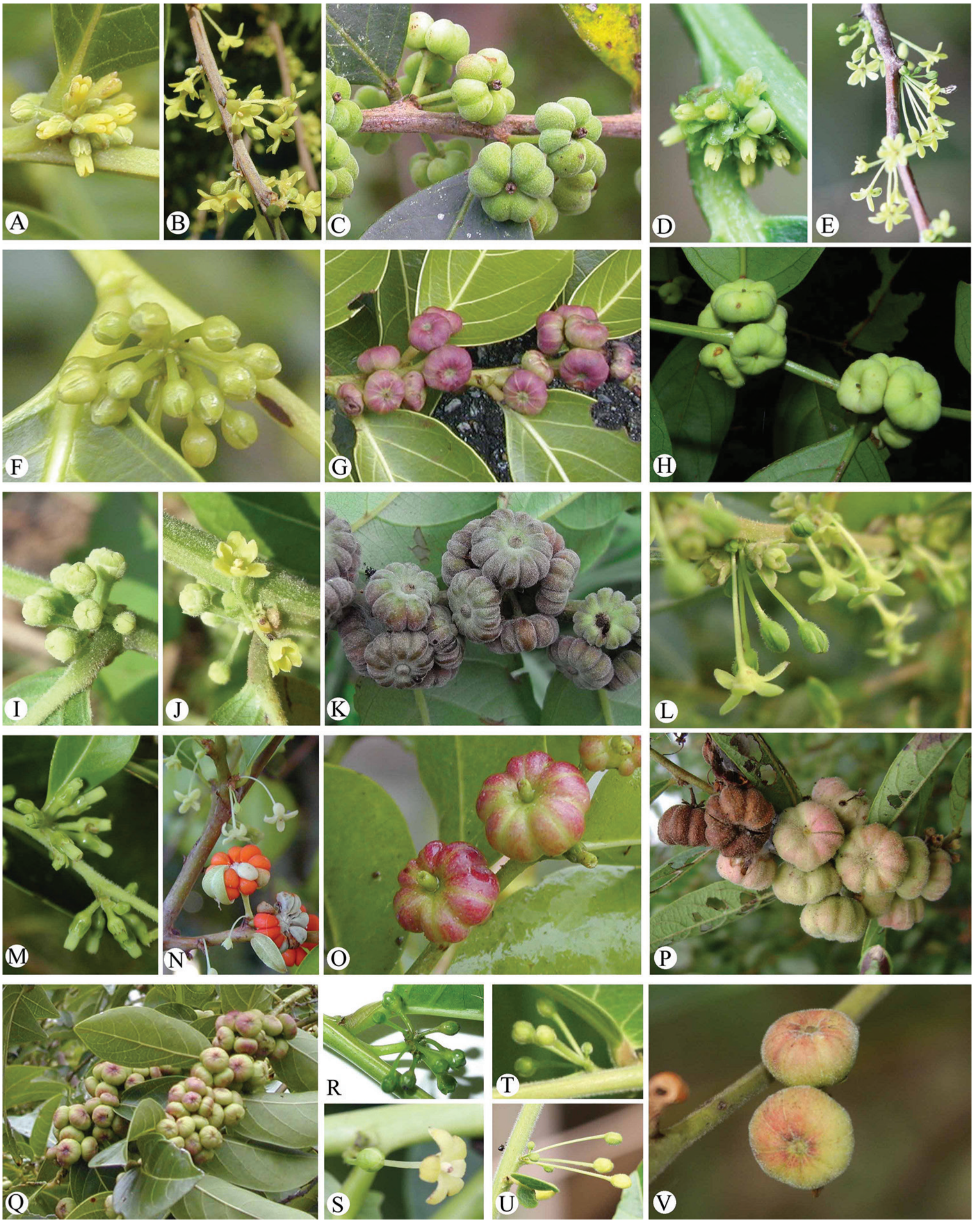

Figure 2. General morphology of *Glochidion* **A–C** *G. acuminatum* var. *acuminatum* Müll. Arg **D, E, H** *G. ellipticum* Wight **F, G** *G. lanceolatum* Hayata **I–K** *G. philippicum* (Cav.) C.B. Rob **L, P** *G. puberum* (L.) Hutch **M–O** *G. rubrum* Blume **Q–S** *G. zeylanicum* var. *zeylanicum* (Gaertn.) A. Juss **T–V** *G. zeylanicum* var. *tomentosum* Trimen **A, D, F, I, M, R, T** female flowers **B, E, J, S, U** male flowers **C, G, H, K, N–Q, V** fruits **L** female flowers and male flowers **N** male flowers and fruits. Photographs: **A–C, F, G, I–K, M–O, Q–U** by A. Kawakita (Kyoto University, Japan) **D–E, H, L, P** by G. Yao **V** Z.Q. Song.

2. ***Glochidion ellipticum*** Wight in Icon. Pl. Orient. 5: t. 1906. 1852

Figures 1A, 2D, E, H, 3

Phyllanthus assamicus Müll. Arg. in Flora 48: 378. 1865. *Glochidion assamicum* (Müll.-Arg.) Hook. f. in Fl. Brit. India 5(14): 319. 1887. Type: India, upper Assam, 1861, *J.D. Hooker* & *T. Thomson s.n.* [*Glochidion* 51] (lectotype: G -00324994, designated by Chakrabarty and Balakrishnan 2018); Remaining syntypes: India, Sikkim, 100 ft, 1861, *J.D. Hooker s.n.* [*Bradleia* 45] (CAL, herb. acc, no. 403548; G-00324992; NY-00263421); India, Assam, *Jenkins 530* (CAL).

Glochidion assamicum var. *magnicapsulum* Croiatz & Hara, in J. Jap. Bot. 16: 319. 1940. Type: China. Formosa (now Taiwan), September 1938, *A. Henry 117* (holotype: A!; isotype: NY) (Figure 1A).

Glochidion ovalifolium F.Y. Lu & Y.S. Hsu, in Quarterly J. For. Res. 25(4): 87. 2003. syn. nov. Type: China. Taiwan: Chiayi Hsien, Chungpu, 3 March 2002, *F.Y. Lu* & *Y.S. Hsu 242* (holotype: NCAI!, Figure 3; isotype: NCAI!).

Type. India, Malabar, *R. Wight* Kew Distrib. No. 2663 (lectotype: K-000246408, photo!, designated by Chakrabarty and Balakrishnan 2018; isolectotypes: CAL; L-0030051, photo!); Remaining syntype: India, Malabar, *R. Wight 2576* (K!, K00024606; S!, S08-1933).

Distribution and habitat. The species is widely distributed from northeastern India, Nepal, through Indo-China Peninsula, to China. In China, it occurs widely from the southwestern area to Taiwan. It usually occurs in evergreen broad-leaved forests, scrub on stream banks, roadsides, usually from low altitude to 1800 m. In Taiwan, the species is widely distributed from Keelung and Taoyuan, to Chiayi, Kaosiung, Nantou, Pingtung, Taichung and Tainan.

