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Authors: Pineda, Yam M., Keller, Héctor A., Balderrama-Torrice, José A., Meve, Ulrich, Nürk, Nicolai M., et al.

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Phylogenetics in *Scyphostelma* (*Apocynaceae*: *Orthosiinae*) and description of new species

Yam M. Pineda¹, Héctor A. Keller², José A. Balderrama-Torrico³, Ulrich Meve¹, Nicolai M. Nürk¹ & Sigrid Liede-Schumann¹

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Abstract: In the tropical Americas, the *Orthosiinae* (*Apocynaceae*) comprises plant species with small but intricate flowers and harbours a tremendous, still understudied diversity currently classified in four genera, *Jobinia*, *Monsanima*, *Orthosia* and *Scyphostelma*. In this study, we describe and illustrate four new species of *Scyphostelma*: *S. bolivianum*, *S. gracile*, *S. rotorum* and *S. solomonii*, based on specimens collected in Bolivia and Peru. Phylogenetic analysis places *S. bolivianum* and *S. gracile* in a clade with *S. harlingii*, a species from southern Ecuador and central Peru, together as sister clade to the rest of *Scyphostelma*. Due to the size of flowers and the long-filiform peduncles and pedicels, we consider the two new species *S. rotorum* and *S. solomonii* and the new combination *S. erikseniae* a part of the *S. harlingii* group, for which an identification key is presented. Furthermore, four species names are lectotypified and six new combinations in *Scyphostelma* are made: *S. fasciculiflorum*, *S. jaramilloi*, *S. purpurascens*, *S. quitense*, *S. stenospira* and *S. unguiculatum*.

Keywords: Andes mountains, *Apocynaceae*, *Asclepiadeae*, endemism, lectotypification, *Orthosiinae*, phylogenetic analysis, *Scyphostelma*, South America, taxonomy

Resumen: En las Américas tropicales, *Orthosiinae* (*Apocynaceae*) comprende especies de plantas con flores pequeñas pero complejas y alberga una alta diversidad, aún poco estudiada, actualmente clasificada en cuatro géneros: *Jobinia*, *Monsanima*, *Orthosia* y *Scyphostelma*. En este estudio, describimos e ilustramos cuatro especies nuevas de *Scyphostelma*: *S. bolivianum*, *S. gracile*, *S. rotorum* y *S. solomonii*, con base en especímenes recolectados en Bolivia y Perú. El análisis filogenético ubica a *S. bolivianum* y *S. gracile* en un clado con *S. harlingii*, una especie del sur de Ecuador y el centro de Perú, juntas como clado hermano del resto de *Scyphostelma*. Debido al tamaño de las flores y a los pedúnculos y pedicelos filiformes largos, consideramos a las dos nuevas especies *S. rotorum* y *S. solomonii* y la nueva combinación *S. erikseniae* una parte del grupo *S. harlingii*, para el cual se presenta una clave de identificación. Además, se lectotifican cuatro nombres de especies y se realizan seis nuevas combinaciones en *Scyphostelma*: *S. fasciculiflorum*, *S. jaramilloi*, *S. purpurascens*, *S. quitense*, *S. stenospira* y *S. unguiculatum*.

Palabras clave: América del Sur, análisis filogenético, *Apocynaceae*, *Asclepiadeae*, Cordillera de los Andes, endemismo, lectotipificación, *Orthosiinae*, *Scyphostelma*, taxonomía

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Introduction

Orthosiinae (*Apocynaceae*: *Asclepiadoideae*: *Asclepiadeae*) is one of the eight subtribes of *Asclepiadeae* that are endemic to the Americas (12 globally; Endress & al. 2018; Keller & Liede-Schumann 2017). It includes more than 100 species classified in *Jobinia* E. Fourn. (c. 25 spp.), *Monsanima* Liede & Meve (2 spp.), *Orthosia* Decne. (55 spp.) and *Scyphostelma* Baill. (>50 spp.; Endress & al. 2018; Liede-Schumann & Meve, pers. obs.).

With the exception of *Monsanima*, with only two species narrowly endemic in the Atlantic rainforest and the grasslands of the *campos rupestres* of Brazil (Silva & al. 2014), the remaining three genera are insufficiently documented and in need of additional research. Many species now assigned to *Orthosiinae* have been originally described under *Cynanchum* L. over the overbroad concept of Woodson (1941). The phylogenetic independence of the neotropical *Orthosia* from the predominantly palaeotropical *Cynanchum* was first suggested by Rapini &

¹ Department of Plant Systematics, University of Bayreuth, 95440 Bayreuth, Germany.

² Facultad de Ciencias Forestales, Universidad Nacional de Misiones, Instituto de Botánica del Nordeste, Casilla de Correo 209, 3400 Corrientes, Argentina; kellerhector@hotmail.com

³ Centro de Biodiversidad y Genética, UMSS-Casilla 538, Cochabamba, Bolivia; tangara_sp@hotmail.com

Author for correspondence: Yam M. Pineda, melissa.pineda@uni-bayreuth.de

al. (2003), and Liede-Schumann & al. (2005) coined the name *Orthosiinae*, now understood to comprise *Jobinia*, *Monsanima*, *Orthosia* and *Scyphostelma*. The monophyly of the subtribe was confirmed by Rapini & al. (2007), while Fishbein & al. (2018) retrieved *Monsanima* in a different position. In recent years, many species have already been transferred from *Cynanchum* to *Jobinia*, *Orthosia* or *Scyphostelma* (e.g. Liede-Schumann & Meve 2013), and seven more species are transferred here.

Scyphostelma remains one of the least known genera of American *Asclepiadoideae*. Its more than 50 species are predominantly distributed in the Andean mountain range, inhabiting moist-tropical to arid valleys and mountains including altitudes up to 4200 m (Liede-Schumann & Meve 2013; Endress & al. 2018). The genus was described in 1890 based on *S. granatense* Baill. (Baillon 1810: 252; holotype: Colombia, *Goudot 1844*, P00106949!) and later proposed as one of 23 synonyms of *Cynanchum* (sensu Woodson 1941) by Morillo (1992). *Scyphostelma* remained monotypic until Liede-Schumann & Meve (2013), based on molecular evidence, resurrected the genus and added 26 species to it, most of them previously assigned to *Cynanchum* sect. *Microphyllum* Liede (Liede 1997). Liede-Schumann & Meve (2013) also included the monotypic genus *Liedea* W. D. Stevens (*L. filisepala* (Standl.) W. D. Stevens) from Costa Rica in *Scyphostelma*. A further species, *S. rugosum* (Turcz.) Morillo from Colombia was later transferred by Morillo (in Bernal & al. 2015).

Morphologically, *Scyphostelma* is characterized by small flowers that are typically < 6 mm in diameter but display considerable variation in structure and coloration (Liede-Schumann & Meve 2013). Flower size can be assessed by measuring individual floral traits, but it is often determined by the length of the corolla (Herrera 2005; Tavares 2016). *Scyphostelma* flowers, like the entire subfamily, exhibit distinctive characteristics, such as a gynostegial corona, gynostegium and pollinaria. The specific appearance of these structures has been widely used as most important diagnostic criteria across *Asclepiadoideae* (Güven & al. 2015). Additionally, details in the specific form of growth, such as the presence of long and short shoots and the position of inflorescences in general on short shoots only, have been considered important in the taxonomy of the group (Liede-Schumann & Meve 2013). However, morphological characters are not always sufficient for generic placement of samples that are not also molecularly analysed, especially in the genera *Orthosia* and *Scyphostelma*.

Among *Scyphostelma* species, *S. harlingii* (Morillo) Liede & Meve is distinguished by its unique inflorescences characterized by (long) slender peduncles and pedicels and large subglabrous flowers (Liede-Schumann & Meve 2013). Originally, it was described as producing only long shoots, which distinguishes *S. harlingii* from the other species in the genus (Liede-Schumann & Meve 2013). The distinction of this taxon from other *Scyphostelma* species was evident, to the point that it was transferred to *Blepha-*

rodon Decne. (Liede & Meve 2001). However, the molecular analysis unequivocally places another Ecuadorian accession of this species within the *Scyphostelma* clade (Liede-Schumann & Meve 2013). Further study of herbarium material from Peru and Bolivia produced specimens similar to *S. harlingii* but with morphological characters and/or phylogenetic placement supporting in summary recognition of four species new to science. In the present paper, we describe and illustrate these new species, two of which are retrieved in phylogenetic analysis together with *S. harlingii* in a clade sister to the remaining species of *Scyphostelma* (Fig. 1). The two other new species and *S. erikseniae*, here newly combined, are referred to the *S. harlingii* group for morphological reasons. A key to the six species recognized in the *S. harlingii* group is provided. Additionally, four species names are lectotypified and six new combinations in *Scyphostelma* are presented.

Material and methods

Phylogenetic analyses

Taxon sampling — The phylogenetic data used in this work are based on the specimens and markers used in Liede-Schumann & Meve (2013). Forty-four additional samples representing at least 13 *Jobinia* or *Scyphostelma* species were obtained from herbarium specimens held in B, CTES, HUA, K, LPB, MO, NY, QCA and UBT (Appendix 1; herbarium codes follow Thiers 2020+). The two species of *Monsanima* were selected as outgroup, following the results of Liede-Schumann & Meve (2013).

DNA isolation, PCR amplification and sequencing — DNA was extracted from silica-dried leaf samples (vouchers held at UBT) or from leaf fragments of the herbarium specimens. Extraction and amplification followed the methods described in Liede-Schumann & Meve (2013) for the chloroplast regions used in this paper (*trnT-trnL* and *trnL-trnF* intergenic spacers, *trnL* and *rps16* introns and *trnD-trnT* intergenic spacer). In addition, the *psbA-trnH* intergenic spacer was amplified with the primers designed by Sang & al. (1997) and the *trnS-trnG* intergenic spacer with the primers designed by Hamilton (1999). The same primers were used for both PCR and Sanger sequencing. Both strands were sequenced for all PCR products. In total, 242 partial sequences were newly created for the present study. Voucher information and GenBank accession numbers are provided in Appendix 1.

Phylogenetic analysis — For all regions, forward and reverse sequences were aligned with CodonCode Aligner, v.3.0.3 (CodonCode Corp., Dedham, Massachusetts, U.S.A.), and the consensus was exported in fasta format. Sequences from GenBank were added, provided the taxon identification was reliable, sequences of at least two loci were available for the specimen and the sequence covered more than half of the locus. The consensus se-

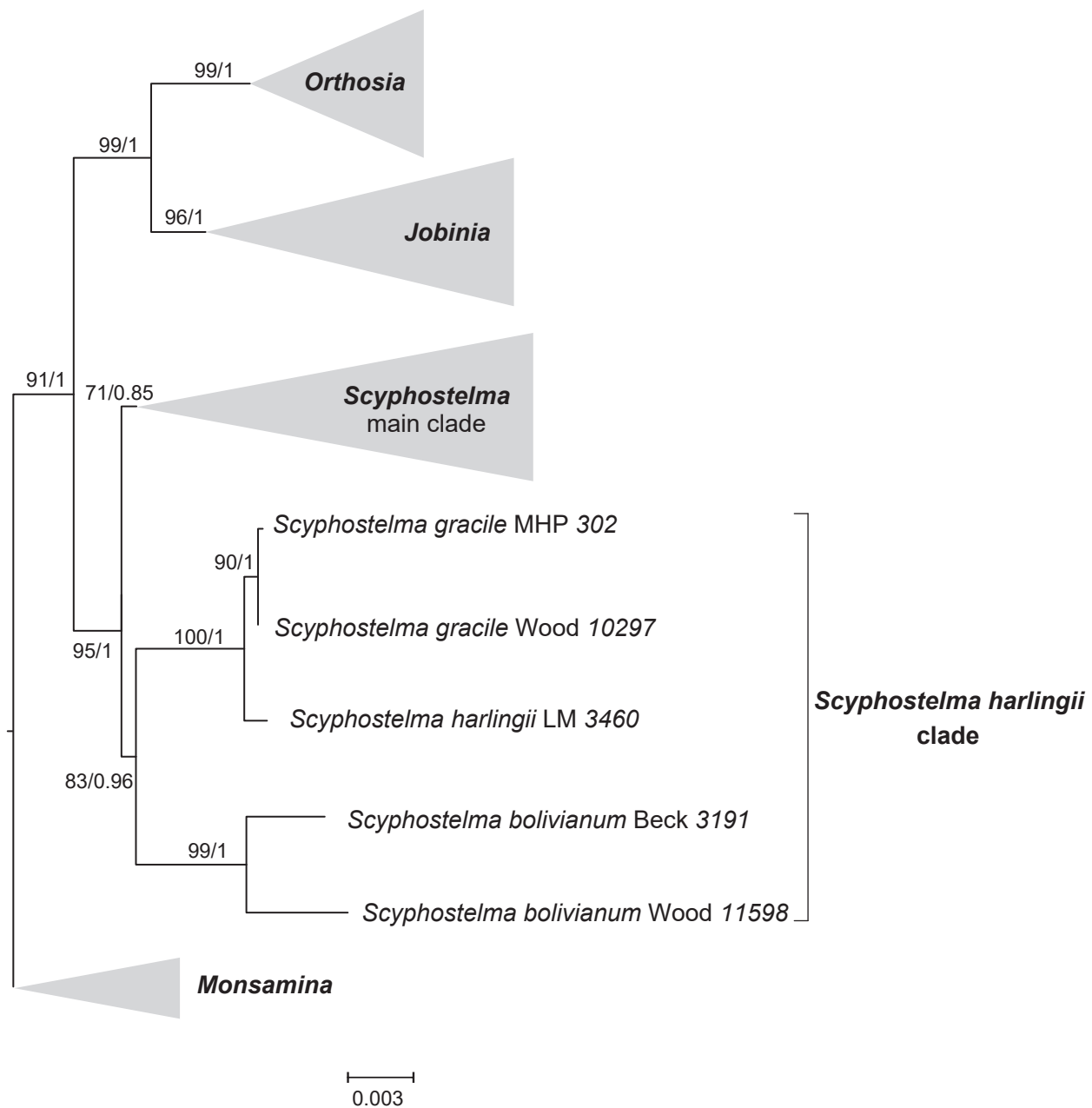


Fig. 1. Phylogenetic reconstruction of *Orthosiinae* based on six cpDNA markers (see text), highlighting the position of the *Scyphostelma harlingii* clade. The remaining genera of *Orthosiinae*, *Jobinia*, *Monsamina* and *Orthosia*, with a sampling identical to Liede-Schumann & Meve (2013), are summarized by triangles, and so is the remainder of *Scyphostelma*. Numbers on branches indicate Bootstrap percentages / posterior probabilities. The root of the tree is that of Liede-Schumann & Meve (2013).

quences of each locus were aligned with the MAFFT package (Kato & Standley 2013) in Mesquite (Maddison & Maddison 2018), using standard settings, and the resulting alignments were corrected manually to fix gap and alignment ambiguities (alignments available in Appendix S1 in Supplemental content online). For maximum likelihood (ML) estimation, RAxML v.8.2.12 (Stamatakis 2014) was used to search for the ML tree and to conduct the bootstrap search. All partitions were allowed to evolve independently under the GTR+ Γ substitution model. ML analyses were conducted using the CIPRES Gateway (<https://www.phylo.org/>, Miller & al. 2010)

with the number of bootstrap replicates set automatically (Pattengale & al. 2010).

For Bayesian inference (BI) using MrBayes v.3.2.2 (Ronquist & al. 2012), two independent runs with one cold and three heated chains each were initiated with random trees and saving a tree and branch lengths every 1000 generations. Following Huelsenbeck & Rannala (2004), the most complex model GTR+ Γ +I was implemented for each partition; the parameters statefreq, revmat, shape and pinvar were all unlinked between the partitions. Ten million generations were run on the CIPRES Gateway (Miller & al. 2010) resulting in a final deviation

of split frequencies of 0.0032. Parameters and convergence of the independent runs were inspected with Tracer v.1.6 (Rambaut & al. 2014). The first 10 000 trees (50%) of each run were discarded as burn-in and the remaining 10 000 trees summarized in a 50% majority rule consensus tree, with posterior probabilities (PP) as an estimate of support for nodes of the tree.

