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

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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 &

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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-

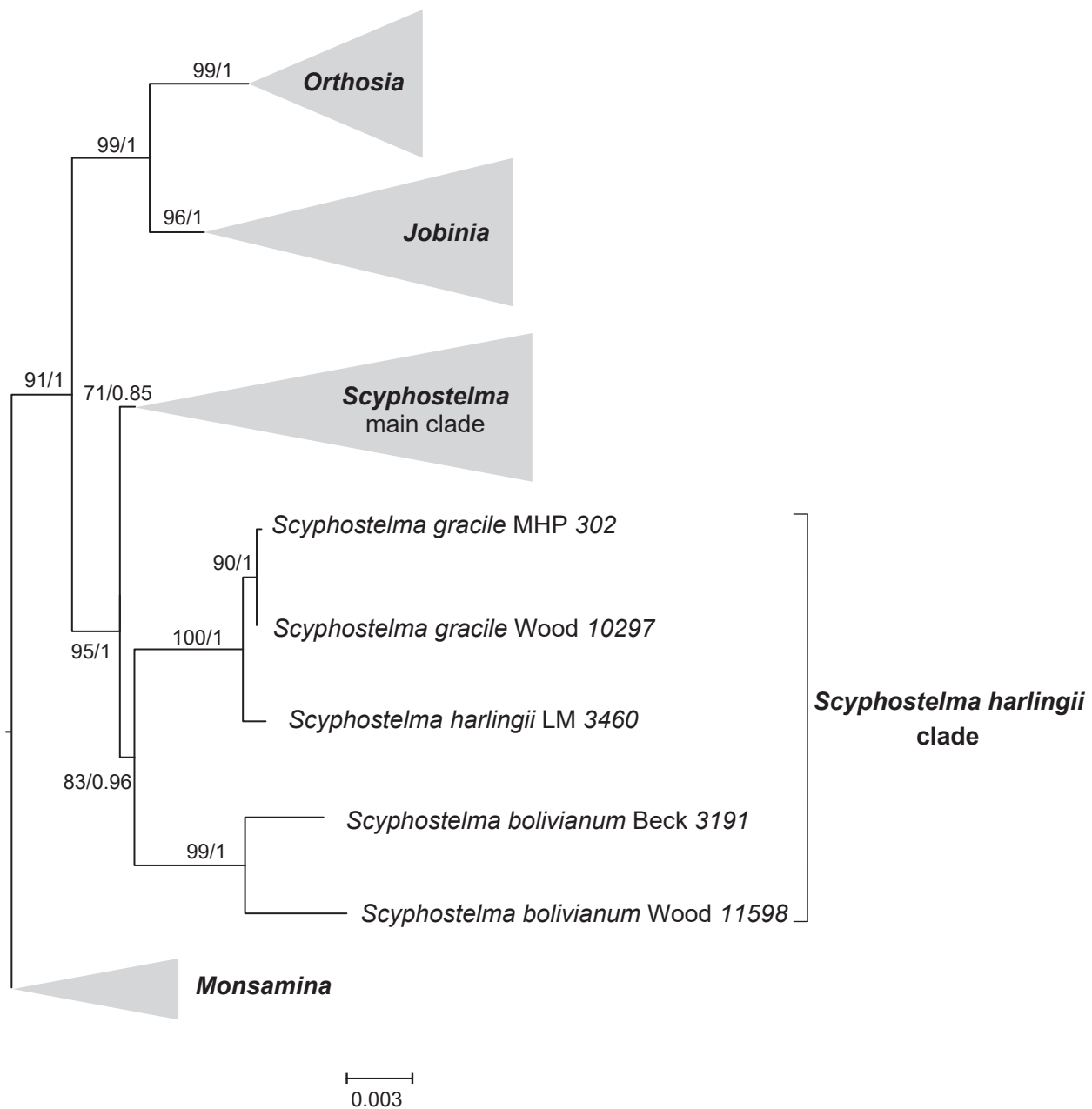


Fig. 1. Phylogenetic reconstruction of *Orthosiinae* based on six cpDNA markers (see text), highlighting the position of the *Scyphostelma harlingii* clade. The remaining genera of *Orthosiinae*, *Jobinia*, *Monsamina* and *Orthosia*, with a sampling identical to Liede-Schumann & Meve (2013), are summarized 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+ $\Gamma$  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+ $\Gamma$ +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

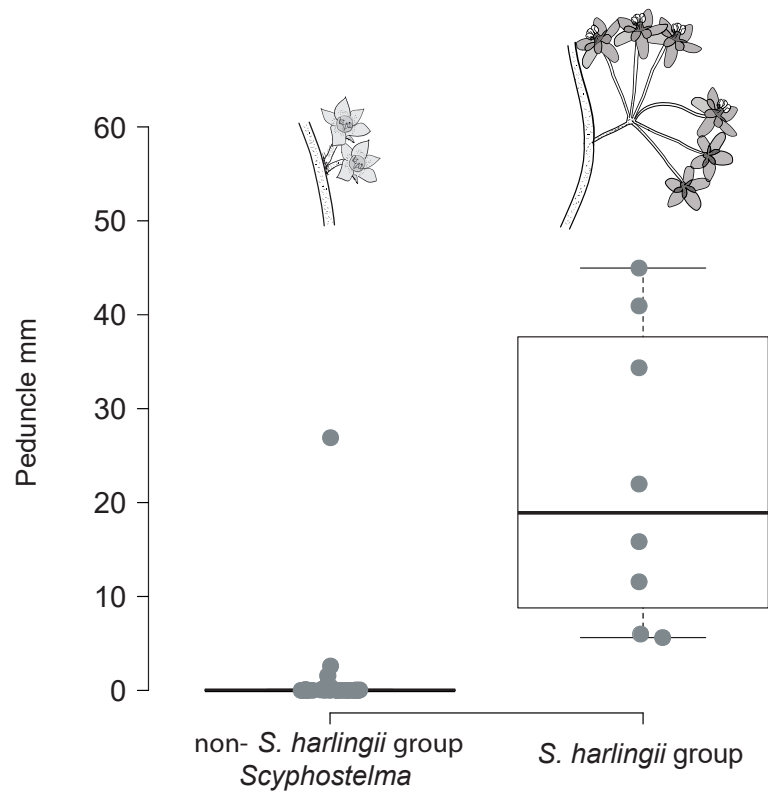


Fig. 2. Boxplot comparing the size of the peduncles between the species within the *Scyphostelma harlingii* group ( $n = 8$ ) and the remaining species in the genus ( $n = 31$ ). t-test: mean diff. = 21.55,  $df = 7.3$ ,  $p = 0.005$ . Schemes above boxplots illustrate the characteristic shape of inflorescences 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!).