Taxonomic discussion. Croizat and Hara (1940) described the variety *G. assamicum* var. *magnicapsulum* from Taiwan, and considered that it differed from the typical variety *G. assamicum* var. *assamicum* by its large female flowers (ca. 2.5 mm in diameter) and the pubescent and large capsules (8–10 mm in diameter). However, this variety had long been treated as a dubious taxa, or even not referred to in latter taxonomic treatments since its publication (e.g. Keng 1955; Hsieh 1977; Deng and Wang 1993; Hsu et al. 2006), until it was reduced to be a synonym of *G. ellipticum* (*G. assamicum* was cited as one of its synonyms) in *Flora of China* (Li and Gilbert 2008). After observing the types and many non-type specimens of *G. ellipticum*, it was found that the species showed much variation in morphology, such as its leaves are elliptic, lanceolate, oblong or ovoid in shapes; ovary usually 3–4-locular, and rarely 5-locular; fruits subglabrous or sparsely pubescent, usually 6–8 mm in diameter, and sometimes could be up to 10 mm in diameter. So the treatment of Li and Gilbert (2008) is accepted and the distribution of *G. ellipticum* in Taiwan is confirmed here. More Taiwanese specimens of *G. ellipticum* were also found and examined in the present study.

Glochidion ovalifolium was described from Chiayi, Taiwan, China, and it was suggested to be similar to *G. lanceolatum* in morphology, but differs in having hairy ovaries and fruits (Lu and Hsu 2003). However, results from checking the types of *G. ovalifolium* (Figure 3) revealed that the species is actually conspecific with *G. ellipticum* (Figure 1A), which is very different from *G. lanceolatum* by its female flowers and fruits cluster in axillary (vs. usually pedunculated supra-axillary cymes), ovary and fruits sub-glabrous or sparsely pubescent (vs. glabrous), stamens 3 (vs. 4–6). The pedunculated supra-axillary cymes of *G. ovalifolium* as described in its protologue, and observed in its line drawing provided in Lu and Hsu (2003), are incongruous with its types (Figure 3). Hence, based on a careful study of its type and non-type specimens, *G. ovalifolium* is here reduced to a new synonym of *G. ellipticum*.

Representative specimens examined. China. Taiwan. Chiayi Hsien, Meishan Hsiang, Juifeng Bridge-Juili, 23°33'N, 120°39'E, at an elevation of 600 m, 25 August 2001, *C.M. Wang 05251* (IBSC); Zhuqi Hsiang, 5 October 2014, *H.Y. Chen 011* (NCAI); Kaosiung Hsien, Maoning Hsiang, at an elevation of 800 m, 27 January 1989, *J.C. Wang 5177* (HAST); Kaosiung Hsien, Liouhguei, roadside, at an elevation of 250–350 m, 5 May 1991, *M.J. Deng & S.L. Chen 463* (HAST); Keelung Hsien, Denryoko, 25°8'2"N, 121°44'26"E, May 1931, *Y. Yamamoto s.n.* (TAI); Nantou Hsien, Chingshuikou, 23°47'16"N, 120°46'55"E, 16 February 1959, *K.K. Huang 839* (PH); Nantou Hsien, Lienhuachih-Yuchih, 24 July 1955, *H. Keng* & *K. Liu s.n.* (PH); Nantou Hsien, 11 May 1991, *Y.S. Hsu* & *J.C. Liaw 198*, *199*, *201*, *202*, *203*, *204*, *207*, *208*, *209* (NCAI); Pingtung Hsien, at an elevation of 1427 m, 8 February 2015, *Y.J. Lin 021* (NCAI); Taichung Hsien, 25 July 1955, *H. Keng, Liu & Kao s.n.* (PH); Tainan Hsien, Kuantzuling, 23°20'32"N, 120°29'33"E, 3 May 1943, *Senben 390* (TAI); Taoyuan, 9 September 1990, *Y.S. Hsu* & *J.C. Liaw 70* & *71* (NCAI).

3. *Glochidion lanceolatum* Hayata in J. Coll. Sci. Univ. Tokyo 20: 16. 1904

Figures 1B, C, 2F, G, 5A, C, E, G, I, L

Glochidion kotoense Hayata in Icon. Pl. Form. 9: 96. 1920. Type: China. Formosa (now Taiwan), Kôtôshô, *Anonymous s.n.* (holotype: TI-01807, photo!).

Glochidion sphaerostigmum Hayata in Icon. Pl. Form. 9: 96. 1920. Type: China. Formosa (now Taiwan), Suisha, *Anonymous s.n.* (holotype: TI-01817, photo!).

Glochidion kusukusense Hayata in Icon. Pl. Formos. 9: 96. 1920. syn. nov. Type: China. Formosa (now Taiwan), Kusukusu, July 1912, *B. Hayata* & *S. Sasaki s.n.* (holotype: TI-01808, photo!, Figure 1B).

Type. China. Formosa (now Taiwan), Kelung, 31 October 1896, *T. Makino s.n.* (lectotype: TI-01810, photo!, Figure 1C; here designated); Remaining syntype: Taiwan, Kelung, 1 November 1896, *C. Owatari s.n.* (TI-01811, photo!).

Distribution and habitat. *Glochidion lanceolatum* is distributed in China (only in Taiwan) and south Japan, and also recorded from the Philippines (Govaerts et al.

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A133
Fam.: Euphorbiaceae (大戟科) Field no.: 242
Scientific Name: Glochidon ovalifolium Lu et Hsu (卵葉饅頭果)
Coll.: Y. S. Hsu 許媖素 Local.: 嘉義中埔 天望崎
Det.: Y. S. Hsu 許媖素 Date: Mar. 3 2002
Note:

Figure 3. Holotype of *Glochidion ovalifolium* F.Y. Lu & Y.S. Hsu. (*F.Y. Lu* & *Y.S. Hsu 242*, NCAI!).

2019). It usually occurs in open forests, roadsides, and at low altitudes. The species is widely distributed from northern to southern Taiwan.

Taxonomic discussion. The morphological description of *G. kusukusense* provided by Hayata (1920) is brief and short, and it is in accordance with its type that has only a short branch and several leaves (Figure 1B). In the protologue, *G. kusukusense* was compared morphologically with *G. wrightii* Benth, a species widely distributed in southern and southwestern China. After observing the type of *G. kusukusense* deposited in herbarium TI (Figure 1B), we found that its glabrous habit and lanceolate leaves were identical to that of the species *G. lanceolatum* (Figure 1C), which is widely distributed in Taiwan. Thus, we considered that *G. kusukusense* is conspecific with *G. lanceolatum* (Figure 1C) and reduced it to be a new synonym of the latter.

In Hsu et al. (2006) study, some specimens collected from Nantou and Taoyuan of Taiwan (out of the type locality of *G. kusukusense*) cannot be identified as *Glochidion* species usually known to Taiwan, while their lanceolate leaves and glabrous pedicel of male flowers observed seemed to be consistent with the diagnostic traits of *G. kusukusense*, when compared with another dubious species *G. chademenosocarpum* also described in Taiwan, as suggested by Li (1994) based on the protologues of the two species. Thus the distribution of *G. kusukusense* in Taiwan was accepted by Hsu et al. (2006), although the type of the species was unavailable in their study. However, the detailed morphological description and line drawing of *G. kusukusense* provided in Hsu et al. (2006) are very different from the type of the species but well identical with *G. ellipticum*, a species distributed in Taiwan but omitted in most literature of Taiwanese *Glochidion*, including Hsu et al. (2006). The result from rechecking the specimens cited as *G. kusukusense* in Hsu et al. (2006) further confirmed our conclusion. More specimens of *G. ellipticum* collected from Chiayi, Kaosiung, Keelung, Pingtung, Nantou, Taichung and Tainan of Taiwan were also found and studied in the current study (see 'Representative specimens examined' under the species *G. ellipticum*).