Morphological study

Taxon sampling — About 700 specimens of *Orthosiinae* were inspected, available in the herbaria B, CTES, GB, K, LPB, MO, NY, QCA, S, UBT, ULM and USM, of which 56 morphologically resembling *Scyphostelma* were selected to be studied in more detail. Additionally, fresh material collected during fieldwork was studied and documented as herbarium specimens (e.g. *Porcel & al.* 302, CTES; for voucher information see Appendix 1).

Morphological measurements — For the selected specimens, foliar traits were measured using an electronic calliper of a millimetre precision. A high-resolution photographic camera and a stereoscopic microscope (Leica MZ75) were used to study floral traits of the material, to obtain images and to illustrate the species described here. Indumentum and pollinaria were examined with an optical microscope (Leica Laborlux 12) with a built-in photographic camera. To extract the pollinaria and study the reproductive characteristics, the flowers were softened by gently heating them in restitution fluid (H_2O :Ethanol:Glycerin = 5:4:1); resulting in described floral dimensions corresponding to the rehydrated material. The length of the peduncle (inflorescence stalk), pedicel (flower stalk) and corolla lobe (petal) were measured on 39 specimens, all of which were correctly preserved in their respective traits (Appendix 1). Molecular phylogenetic groupings of *Scyphostelma* were tested for significant differences in floral traits among retrieved clades using the one-sided student's t-test (R Core Team 2022).

Results

Phylogenetic analyses

In accordance with previous results, *Jobinia* ($BS_{ML} = 96\%$, $PP = 100$), *Orthosia* ($BS_{ML} = 99\%$, $PP = 1$) and *Scyphostelma* ($BS_{ML} = 95\%$, $PP = 1$) are retrieved as monophyletic (Fig. 1). The *S. harlingii* clade, containing newly described species *S. bolivianum* sister to *S. harlingii* + (newly described) *S. gracile* ($BS_{ML} = 100\%$, $PP = 1$) is

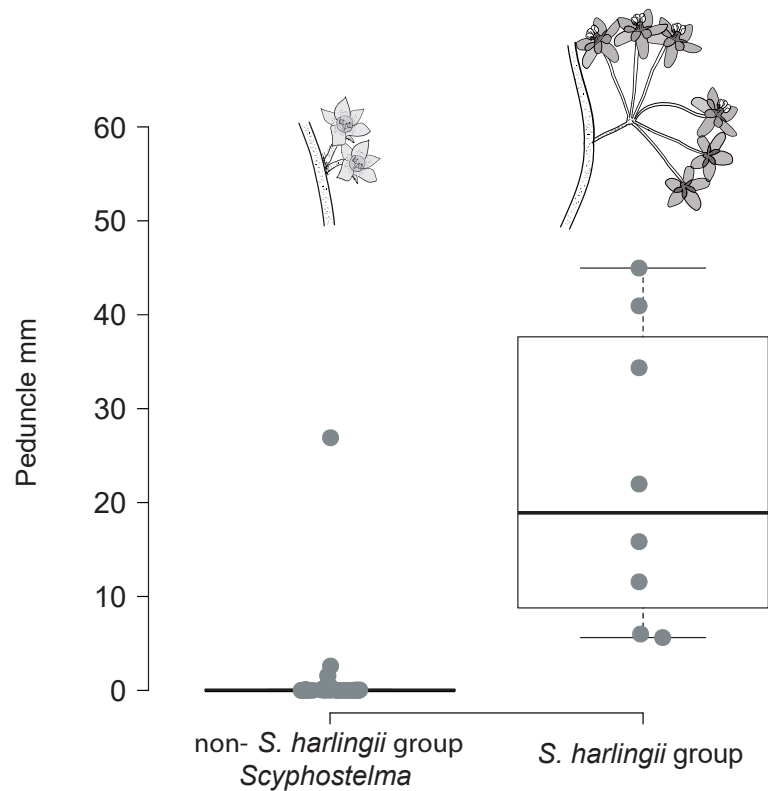


Fig. 2. Boxplot comparing the size of the peduncles between the species within the *Scyphostelma harlingii* group ($n = 8$) and the remaining species in the genus ($n = 31$). t-test: mean diff. = 21.55, $df = 7.3$, $p = 0.005$. Schemes above boxplots illustrate the characteristic shape of inflorescences in the two groups; *Wurdack 1077* (USM), *J. R. I. Wood 11598* (K).

moderately supported ($BS_{ML} = 88\%$, $PP = 0.98$) and well-supported sister to the remaining members of *Scyphostelma* ($BS_{ML} = 95\%$, $PP = 1$; Fig. 1, Appendix S2, S3 in Supplemental content online). The three species in the *S. harlingii* clade are distinguished from the remainder of *Scyphostelma* by long-filiform peduncles and pedicels.

Morphological study

Based on similarities in growth form and floral traits, we recognize five species as being closely related to *Scyphostelma harlingii*. The species in this “*S. harlingii* group” are characterized by the appearance of inflorescences also on long shoots (i.e. not only on short shoots as is typical for non-*S. harlingii*-group *Scyphostelma* species) and the significantly larger appearance of three floral characters, peduncles, pedicels and corolla lobes, compared to the other *Scyphostelma* species included in the phylogenetic analysis (Fig. 2). We measured these traits on 39 specimens, consisting of 31 specimens from 11 species belonging to non-*S. harlingii* *Scyphostelma* and eight specimens representing the six species together referred to here as the *S. harlingii* group. Peduncles in the *S. harlingii* group are (5–)10–36(–45) mm long, significantly filiform and longer compared to the remainder in the genus (t-test: mean diff. = 21.55, $df = 7.3$, $p = 0.005$). In non-*S. harlingii* *Scy-*

phostelma, flowers are typically (sub)sessile, except for an outlier sample (*Luteyn & Berg 14375*, NY, QCA; Appendix 1), in which peduncles are 20–32 mm long (Fig. 2). Pedicels are also significantly longer in the *S. harlingii* group, measuring (7)13–20(–22) mm long, compared to (0.5–)1.6–4.2(–20) mm long in non-*S. harlingii* *Scyphostelma* (t-test: mean diff. = 12.2, df = 8.9, $p < 0.001$; outlier: *Luteyn & Berg 14375*, has longer pedicels). Corolla lobe length indicates that the species in the *S. harlingii* group are characterized by larger flowers with corolla lobes (2.2–)3.3–4.8(–5.8) mm long in the *S. harlingii* group and (1–)1.5–2.8(–4.9) mm long in non-*S. harlingii* *Scyphostelma* (t-test: mean diff. = 2, df = 9.2, $p = 0.002$; outlier: *Luteyn & Berg 14375*, has longer corolla lobes).

Out of the 32 specimens mentioned in the taxonomic treatment, 16 are classified under the *Scyphostelma harlingii* group, six of them represent the four newly described species in this study and the remaining 16 correspond to the new combinations.

Discussion and Conclusions

The *Scyphostelma harlingii* group, recognized and named as such for the first time here, comprises the species *S. bolivianum*, *S. erikseniae*, *S. gracile*, *S. harlingii*, *S. rotorum* and *S. solomonii*. The group is supported by molecular phylogenetic results grouping included species (*S. bolivianum*, *S. gracile* and *S. harlingii*) in a clade sister to the remaining species of *Scyphostelma* (Fig. 1, Appendix S2, S3). Morphologically, longer filiform peduncles and pedicels together with generally larger flowers distinguish the species in the *S. harlingii* group from remaining *Scyphostelma*, although exceptions exist (see paragraph below). The larger flowers also affected internal floral features such as pollinaria, which are considerably larger compared to the remaining species in the genus. In contrast to Liede-Schumann & Meve (2013), we observed several specimens from most species assigned here to the *S. harlingii* group that exhibit both long and short shoots (e.g. *Matezki & Homeier 174*; *Wood 10297*) and with inflorescences on both shoot forms. That is, long shoots with inflorescences exist in the *S. harlingii* group, a feature that distinguishes species in the group from non-*S. harlingii* *Scyphostelma* where inflorescences appear typically on short shoots.

The molecular phylogenetic analysis did not include *Scyphostelma erikseniae*, *S. rotorum* and *S. solomonii* due to missing samples suitable for Sanger sequencing. Morphology suggests these species to belong to the *S. harlingii* clade, although not unequivocally. For instance, *S. erikseniae* and *S. bolivianum* exhibit shorter peduncles (3.5–7 mm) and pedicels (4.5–12.5 mm) than in the other *S. harlingii* group species. Similar exceptions exist vice versa in some samples that are placed in the molecular phylogeny in the *Scyphostelma* main clade (Fig. 1). For example, the undetermined specimen *Luteyn & Berg 14375* (QCA, Appendix 1) exhibits morphological traits

typical of the *S. harlingii* group (average lengths: peduncle 29 mm, pedicel 20 mm, corolla lobe 3 mm, Fig. 2). In the phylogenetic analysis, however, it is placed in the *Scyphostelma* main clade (Appendix S2, S3). Therefore, phylogenetic relationships within *Scyphostelma* need further investigation.

We acknowledge the challenges associated with describing new species based on a single specimen, as in the cases of *Scyphostelma rotorum* and *S. solomonii*. This can be problematic due to the absence of knowledge on intraspecific variation, especially when the respective specimen is atypical by chance. We emphasize the importance of exploring and collecting additional specimens belonging to the *S. harlingii* group, and *Scyphostelma* in general, of which many species have very limited records. We hope that the newly described species and the proposed combinations will contribute to the systematic understanding of *Scyphostelma*.

Taxonomy

Key to the species of the *Scyphostelma harlingii* group

1. Corolla glabrous, gynostegial corona flat, spreading, \pm appressed to corolla; peduncles < 10 mm long **2**
- Corolla with indumentum, gynostegial corona suberect or erect and appressed to gynostegium or gynostegial stipe; peduncles > 10 mm long **3**
2. Leaves ovate to ovate-lanceolate; staminal corona lobes 1.4–1.8 mm long, rounded rectangular, only basally fused **1. S. bolivianum**
- Leaves narrowly lanceolate; gynostegial corona fused to a collar-like structure **2. S. erikseniae**
3. Leaves, if present at all, linear-lanceolate, to 10 mm long; staminal corona lobes deltate **6. S. solomonii**
- Leaves lanceolate, 15–45 mm long; staminal corona lobes not deltate **4**
4. Staminal corona lobes plane, rectangular with rounded shoulders, suberect with a vertical wave, basally fused and forming a bowl-like structure **3. S. gracile**
- Staminal corona lobes 3-dimensional, spreading, reflexed, laterally attached to a gynostegial stipe **5**
5. Corona about as long (high) as gynostegium, staminal corona lobes \pm appressed to gynostegial stipe **4. S. harlingii**
- Corona only c. 1/2 as long (high) as gynostegium, free staminal corona lobes much protruding, each spreading horizontally for c. 0.8 mm with margins approaching at lower edges **5. S. rotorum**

Taxonomic descriptions

1. *Scyphostelma bolivianum* Y. M. Pineda, Liede & Meve, **sp. nov.** – Fig. 1, 3, 4.

Holotype: Bolivia, Cochabamba, Carrasco, 18–20 km from Montepuncu below Sehuena, 19 Oct 1996, *J. R. I. Wood 11598* (K!; isotype: UBT!).

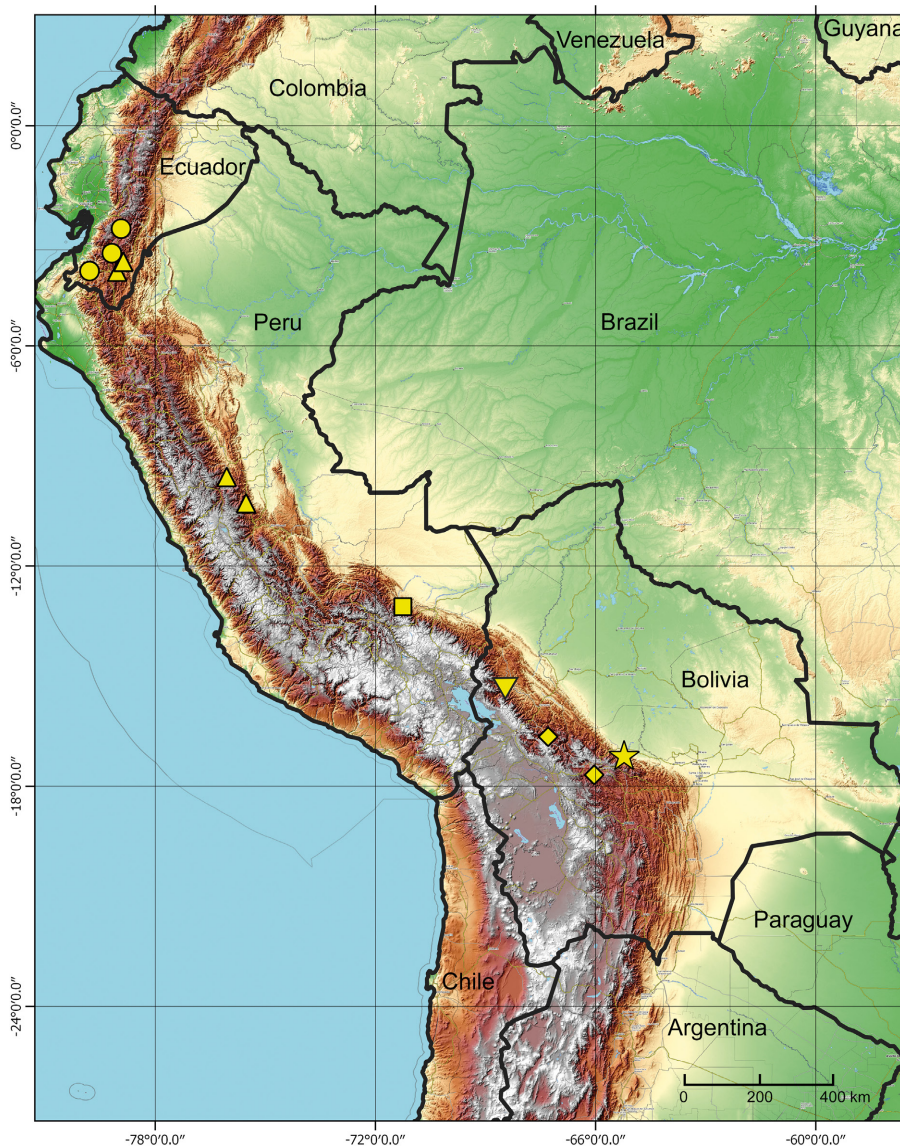


Fig. 3. Distribution map of *Scyphostelma bolivianum* (diamonds), *S. erikseniae* (circles), *S. gracile* (stars), *S. harlingii* (upright triangles), *S. rotorum* (square) and *S. solomonii* (inverted triangle). – Map created in QGIS (QGIS Development Team 2009).

Diagnosis — Similar to *Scyphostelma erikseniae* (Morillo) Liede, Meve & Y. M. Pineda but with leaves ovate-lanceolate (vs narrowly lanceolate in *S. erikseniae*), corona c. 4 mm in diam. with free staminal corona lobes c. 1.5 mm long (vs corona c. 5 mm in diam. and completely fused to a collar-like structure in *S. erikseniae*) and guide rails c. 1 mm long (vs c. 1.75 mm long in *S. erikseniae*).

Morphological description — Twining plants, to 4 m tall; stems densely pubescent with scattered trichomes; internodes of long shoots 40–53 × 1.2–2 mm, internodes of short shoots 25–31 × 1–1.5 mm. Leaves: petiole 9–17 mm long, with pubescence like that of stems; lamina ovate-lanceolate, 24–40 × 18–27 mm, base rounded, truncate to subcordate, apex acute to attenuate, usually mucronate; abaxial surface with short trichomes

on veins, adaxial surface with sparse trichomes appressed, often with 2 conic colleters at base; venation brochidodromous with 3–7 pairs of secondary veins. Inflorescences axillary, alternate, with 5–8 flowers per cyme, all in simultaneous anthesis; peduncle 4.5–7 × c. 0.6 mm, with pubescence similar to shoots; bracts 0.7–1 × 0.2–0.4 mm. Flowers: pedicel 11–12.5 × 0.2–0.35 mm, with scattered, wrinkled trichomes; calyx purple, lobes oblong, c. 1.5 × 1 mm, glabrous except for ciliate margin, apex acute; corolla maroon, rotate, c. 8 mm in diam., tube short, c. 0.1 mm long, free lobes elliptic, 3–3.2 × 1.8–2 mm, spreading, abaxially and adaxially glabrous. Gynostegial corona cream in vivo to yellowish in sicco, c. 4 mm in diam., spreading flat on corolla, basally fused, free staminal corona lobes rounded rectangular, 1.4–1.8 × 1.1–1.3 mm; gynostegium stipitate, 1.5–2.1 × 2–3.2 mm, stipe 0.8–0.1 mm long; anthers rectangular, c. 1.2 × 1 mm, fertile part of anthers c. 1/2 as long as guide rails, abaxially bulging hemispherically, anther appendages suborbicular, c.