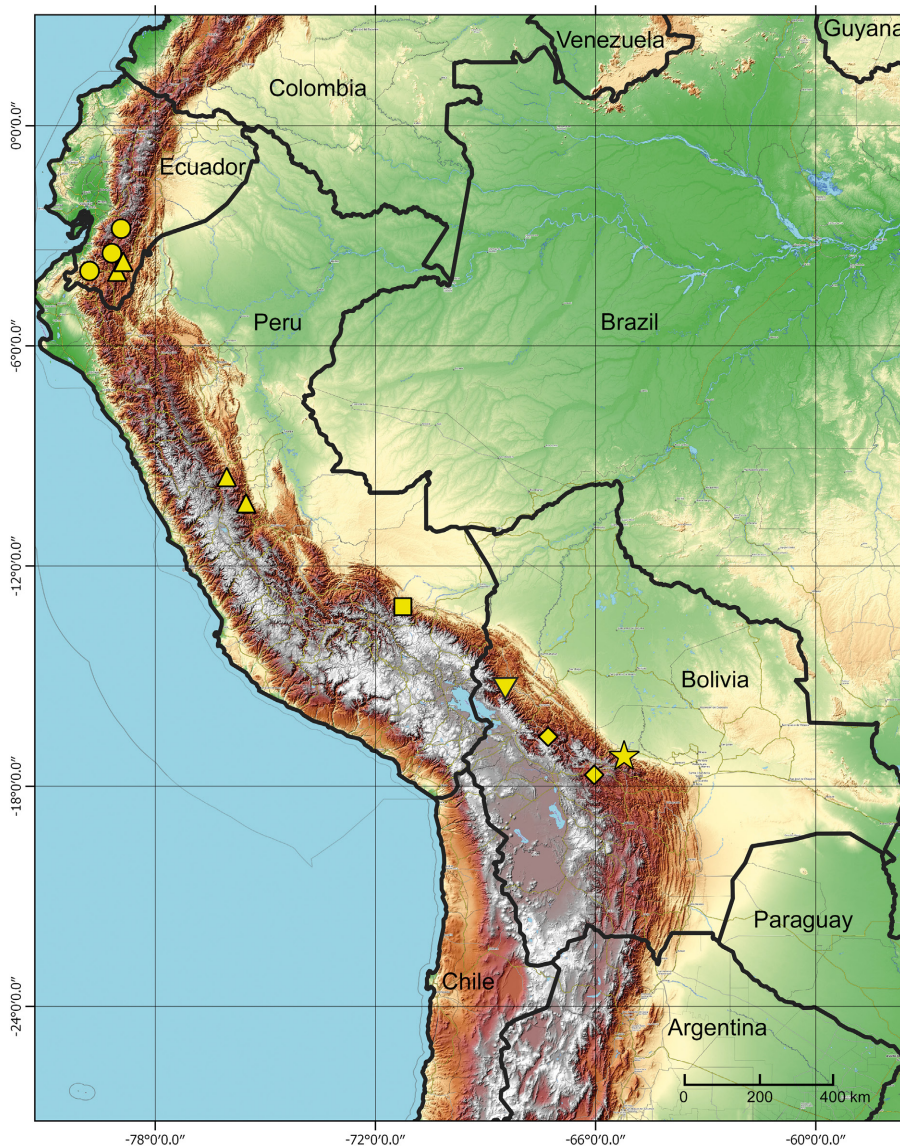


Fig. 3. Distribution map of *Scyphostelma bolivianum* (diamonds), *S. erikseniae* (circles), *S. gracile* (stars), *S. harlingii* (upright triangles), *S. rotorum* (square) and *S. solomonii* (inverted triangle). – Map created in QGIS (QGIS Development Team 2009).

**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.

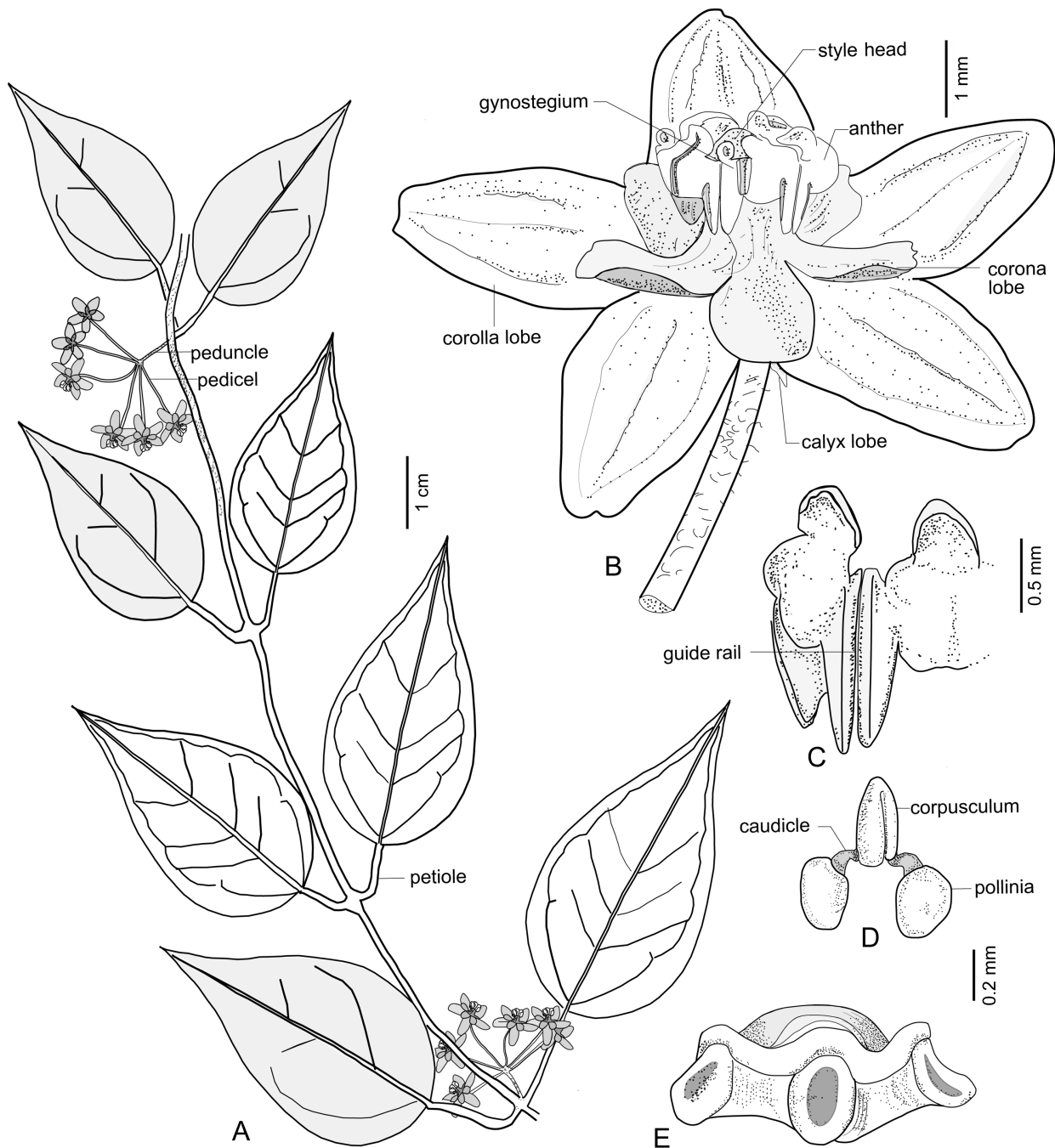


Fig. 4. *Scyphostelma bolivianum* – A: flowering branch; B: flower; C: two anthers and guide rail; D: pollinarium; E: style head. – A–E from the holotype, *J. R. I. Wood 11598* (K). – Drawn by Y. M. Pineda.