Morphologically, the species *G. lanceolatum* is similar to the typical variety of *G. zeylanicum*, but differs by its smaller leaves (6–13 × 2.5–4 cm), ovaries 4–6-locular, and capsules 6–7 mm in diameter (Figure 2G). In contrast, *G. zeylanicum* var. *zeylanicum* has larger leaves (8.5–23.5 × 5–9 cm), ovaries 6–8-locular, and capsules 8–12 mm in diameter (Figure 2Q). Additionally, as revealed in previous studies, pollen morphology of the two taxa also showed differences in terms of pollen size and aperture system (Deng 1992; Yao and Zhang 2016). Pollen grains of *G. lanceolatum* are smaller in size [polar axis (P) = 17.25 μm, equatorial axis (E) = 15.47 μm] and showed a 3–4-colporate aperture pattern (Yao and Zhang 2016). In contrast, pollen grains of *G. zeylanicum* var. *zeylanicum* are larger in size (P = 22.28 μm, E = 19.49μm) and showed a 4-colporate aperture pattern (Yao and Zhang 2016).

Representative specimens examined. China. Taiwan. Hsinchu Hsien, Peipu, 24°42'0"N, 121°3'5"E, 12 January 1908, *U. Mori s.n.* (TAI); Hualien Hsien, Tungmen, Wunlan, at an elevation of 180–250 m, 23 November 1982, *Y. Tateishi 16250* (HAST); Keelung, 25°7'43"N, 121°44'9"E, 8 September 1928, *S. Sasaki s.n.* (TAI); Kaohsiung, Shoushan, al. 400 m, 16 October 1985, *S.Y. Lu 17379* (HAST); Keelung, Ensorei, 25°7'32"N, 121°45'56"E, 14 April 1929, *S. Suzuki s.n.* (TAI); Keelung, Hopingtao, 25°9'33"N, 121°45'5"E, 8 December 1963, *C.C. Chuang & M.T. Kao 5541* (PH, TAI); Ilan Hsien, Lotung, 24°40'58"N, 121°47'13"E, 13 November 1932, *S. Suziki 12348* (TAI); Ilan Hsien, Suao, 24°35'34"N, 121°50'38"E, *Y.M. Hsu 113* (TAI); Ilan Hsien, Lungtanhu, along the paved road surrounding the lake, at an elevation of

100 m, 23 January 1997, *S.M. Liu 556* (HAST); Ilan Hsien, Toucheng Town, TaHSI, Taoyuanku trail, at an elevation of 50 m, 16 November 2000, *J.J. Chen 539* (HAST); Miaoli Hsien, Zhuolan, at an elevation of 0–300 m, 10 July 2001, *C.M. Wang 5060* (IBSC); Pingtung Hsien, Manchou Hsiang, Chunhsing Bridge-Chiatulu, 22°01'17"N, 120°48'29"E, at an elevation of 60–100, on broadleaf forest, 11 April 1998, *C.M. Wang et al. 03069* (PE); Pingtung Hsien, Peiyeh-Shanpaiwan, 22°42'6"N, 120°38'31"E, 25 December 1930, *S. Suzuki 6798* (TAI); Pingtung Hsien, Shihtzu Hsiang, Shouchia-Mutan, 22°14'46"N, 120°49'49"E, at an elevation of 420 m, roadside, 26 March 1999, *C.M. Wang 03936* (PE); Taipei, Muchihshan, 25°1'15"N, 121°35'3"E, 12 April 1985, *S.F. Huang 2780* (TAI); Taipei, Peitou, 25°7'42"N, 121°29'42"E, 13 December 1931, *T. Suzuki 5904* (TAI); Taipei, Tatungshan, 25°10'22"N, 121°31'33"E, 30 December 1929, *Y. Simada 1743C* (TAI); Taipei, Wantan, 24°56'39"N, 121°31'49"E, 21 March 1949, *H. Keng 1008* (TAI); Taipei, Chungho Shih: Yuan-Tung-Ssu, at an elevation of 50 m, 6 October 1989, *C.H. Lin 258* (HAST); Taipei, Linkou Hsien, Hou-hu, roadside, at an elevation of 100–200 m, 23 September 2000, *C.L. Huang & H.M. Chang 134* (HAST); Taitung Hsien, Hungtou river, Lanyu, 22°1'49"N, 121°33'13"E, *T. Hosokawa 8048* (TAI); Taitung Hsien, Lanyu Hsiang, Bridge Chungaichiao, roadside, 4 December 1996, *T.Y.A. Yang et al. 07749* (KUN); Taitung Hsien, Lanyu Hsiang, Langtao, Pond Hsiaotienchih, at an elevation of 180 m, roadside, 18 December 1997, *T.Y.A. Yang et al. 09881* (IBSC); Taitung Hsien, Lanyu Hsiang, Langtao, Pond Hsiaotienchih, at an elevation of 150–180 m, 9 July 1997, *T.Y.A. Yang et al. 08598* (IBSC); Taitung, Lanyu, Orchid Is., 22°3'23"N, 121°30'52"E, *T.C Huang et al. 10552* (TAI).

4. *Glochidion lanyuense* Gang Yao & S.X. Luo, sp. nov.

urn:lsid:ipni.org:names:77211389-1

Figures 4, 5B, D, F, H, J, K, M

Diagnosis. The species is morphologically similar to *G. lanceolatum*, but differs by its female flowers usually solitary or rarely two in axillary, pedicel of female flowers and ovaries usually densely strigose, styles ovoid column and strigose at base, and fruits ca. 10 mm in diameter.

Type. China. Taiwan, Taitung Hien, Lanyu Hsiang, Hongtoucun, on roadsides of broadleaf forest, 22°01'00"N, 121°33'27"E, at an elevation of 1–10 m, 16 September 1998, *C.M. Wang 03521* (holotype: IBSC-0330741!).