0.5 × 0.7 mm, translucent, guide rails forming a protruding triangle, 0.8–1 mm long; style head umbonate, c. 1.5 mm in diam. Pollinarium: corpusculum ovoid, 0.3–0.38 × 0.18–0.2 mm; caudicles strap-like with bend in central region, c. 0.15 mm long; pollinia ovoid-oblate, 0.3–0.34 × 0.2–0.22 mm, subapically attached to caudicles. Follicles and seeds not seen.

Phenology — Found with flowers in October.

Distribution and ecology — *Scyphostelma bolivianum* is presently known from two localities in Bolivia, one in La Paz and the other one in Cochabamba (Fig. 3, 4). The species inhabits well-developed moist cloud forests with areas of disturbance; scattered plants at the forest edge on a steep, scrubby bank by a river cliff; at altitudes between 2000–2500 m.

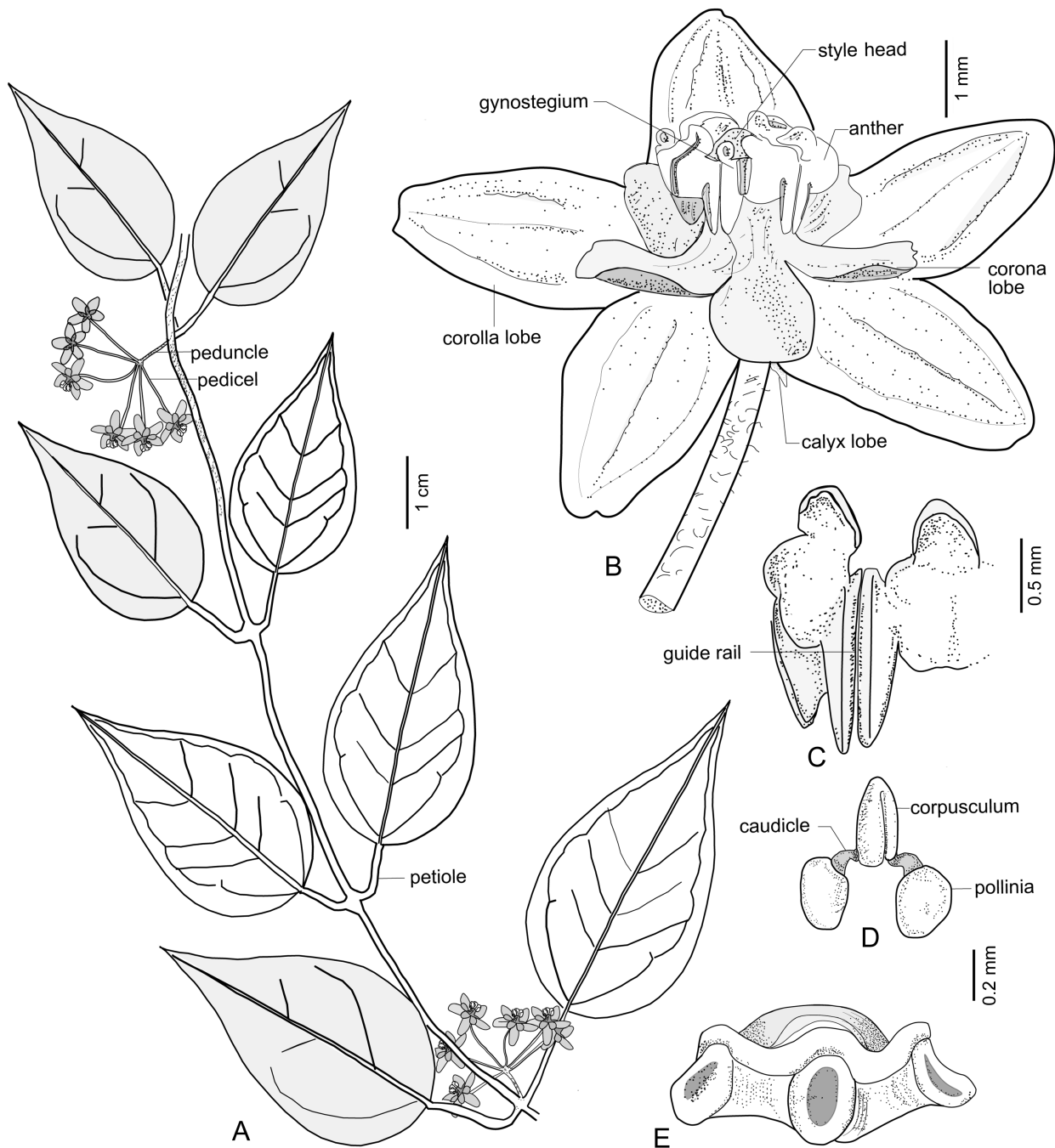


Fig. 4. *Scyphostelma bolivianum* – A: flowering branch; B: flower; C: two anthers and guide rail; D: pollinarium; E: style head. – A–E from the holotype, *J. R. I. Wood 11598* (K). – Drawn by Y. M. Pineda.

Etymology — The specific epithet refers to Bolivia, the country in which the new species has been recorded so far.

Additional specimens (paratypes) — BOLIVIA: La Paz, Sud Yungas, Huancané, 7.5 km hacia el sud sobre el camino nuevo, 2410 m, 10–20° SW, 9 Mar 1980 (sterile), *S. G. Beck 3191* (LPB!, MO, UBT!).

2. *Scyphostelma erikseniae* (Morillo) Liede, Meve & Y. M. Pineda, **comb. nov.** \equiv *Cynanchum erikseniae* Morillo

in *Ernstia* 2(3–4): 61. 1992. – Holotype: Ecuador, Loja, road El Cisne to Loja, 2 km S of El Cisne, on road to Loja, 79°26'W, 03°52'S, 2500 m, 19 Feb 1988, *U. Molau & B. Erikson 3108* (GB!; isotype: QCA7980!). – Fig. 3, 5.

Morphological description — Twining plants, at least 1 m tall; stems glabrous, except for scattered erect trichomes at nodes; internodes of long shoots 71–75 \times 1.2–1.7 mm, internodes of short shoots 22–33 \times 0.5–0.7 mm. Leaves: petiole 4–7 mm long, glabrous; lamina lanceolate-oblong or suboblong, 23–45 \times 2–8 mm,

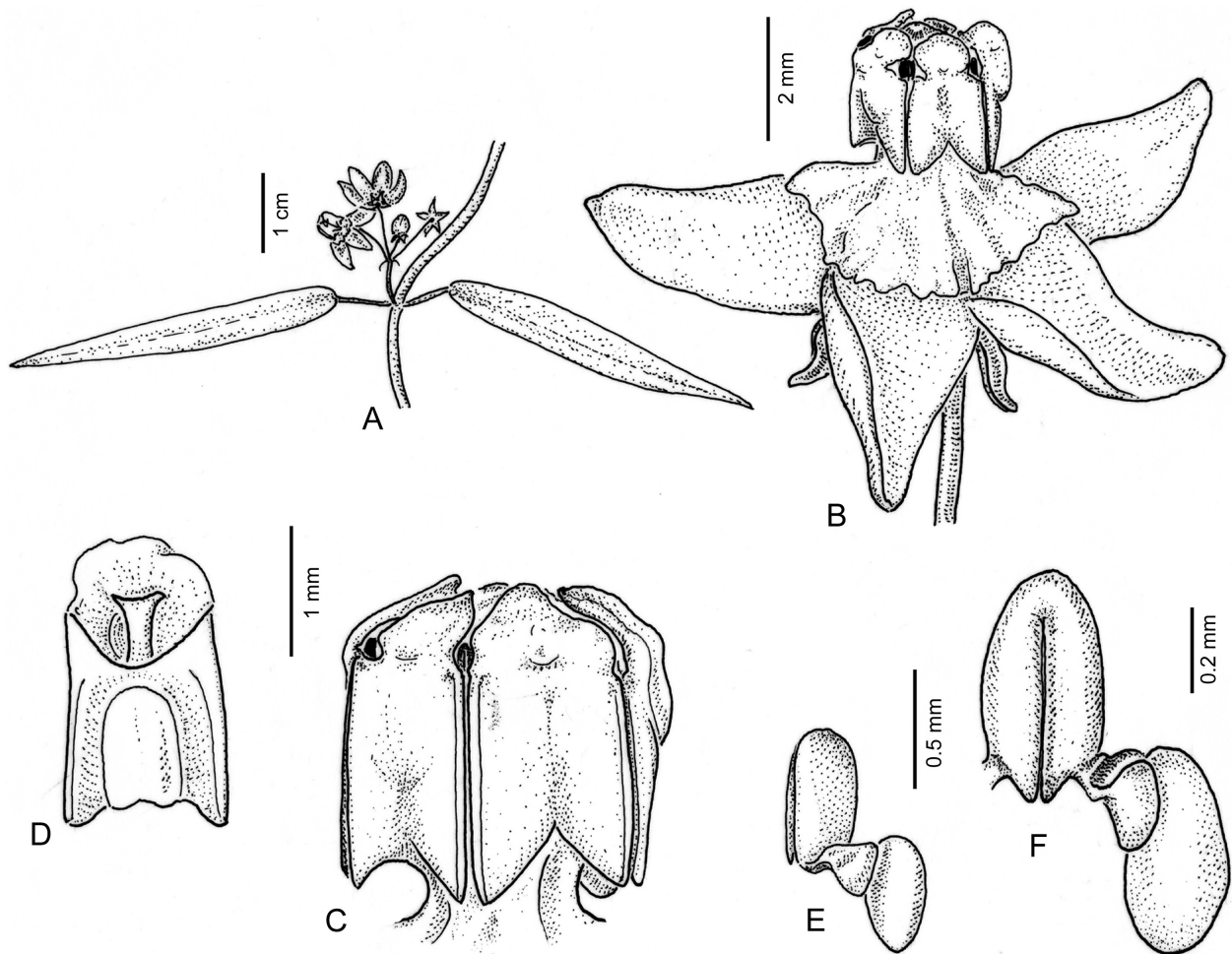


Fig. 5. *Scyphostelma erikseniae* – A: stem node with two leaves and inflorescence; B: flower; C: gynostegium; D: anther, adaxial view; E: pollinarium, one pollinium missing, lateral view; F: pollinarium, one pollinium missing, frontal view. – A–F from *G. Harling 745* (S). – Drawn by U. Meve.

ciliate, base obtuse to rounded, apex acuminate; abaxial surface glabrous or sparsely puberulous with appressed trichomes, adaxial surface also sparsely puberulous; lateral veins 6–8. Inflorescences subaxillary, with 3 or 4 flowers per cyme; peduncle 3.5–7 mm, uniseriate pubescent with appressed trichomes, bracts linear-lanceolate 1.2–2.2 mm long, ciliate. Flowers: pedicel 4.5–7.5 × c. 0.3 mm, pubescent; calyx lobes ovate-oblong, 3–3.2 × 1–1.2 mm, glabrous, apex acute; corolla rotate, abaxially purple, adaxially green, 12–13 mm in diam., tube 1–1.2 mm long, free lobes ovate or ovate-elliptic, 4.8–5.1 × 3.2–3.6 mm, veined, glabrous on both sides, apex obtuse-emarginate. Gynostegial corona colour unrecorded, 4–4.3 mm in diam., membranous, staminal corona lobes fused to a subdiscoïd, denticulate collar appressed to corolla tube; gynostegium stipitate, 2.4–2.6 × 2.5–2.6 mm, stipe slightly angular, 0.5–0.8 mm long; anthers rectangular, c. 1.5 mm long, guide rails c. 2 mm long, anther appendages suborbicular-subdeltate, c. 0.5 × 1 mm, translucent, laid on style head; style head flat, c. 1.8 mm in diam. Pollinarium: corpusculum obovoid-ellipsoid, c. 0.5 × 0.22 mm; caudicles trapezoidal, c. 0.15 mm long;

pollinia ovoid, 0.45–0.5 × c. 0.3 mm. Follicles and seeds not seen. (Description modified and supplemented from Morillo 1992: 61.)

Phenology — Found with flowers in February and May.

Distribution and ecology — *Scyphostelma erikseniae* is presently known from two localities in Loja, Ecuador. The species inhabits disturbed shrubby montane forests and secondary scrub, at altitudes between 2500–2700 m.

Remarks — *Scyphostelma erikseniae* is a rare species from Ecuador (Azuay, Loja). With its long slender leaves and its relatively large flowers borne on slender pedicels and peduncles, as well as the collar-shaped corona, it clearly belongs in the *S. harlingii* clade, even though no sequenceable material was available.

Additional specimens — ECUADOR: Azuay, Baños, 2500 m, 6 May 1947, *G. Harling 745* (S!); Loja, road Celica-Guachanamá, km 8 at Roldod monument, 2700 m, Feb 1985, *G. Harling & L. Andersson 22257* (GB paratype).

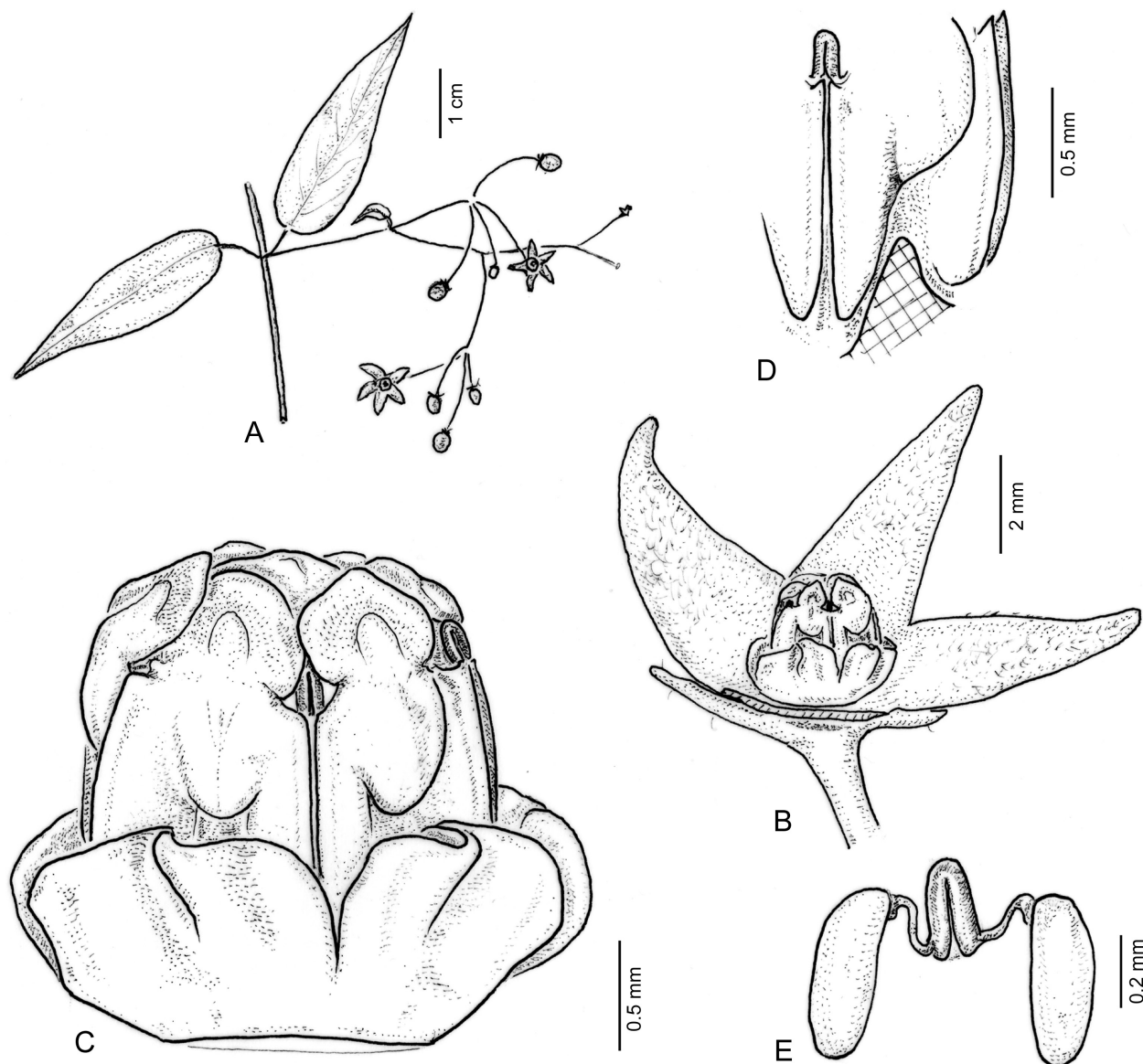


Fig. 6. *Scyphostelma gracile* – A: stem node with two leaves and inflorescence; B: flower, two petals removed; C: gynostegium with corona; D: details of guide rails (one in frontal, one in lateral view), with area of attachment of the corona (cross-hatched); E: pollinarium. – A–E from the isotype, *J. R. I. Wood 10297* (UBT). – Drawn by U. Meve.