*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.** ≡ *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 × 1.2–1.7 mm, internodes of short shoots 22–33 × 0.5–0.7 mm. Leaves: petiole 4–7 mm long, glabrous; lamina lanceolate-oblong or suboblong, 23–45 × 2–8 mm,



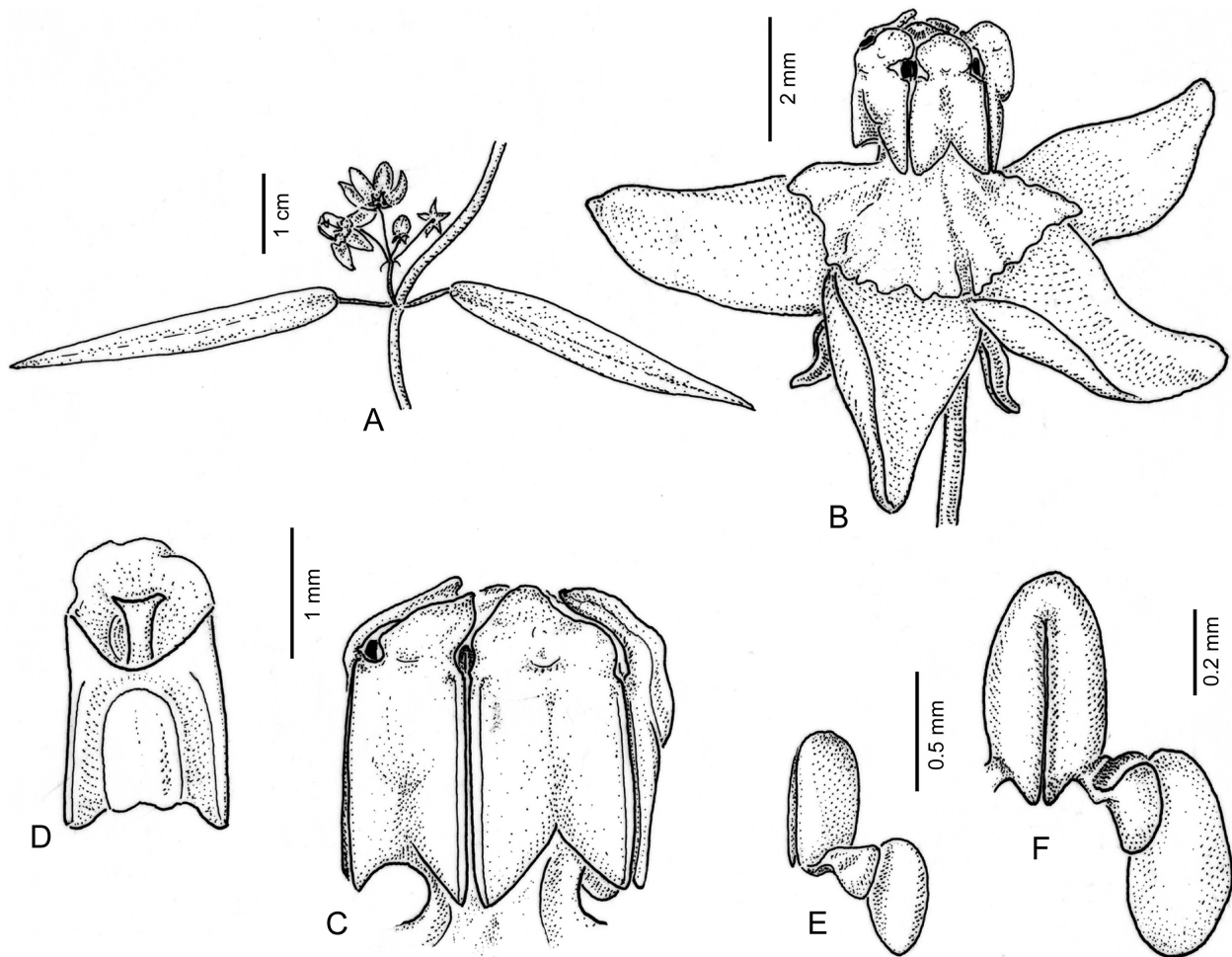


Fig. 5. *Scyphostelma erikseniae* – A: stem node with two leaves and inflorescence; B: flower; C: gynostegium; D: anther, adaxial view; E: pollinarium, one pollinium missing, lateral view; F: pollinarium, one pollinium missing, frontal view. – A–F from *G. Harling 745* (S). – Drawn by U. Meve.

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).



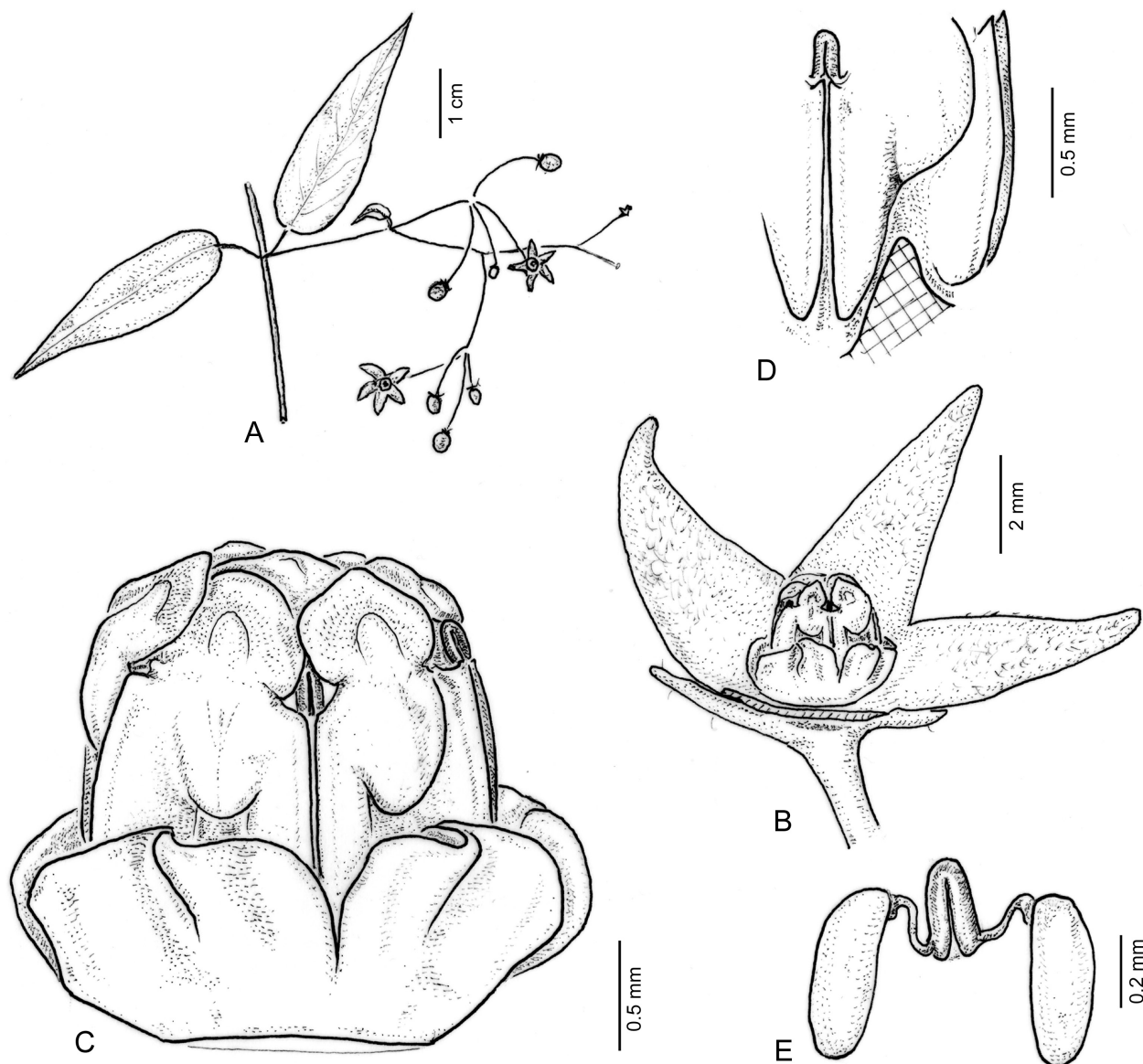


Fig. 6. *Scyphostelma gracile* – A: stem node with two leaves and inflorescence; B: flower, two petals removed; C: gynostegium with corona; D: details of guide rails (one in frontal, one in lateral view), with area of attachment of the corona (cross-hatched); E: pollinarium. – A–E from the isotype, *J.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