Description. Shrubs or treelets, monoecious; branchlets pubescent. Leaf blade oblong ovate, or elliptic, 6–10 × 3–4.5 cm, papery, slightly leathery, with apex acuminate or acute, and base broadly cuneate or rounded, glabrous in both surface; lateral veins 6–7 pairs, prominent beneath. Petiole 4–7 mm long, glabrous. Stipules broadly triangular, 1–1.5 mm long. Flowers in axillary solitarily or two. Male flowers: pedicles ca. 5 mm long, glabrous; sepals 6, oblong or ovate, biseriate, glabrous; stamens 3, 1–1.2 mm long. Female flowers: pedicles ca. 1 mm long, usually densely strigose; sepals 6, ovoid-triangular or ovate, biseriate, sparsely tomentose; ovary depressed globose, 5–6-locular, densely strigose; style connate into a cylindrical column, ca. 0.5 mm

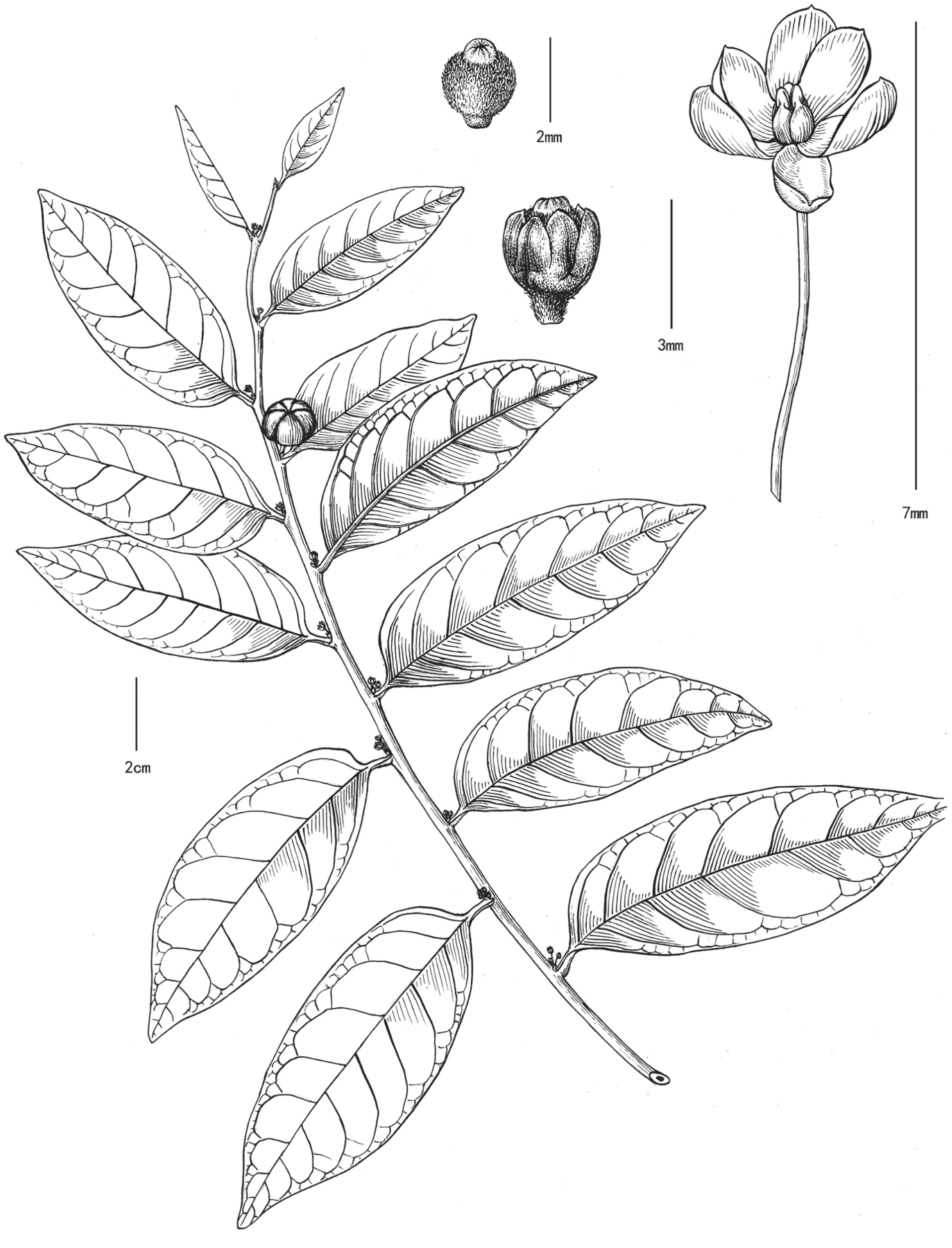

Figure 4. *Glochidion lanyuense* Gang Yao & S.X. Luo, sp. nov. (based on the holotype, drawn by Y.X. Liu) **A** habit **B** ovary and style **C** female flower **D** male flower.

long, truncate at apex, densely strigose at base, 5–6-lobed apex, and then shallowly 2-lobed for each lobes. Capsules depressed globose, ca. 10 mm in diameter, sub-glabrous, 5–6-grooved.

Distribution and habitat. The species is known only from its type locality, Lanyu island of Taiwan, China. It grows on roadsides of broadleaf forest at low altitude.

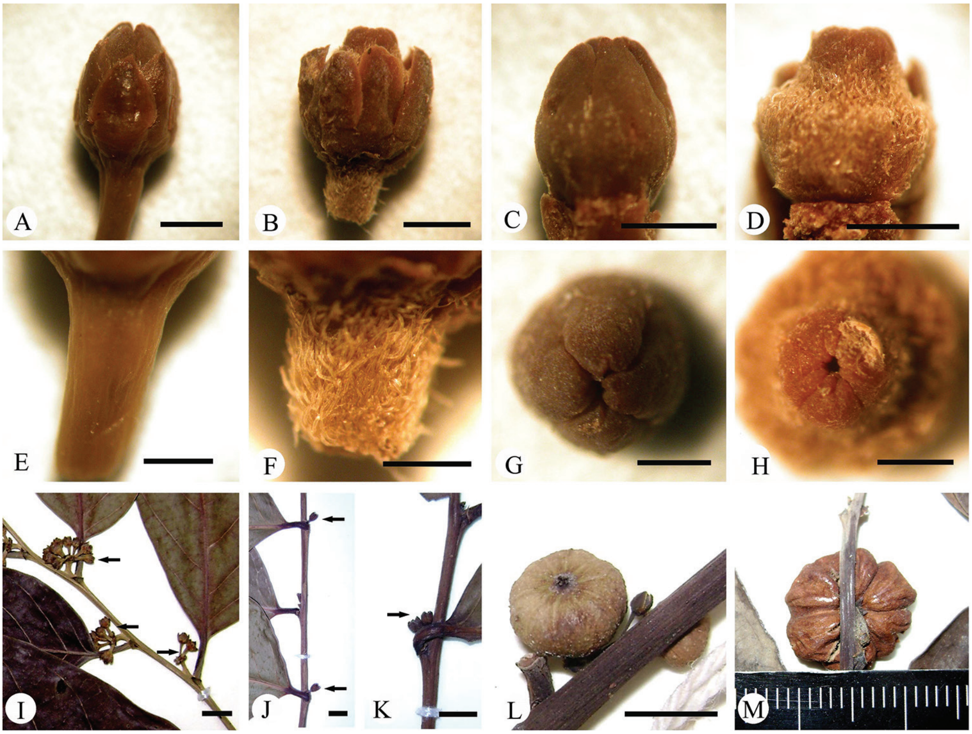

Figure 5. Morphological comparison between *Glochidion lanyuense* Gang Yao & S.X. Luo and *G. lanceolatum* Hayata **A, C, E, G, I, L** *G. lanyuense* **B, D, F, H, J, K, M** *G. lanceolatum* **A, B** female flower **C, D** ovary and style **E, F** pedicle of female flower **G, H** general view of style **I–K** female flowers (shown by arrowheads) **L, M** fruit. Scar bars: 1 mm (**A–H**); 3 mm (**I–K**); 5 mm (**L**).

Etymology. *Glochidion lanyuense* is named after its type locality, Lanyu island of Taiwan.