3. *Scyphostelma gracile* H. A. Keller, Meve & Liede, sp. nov. – Fig. 1, 3, 6, 7.

Holotype: Bolivia, Cochabamba, Chapare, 6 km below Sehuencas, roadsides/gullies, 17°29'S, 65°15'W, 2200 m, 26 Dec 1995, *J. R. I. Wood 10297* (K 62678!; isotype: UBT!).

Diagnosis — Similar to *Scyphostelma harlingii* (Morillo) Liede & Meve but with gynostegium sessile (vs seated on barrel-shaped filament tube [stipe] in *S. harlingii*); corona basally fused to form a cup-like structure (vs basally connected only by a basal fringe in *S. harlingii*), corona lobes suberect with a vertical wave (vs spreading and bent together in *S. harlingii*) and anthers nearly as long as wide (vs c. 1/2 as long as wide in *S. harlingii*).

Morphological description — Twining plants, 1.5–6 m tall; stems reddish, with uniseriate, scattered, retrorse adpressed trichomes; internodes of long shoots 60–76 × 1–1.2 mm, internodes of short shoots 15–58 × c. 0.7 mm. Leaves: petiole 4–10 mm long, reddish, with pubescence similar to that of shoots; lamina ovate-lanceolate, 16–42 × 5–12 mm, base rounded, truncate to subcordate, apex acute to acuminate; abaxial surface with short trichomes on veins only, adaxial surface with sparse appressed trichomes, with 2 conic colleters at base; venation brochidodromous with 4–8 pairs of secondary veins. Inflorescences extra-axillary, alternate, with 3–9 flowers per cyme, 2 or 3 in simultaneous anthesis; peduncle filiform, 25–40 mm long, with pubescence like that of stems; bracts 2–3 × 0.8–1 mm. Flowers: pedicel filiform, 12–16 × 0.2–0.35 mm, with scattered, ap-



Fig. 7. *Scyphostelma gracile* – A: floriferous branches; B: inflorescences; C: leaves; D: venation; E: flower with diptera. F: flower detail showing the gynostegium. – A–F from M. H. Porcel & al. 302 (CTES). – Scale bars: A = 5 cm; B = 1 cm; C, D, E = 5 mm; F = 1 mm. – Photographs by J. A. Balderrama-Torrico & M. H. Porcel.



Fig. 8. *Scyphostelma harlingii* – A: plant with inflorescences; B: flower. – From R. Vásquez & al. 35067 (USM). – Scale bars: A = 2 cm; B = 5 mm. – Photographs by R. Vásquez.

pressed trichomes; calyx lobes ovate, 1.5–2 × 0.9–1.1 mm, abaxially with scattered trichomes, margin ciliate, apex acute; corolla pale purple, rotate, tube c. 1.8 mm in diam., free lobes triangular-lanceolate, 4.5–5 × c. 2 mm, spreading, abaxially glabrous, adaxially densely covered with short, verrucose trichomes (becoming longer toward tip). Gynostegial corona green in vivo to yellowish in sicco, bowl-shaped, c. 1 × 3 mm, fused for basal 1/3, free staminal corona lobes rectangular with rounded shoulders, 0.2–0.8 × 1.5–1.8 mm, suberect, membranous, with a vertical wave, closely and firmly attached just to gynostegium base; gynostegium sessile, 1.7–1.9 × 1.2–1.3 mm; anthers subrectangular, c. 1.2 × 1 mm, anther appendages suborbicular, c. 0.5 × 1 mm, translucent, adpressed to style head, guide rails broadly protruding, 0.9–1.1 mm long; style head umbonate c. 1.2 mm in diam. Pollinarium: corpusculum ovoid, 0.22–0.28 × 0.11–0.12 mm; caudicles sigmoid, 0.2–0.23 mm long; pollinia oblong-subreniform, 0.45–0.5 × 0.20–0.24 mm, subapically attached to caudicles, apex rounded. Follicles and seeds not seen.

Phenology — Found with flowers from November to December. Flowers are visited by small diptera (Fig. 7E).

Distribution and ecology — *Scyphostelma gracile* is known at present from two Andean localities, both in Cochabamba, Bolivia (Fig. 3). The species inhabits moist cloud forests in deep valleys with steep slopes and high rainfall. Scattered plants on the edge of the forest and scrubland at altitudes between 2200–2500 m.

Etymology — The specific epithet refers to its graceful inflorescences with filiform peduncles and pedicels.

Additional specimens (paratypes) — BOLIVIA: Cochabamba, Prov. Chapare, Parque Nacional Carrasco, 17°27'43.76"S, 65°16'26.67"W, 2325 m, 16 Jan 2021, M. H. Porcel & al. 302 (BOLV, CTES).

4. *Scyphostelma harlingii* (Morillo) Liede & Meve in Ann. Missouri Bot. Gard. 99: 70. 1999 ≡ *Cynanchum harlingii* Morillo in Ernstia, n.s., 2(3–4): 62. 1992 ≡ *Blepharodon harlingii* (Morillo) Liede & Meve in Novon 11: 173. 2001. — Holotype: Ecuador, Zamora-Chinchipe, above Valladolid, on road to Yangana, mountain rainforest, 2300 m, 1 Feb 1985, G. Harling & L. Andersson 21422 (GB!). — Fig. 1, 3, 8.

Morphological description — Twining plants, to 3 m tall; stems moderately or densely pubescent with appressed trichomes; internodes of long shoots 30–68 × 1.4–2 mm, internodes of short shoots 15–27 × 1–1.4 mm. Leaves: petiole 4–19 mm long, moderately or densely puberulent with appressed trichomes; lamina ovate to oblong-ovate, 30–70 × 7–27 mm, base truncate or subcordate, apex long acuminate; both surfaces sparsely puberulent, usu-

ally with appressed trichomes, usually with densely appressed puberulent lateral veins, adaxial surface with 2 or 3 conic colleters at base; venation brochidodromous with 6–8 pairs of secondary veins. Inflorescences subaxillary, with 3–6 flowers per cyme, most in simultaneous anthesis; peduncle filiform, 15–48 mm long, puberulent with erect or retrorse trichomes; bracts ovate, 0.4–0.7 × 0.2–0.4 mm long, densely ciliate. Flowers: pedicel filiform, 14–24 × c. 0.5 mm, glabrous; calyx lobes narrowly ovate, 1.2–1.3 × 0.8–0.85 mm, glabrous; corolla rose to bright pinkish (or brownish purple when dry), central parts often whitish, 6–12 mm in diam., tube c. 1 mm long, free lobes narrowly ovate-elliptic or oblong-elliptic, 2.5–6 × 1.8–2.3 mm, expanded to reflexed, abaxially glabrous, adaxially densely and shortly puberulent with appressed to spreading, verrucose trichomes on upper half, apex narrowly obtuse. Gynostegial corona whitish (occasionally with rose tinge), 2–2.5 mm in diam., staminal corona lobes connate to stipe, semi-ovate in outline, concave at front, obtuse at apex, c. 1 × 0.8 mm; gynostegium stipitate, c. 1.7 × 2 mm, stipe 0.8–0.9 mm long; anthers broadly rectangular, erect, slightly bulging, c. 0.8 × 1 mm, guide rails c. 0.8 mm long, anther appendages broadly kidney-shaped, c. 0.3 × 0.75 mm, translucent, adpressed to style head; style head flattened convex, c. 1.5 mm in diam. Pollinarium: corpusculum narrowly ovoid, 0.2–0.5 × 0.08–0.2 mm; caudicles sigmoid, 0.2–0.3 mm long; pollinia suboblong-elliptic, 0.5–0.55 × c. 0.15 mm. Follicles and seeds not seen. (Description modified and supplemented from Morillo 1992: 62–63.)

Phenology — Found with flowers from October to March.

Distribution and ecology — *Scyphostelma harlingii* was previously known (Liede-Schumann & Meve 2013) from southern Ecuador (Zamora-Chinchipe) and central Peru (Huánuco). Here, a southward extension into the Pasco region of Peru is reported. The species inhabits montane rainforest or subtropical forest, near streams, at altitudes between 2300–2750 m.

Additional specimens — ECUADOR: Zamora-Chinchipe, Est. Cient. San Francisco, Quebrada Milagro, 4 Oct 2000, S. Liede & U. Meve 3460 (UBT); same locality, 18 Dec 2001, D. Wolff 167 (UBT); same locality, 2300 m, 28 Jan 2001, D. Wolff 57 (UBT); along T4, 03°58'18"S, 79°04'44"W, 23 Feb 2000, S. Matezki & J. Homeier 174 (UBT). — PERU: Húanuco, Húanuco, Carpish, 2700–2750 m, 11 Nov 1964, R. Ferreyra 16159 (USM); Pasco, Oxapampa, 10°17'19"S, 75°31'06"W, 1760 m, 3 Feb 2009 (fl.), R. Vásquez & al. 35067 (HOXA!, HUT!, MO!, USM!).

5. *Scyphostelma rotorum* Meve & Y. M. Pineda, sp. nov. — Fig. 3, 9.

Holotype: Peru, Cusco, Paucartambo, Valle del Pilcopata, roadside near Pillahuata, at km 121–126, 13°10'S,

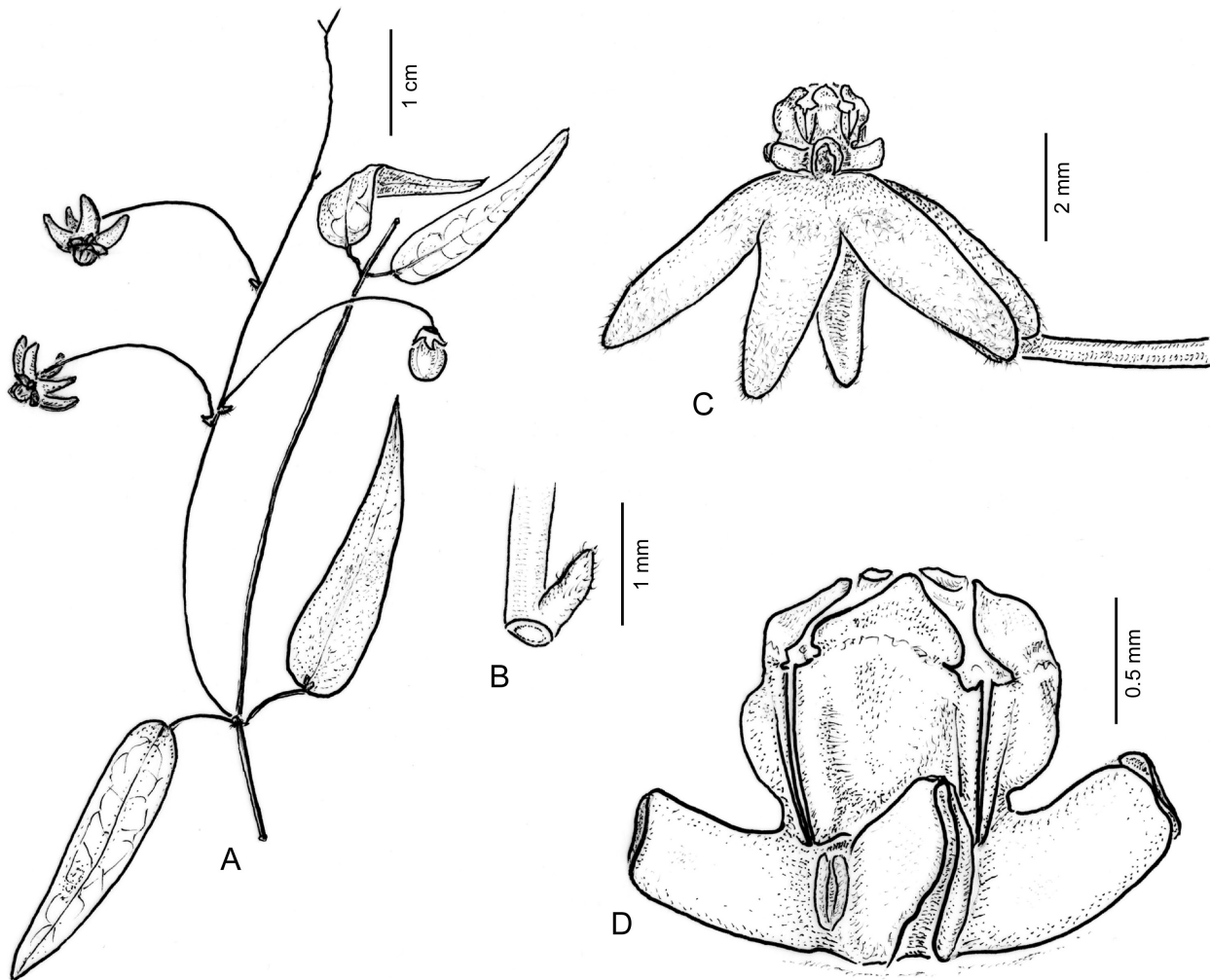


Fig. 9. *Scyphostelma rotorum* – A: flowering branch; B: inflorescence bract; C: flower; D: gynostegium and corona (reconstructed). – A–D from the holotype, R. B. Foster & T. S. Wachter 7498 (USM). – Drawn by U. Meve.

71°30'W, 2500 m, 14 Dec 1983, R. B. Foster & T. S. Wachter 7498 (USM!; isotype: MO-423395).

Diagnosis — Similar to *Scyphostelma harlingii* (Morillo) Liede & Meve but with gynostegial stipe (and corona) reaching just 1/3 of length of gynostegium (vs at least 1/2 of length in *S. harlingii*), corona lobes green, extending horizontally into c. 0.8 mm long, spreading, subrectangular tubes open at bottom (vs corona lobes white to purplish, spreading to 0.3 mm in *S. harlingii*).

Morphological description — Twining plants; stems bright brown, with scattered, retrorse appressed trichomes; internodes of long shoots 55–62 × 1.2–1.5 mm, internodes of short shoots 20–35 × 0.7–1 mm. Leaves discolorous; petiole 4–6 mm long, channelled, densely pilose on upper margin; lamina lanceolate, 15–40 × 4–7 mm, base rounded to subtruncate, apex acute to acuminate; abaxial surface scattered pilose, densely pilose on main veins, adaxial surface with scattered trichomes, with 2 or 3 conic colleters at base; venation brochidodromous with 4–7 pairs of secondary veins. Inflorescenc-

es extra-axillary, alternate, with 3–7 flowers per cyme, at most 2 in simultaneous anthesis; peduncle filiform, 25–45 × 0.4–0.5 mm, glabrous or nearly so; bracts ovate, c. 0.7 × 0.4 mm, abaxially pilose. Flowers: pedicel filiform, 15–25 × 0.2–0.3 mm, glabrous; calyx lobes ovate, c. 0.8 × 0.4 mm, abaxially pilose, margin ciliate, apex subacute; corolla dark purple, rotate, tube c. 2.5 mm in diam., lobes reflexed, oblong-lanceolate, 4–4.5 × 1.2–1.7 mm, abaxially glabrous, adaxial base with scattered trichomes, adaxial distal half covered with short, verrucose trichomes (becoming densely pilose toward tip). Gynostegial corona green with purplish tinge, c. 2 mm in diam., lobes connected to gynostegial stipe, arching upright, c. 0.8 mm high and then horizontally extending to c. 0.5 mm, forming spreading, subrectangular tubes open at bottom; gynostegium stipitate, c. 1 × 1.4 mm, c. 2 × as long as corona lobes, basally narrowing, stipe c. 0.5 × 1 mm; anthers subrectangular, c. 1.1 × 0.8 mm, anther appendages deltate, c. 0.45 × 0.7 mm, translucent, appressed to style head, guide rails c. 0.8 mm long, narrowly triangular, inclined. Style head and pollinaria not seen. Follicles and seeds not seen.