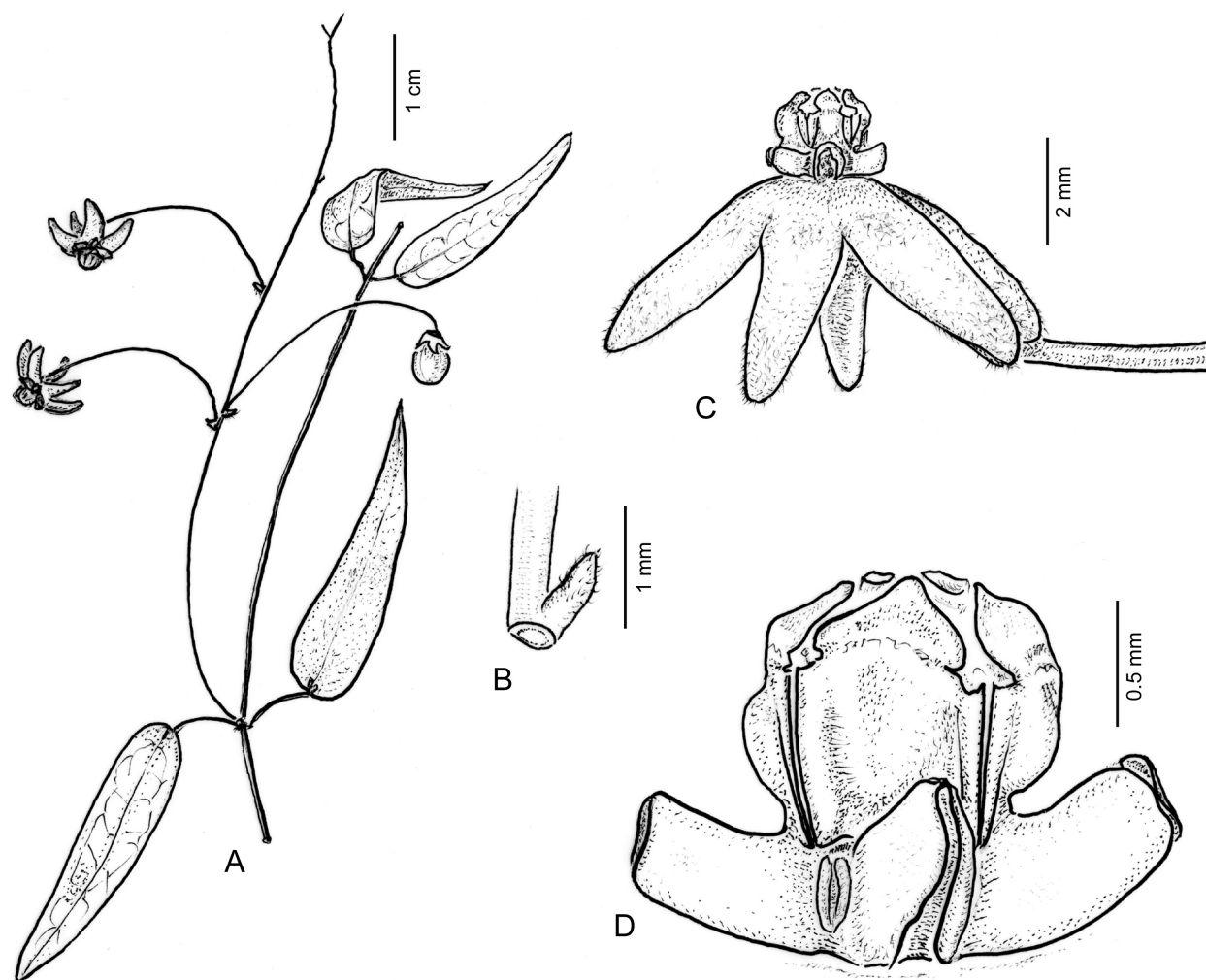


Fig. 9. *Scyphostelma rotorum* – A: flowering branch; B: inflorescence bract; C: flower; D: gynostegium and corona (reconstructed). – A–D from the holotype, R. B. Foster & T. S. Wachter 7498 (USM). – Drawn by U. Meve.

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-

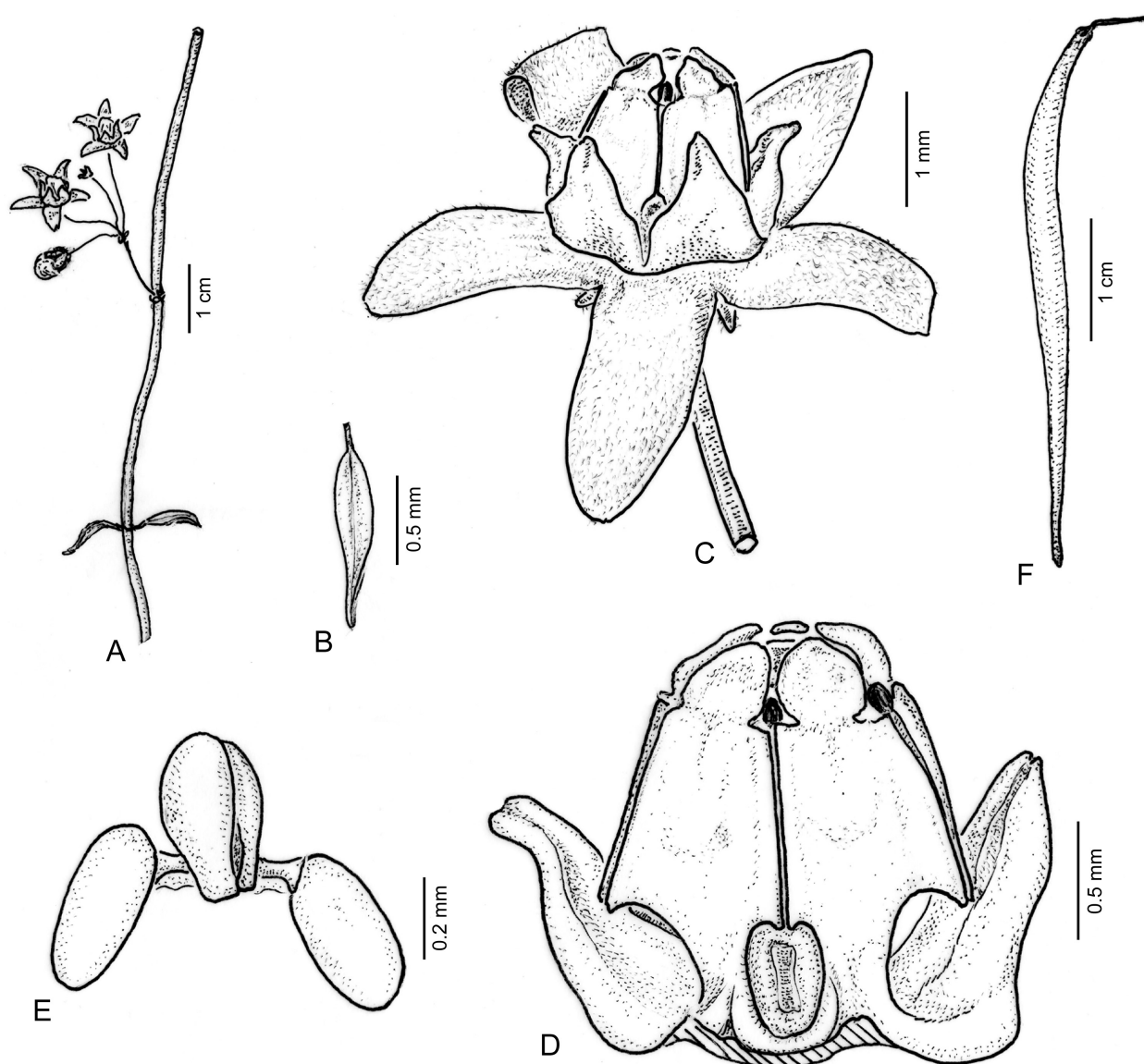


Fig. 10. *Scyphostelma solomonii* – A: flowering branch; B: leaf; C: flower; D: gynostegium; E: pollinarium; F: follicle. – A, C–E from the isotype, *J. C. Solomon 16120* (K); B, F from the holotype, *J. C. Solomon 16120* (MO). – Drawn by U. Meve.