Taxonomic discussion. *Glochidion lanyuense* is quite different from all of the other *Glochidion* species recorded from China, Japan, and the Philippines by its special characters of female flowers. It is similar to *G. lanceolatum* in habit, but differs (Table 1) in its female flowers which are usually solitary or rarely two in axillary (Figure 5J, K), pedicel of female flowers and ovaries are usually densely strigose (Figure 5B, D, F), style connate into a short cylindrical column (Figure 5D, H), stamens 3, capsules ca. 10 mm in diameter and 5–6-grooved (Figure 5M). In contrast, the species *G. lanceolatum* has multiple female flowers (usually 6–15) in supra-axillary cymes (Figures 2F, 5I) or rarely axillary, pedicel of female flowers and ovaries are glabrous (Figure 5A, C, E), styles sub-conical Figure 5C, G), stamens 4–6, fruits 6–7 mm in diameter and shallowly 4- or 6-grooved or obscurely grooved (Figures 2G, 5L). Additionally, as revealed in our previous palynological study (Yao and Zhang 2016), pollen grains of *G. lanyuense* (recorded as *Glochidion sp.3* in Yao and Zhang 2016) were much larger in size (P = 21.01 μm, E = 21.12 μm), 4-colporate in aperture system, and rugulate in exine ornamentation. While pollen grains of *G. lanceolatum* were smaller in size

Table 1. Morphological comparison between *Glochidion lanceolatum* Hayata and *G. lanyuense* Gang Yao & S.X. Luo.

Traits	*Glochidion lanceolatum*	*Glochidion lanyuense*
Female flower	6–15 female flowers usually in supra-axillary cymes or rarely axillary	Solitary or rarely two in axillary
Pedicel of female flower	Glabrous	Densely strigose
Ovary	Glabrous, or rarely pubescent	Densely strigose
Style	Sub-conical	Short cylindric column
Stamen	4–6	3
Fruit	Glabrous, 6–7 mm in diameter, usually grooved obscurely or shallowly 4–6-grooved	Sub-glabrous, ca. 10 mm in diameter, 5–6-grooved

(P = 17.25 µm, E = 15.47 µm), 3–4-colporate, and regular reticulate in exine ornamentation, all of these characters are also consistent with the observation of Deng (1992). The rugulate ornamentation observed in pollen grains of the new species seems to be very different from those of other Taiwanese *Glochidion* species observed previously (Deng 1992; Yao and Zhang 2016).

5. *Glochidion philippicum* (Cav.) C.B. Rob., in Philipp. J. Sci. Bot. 4: 103. 1909
Figure 2I–K

Glochidion formosanum Hayata, in J. Coll. Sci. Univ. Tokyo 20: 20. tab. 2G. 1904. Type: China. Formosa (now Taiwan), Tai-tong-thian, Pi-Iam, 23 December 1899, *K. Miyake s.n.*, (holotype: TI-01802, photo!).
Bradleia philippica Cav., in Icon. 3: 48. tab. 371. 1797. Basionym.

Type. Philippines, *L. Née s.n.* (lectotype: MA-475455, photo!, designated by Yao et al. 2017; isolectotype: MA-475454, photo!).

Distribution and habitat. *Glochidion philippicum* is distributed in China (only in Taiwan), Malaysia, and the Philippines. The species usually occurs beside a gravelly road, forest margins, and roadsides, at low and medium altitudes. In Taiwan, the species is widely distributed from Ilan, Taichung, Changhua and Chiayi, to Hualian, Kaohsiung, Pingtung, Tainan and Taitung.

Taxonomic discussion. *Glochidion philippicum* differs from all other *Glochidion* species in Taiwan by its sub-hemispherical or sub-conical styles (Figure 2I), capsules that are deeply 10–16-grooved, and persistent sub-hemispheric styles (Figure 2K).

Representative specimens examined. China. Taiwan. Changhua, 30 November 1991, *M.J. Deng 751* (HAST); Changhua, Pakuashan, at an elevation of 50–200 m, 7 April 1991, *S.L. Chen 382* (HAST); Chiayi, Chungpu, 23°25'6"N, 120°30'57"E, December 1934, *K. Mori 2339* (TAI); Chiayi, Chuchi District, Kuanghua Village: Chiehtung, at an elevation of 600–800 m, 26 October 1985, *C.I. Peng 8762* (HAST); Hualian Hsien, Chuolu, at an elevation of 250 m, 17 November 1982, *Y. Tateishi & J. Murata 15540* (IBSC); Hualien, Sanmin, 23°26'51"N, 121°24'25"E, 15 December 1939, *Suzuki-Tokio 19781* (TAI); Hualien Hsien, Wanjung District, Hungyeh Village, Hungyeh Hot Spring, at an elevation of ca. 200–400 m, 3 July 1988, *C.I. Peng et al. 11618* (PE); Hualian Hsien, Zuepei, at an elevation of 250 m, 18 November 1982, *Y. Tateishi & J. Murata 15583* (IBSC); Ilan Hsien, Lotung, at an elevation of 10–20 m, 10 February 1992, *S.L. Chen 807* (HAST); Kaohsiung, 22°37'39"N, 120°16'55"E, 7 August 1938, *Tsuchiya 27* (TAI); Kaohsiung, Chaishan, broadleaf forest on mountain slope, at an elevation of 100 m, 24 June 1999, *K.F. Chung 1389* (HAST); Pingtung Hsien, Hengchun Town, Kengting Park, 21°58'12"N, 120°48'27"E, at an elevation of 300 m, 15 July 1997, *C.M. Wang & H.M. Lin 02675* (IBSC, PE); Pingtung Hsien, Kentin, at an elevation of 300 m, 16 August 1969, *Y. Ando et al. 601* (KUN); Pingtung, Kenting, 21°57'6"N, 120°47'26"E, 26 September 1966, *C.C. Chuang & M.T. Kao 3946* (TAI); Pingtung, Oluanpi, South Cape, 21°54'9"N, 120°50'45"E, 30 December 1928, *Y. Kudo & S. Suzuki 15811* (TAI); Pingtung Hsien, Mt. Nanjen-shan, at an elevation of 450 m, 3 November 1982, *H. Ohashi & Y. Tateishi 13495* (IBSC); Pingtung Hsien, Mutan Hsiang, Kaoshih-Kaoshihfo, 22°07'39"N, 120°49'35"E, at an elevation of 200–300 m, beside a gravelly road, 5 September 1998, *C.M. Wang 03487* (IBSC, PE); Pingtung, Sheting Nature Park, 21°57'20"N, 120°48'32"E, 22 November 1984, *J.C. Wang 2656* (TAI); Pingtung Hsien, Wutai Hsiang, on the way from Haocha to Old Haocha, 22°42'37"N, 120°41'31"E, at an elevation of 250–430 m, roadside, 19 July 1995, *T.Y. Liu et al. 771* (IBSC, PE); Taichung, Fungyuan, secondary forest, roadside, at an elevation of 300–350 m, 18 July 1991, *M.J. Deng 609* (HAST); Tainan, Chentoushan, 23°19'50"N, 120°30'2"E, 20 June 1937, *Mori 2329* (TAI); Tainan, Mado, 23°10'38"N, 120°13'36"E, 10 August 1988, *S.F. Huang & T.C. Huang 13740* (TAI); Tainan, Nanhsi Hsiang, along a paved road to Hsienkungmiao, at an elevation of 300–500 m, 16 October 2002, *P.J. Lin 74* (HAST); Taitung Hsien, Chihen Hot Spring, 22°41'46"N, 120°59'49"E, 1967, *C.C. Hsu & M.T. Kao 3382* (TAI); Taitung, Kannatolo, 22°51'38"N, 121°7'0"E, 28 July 1937, *Y. Yamamoto & K. Mori s.n.* (TAI).