Phenology — The single gathering documented was found flowering in December.

Etymology — The specific epithet refers to the unusual gynostegial corona with the single corona lobes reminiscent of rotor blades.

Remarks — *Scyphostelma rotorum* appears to belong to the *S. harlingii* group for morphological reasons. Particularly in the filiform inflorescence structures and the corolla, *S. rotorum* closely resembles *S. harlingii*, differing only in minor quantitative aspects. Unfortunately, we failed to separate pollinaria. In addition, leaf shape is virtually identical in the two species, even though the leaves of *S. rotorum* are much smaller (15–40 × 4–7 mm vs 30–70 × 7–27 mm in *S. harlingii*). *Scyphostelma harlingii* occurs also in Peru (Fig. 3; two gatherings, see above); therefore *S. rotorum* could be regarded as the most southern extension of *S. harlingii* (into Cusco). However, as we did not observe any floral variability in *S. harlingii*, and as the gynostegial dimensions and coronal structures, though based on the same general structure, are so different from each other in terms of corona lobe shape, size and colour, we propose this as new species endemic to Valle del Pilcopata.

6. *Scyphostelma solomonii* Meve & Y. M. Pineda, sp. nov. — Fig. 3, 10.

Holotype: Bolivia, La Paz, Prov. Murillo, 20.8 km al norte de La Cumbre del valle del Río Zongo, 16°09'S, 68°07'W, 3200 m, 28 Feb 1987, *J. C. Solomon 16120* (MO-3147137!; isotype: K!).

Diagnosis — Similar to *Scyphostelma bolivianum* Y. M. Pineda, Liede & Meve (this paper) but with leaves linear-lanceolate, to 1 cm long (vs ovate-lanceolate, to 4 cm long in *S. bolivianum*), corolla lobes adaxially pubescent (vs glabrous in *S. bolivianum*), gynostegium as long as wide (vs wider than long in *S. bolivianum*), corona lobes deltate, channelled above (vs rounded rectangular and plain in *S. bolivianum*) and nectarial orifices present below each guide rail (vs no such orifices present in *S. bolivianum*).

Morphological description — Twining plants; stems bright green, glabrous or nearly so, internodes of long shoots 100–120 × c. 1.5 mm, internodes of short shoots 15–43 × c. 1 mm. Leaves reduced to scales, shortly petiolate; lamina linear-lanceolate, 4–10 × c. 1 mm, glabrous. Inflorescences subaxillary, with 2–5 flowers per cyme, most in simultaneous anthesis; peduncle (1.5–)10–13 × c. 0.5 mm; bracts ovate, c. 0.8 × 0.2–0.4 mm, glabrous. Flowers: pedicel filiform, 10–15 × c. 0.3 mm, glabrous; calyx purplish, lobes narrowly deltate, c. 2.5 × 1 mm, abaxially with scattered trichomes, margin ciliate; corolla rotate, creamish reddish, 10–14 mm in diam., tube c. 0.2 mm long, free lobes oblong-elliptic, 4.2–5 × 1.8–2.2 mm, spreading, abaxially glabrous, adaxially pubescent, more so api-

cally, trichomes 0.05–0.1 mm long, left side margin and base glabrous. Gynostegial corona creamish, c. 4 mm in diam., shallowly cup-shaped, only very basally fused, free corona lobes suberect (in sicco), deltate, adaxially channelled and apically pointed and notched (retuse), 2–2.3 × 1.5–2 mm; gynostegium stipitate, 2.8–3.7 × 3–4 mm, stipe c. 0.7 mm long; anthers narrowly trapezoidal, c. 2.5 × 1.75 mm, fertile part of anthers c. 1/2 as long as guide rails, abaxially almost flat, anther appendages broadly deltate, c. 0.7 × 0.8 mm, suberect, translucent, guide rails straight, slightly protruding, to 2.7 mm long; style head flattened, c. 1.5 mm in diam., constricted below a salver-shaped apex c. 0.5 mm in diam. Pollinarium: corpusculum broadly obovoid, 0.33–0.4 × 0.24–0.25 mm; caudicles flattened bone-shaped, 0.11–0.17 mm long, spreading; pollinia flattened ellipsoid, 0.40–0.5 × 0.20–0.26 mm, subapically attached to caudicles. Follicles solitary, drooping, reddish brown, straight fusiform, long beaked, 110–120 × 0.7–0.8 mm, glabrous; seeds not seen.

Phenology — The single gathering documented was found flowering and fruiting in February.

Distribution and ecology — *Scyphostelma solomonii* is known from only one locality in the Bolivian Andes at around 3200 m altitude. It was recorded in dense, low-growing (3–5 m tall) cloud forest, together with species of *Barnadesia* Mutis ex L. f., *Chusquea* Kunth, *Myrsine* L. and *Solanum* L.

Etymology — The specific epithet refers to the collector of the type specimen, James C. Solomon, MO senior botanist, collector and collaborator (for *Cactaceae* and *Vitaceae*) in the “Flora of Bolivia” project.

Remarks — Only three narrow leaves, better described as leaf scales, were found to be present in the holotype. In contrast to *Orthosia*, where reduced foliage is regularly observed, the new species represents the first *Scyphostelma* with foliage so strongly reduced in size and number. The large, rotate flowers seated on filiform pedicels and the large and solid pollinaria immediately mark *S. solomonii* as a member of the *S. harlingii* group. These features are particularly reminiscent of *S. bolivianum*. However, the flowers are larger and the corolla pubescent in *S. solomonii* (vs glabrous in *S. bolivianum*); above all, gynostegial and coronal structures are so different in the two taxa that a treatment within a single species is impossible. The staminal corona is deltate, adaxially channelled and apically pointed and notched (retuse) in *S. solomonii*, whereas those of *S. bolivianum* are rounded rectangular, flat and plain. Moreover, the gynostegium is as long as wide in *S. solomonii*, the anther wings (guide rails) c. 2 mm long, straight and slightly protruding, whereas in *S. bolivianum* the gynostegium is wider than long, with guide rails c. 1.3 mm long, slightly convex and curved inward. Below each guide rail, deeply sunken in the fila-

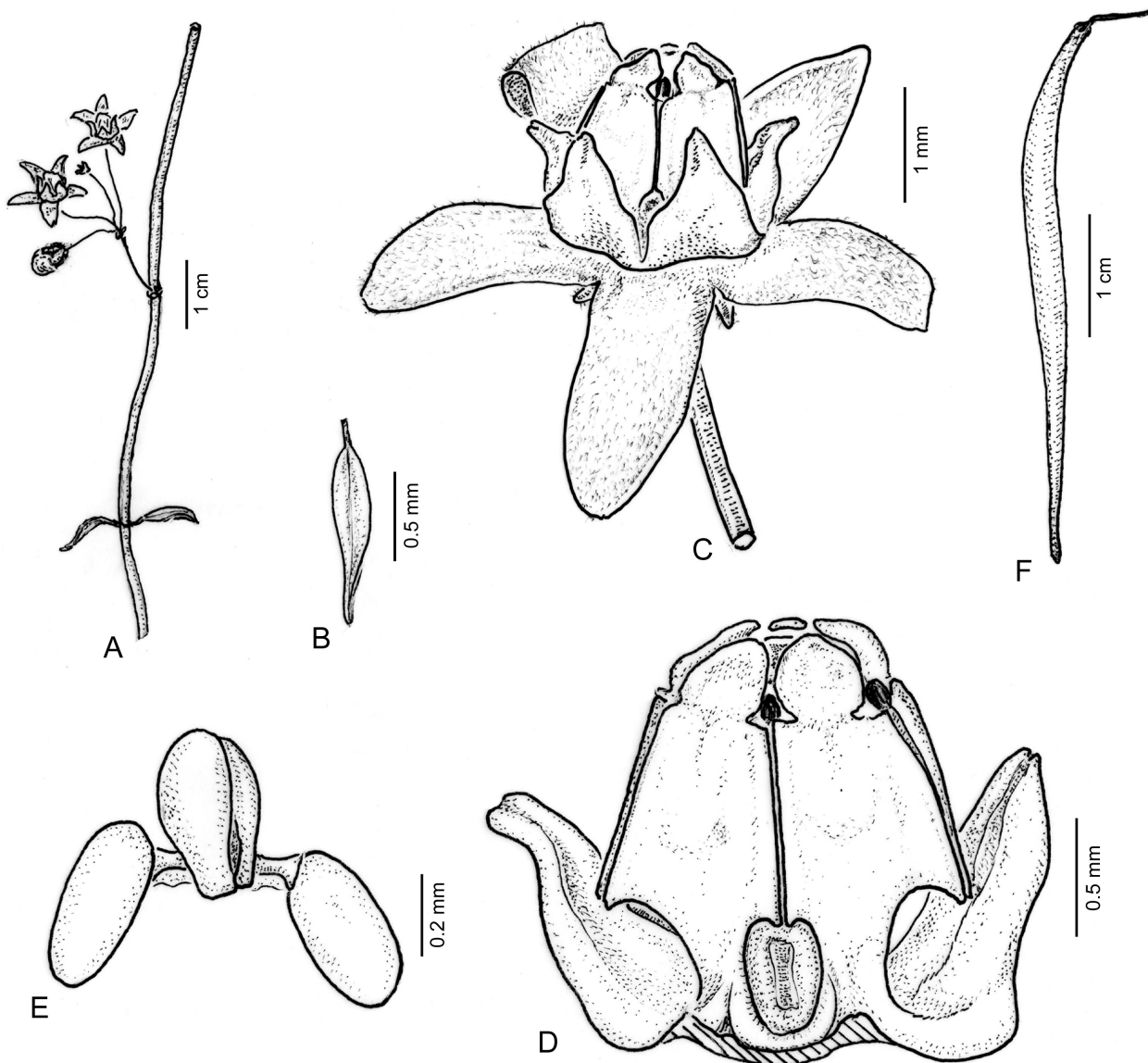


Fig. 10. *Scyphostelma solomonii* – A: flowering branch; B: leaf; C: flower; D: gynostegium; E: pollinarium; F: follicle. – A, C–E from the isotype, *J. C. Solomon 16120* (K); B, F from the holotype, *J. C. Solomon 16120* (MO). – Drawn by U. Meve.

ment tube, *S. solomonii* has a distinct nectarial orifice, which is absent in *S. bolivianum*. The massive and stout pollinaria of *S. solomonii* are remarkable (Fig. 10E); no other species in *Scyphostelma* has larger pollinaria. Ripe follicles are rarely documented on herbarium specimens, especially within the *S. harlingii* group. The holotype of *S. solomonii* represents a lucky exception, because it possesses solitary follicles that are drooping, fusiform and exceptionally large (to 12 cm long). These fruits are more than twice as long as those typically found in *Scyphostelma* (cf. Fig. 14A).

New combinations in *Scyphostelma*

Scyphostelma fasciculiflorum (Morillo) Liede, Meve & Y. M. Pineda, **comb. nov.** \equiv *Cynanchum fasciculiflorum* Morillo in *Ernstia* 2(3–4): 62. 1992. – Holotype: Ecua-

dor, Azuay, Partidero Llantera-Chiquitad-Saucay, bosque húmedo, 3130 m, 7 Feb 1978, *F. I. Ortíz & J. Jaramillo 148* (AAU!; isotype: QCA7980!). – Fig. 11.

Remarks — The ovate, apically rounded, occasionally shortly mucronate leaves with an abaxially yellowish, adaxially whitish indumentum, the dense, rich inflorescences and the trichomes along the upper margin of the adaxial side of the corolla lobes are reminiscent of *Scyphostelma ecuadorensis* (Schltr.) Liede & Meve. The corona lobe shape, however, clearly differentiates the two species: lanceolate-ligulate with a central dorsal fold near the base and a recurved margin in *S. ecuadorensis* vs corona lobes trapezoidal, shouldered and terminating in a central tooth in *S. fasciculiflorum* (cf. Fig. 11).

This species was not included in the phylogenetic analysis.

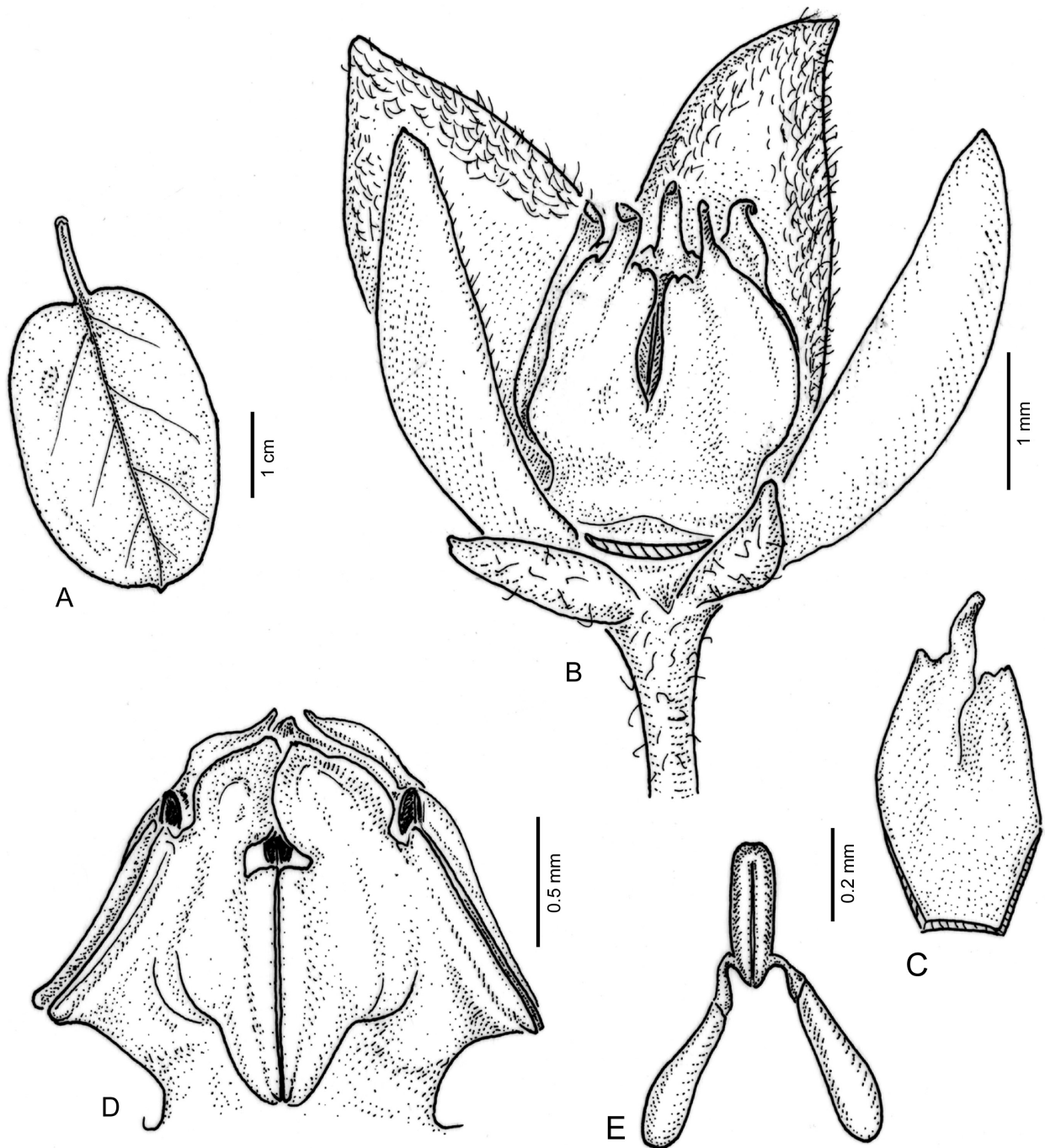


Fig. 11. *Scyphostelma fasciculiflorum* – A: leaf; B: flower, one corolla lobe removed; C: corona lobe, adaxial view; D: gynostegium; E: pollinarium. – A–E from the isotype, F. I. Ortíz & J. Jaramillo 148 (QCA). – Drawn by U. Meve.