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.

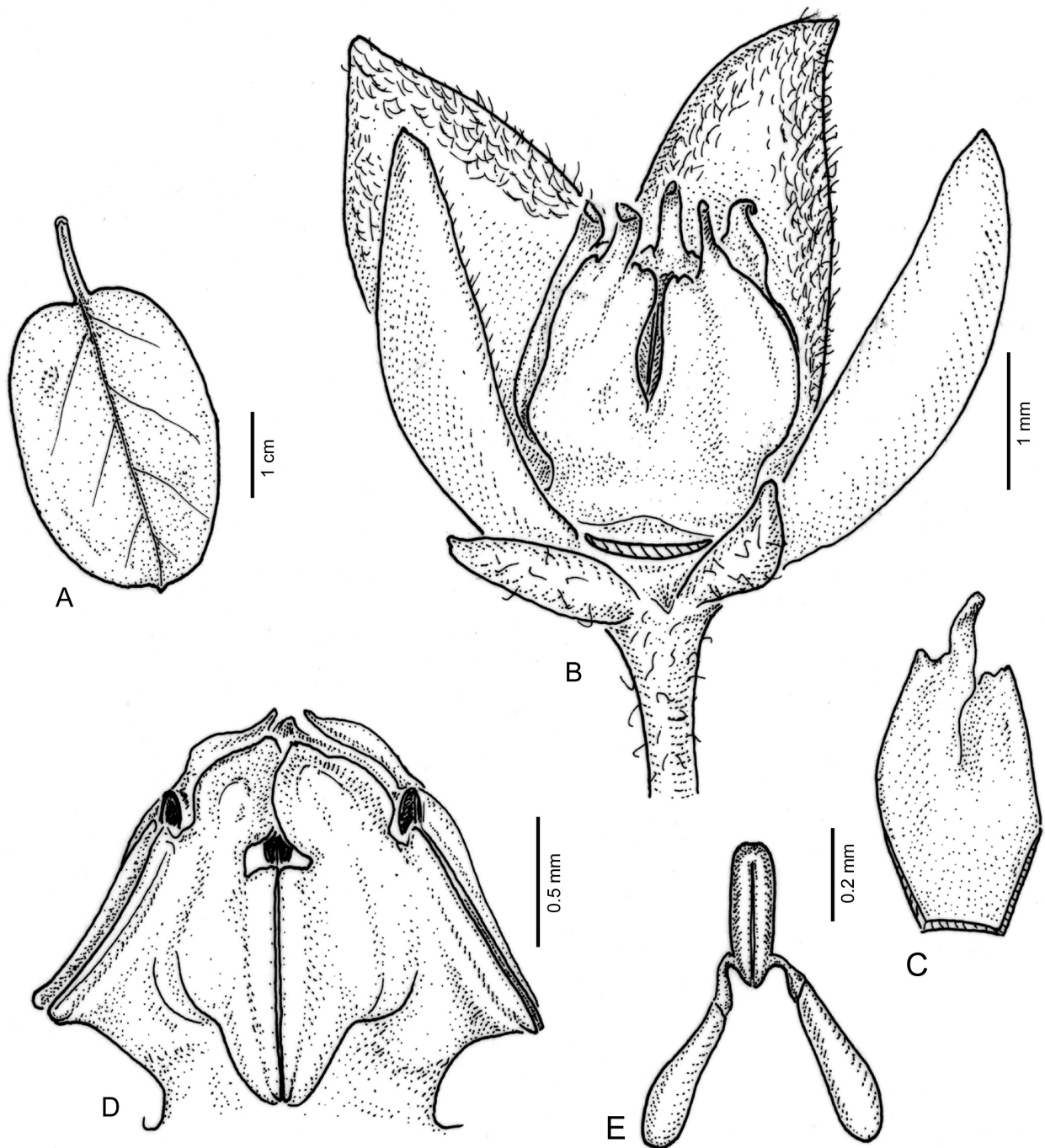


Fig. 11. *Scyphostelma fasciculiflorum* – A: leaf; B: flower, one corolla lobe removed; C: corona lobe, adaxial view; D: gynostegium; E: pollinarium. – A–E from the isotype, F. I. Ortíz & J. Jaramillo 148 (QCA). – Drawn by U. Meve.

*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.