6. *Glochidion puber* (L.) Hutch., in Sarg. Pl. Wilson. 2: 518. 1916 [as *G. puberum*]

Figure 2L, P

Agyneia pubera L., Mant. 2: 296. 1771. Basionym.

Type. China. *Anon s.n.* (holotype: LINN, sheet no. LINN-1145.2, photo!).

Distribution and habitat. *Glochidion puber* is widely distributed in China and also recorded in Kyushu of Japan. It occurs usually on slopes, or in scrub on stream banks, forest margins, roadsides, at altitudes between 100 and 2200 m. In Taiwan, the species is distributed from Miaoli, to Changhua, Nantou and Taichung.

Taxonomic discussion. The species differs from all other *Glochidion* species in Taiwan by its annular styles (Figure 2L), and the persistent annular styles on capsules which are not, or only slightly, elevated (Figure 2P).

Representative specimens examined. China. Taiwan. Detailed locality unknown, 23 October 1929, *Anonymous s.n.* (PE-00961458); Detailed locality unknown, 24 October 1929, *Anonymous s.n.* (IBSC-0314244); Changhua Hsien, Puhsin, 13 October

1988, *S.M. Chaw 742* (HAST); Miaoli Hsien, Cholan Town, the First Cemetery, at an elevation of 450 m, 1 November 2008, *P.F. Lu 17251* (HAST); Nantou Hsien, Chungming, 23°52'50"N, 120°54'42"E, 23 September 1929, *K. Sasaki 15713* (TAI); Nantou Hsien, Sun Moon Lake, 23°50'26"N, 120°55'26"E, 20 September 1929, *K. Sasaki 15509* (TAI); Nantou Hsien, Yuechih-Sunmoonlake, 23°52'35"N, 120°55'5"E, 23 October 1930, *S. Suzuki 6513* (TAI); Nantou Hsien, 8 June 1991, *Y.S. Hsu* & *J.C. Liaw 222* (NCAI); Nantou Hsien, 24 August 1991, *Y.S. Hsu* & *J.C. Liaw 250*, *251*, *252*, 253, *255*, *256*, *258 & 259* (NCAI); Nantou Hsien, Yuchi Hsiang, Sun-moonlake, at an elevation of 700 m, 2 November 2007, *P.F. Lu 14821* (HAST); Taichung Hsien, 27 April 1991, *Y.S. Hsu* & *J.C. Liaw 185* (NCAI); Taichung Hsien, 2 November 1933, *Suzuki-Tokio 10796* (NAS); Taichung, Shihpikeng, 24°18'6"N, 120°46'26"E, 15 December 1922, *S. Suzuki s.n.* (TAI); Taichung, Fengyuan, secondary forest, roadside, at an elevation of 350–450 m, 18 July 1991, *M.J. Deng 605* (HAST).

7. *Glochidion rubrum* Blume in Bijdr. Fl. Nederl. Ind. 586. 1825

Figures 1D–F, 2M–O

Glochidion chademenosocarpum Hayata in Icon. Pl. Formos. 9: 94. 1920. syn. nov. Type: China. Formosa (now Taiwan), Inter Onô et Kôsenpo, October 1917, *B. Hayata s.n.* (holotype: TI-01801, photo!, Figure 1D).

Glochidion fortunei Hance var. *longistylum* H. Keng in Journ. Acard. Washington Sci. 41(6): 200. 1951. Type: China. Taiwan, Kaohsiung, 14 August 1937, *Yamomoto & Mori 790* (holotype: TAI, photo!).

Glochidion fortunei Hance var. *megacarpum* H. Keng in Journ Acad. Washington Sci. 41(6): 200. 1951. Type: China. Taiwan, Kaoshiung, 8 April 1929, *Kudo* & *Suzuki 96* (holotype: TAI).

Glochidion suishaense Hayata in Icon. Pl. Formos. 9: 97. 1920. Type: China. Formosa (now Taiwan), Suisha, 29 Apr. 1916, *B. Hayata s.n.* (lectotype: TI-01820, photo!, here designated; isolectotype: TI-01821, photo! Figure 1F); Remaining syntype: Taiwan, *B. Hayata s.n.* (TI-01823 & TI-01824, photos!).

Type. Indonesia, Java, *C.L. von Blume s.n.* (holotype: not traced; isotypes: CAL; NY-00263451, photo!, Figure 1E).

Distribution and habitat. *Glochidion rubrum* is recorded widely from India to Cambodia, China, south Japan, Malaysia, Indonesia, Philippines and Vietnam. In China, it occurs in Anhui, Fujian, Guangdong, Hainan, Hong Kong, Taiwan and Zhenjiang. It grows in broad-leaved evergreen forests, roadsides from low altitude to 1800 m. The species is widely distributed from northern to southern Taiwan.

Taxonomic discussion. Hayata (1920) described *G. chademenosocarpum* based on one of his collections (*B. Hayata s.n.*, TI, photo!; Figure 1D) from Taiwan, and he suggested that the species differed from *G. rubrum* (recorded as *G. fortunei* in his study) by its much more densely clustered and sessile female flowers. After checking the protologue and observing the type of *G. chademenosocarpum* (Figure 1D), it was concluded that the species is well conspecific with *G. rubrum* (Figure 1E) and should be treated as a new synonym of the latter. Based on morphological description (Hayata 1920) as well as our observation of the type, we found that the type of *G. chademenosocarpum* might represent an unripe flower branch of *G. rubrum* because the morphology of branch, leaves, ovaries and styles observed are all identical with those of *G. rubrum*, except the ovaries and styles are smaller in size compared with those of the ripe female flowers described by Hsu et al. (2006) as well as those observed in living plants. Additionally, most male flowers observed from the type of *G. chademenosocarpum* also seem to be unripe because sepals of most male flowers were unopen (Figure 1D).

The taxonomic history of *G. suishaense* was similar to that of *G. chademenosocarpum* and *G. kusukusense*, except Hsu et al. (2006) treated it as a synonym of *G. rubrum* based on its protologue. In the present study, the result from observing the type of *G. suishaense* (Figure 1F) further confirmed its taxonomic status.

Morphologically, *G. rubrum* could be distinguished from all other Taiwanese *Glochidion* species by its styles which are cylindrical in shape and 1–3 mm in length (Figure 2M).