Scyphostelma jaramilloi (Morillo) Liede, Meve & Y. M. Pineda, **comb. nov.** \equiv *Cynanchum jaramilloi* Morillo in *Pittieria* 23: 41. 1995. – **Lectotype (designated here):** Ecuador, Pichincha, carretera Chillogallo-San Juan-Chiriboga, empalme alrededor de San Juan, 00°18'S, 78°39'W, 3100–3260 m, Sep 1985, V. Zak & J. Jaramillo 653 (QCA! [determined by W. D. Stevens as “*Cynanchum pichinchense*”]; isoelectotypes: F V0043979F digital image!, GB!, MERF!, MO-078342 digital image!, QCA! [marked “duplicado”], S!). – Fig. 12, Appendix S2, S3.

Iconography — Morillo (1995: 42, fig. 2).

Nomenclatural note — In the protologue of *Cynanchum jaramilloi* (Morillo 1995: 41), the holotype was designated as being in QCA, where in fact there are two specimens belonging to the same gathering. Zak & J. Jaramillo 653. There is no cross-labelling to indicate that they are two parts of a single specimen (Turland & al. 2018: Art. 8.3). Because the type was indicated by reference to a single gathering, the name is validly published but the two specimens are syntypes (Art.

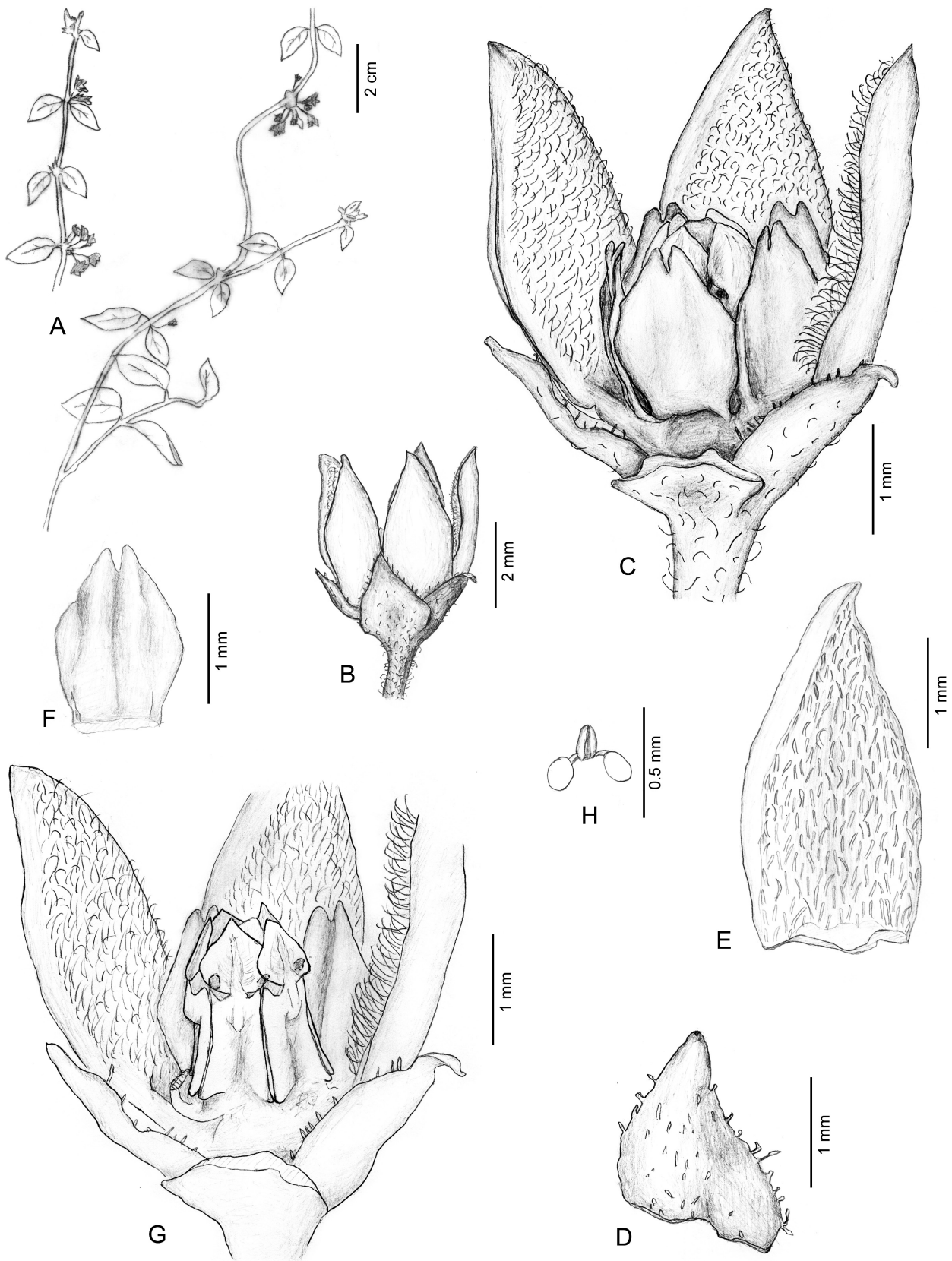


Fig. 12. *Scyphostelma jaramilloi* – A: branch with leaves and inflorescences; B: flower; lateral view; C: flower, two corolla lobes removed; D: sepal; E: corolla lobe; F: corona lobe; G: gynostegium; H: pollinarium; – A–H from the lectotype, *V. Zak & J. Jaramillo* 653 (QCA). – Drawn by B. Neugeboren.

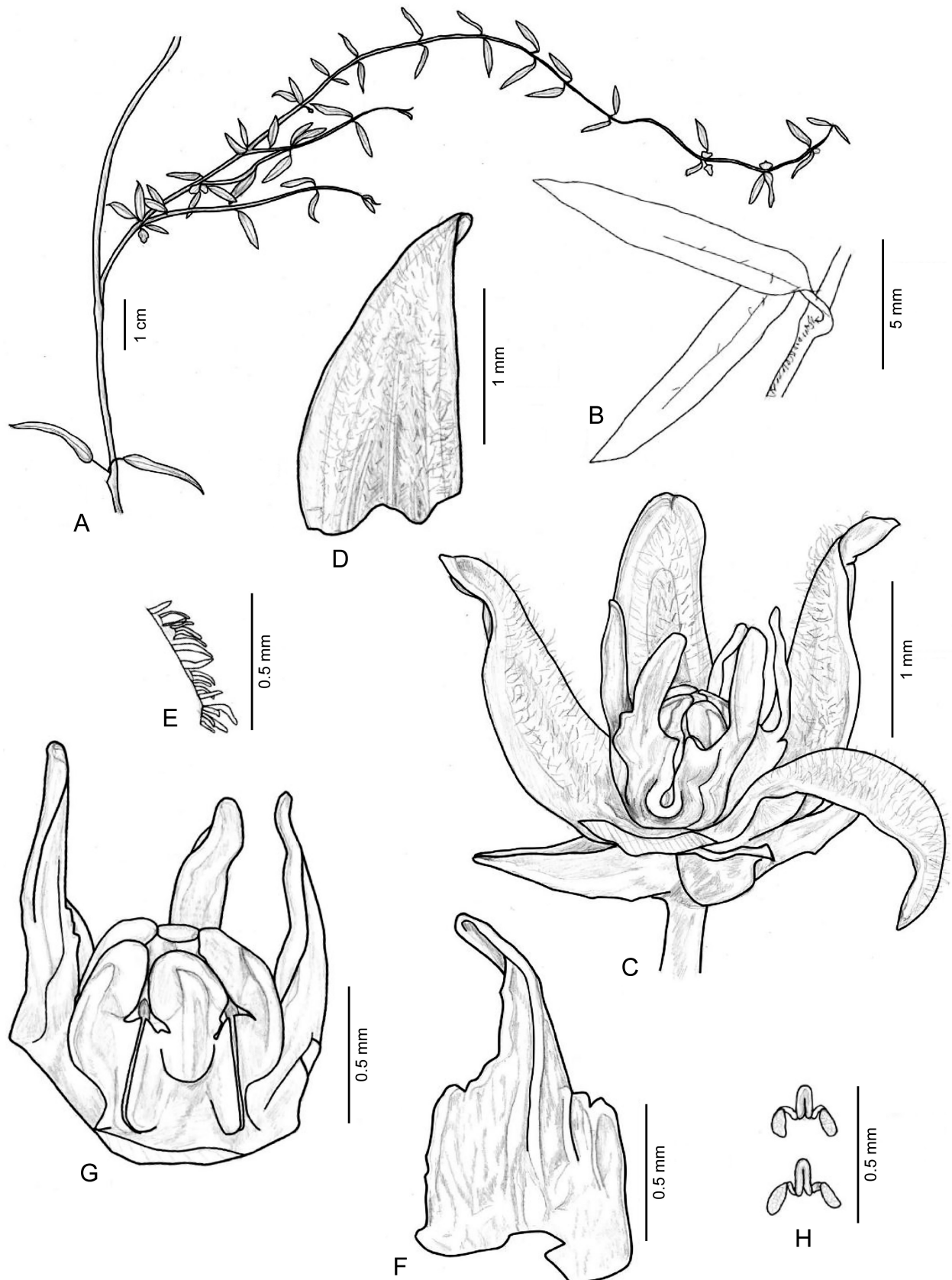


Fig. 13. *Scyphostelma purpurascens* – A: branch with leaves; B: pair of leaves; C: flower; D: corolla lobe; E: corolla trichomes; F: corona lobe; G: gynostegium with corona; H: pollinaria. – A–H from C. Cerón 2765 (QCNE). – Drawn by N. Arzt.

40 Note 1), one of which is therefore selected here as the lectotype.

Remarks — *Scyphostelma jaramilloi* is similar morphologically to other Ecuadorian species of *Scyphostelma* with ovate, acute leaves, such as *S. pichinchense* (K. Schum.) Liede & Meve (the type specimen of *S. jaramilloi* was first identified as *S. pichinchense*) and *S. sodiroi* (K. Schum.) Liede & Meve. Leaf size of *S. jaramilloi* (15–25 × 0.7–1.7 mm) is intermediate between *S. pichinchense* (25–70 × 8–25 mm) and *S. sodiroi* (6–20 × 3–8 mm). In addition, *S. pichinchense* is entirely glabrous, whereas *S. jaramilloi* and *S. sodiroi* bear trichomes both along the stem and on the leaves. Morillo (1995: 23) differentiated *S. jaramilloi* from *S. sodiroi* by its larger leaves, longer pedicels, larger gynostegium and corona lobes slightly shorter than the gynostegium (vs slightly longer than the gynostegium in *S. sodiroi*).

Scyphostelma purpurascens (Benth.) Liede, Meve & Y. M. Pineda, **comb. nov.** ≡ *Metastelma purpurascens* Benth., Pl. Hartw.: 215. 1845. – Holotype: Ecuador, near the town of Quito, 1844, *Hartweg 1191* (K000197128!; isotypes: BM000796239 digital image!, E00259776 digital image!, F V0043858F digital image!, G00177152, G00177153 digital image!, LD1219349 digital image!). – Fig. 13.

Remarks — *Scyphostelma purpurascens* belongs to the *S. microphyllum* group of species as suggested by the small leaves (4–15 × 2–3 mm) on long as well short shoots and flowers (< 5 mm in diam.). Significant for *S. purpurascens* is a gynostegial corona much overtopping a sessile gynostegium, consisting of staminal corona lobes that are transversely rectangular in the basal half while the apical half terminates into a narrowly lanceolate, adaxially canaliculate tooth.

This species was not included in the phylogenetic analysis.

Scyphostelma quitense (K. Schum.) Liede, Meve & Y. M. Pineda, **comb. nov.** ≡ *Cynanchum quitense* K. Schum. in Bot. Jahrb. Syst. 25: 728. 1898. ≡ *Metastelma quitense* (K. Schum.) Liede in Novon 7: 43. 1997. – **Lectotype (designated here)**: Ecuador, Chimborazo, “Inter virgult. prp. pagum Pallatanga”, Sep 1891, *L. Sodiro 107/17* (QPLS7008224). – Appendix S2, S3.

Iconography — Liede & Meve (1997: 43, fig. 4, as *Metastelma quitense*).

Nomenclatural note – Of the two syntypes, *L. Sodiro 107/16* (“In coll. Panecillo ca. Quito”) and *107/17*, none is still extant in B, where Schumann’s original material was housed. QPLS holds a specimen of *Sodiro 107/17* annotated by Schumann’s hand, which is selected as the lectotype here. Of *Sodiro 107/16*, a well-preserved specimen is extant in P (P00644874).

Remarks — The habit of the plants, which at first grow erect, later twining, the slender, linear to lanceolate leaves, the spindle-shaped follicles and in particular the densely bearded corolla lobes support the view expressed by Liede & Meve (1997) that the species belongs in *Metastelma*. However, the present molecular analysis shows that the species is a member of *Scyphostelma* (Appendix S2, S3), in which all the above characters can occur but are not combined in any other species. Therefore, the transfer of this species, which is endemic to central Ecuador (Chimborazo, Pichincha, Tungurahua), to *Scyphostelma* is carried out here. In consequence, no member of *Metastelma* s. str. is presently known to occur in Ecuador.

Scyphostelma stenospira (K. Schum.) Liede, Meve & Y. M. Pineda, **comb. nov.** ≡ *Cynanchum stenospira* K. Schum. in Bot. Jahrb. Syst. 25: 729. 1898. – **Lectotype (designated here)**: Ecuador, Pichincha, near Pomasqui, Sep 1894, *L. Sodiro 107/15* (QPLS210834 digital image!; isolectotypes: F V0043840F digital image!, P00140189!).

Nomenclatural note — Because the original material in B has been destroyed, lectotypification is necessary. Of the three located duplicates, the specimen in QPLS is particularly well preserved and therefore selected to serve as the lectotype. The isotype in F consists of a single short shoot only (“kleptotype”) together with a photograph of the destroyed holotype in B.

Remarks — The affinities of *Scyphostelma stenospira* are unclear. The species shares narrowly linear leaves with *S. purpurascens* and *S. quitense*, but its leaf texture is much more membranous than in those species. The corona is reminiscent of *S. fasciculiflorum* (Fig. 11) and *S. purpurascens* with staminal lobes broadly rectangular in the basal half but then suddenly shouldered and terminating in a longer tooth.

This species was not included in the phylogenetic analysis.

Scyphostelma unguiculatum (Britton) Liede, Meve & Y. M. Pineda, **comb. nov.** ≡ *Vincetoxicum unguiculatum* Britton in Bull. Torrey Bot. Club 25: 499. 1898 ≡ *Cynanchum unguiculatum* (Britton) Markgr. in Notizbl. Bot. Gart. Berlin-Dahlem 11: 788. 1933. – **Lectotype (designated here)**: Bolivia, La Paz, Unduavi, 8000 ft, Oct 1885, *H. H. Rusby 1044* (NY01288243!). – Fig. 14, Appendix S2, S3.

Nomenclatural note — Of the syntypes cited in the protologue, *Rusby 2518* (NY01288245!, NY01288246!) and *Rusby 1044* (NY01288243!, NY01288244!), one specimen bears a pollinarium drawing, and the printed description by Britton, and is therefore selected here as the lectotype of *Vincetoxicum unguiculatum*.