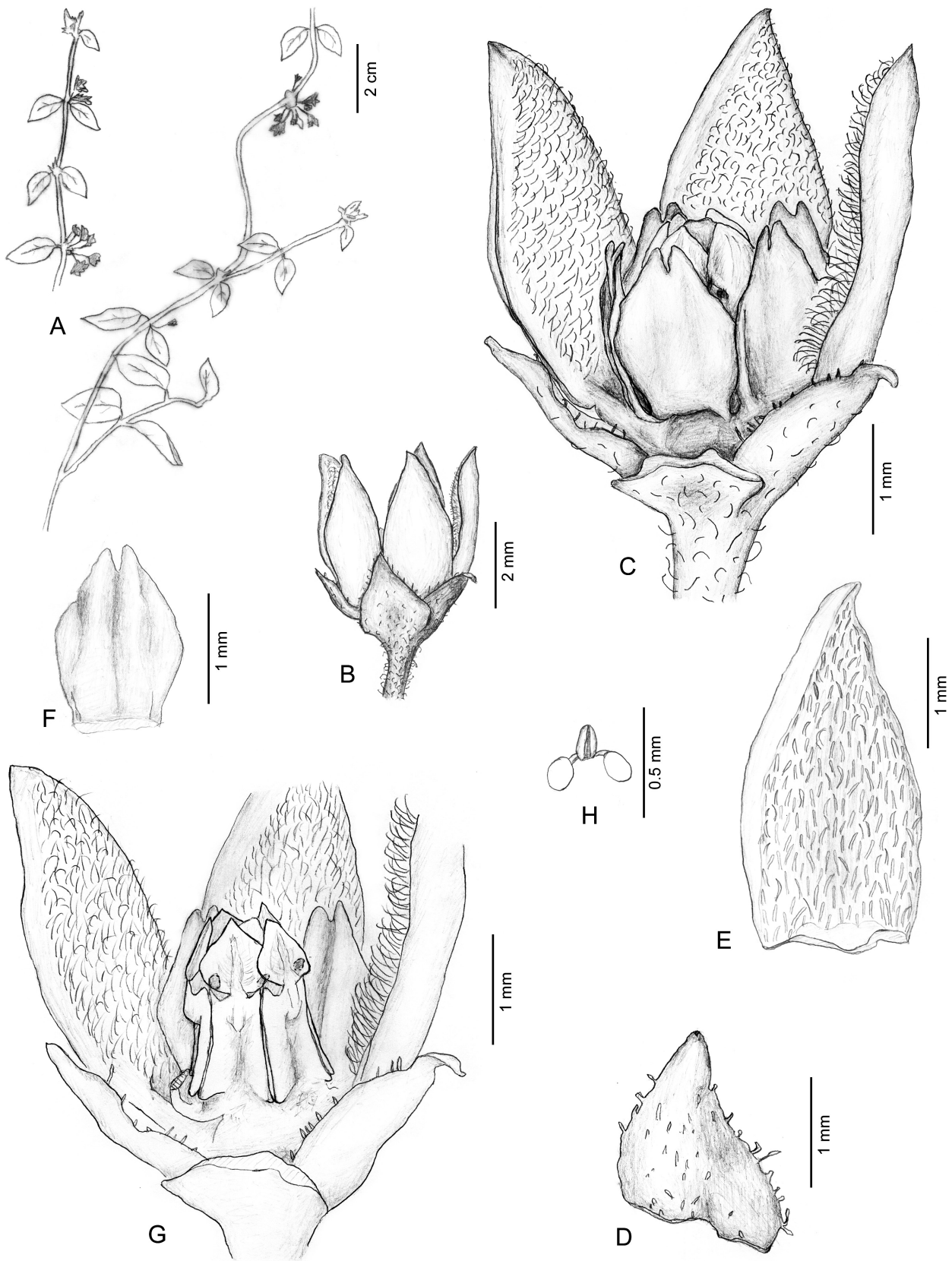


Fig. 12. *Scyphostelma jaramilloi* – A: branch with leaves and inflorescences; B: flower; lateral view; C: flower, two corolla lobes removed; D: sepal; E: corolla lobe; F: corona lobe; G: gynostegium; H: pollinarium; – A–H from the lectotype, *V. Zak & J. Jaramillo* 653 (QCA). – Drawn by B. Neugeboren.

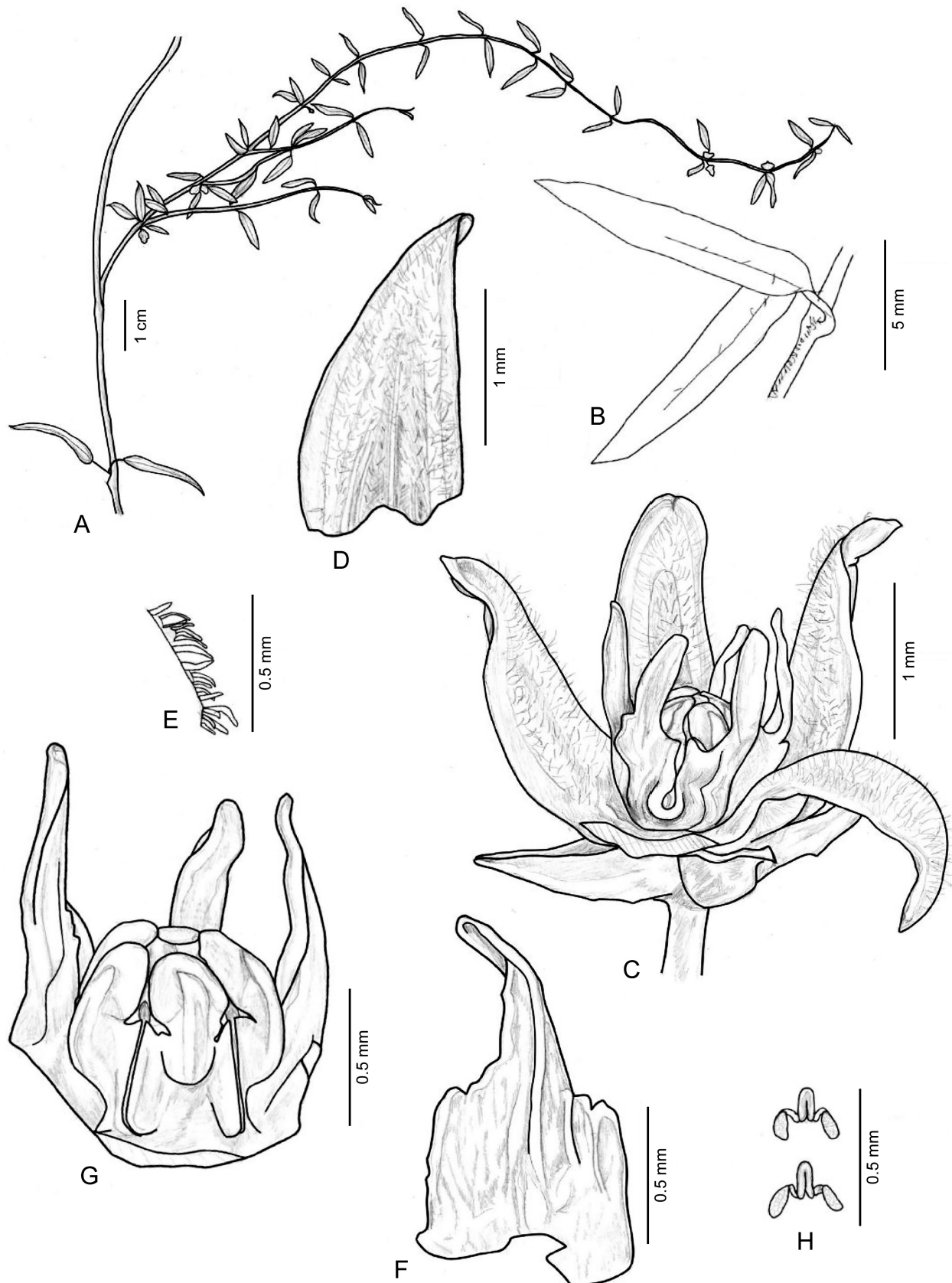


Fig. 13. *Scyphostelma purpurascens* – A: branch with leaves; B: pair of leaves; C: flower; D: corolla lobe; E: corolla trichomes; F: corona lobe; G: gynostegium with corona; H: pollinaria. – A–H from C. Cerón 2765 (QCNE). – Drawn by N. Arzt.



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*.