Representative specimens examined. China. Taiwan. Chiayi, at an elevation of 700–1300 m, 1 November 1985, *C.I. Peng 8789* (HAST); Hsinchu, Senkyakuseki, 25 June 1927, Y. Simada 4147 (HAST); Hsinchu, Lienhuassu, at an elevation of 50–100 m, 30 August 1996, *K.C. Yang 4908* (HAST); Hualien Hsien, Yueh-wang-ting to Yen-hai logging tract, 3 April 1991, *J.C. Wang et al. 6757* (HAST); Hualien Hsien, Hsiulin Hsiang, Hoping Forest Road, 24°18'26"N, 121°41'57"E, at an elevation of ca. 875 m, 22 August 1996, *S.M. Liu et al. 362* (PE); Ilan Hsien, Mohen, 24°26'54"N, 121°37'30"E, 30 September 1930, *S. Suzuki 6097* (TAI); Ilan Hsien, Nanao Hsiang, on the way from hiking entrance to Machialanshan, at an elevation of 270 m, 13 January 1994, *Y.R. Lin 294* (HAST); Ilan Hsien, Nanaonanhsi, at an elevation of 440 m, 16 August 1995, *T.Y. Liu 817* (HAST); Kaosiung Hsien, Taoyuan Hsiang, southern Cross-Island Hwy near Likuan, broadleaf forest, 23°16'57"N, 120°52'24"E, at an elevation of ca. 1800 m, 1 April 1995, *T.Y. Liu et al. 509* (IBSC); Nantou Hsien, Chen-you-lan-chi, at an elevation of 1650 m, 7 May 1988, *W.H. Hu 663* (IBSC); Pingtung, Kaoshih, 22°7'54"N, 120°50'42"E, 1 January 1929, *S. Suzuki 16046* (TAI); Pingtung Hsien, Mutan Hsiang, Gaushr-Mutan, 22°08'22"N, 120°49'49"E, at an elevation of 250 m, roadside, 26 March 1999, *C.M. Wang 03970* (IBSC, PE); Pingtung Hsien, Mutan Hsiang, Mutan-Hsushai, 22°11'13"N, 120°51'17"E, on roadside, 12 April 1998, *C.M. Wang et al. 03099* (IBSC); Pingtung Hsian, Shihtzu Hsiang, on the way from Neiwen to Shouka, along Hsien road 199, broadleaf forest, 22°13'57"N, 120°51'58"E, at an elevation of ca. 390 m, 6 December 1995, *S.M. Liu et al. 140* (PE); Pingtung Hsien, Tahanshan, 22°24'N, 120°46'E, at an elevation of 600 m, 20 September 1996, *T.T. Chen 7883* (PE); Taichung Hsien, Hoping Hsiang, on Hsuehshan forest, at road mileage sign 23.7 km, 24°14'57"N, 120°55'30"E, at an elevation of 1600 m, 5 May 1999, *S.H. Wu 1277* (KUN); Taichung Hsien, Hoping Hsiang, at an elevation of ca. 1100 m, 29 May 1999, *C.H. Chen et al. 2737* (HAST); Tainan, Lungtien, 23°12'5"N, 120°16'33"E, 17 May 1942, *Senbenlin 303* (TAI); Taipei Hsien, Nankang, local hills up the Hu-Shih Park, at an elevation of ca. 50–100 m, 14 April 1991, *C.I. Peng et al. 13898* (PE); Taipei, Peitou, 25°7'42"N, 121°29'42"E, 5 May 1935, *H. Shimada 360* (TAI); Taipei Hsien, Yangmingshan National Park, Tatunshan, 25°22'00"N, 121°31'31"E, at an elevation of ca. 825–840 m, on exposed trail, 10 November 1994, *H.Y. Shen et al. 275* (KUN); Taitung Hsien, Lanyu Hsiang, Hsiangtienchih, 22°04'50"N, 121°30'05"E, at an elevation of 180 m, semi-shaded, 28 April 1997, *S.T. Chiu & J.N. Chen 04099* (IBSC); Taitung Hsien, Lanyu Hsiang, Langtao, Pond Hsiaotienchih, at an elevation of 150–180 m, 9 July 1997, *T.Y.A. Yang et al. 08597* (IBSC); Taitung Hsien, Lutao Hsiang, along the paved road from Nanliao to Huoshaoshan, at an elevation of 100 m, 9 October 2001, *Y.Y. Huang 753* (PE); Taoyuan Hsien, Fuhsiang Hsiang, Litungshanchuang-Shankuang, 24°40'47"N, 121°20'23"E, at an elevation of 960 m, on roadside of broadleaf forest, 4 January 1996, *C.M. Wang & H.M. Lin 01953* (IBSC); Taoyuan Hsien, Nankan, 24°59'17"N, 121°18'22"E, 5 May 1929, *Y. Yamamoto s.n.* (TAI).

8. *Glochidion zeylanicum* (Gaertn.) A. Juss., in Tent. Euphor. 107. 1824

Bradleia zeylanica Gaertn., in Fruct. 2: 128. 1791.Basionym.

Type. Gaertner, Fruct. Sem. Pl. 2: t. 109.1791 (lectotype designated by Chakrabarty and Gangopadhyay 1995).

a. var. *zeylanicum*

Figure 2Q–S

Distribution and habitat. The typical variety *G. zeylanicum* var. *zeylanicum* is widely distributed from India, Sri Lanka, through Myanmar, Thailand, Vietnam, to China, south Japan, Indonesia, and the Pacific islands. In China, it occurs widely from the southwest of the mainland to Taiwan island. It usually grows in sparse forests, margins of woods, humid valleys, scrub on stream banks, roadsides, and at low and medium altitudes. In Taiwan, the variety is widely distributed from Hsinchu, Ilan, Taoyuan and Taipei, to Nantou, Taichung and Pingtung.

Taxonomic discussion. The typical variety *G. zeylanicum* var. *zeylanicum* is similar to *G. lanceolatum* in habit, and morphological differences between them have been discussed under the latter species.

Representative specimens examined. China. Taiwan. Hsinchu Hsien, Kuanhsi, at an elevation of 200 m, 24 September 1985, *S.Y. Lu 17142* (HAST); ILan Hsien, Chiaohsi Hsiang, Lungtanhu, 24°48'00"N, 121°44'06"E, at an elevation of ca. 100 m, slope above the road with some trees, 23 January 1997, *S.M. Liu et al. 556* (PE); ILan Hsien, Yuanshan, roadside, 15 April 1991, *M.J. Deng 404* (HAST); Nantou, Meifeng Farm, 24°6'0"N, 121°10'55"E, 1 August 1939, *Masamune et al. 2441* (TAI); Nantou, Sun Moon Lake, 23°50'26"N, 120°55'26"E, 24 October 1930, *S. Suzuki 6722* (TAI); Pingtung, Kengting, at an elevation of 200–300 m, *M.J. Deng & S.L. Chen 834* (HAST); Taichung Hsien, Wufeng Hsiang, Tingtai, 24°03'15"N, 120°40'24"E, open place, 22 January 2000, *J.N. Chen 00047* (PE); Taihoku, September 1922, *S. Sasaki s.n.* (NAS); Taipei, Chihshanyen, 25°5'38"N, 121°30'57"E, 15 May 1932, *T. Nonaka & K. Mori s.n.* (TAI); Taipei, NTU campus, 25°0'57"N, 121°32'9"E, 9 February 1964, *J.G. Kung 42* (TAI); Taipei, Tanshui, 25°9'50"N, 121°26'11"E, 10 December 1921, *S. Sasaki 1910* (TAI); Taipei, Taihoku, 25°2'46"N, 121°30'43"E, September 1922, *S. Sasaki 1911* (TAI); Taipei, Taihoku, 25°2'46"N, 121°30'43"E, 2 August 1927, *Y. Shimada 3404* (TAI); Taipei, Wantan, 24°56'39"N, 121°31'49"E, 18 June 1936, *H. Siizu 2342* (TAI); Taipei, Nei-Shuang-His, 12 December 1997, *M.F. Kao 3304* (HAST); Taoyuan Hsien, Lungtan, at an elevation of 220 m, 21 July 1990, *C.H. Lin 13301* (HAST, PE); Taoyuan Hsien, Yangmei, roadside, at an elevation of 50–150 m, 12 December 1990, *M.J. Deng 25* (HAST); Taoyuan Hsien, Gueishan, Fongshu, at an elevation of 100–200 m, 28 September 2002, *C.C. Chen 458* (HAST).