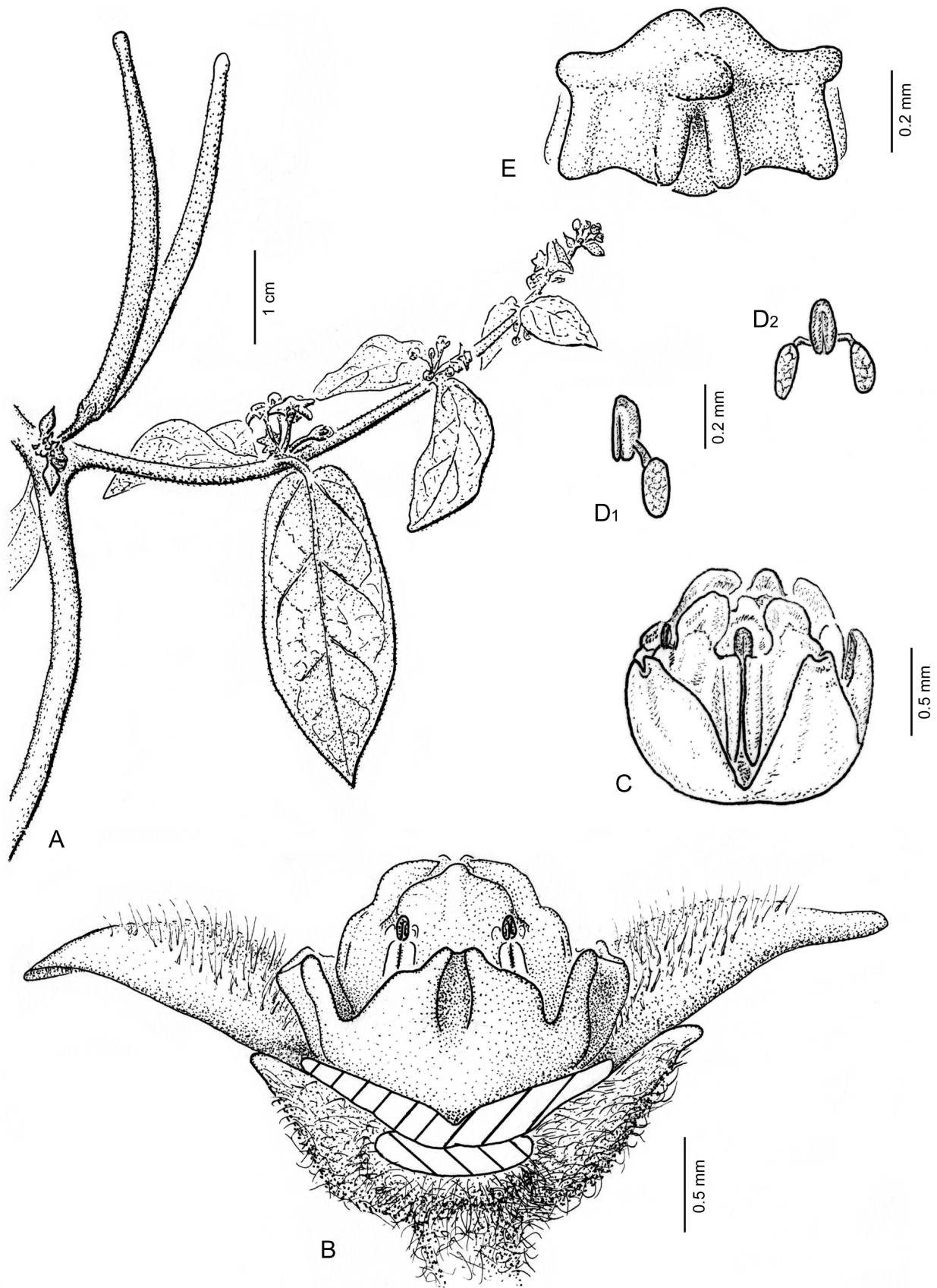


Fig. 14. *Scyphostelma unguiculatum* – A: branch with inflorescences and twin follicles; B: flower, two corolla lobes removed; C: gynostegium and corona; D₁: pollinarium, one pollinium removed; D₂: pollinarium; E: style head. – A, B, E from S. Liede & J. Conrad 3140 (UBT); C, D, from H. Ruiz & J. A. Pavón 5/80 (MA814543); D₂ from J. R. I. Wood 10086 (LPB). – A, B, E drawn by J. Conrad; C, D drawn by U. Meve.

Markgraf's (in Pilger 1933: 788) citing "Peru: Ruiz et Pavon" on publishing *Cynanchum unguiculatum* can be considered an indirect reference to Britton's (in Rusby 1898: 499) "*Vincetoxicum unguiculatum* (R. & P.) Britton" (cf. Turland & al. 2018: Art. 41 Ex. 3 and 7). The Peruvian specimens of Ruiz and Pavón to which Markgraf (1933) was referring, *H. Ruiz & J. A. Pavón 5/80* (F V0040239F digital image!, MA814543!, MA814544!, MO-2290015!), conform to the concept of *S. unguiculatum*.

Remarks — *Scyphostelma unguiculatum* is one of the most frequent species of *Scyphostelma* around La Paz. It is multi-leaved with fairly stout stems covered by an obvious hispid to tomentose indumentum; the flowers are medium-sized (c. 5 mm in diam.), the corolla whitish and tomentose and the bowl-shaped corona whitish to rose-coloured; the follicles are puberulent to pubescent (Fig. 14).

Author contributions

Designing the research: HAK, UM, NMN, SLS; performing the research: YMP, HAK, JABT, UM, SLS; methodology: YMP, UM, SLS; field work: HAK, JABT; statistical analysis: YMP; visualization: YMP, HAK, UM; curation and analysis of data: YMP, UM, SLS; taxonomic descriptions: YMP, HAK, UM, SLS; writing the paper: YMP, HAK, UM, SLS; reviewing and editing the paper: YMP, UM, NMN, SLS; resources: NMN; funding acquisition: SLS; project administration: UM, NMN, SLS; supervision: NMN, SLS.

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Supplemental content online

See <https://doi.org/10.3372/wi.53.53201>

Appendix S1. Alignment. DNA matrix comprising 108 taxa (57 outgroup, 51 ingroup) and 5607 characters from six cpDNA regions.

Appendix S2: GTR+ Γ . Maximum likelihood tree of the concatenated dataset under GTR+ Γ . Numbers on branches indicate bootstrap percentages. Colours indicate the origin of a sample; blue: Bolivia; blue-green: Ecuador; green: Peru; pink: Venezuela-Colombia.

Appendix S3. GTR+ Γ +I. Bayesian tree of the concatenated dataset under GTR+ Γ +I. Numbers on branches indicate Posterior Probabilities. Colours indicate the origin of a sample; blue: Bolivia; blue-green: Ecuador; green: Peru; pink: Venezuela-Colombia.

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Appendix 1. Species of *Orthostinae* included in this study, with herbarium vouchers and GenBank accession information in support of the molecular phylogeny (cf. Fig. 1). Sequences generated for the present study are indicated in **bold** and specimens included in the morphological analysis are indicated by a superscript ^m. Under *trnL-trnF*, two accession numbers refer to the *trnL* intron and the *trnL-trnF* intergenic spacer, respectively, whereas a single accession number refers to the whole region, i.e. intron and spacer.

Species	Voucher	Geographic origin	<i>trnT-trnL</i>	<i>trnL-trnF</i>	<i>rps16</i>	<i>trnD-trnT</i>	<i>psbA-trnH</i>	<i>trnS-trnG</i>
Outgroup								
<i>Jobinia formosa</i> (N. E. Br.) Liede & Meve	<i>Liede & Conrad 3061</i> (MSUN)	Chile: Coquimbo	AJ428639	(AJ428640, AJ428641)	AJ699346	HE611900	OM128312	OM032690
<i>Jobinia hatschbachii</i> Fontella	<i>Konno 856</i> (SP)	Brazil: São Paulo	HE611705	(HE611763, HE611802)	HE611842	HE611894	OM128313	OM032691
<i>Jobinia latipes</i> (Malme) Liede & Meve	<i>Keller 9727</i> (CTES)	Argentina: Misiones	ON571739	ON571787	ON571838	ON571936	ON571973	ON571887
<i>Jobinia latipes</i>	<i>Tressens & al. 6647</i> (CTES, UBT)	Argentina: Misiones	HE611706	(HE611764, HE611803)	HE611843	HE611895	OM128314	OM032692
<i>Jobinia lindbergii</i> E. Fourn.	<i>Keller & Hildt 11694</i> (CTES)	Argentina: Misiones	ON571740	ON571788	ON571839	ON571937	ON571974	ON571888
<i>Jobinia lindbergii</i>	<i>Farinaccio 194</i> (SPF)	Brazil	AJ704491	AY163694	AJ704490	–	–	DQ026770
<i>Jobinia longirostris</i> ined.	<i>Wood 8727</i> (K)	Bolivia: Chuquisaca	ON571741	ON571789	ON571840	–	ON571975	ON571889
<i>Jobinia longirostris</i>	<i>Wood 8762</i> (K)	Bolivia: Chuquisaca	ON571742	ON571790	ON571841	–	ON571976	ON571890
<i>Jobinia longirostris</i>	<i>Wood & Goyder 15578</i> (K, UBT)	Bolivia: Santa Cruz	AJ704313 ^a	(AJ704315 ^a , AJ704314 ^b)	AJ704312 ^a	HE611901 ^a	OM128321	OM032699
<i>Jobinia peruviana</i> Liede & Meve	<i>Hutchinson & Wright 5439</i> (S)	Peru: Cajamarca	HE611707	(HE611765, HE611804)	HE611844	HE611896	OM128315	OM032693
<i>Jobinia</i> sp. nov.	<i>Wolff 110</i> (UBT)	Ecuador: Zamora-Chinchipe	HE611704	HE611751	HE611842	HE611893	OM128311	OM032689
<i>Jobinia streptantha</i> (Malme) Liede & Meve	<i>Liede & Meve 3550</i> (UBT)	Ecuador: Bolivar	HE611708	(HE611766, HE611805)	HE611845	HE611897	OM128316	OM032694
<i>Jobinia tarmensis</i> (Schltr.) Liede & Meve	<i>Tupayachi & Galiano 761</i> (NY)	Peru: Cuzco	AJ428744	(AJ428745, AJ428746)	AJ699349	–	–	–
<i>Jobinia tarmensis</i>	<i>Becker & Terrones 728</i> (ULM)	Colombia: Quindio	OL907316	OL907376	OL907442	–	OM128317	OM032695
<i>Jobinia tarmensis</i>	<i>Liede & Meve 3452</i> (UBT)	Peru: Huanuco	OL907317	OL907377	–	OM049003	–	–
<i>Jobinia trifurcata</i> (Griseb.) Liede & Meve	<i>Liede-Schumann & al. 3636</i> (CORD)	Argentina: La Rioja	HE611709	HE611752	HE611846	HE611898	OM128318	OM032696

<i>Jobinia trifurcata</i>	Wood & al. 15308 (K, UBT)	Bolivia: Chuquisaca	HE611710	HE611753	HE611847	HE611899	OM128319	OM032697
<i>Jobinia umbellata</i> (Rusby) Liede & Meve	Beck 17838 (LPB)	Bolivia: La Paz	ON571743	ON571791	ON571842	ON571938	ON571977	ON571891
<i>Jobinia umbellata</i>	Beck 22892 (LPB)	Bolivia: La Paz	ON571744	ON571792	ON571843	–	ON571978	ON571892
<i>Jobinia umbellata</i>	Mello-Silva 2104 (LPB)	Bolivia: Cochabamba	ON571745	ON571793	ON571844	–	ON571979	ON571893
<i>Jobinia umbellata</i>	Nee 40327 (LPB)	Bolivia: Santa Cruz	ON571746	ON571794	ON571845	–	ON571980	ON571894
<i>Jobinia umbellata</i>	Goyder sub Wood 15798 (K, UBT)	Bolivia: La Paz	AJ704317	(AJ704316, AJ704318)	AJ704319	HE611902	OM128320	OM032698
<i>Monsamina morrenioides</i> (Goyder) Liede & Meve	Omlor 160 (MJG)	Brazil: Bahia	AJ428684	(AJ428685, AJ428686)	AJ699348	HE611903	OM128310	OM032688
<i>Monsamina tinguanaensis</i> R. G. P. Santos & Fontella	J. Silva Neto & al. 1654 (RB)	Brazil: Rio de Janeiro	KJ566592	KJ566593	KJ566594	–	–	–
<i>Orthostia angustifolia</i> (Turcz.) Liede & Meve	Nee 33059 (NY)	Mexico: Veracruz	HE611711	(HE611767, HE611806)	HE611848	HE611904	OM128323	OM032701
<i>Orthostia angustifolia</i>	Reyes A-5219 (XAL)	Mexico: Veracruz	HE611712	HE611754	HE611849	HE611905	OM128324	OM032702
<i>Orthostia boliviana</i> Liede & Meve, ined.	Wood & Goyder 15776 (K, UBT)	Bolivia: Santa Cruz	HE611732 ^b	(HE611786 ^b , HE611825)	HE611868 ^b	HE611926 ^b	OM128328	OM032706
<i>Orthostia calycina</i> (Schltr.) Liede & Meve	Weigend & al. 7530 (B)	Peru: Cajamarca	HE611716	HE611755	HE611853	HE611909	OM128330	OM032708
<i>Orthostia congesta</i> (Vell.) Decne.	Konno 855 (SP)	Brazil: Rio de Janeiro	HE611717	(HE611771, HE611810)	HE611854	HE611910	OM128332	OM032710
<i>Orthostia ellemannii</i> (Morillo) Liede & Meve	Liede & Meve 3457 (UBT)	Ecuador: Loja	AJ428780	(AJ428781, AJ428782)	AJ699350	HE611918	OM128336	OM032714
<i>Orthostia ellemannii</i>	Matezki 161 (UBT)	Ecuador: Loja	HE611719	(HE611773, HE611812)	HE611856	HE611912	OM128337	OM032715
<i>Orthostia florida</i> (Vell.) Liede & Meve	van der Werff & Wingsfield 7441 (NY)	Venezuela: Falcón	HE611730 ^b	(HE611784 ^b , HE611823 ^b)	HE611866 ^b	–	OM128346	OM032724
<i>Orthostia goyderiana</i> Liede & Meve	Wood 15994 (K, UBT)	Bolivia: Cochabamba	HE611739 ^c	HE611759 ^c	OL907468	HE611933 ^c	OM128364	OM032733
<i>Orthostia meridensis</i> (Morillo) Liede & Meve	Liede & Meve 3310 (UBT)	Venezuela: Barinas	HE611721	(HE611775, HE611814)	HE611858	HE611914	OM128363	OM032741

Species	Voucher	Geographic origin	<i>trnT-trnL</i>	<i>trnL-trnF</i>	<i>rps16</i>	<i>trnD-trnT</i>	<i>psbA-trnH</i>	<i>trnS-trnG</i>
<i>Orthostia mexicana</i> (S. Watson) Liede & Meve, ined.	Hinton & al. 24347 (NY)	Mexico: Nuevo Leon	AJ428783	(AJ428784, AJ428785)	AJ699351	HE611919	OM128364	OM032742
<i>Orthostia mexicana</i>	Valdés & al. 1961 (NY)	Mexico: Nuevo León	HE611720 ^e	(HE611774 ^e , HE611813 ^c)	HE611857 ^e	HE611913 ^e	OM128366	OM032744
<i>Orthostia pallida</i> (Rusby) Liede & Meve	Liede & Meve 3311 (UBT)	Venezuela: Mérida	HE611714 ^f	(HE611769 ^f , HE611808 ^b)	HE611851 ^f	HE611907 ^f	OM128371	OM032749
<i>Orthostia pearcei</i> (Rusby) Liede & Meve	Wood 10514 (K, UBT)	Bolivia: Cochabamba	HE611723	(HE611777, HE611816)	–	HE611916	OM128376	OM032754
<i>Orthostia pubescens</i> (Greenman) Liede & Meve	Prinzle & al. 207 (TEX)	Mexico: México	HE611724	(HE611778, HE611817)	HE611860	HE611917	OM128378	OM032756
<i>Orthostia pubescens</i>	Ventura 555 (NY)	Mexico: México	HE611725	(HE611779, HE611818)	HE611861	–	OM128379	OM032757
<i>Orthostia retinaculata</i> (Schltr.) Liede & Meve	Wood & al. 13292 (K)	Bolivia: Chuquisaca	HE611715 ^f	OL907424	HE611909 ^f	HE611908 ^f	OM128384	OM032762
<i>Orthostia scoparia</i> (Nutt.) Liede & Meve	Acevedo & al. 7714 (NY)	Puerto Rico	AJ704320	(AJ704322, AJ704321)	OL907488	HE611920	OM128389	OM032767
<i>Orthostia scoparia</i>	Axelrod 8409 (NY)	Puerto Rico	HE611726	(HE611780, HE611819)	HE611862	HE611921	OM128390	OM032768
<i>Orthostia scoparia</i>	Easley 542 (NY)	U.S.A.: Florida	HE611727	(HE611781, HE611820)	HE611863	HE611922	OM128391	OM032769
<i>Orthostia scoparia</i>	Mangelsdorff RMC 246 (UBT)	Cuba: Guantanamo	HE611728	(HE611782, HE611821)	HE611864	HE611923	OM128392	OM032770
<i>Orthostia scoparia</i>	Mangelsdorff RMC 3125 (FR)	Cuba: Cienfuegos	HE611729	(HE611783, HE611822)	HE611865	HE611924	OM128393	OM032771
<i>Orthostia scoparia</i>	Fishbein 5280 (OKLA)	U.S.A.: Florida	KF539851	KF539851	KF539851	KF539851	KF539851	KF539851
<i>Orthostia scoparia</i> subsp. <i>crassiuscula</i> (Schltr.) Liede & Meve	Mika & al. 072 (FR)	Dominican Republic: La Vega	HE611733 ^g	HE611756 ^g	HE611869 ^g	HE611927 ^g	OM128394	OM032772
<i>Orthostia scoparia</i> subsp. <i>crassiuscula</i>	Mika & al. 073 (FR)	Dominican Republic: La Vega	HE611734 ^h	(HE611787 ^g , HE611826 ^g)	OL907489	HE611928 ^h	OM128395	OM032773