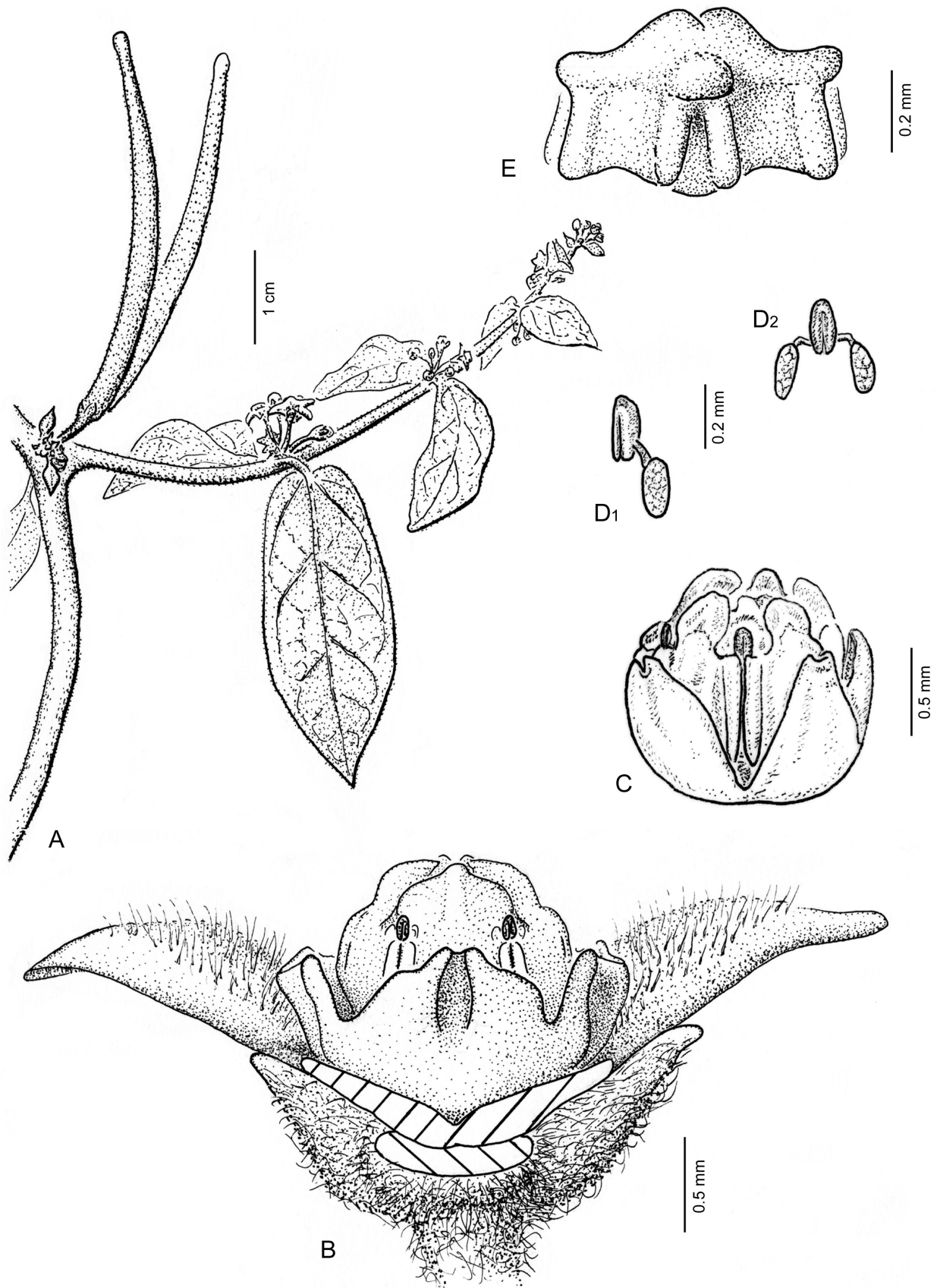


Fig. 14. *Scyphostelma unguiculatum* – A: branch with inflorescences and twin follicles; B: flower, two corolla lobes removed; C: gynostegium and corona; D<sub>1</sub>: pollinarium, one pollinium removed; D<sub>2</sub>: pollinarium; E: style head. – A, B, E from S. Liede & J. Conrad 3140 (UBT); C, D<sub>1</sub> from H. Ruiz & J. A. Pavón 5/80 (MA814543); D<sub>2</sub> 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+ $\Gamma$ . Maximum likelihood tree of the concatenated dataset under GTR+ $\Gamma$ . 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+ $\Gamma$ +I. Bayesian tree of the concatenated dataset under GTR+ $\Gamma$ +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 <sup>m</sup>. 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> |
|--|---|---------------------------|-----------------------|--|-----------------------|-----------------------|------------------|------------------|
| <b>Outgroup</b>                                  |   |                           |                       |  |                       |                       |                  |                  |
| <i>Jobinia formosa</i> (N. E. Br.) Liede & Meve  | <i>Liede &amp; 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       | <b>ON571739</b>       | <b>ON571787</b>                                  | <b>ON571838</b>       | <b>ON571936</b>       | <b>ON571973</b>  | <b>ON571887</b>  |
| <i>Jobinia latipes</i>                           | <i>Tressens &amp; al. 6647</i> (CTES, UBT)  | Argentina: Misiones       | HE611706              | (HE611764, HE611803)                             | HE611843              | HE611895              | OM128314         | OM032692         |
| <i>Jobinia lindbergii</i> E. Fourn.              | <i>Keller &amp; Hildt 11694</i> (CTES)      | Argentina: Misiones       | <b>ON571740</b>       | <b>ON571788</b>                                  | <b>ON571839</b>       | <b>ON571937</b>       | <b>ON571974</b>  | <b>ON571888</b>  |
| <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       | <b>ON571741</b>       | <b>ON571789</b>                                  | <b>ON571840</b>       | –                     | <b>ON571975</b>  | <b>ON571889</b>  |
| <i>Jobinia longirostris</i>                      | <i>Wood 8762</i> (K)                        | Bolivia: Chuquisaca       | <b>ON571742</b>       | <b>ON571790</b>                                  | <b>ON571841</b>       | –                     | <b>ON571976</b>  | <b>ON571890</b>  |
| <i>Jobinia longirostris</i>                      | <i>Wood &amp; Goyder 15578</i> (K, UBT)     | Bolivia: Santa Cruz       | AJ704313 <sup>a</sup> | (AJ704315 <sup>a</sup> , AJ704314 <sup>b</sup> ) | AJ704312 <sup>a</sup> | HE611901 <sup>a</sup> | OM128321         | OM032699         |
| <i>Jobinia peruviana</i> Liede & Meve            | <i>Hutchinson &amp; 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 &amp; Meve 3550</i> (UBT)          | Ecuador: Bolivar          | HE611708              | (HE611766, HE611805)                             | HE611845              | HE611897              | OM128316         | OM032694         |
| <i>Jobinia tarmensis</i> (Schltr.) Liede & Meve  | <i>Tupayachi &amp; Galiano 761</i> (NY)     | Peru: Cuzco               | AJ428744              | (AJ428745, AJ428746)                             | AJ699349              | –                     | –                | –                |
| <i>Jobinia tarmensis</i>                         | <i>Becker &amp; Terrones 728</i> (ULM)      | Colombia: Quindio         | OL907316              | OL907376   | OL907442              | –                     | OM128317         | OM032695         |
| <i>Jobinia tarmensis</i>                         | <i>Liede &amp; Meve 3452</i> (UBT)          | Peru: Huanuco             | OL907317              | OL907377   | –                     | OM049003              | –                | –                |
| <i>Jobinia trifurcata</i> (Griseb.) Liede & Meve | <i>Liede-Schumann &amp; 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 <sup>b</sup> | (HE611786 <sup>b</sup> , HE611825)               | HE611868 <sup>b</sup> | HE611926 <sup>b</sup> | 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 <sup>b</sup> | (HE611784 <sup>b</sup> , HE611823 <sup>b</sup> ) | HE611866 <sup>b</sup> | –                     | OM128346 | OM032724 |
| <i>Orthostia goyderiana</i> Liede & Meve                  | Wood 15994 (K, UBT)                  | Bolivia: Cochabamba    | HE611739 <sup>c</sup> | HE611759 <sup>c</sup>                            | OL907468              | HE611933 <sup>c</sup> | 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 <sup>e</sup> | (HE611774 <sup>e</sup> , HE611813 <sup>c</sup> ) | HE611857 <sup>e</sup> | HE611913 <sup>e</sup> | OM128366         | OM032744         |
| <i>Orthostia pallida</i> (Rusby) Liede & Meve                               | Liede & Meve 3311 (UBT)    | Venezuela: Mérida           | HE611714 <sup>f</sup> | (HE611769 <sup>f</sup> , HE611808 <sup>b</sup> ) | HE611851 <sup>f</sup> | HE611907 <sup>f</sup> | 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 <sup>f</sup> | OL907424   | HE611909 <sup>f</sup> | HE611908 <sup>f</sup> | 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 <sup>g</sup> | HE611756 <sup>g</sup>                            | HE611869 <sup>g</sup> | HE611927 <sup>g</sup> | OM128394         | OM032772         |
| <i>Orthostia scoparia</i> subsp. <i>crassiuscula</i>                        | Mika & al. 073 (FR)        | Dominican Republic: La Vega | HE611734 <sup>h</sup> | (HE611787 <sup>g</sup> , HE611826 <sup>g</sup> ) | OL907489              | HE611928 <sup>h</sup> | OM128395         | OM032773         |