b. var. *tomentosum* Trim., in Cat. Ceyl. Pl. 79. 1885

Figure 2T–V

Type. Sri Lanka, *G.H.K. Thwaites 3432* (lectotype: BM-000617461, designated by Chakrabarty and Balakrishnan 2018; Isolectotypes: CAL, K-001081200 & K001081201).

Distribution and habitat. This variety *G. zeylanicum* var. *tomentosum* is widely distributed from India, Myanmar, Thailand, Vietnam, to China and south Japan. In China, it occurs widely from southwestern areas to Taiwan. It shares a similar habitat with the typical variety *G. zeylanicum* var. *zeylanicum*. In Taiwan, *G. zeylanicum* var. *tomentosum* is distributed from Hsinchu and Taipei to Nantou. Hsu et al. (2006) recorded the distribution of this variety in Ilan Hsien, but relevant specimens were unavailable in the present study.

Taxonomic discussion. Morphologically, the variety *G. zeylanicum* var. *tomentosum* differs from the typical variety *G. zeylanicum* var. *zeylanicum* by its hairy habit. For the hairy taxon, the name *G. zeylanicum* var. *tomentosum* was accepted by several authors in their treatment of Taiwanese *Glochidion* (Hsieh 1977; Deng and Wang 1993) and further appreciated recently (TPL 2013 continuously updated, Yao and Zhang 2015a), but in some other treatments the name *G. hirsutum* (Roxb.) Voigt was adopted (Li 1994; Hsu et al. 2006; Li and Gilbert 2008). In our taxonomic study of the genus *Glochidion*, it was found that the hairy variety (Figure 2T–V) and the typical glabrous variety *G. zeylanicum* var. *zeylanicum* (Figure 2Q–S) are very similar in habit and also shared similar distribution areas, so the name *G. zeylanicum* var. *tomentosum* is accepted here.

Representative specimens examined. China. Taiwan. Detailed locality unknown, 10 June 1929, *S. Sasaki s.n.* (NAS); Hsinchu Hsien, Hsinfeng Hsiang, Fengshan Margin of fallow paddy, at an elevation of 5–10 m, 30 May 1991, *W.P. Leu 946* (HAST); Hsinchu Hsien, Chupei Hsiang, on the slope along the riverbank of Fengshanhsi, at an elevation of 50–100 m, 27 November 1992, *W.P. Leu 1645* (HAST); Hsinchu Hsien, Hsinfeng Hsiang, 22 March 2014, *P.M. Zeng PM14* (NCAI); Nantou Hsien, Hsianshan-Sunmoon Lake, 23°50'29"N, 120°53'19"E, 19 September 1929, *K. Sasaki 15394* (TAI); Nantou Hsien, Sun Moon Lake, 23°50'26"N, 120°55'26"E, September 1929, *S. Sasaki* *s.n.* (TAI); Nantou Hsien, Yuchih, at an elevation of 750 m, 25 December 1985, *S.Y. Lu 18170* (HAST); Nantou Hsien, 26 April 1991, *Y.S. Hsu* & *J.C. Liaw 174* (NCAI); Nantou Hsien, 8 June 1991, *Y.S. Hsu* & *J.C. Liaw 216* (NCAI); Taipei Hsien, Shuiyuanti, 25°0'27"N, 121°31'48"E, 14 May 1929, *S. Suzuki 19294* (TAI); Taipei Hsien, Sungshan, 25°2'53"N, 121°34'5"E, 27 April 1933, *S. Sasaki s.n.* (TAI); Taipei Hsien, Taihoku, 25°2'46"N, 121°30'43"E, 10 June 1929, *S. Sasaki 9294* (TAI); Taipei Hsien, Tomitacho, 25°0'43"N, 121°32'7"E, 27 May 1932, *T. Tanaka & Y. Shimada 11071* (TAI); Tomitacho, Taihoku-shi, 27 May 1932, *T. Tanaka et al. 11071* (IBSC, PE); Taipei Hsien, Kungkuan, roadside, at an elevation of 10–20 m, 20 March 1992, *M.J. Deng 883* (HAST).

Key to species of *Glochidion* in Taiwan, China

1 Female flowers in axillary clusters; stamens usually 3 .... **2**
– Female flowers usually supra-axillary cymes or rarely in axillary clusters; stamens more than 3 .... **7**
2 Ovary usually 3–4-locular, or rarely 5-locular **3**
– Ovary 5-locular or more than 5-locular **4**
3 Leaves glaucous and white pubescent abaxially; styles column cylindric; capsules deeply 6–8-grooved; persistent styles obvious, ca. 1 mm long, dilated at apex .... ***G. acuminatum* var. *acuminatum* Müll. Arg.**
– Leaves usually paler abaxially; styles column shortly conical; capsules grooved shallowly or obscurely; persistent styles obscure or slightly elevated .... ***G. ellipticum* Wight**
4 Styles cylindrical, 1–3 mm long; capsules glabrous, 6–10 mm in diameter .... ***G. rubrum* Blume**
– Styles not cylindrical, usually less than 1 mm long; capsules hairy or slightly pubescent, up to 10 mm in diameter **5**
5 Female flower usually solitary or rarely two in axillary; styles ovoid column; ovary 5–6-locular .... ***G. lanyuense* Gang Yao & S.X. Luo**
– Female flowers multiple (usually more than 5) in axillary; styles annular, caliciform or sub-conical; ovary more than 6-locular **6**
6 Lateral veins of leaves 6–7 pairs; styles annular; ovary 6–10-locular; capsules 6–10-grooved, usually reddish when mature; persistent styles annular, not or slightly elevated .... ***G. puber* (L.) Hutch.**
– Lateral veins of leaves 8–9 pairs; styles caliciform or sub-conical; ovary 5–8-locular; capsules 10–16-grooved, usually purplish when mature; persistent styles sub-conical or sub-hemispheric .... ***G. philippicum* (Cavan.) C.B. Rob.**
7 Leaves less than 15 cm long and 5 cm wide; capsules 6–7 mm in diameter .... ***G. lanceolatum* Hayata**
– Leaves up to 20 cm long and 8 cm wide; capsules 8–12 mm in diameter **8**
8 Plant glabrous (except ovary) .... ***G. zeylanicum* var. *zeylanicum* (Gaertn.) A. Juss.**
– Plant hairy .... ***G. zeylanicum* (Gaertn.) A. Juss. var. *tomentosum* Trim.**

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