<i>Orthosia</i> sp.	<i>Conrad 9306</i> (UBT)	Mexico: Michoacán	HE611713 ^f	(HE611768 ^f , HE611807 ^g)	HE611849 ^f	HE611906 ^f	OM128398	OM032776	
<i>Orthosia stenophylla</i> Schltr.	<i>Liede & Meve 3487</i> (ex hort.)	Ecuador: Carehi	HE611718 ^h	(HE611772 ^d , HE611811 ^d)	HE611855 ^d	HE611911 ^d	OM128360	OM032738	
<i>Orthosia subulata</i> (Vell.) Liede & Meve	<i>Wasum & al. 7930</i> (NY)	Brazil: Rio Grande do Sul	HE611731 ^b	(HE611785 ^b , HE611824 ^b)	HE611867 ^b	HE611925 ^b	OM128402	OM032780	
<i>Orthosia teodormeyeri</i> Liede & Meve	<i>Galetto 723</i> (CORD, NY)	Argentina: Córdoba	HE611722 ^h	(HE611776 ^h , HE611815 ^h)	HE611859 ^h	HE611915 ^h	OM128404	OM032782	
<i>Orthosia teodormeyeri</i>	<i>Morero 112</i> (CORD)	Argentina: Córdoba	HE611736 ⁱ	HE611757 ⁱ	–	HE611930 ⁱ	OM128408	OM032786	
<i>Orthosia teodormeyeri</i>	<i>Liede-Schumann & al. 3640</i> (CORD)	Argentina: Catamarca	HE611738 ^h	HE611758 ^h	–	HE611932 ^h	OM128407	OM032785	
<i>Orthosia urceolata</i> E. Fourn.	<i>Carriño 27500</i> (NY)	Brazil: Paraná	AJ704324	(AJ704323, AJ704325)	OL907496	HE611934	OM128410	OM032788	
<i>Orthosia woodii</i> Meve & Liede	<i>Wood 10369</i> (K)	Bolivia: Chuquisaca	HE611737	(HE611789, HE611828)	HE611872	HE611931	OM128415	OM032793	
Ingroup									
<i>Scyphostelma beckii</i> (Morillo) Liede & Meve	<i>Liede & Conrad 3141</i> (MSUN, ULM) ^m	Bolivia: La Paz	AJ704305	(AJ704307, AJ704306)	AJ704304	–	–	–	
<i>Scyphostelma bifidum</i> (Liede & Meve) Liede & Meve	<i>Liede & Meve 3557</i> (UBT) ^m	Ecuador: Azuay	HE611740	(HE611790, HE611829)	HE611873	HE611935	–	–	
<i>Scyphostelma bolivianum</i> Y. M. Pineda, Liede & Meve	<i>Beck 3191</i> (LPB)	Bolivia: Sud Yungas	ON571778	ON571829	ON571878	–	ON572013	ON571927	
<i>Scyphostelma bolivianum</i>	<i>Wood 11598</i> (K) ^m	Bolivia: Cochabamba	ON571779	ON571830	ON571879	–	ON572014	ON571928	
<i>Scyphostelma ecuadorensis</i> (Schltr.) Liede & Meve	<i>Harling & Ståhl 26512</i> (S)	Ecuador: Loja	HE611741	(HE611791, HE611830)	HE611874	HE611936	OM128416	OM032795	
<i>Scyphostelma ecuadorensis</i>	<i>Liede & Meve 3556</i> (UBT) ^m	Ecuador: Chimborazo	HE611748	(HE611797, HE611836)	HE611880	HE611943	OM128417	OM032794	
<i>Scyphostelma gracile</i> H. A. Keller, Meve & Liede	<i>Porcel 302</i> (CTES)	Bolivia: Cochabamba	ON571753	ON571801	ON571852	ON571944	ON571987	ON571901	
<i>Scyphostelma gracile</i>	<i>Wood 10297</i> (K, UBT) ^m	Bolivia: Cochabamba	HE611750 ⁱ	(HE611799 ⁱ , HE611838 ⁱ)	HE611882 ⁱ	HE611945 ⁱ	OM128418	OM032796	

Species	Voucher	Geographic origin	trnT-trnL	trnL-trnF	rps16	trnD-trnT	psbA-trnH	trnS-trnG
<i>Scyphostelma harlingii</i> (Morillo) Liede & Meve	<i>Liede & Meve 3460</i> (UBT) ^m	Ecuador: Zamora-Chunchipe	AJ704309	(AJ704308, AJ704310)	AJ704311	HE611946	OM128419	OM032797
<i>Scyphostelma</i> cf. <i>isidrense</i> (Morillo) Liede & Meve	<i>Liede & Meve 3320</i> (UBT)	Venezuela: Mérida	ON571754	ON571802	ON571853	ON571945	ON571988	ON571902
<i>Scyphostelma jaramilloi</i> (Morillo) Liede, Meve & Y. M. Pineda	<i>Liede & Meve 3502</i> (UBT) ^m	Ecuador: Pichincha	ON571755	ON571803	ON571854	ON571946	ON571989	ON571903
<i>Scyphostelma lechleri</i> (Morillo) Liede & Meve	<i>Liede & Conrad 3136</i> (MSUN, ULM)	Bolivia: La Paz	AJ428753	(AJ428754, AJ428755)	HE611883	HE611947	–	–
<i>Scyphostelma microphyllum</i> (Kunth) Liede & Meve	<i>Cerón & Alcarón 12217</i> (MO)	Ecuador: Pichincha	AJ428681	(AJ428682, AJ428683)	AJ699347	–	OM128420	–
<i>Scyphostelma</i> aff. <i>microphyllum</i>	<i>Homeier s.n.</i> (UBT)	Ecuador: Cotopaxi	ON571756	ON571804	ON571855	ON571947	ON571990	ON571904
<i>Scyphostelma</i> aff. <i>microphyllum</i>	<i>Liede & Meve 3343</i> (UBT) ^m	Ecuador: Pichincha	ON571757	ON571805	ON571856	ON571948	ON571991	ON571905
<i>Scyphostelma</i> aff. <i>microphyllum</i>	<i>Liede & Meve 3473</i> (UBT) ^m	Ecuador: Pichincha	HE611744 ^f	(HE611794 ^f , HE611833 ^g)	HE611876 ^f	HE611939 ^f	OM128421	OM032798
<i>Scyphostelma</i> aff. <i>microphyllum</i>	<i>Liede & Meve 3474</i> (UBT) ^m	Ecuador: Pichincha	HE611745 ^f	HE611760 ^f	HE611877 ^f	HE611940 ^f	OM128422	OM032799
<i>Scyphostelma</i> aff. <i>microphyllum</i>	<i>Liede & Meve 3480</i> (UBT)	Ecuador: Carchi	ON571758	ON571806	ON571857	ON571949	ON571992	ON571906
<i>Scyphostelma microphyllum</i>	<i>Liede s.n.</i> (UBT)	Ecuador: Pichincha	ON571759	ON571807	ON571858	ON571950	ON571993	ON571907
<i>Scyphostelma</i> aff. <i>pichinchense</i> (K. Schum.) Liede & Meve	<i>Liede & Meve 3484</i> (UBT) ^m	Ecuador: Carchi	ON571760	ON571808	ON571859	ON571951	ON571994	ON571908
<i>Scyphostelma quitense</i> (K. Schum.) Liede, Meve & Y. M. Pineda	<i>Céron & Mortesdesca 16008</i> (MO) ^m	Ecuador: Pichincha	ON571761	ON571809	ON571860	ON571952	ON571995	ON571909
<i>Scyphostelma serpyllifolium</i> (Kunth) Liede & Meve	<i>Liede & Meve 3482</i> (UBT) ^m	Ecuador: Carchi	ON571762	ON571810	ON571861	ON571953	ON571996	ON571910
<i>Scyphostelma serpyllifolium</i>	<i>Liede & Meve 3553</i> (UBT) ^m	Ecuador: Bolívar	ON571763	ON571811	ON571862	ON571954	ON571997	ON571911
<i>Scyphostelma</i> sp. <i>Cajanuma</i>	<i>Liede & Meve 3462</i> (UBT)	Ecuador: Loja	ON571764	ON571812	ON571863	ON571955	ON571998	ON571912
<i>Scyphostelma</i> sp. <i>indet. c</i>	<i>Liede & Meve 3551</i> (UBT) ^m	Ecuador: Bolívar	ON571765	ON571813	ON571864	ON571956	ON571999	ON571913

<i>Scyphostelma</i> sp. indet. c	<i>Liede & Meve 3552</i> (UBT) ^m	Ecuador: Bolívar	HE611746	(HE611795, HE611834)	HE611878	HE611941	OM128423	OM032802
<i>Scyphostelma</i> sp. indet. d	<i>Liede & Meve 3563</i> (UBT)	Ecuador: Loja	HE611749	(HE611798, HE611837)	HE611881	HE611944	OM128424	OM032803
<i>Scyphostelma</i> sp. indet. f	<i>Weigend & al. 5821</i> (B) ^m	Peru: Cajamarca	HE611742	(HE611792, HE611831)	HE611875	HE611937	OM128425	OM032804
<i>Scyphostelma</i> sp. indet. g	<i>Ollerton 260</i> (UBT) ^m	Peru: Cuzco	ON571766	ON571814	–	–	–	–
<i>Scyphostelma</i> sp. indet. h	<i>Ortuno 319</i> (LPB) ^m	Bolivia: Cochabamba	–	ON571815	ON571865	–	–	ON571914
<i>Scyphostelma</i> sp. indet. i	<i>Ortuno 508</i> (LPB)	Bolivia: La Paz	ON571767	ON571816	ON571866	–	ON572000	ON571915
<i>Scyphostelma</i> sp. indet. k	<i>Liede 3647</i> (UBT)	Colombia: Antioquia	–	ON571817	ON571867	–	ON572001	ON571916
<i>Scyphostelma</i> sp. indet. k	<i>Liede 3648</i> (UBT)	Colombia: Antioquia	ON571768	ON571818	ON571868	ON571957	ON572002	ON571917
<i>Scyphostelma</i> sp. indet. k	<i>Liede 3649</i> (UBT)	Colombia: Antioquia	ON571769	ON571819	ON571869	ON571958	ON572003	ON571918
<i>Scyphostelma</i> sp. indet. l	<i>Liede & Meve 3489</i> (UBT) ^m	Ecuador: Carchi	ON571770	ON571820	ON571870	ON571959	ON572004	ON571919
<i>Scyphostelma</i> sp. indet. m	<i>Liede & Meve 3490</i> (UBT) ^m	Ecuador: Carchi	ON571771	ON571821	ON571871	ON571960	ON572005	ON571920
<i>Scyphostelma</i> sp. indet. n	<i>Liede & Meve 3494</i> (UBT) ^m	Ecuador: Napo	ON571772	ON571822	–	ON571961	ON572006	ON571921
<i>Scyphostelma</i> sp. indet. o	<i>Fuentes 16333</i> (LPB) ^m	Bolivia: La Paz	ON571773	ON571823	ON571872	ON571962	ON572007	ON571922
<i>Scyphostelma</i> sp. indet. p	<i>Matezki 145</i> (UBT) ^m	Ecuador: Loja	ON571774	ON571824	ON571873	ON571963	ON572008	ON571923
<i>Scyphostelma</i> sp. indet. q	<i>Porcel 254</i> (CTES)	Bolivia: Cochabamba	ON571775	ON571825	ON571874	ON571964	ON572009	ON571924
<i>Scyphostelma</i> sp. indet. r	<i>Morillo 11972</i> (NY)	Venezuela: Mérida	ON571776	ON571826	ON571875	ON571965	ON572010	ON571925
<i>Scyphostelma</i> sp. indet. s	<i>Weigend & al. 7522</i> (B) ^m	Peru: Cajamarca	ON571777	ON571827	ON571876	ON571966	ON572011	ON571926
<i>Scyphostelma</i> sp. indet. t	<i>Luteyn & Berg 14375</i> (OCA) ^m	Ecuador: Pichincha	–	ON571828	ON571877	–	ON572012	–
<i>Scyphostelma</i> aff. <i>unguiculatum</i> (Britton) <i>Liede, Meve & Y. M. Pineda</i>	<i>Beck 7443</i> (LPB) ^m	Bolivia: Cochabamba	ON571781	ON571832	ON571881	ON571967	ON572016	ON571930
<i>Scyphostelma unguiculatum</i>	<i>Beck 22326</i> (LPB) ^m	Bolivia: La Paz	ON571784	ON571833	ON571882	ON571968	ON572017	ON571931
<i>Scyphostelma unguiculatum</i>	<i>Beck 22327</i> (LPB) ^m	Bolivia: La Paz	ON571782	ON571834	ON571883	ON571969	ON572018	ON571932
<i>Scyphostelma unguiculatum</i>	<i>Liede & Conrad 3140</i> (LPB, MO, MSUN, ULM) ^m	Bolivia: La Paz	ON571783	ON571835	ON571884	ON571970	ON572019	ON571933

Species	Voucher	Geographic origin	trnT-trnL	trnL-trnF	rps16	trnD-trnT	psbA-trnH	trnS-trnG
<i>Scyphostelma unguiculatum</i>	Wood 15800 (LPB) ^m	Bolivia: La Paz	ON571785	ON571836	ON571885	ON571971	ON572020	ON571934
<i>Scyphostelma vezizae</i> (Morillo) Liede & Meve	Idarraga & al. 4047 (HUA)	Colombia: Antioquia	ON571786	ON571837	ON571886	–	ON572021	ON571935
<i>Scyphostelma velutinum</i> (Morillo) Liede & Meve	Liede & Meve 3555 (UBT) ^m	Ecuador: Chimborazo	HE611747	(HE611796, HE611835)	HE611879	HE611942	OM128426	OM032800
<i>Scyphostelma wurdackii</i> (Morillo) Liede & Meve	Liede 3342 (UBT) ^m	Ecuador: Cuenca	HE611743	(HE611793, HE611832)	–	HE611938	–	OM032801

^a in GenBank under *Jobinia* sp. SLS-2015

^b in GenBank under *Orthosia scoparia*

^c in GenBank under *Orthosia* sp. Wood 15994 (K)

^d in GenBank under *Orthosia ellemannii*

^e in GenBank under *Orthosia kunthii*

^f in GenBank under *Orthosia bonplandiana*

^g in GenBank under *Orthosia scoparia* (no subspecies indicated)

^h in GenBank under *Orthosia pearcei*

ⁱ in GenBank under *Scyphostelma* sp. Wood 10297 (K)

^j in GenBank under *Scyphostelma* sp.