|   |   |                           |                       |   |                       |                       |                 |                 |  |
|---|---|---------------------------|-----------------------|---|-----------------------|-----------------------|-----------------|-----------------|--|
| <i>Orthosia</i> sp.                                       | <i>Conrad 9306</i> (UBT)                                | Mexico: Michoacán         | HE611713 <sup>f</sup> | (HE611768 <sup>f</sup> ,<br>HE611807 <sup>f</sup> ) | HE611849 <sup>f</sup> | HE611906 <sup>f</sup> | OM128398        | OM032776        |  |
| <i>Orthosia stenophylla</i> Schltr.                       | <i>Liede &amp; Meve 3487</i> (ex hort.)                 | Ecuador: Carehi           | HE611718 <sup>g</sup> | (HE611772 <sup>d</sup> ,<br>HE611811 <sup>d</sup> ) | HE611855 <sup>d</sup> | HE611911 <sup>d</sup> | OM128360        | OM032738        |  |
| <i>Orthosia subulata</i> (Vell.) Liede & Meve             | <i>Wasum &amp; al. 7930</i> (NY)                        | Brazil: Rio Grande do Sul | HE611731 <sup>b</sup> | (HE611785 <sup>b</sup> ,<br>HE611824 <sup>b</sup> ) | HE611867 <sup>b</sup> | HE611925 <sup>b</sup> | OM128402        | OM032780        |  |
| <i>Orthosia teodormeyeri</i> Liede & Meve                 | <i>Galetto 723</i> (CORD, NY)                           | Argentina: Córdoba        | HE611722 <sup>h</sup> | (HE611776 <sup>h</sup> ,<br>HE611815 <sup>h</sup> ) | HE611859 <sup>h</sup> | HE611915 <sup>h</sup> | OM128404        | OM032782        |  |
| <i>Orthosia teodormeyeri</i>                              | <i>Morero 112</i> (CORD)                                | Argentina: Córdoba        | HE611736 <sup>i</sup> | HE611757 <sup>i</sup>                               | –                     | HE611930 <sup>i</sup> | OM128408        | OM032786        |  |
| <i>Orthosia teodormeyeri</i>                              | <i>Liede-Schumann &amp; al. 3640</i> (CORD)             | Argentina: Catamarca      | HE611738 <sup>h</sup> | HE611758 <sup>h</sup>                               | –                     | HE611932 <sup>h</sup> | OM128407        | OM032785        |  |
| <i>Orthosia urceolata</i> E. Fourn.                       | <i>Carriño 27500</i> (NY)                               | Brazil: Paraná            | AJ704324              | (AJ704323,<br>AJ704325)                             | OL907496              | HE611934              | OM128410        | OM032788        |  |
| <i>Orthosia woodii</i> Meve & Liede                       | <i>Wood 10369</i> (K)                                   | Bolivia: Chuquisaca       | HE611737              | (HE611789,<br>HE611828)                             | HE611872              | HE611931              | OM128415        | OM032793        |  |
| <b>Ingroup</b>  |   |                           |                       |   |                       |                       |                 |                 |  |
| <i>Scyphostelma beckii</i> (Morillo) Liede & Meve         | <i>Liede &amp; Conrad 3141</i> (MSUN, ULM) <sup>m</sup> | Bolivia: La Paz           | AJ704305              | (AJ704307,<br>AJ704306)                             | AJ704304              | –                     | –               | –               |  |
| <i>Scyphostelma bifidum</i> (Liede & Meve) Liede & Meve   | <i>Liede &amp; Meve 3557</i> (UBT) <sup>m</sup>         | Ecuador: Azuay            | HE611740              | (HE611790,<br>HE611829)                             | HE611873              | HE611935              | –               | –               |  |
| <i>Scyphostelma bolivianum</i> Y. M. Pineda, Liede & Meve | <i>Beck 3191</i> (LPB)                                  | Bolivia: Sud Yungas       | <b>ON571778</b>       | <b>ON571829</b>                                     | <b>ON571878</b>       | –                     | <b>ON572013</b> | <b>ON571927</b> |  |
| <i>Scyphostelma bolivianum</i>                            | <i>Wood 11598</i> (K) <sup>m</sup>                      | Bolivia: Cochabamba       | <b>ON571779</b>       | <b>ON571830</b>                                     | <b>ON571879</b>       | –                     | <b>ON572014</b> | <b>ON571928</b> |  |
| <i>Scyphostelma ecuadorensis</i> (Schltr.) Liede & Meve   | <i>Harling &amp; Ståhl 26512</i> (S)                    | Ecuador: Loja             | HE611741              | (HE611791,<br>HE611830)                             | HE611874              | HE611936              | OM128416        | OM032795        |  |
| <i>Scyphostelma ecuadorensis</i>                          | <i>Liede &amp; Meve 3556</i> (UBT) <sup>m</sup>         | Ecuador: Chimborazo       | HE611748              | (HE611797,<br>HE611836)                             | HE611880              | HE611943              | OM128417        | OM032794        |  |
| <i>Scyphostelma gracile</i> H. A. Keller, Meve & Liede    | <i>Porcel 302</i> (CTES)                                | Bolivia: Cochabamba       | <b>ON571753</b>       | <b>ON571801</b>                                     | <b>ON571852</b>       | <b>ON571944</b>       | <b>ON571987</b> | <b>ON571901</b> |  |
| <i>Scyphostelma gracile</i>                               | <i>Wood 10297</i> (K, UBT) <sup>m</sup>                 | Bolivia: Cochabamba       | HE611750 <sup>i</sup> | (HE611799 <sup>i</sup> ,<br>HE611838 <sup>i</sup> ) | HE611882 <sup>i</sup> | HE611945 <sup>i</sup> | 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 &amp; Meve 3460</i> (UBT) <sup>m</sup>        | Ecuador: Zamora-Chunchipe | AJ704309              | (AJ704308, AJ704310)                             | AJ704311              | HE611946              | OM128419  | OM032797  |
| <i>Scyphostelma</i> cf. <i>isidrense</i> (Morillo) Liede & Meve       | <i>Liede &amp; Meve 3320</i> (UBT)                     | Venezuela: Mérida         | ON571754              | ON571802   | ON571853              | ON571945              | ON571988  | ON571902  |
| <i>Scyphostelma jaramilloi</i> (Morillo) Liede, Meve & Y. M. Pineda   | <i>Liede &amp; Meve 3502</i> (UBT) <sup>m</sup>        | Ecuador: Pichincha        | ON571755              | ON571803   | ON571854              | ON571946              | ON571989  | ON571903  |
| <i>Scyphostelma lechleri</i> (Morillo) Liede & Meve                   | <i>Liede &amp; Conrad 3136</i> (MSUN, ULM)             | Bolivia: La Paz           | AJ428753              | (AJ428754, AJ428755)                             | HE611883              | HE611947              | –         | –         |
| <i>Scyphostelma microphyllum</i> (Kunth) Liede & Meve                 | <i>Cerón &amp; 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 &amp; Meve 3343</i> (UBT) <sup>m</sup>        | Ecuador: Pichincha        | ON571757              | ON571805   | ON571856              | ON571948              | ON571991  | ON571905  |
| <i>Scyphostelma</i> aff. <i>microphyllum</i>                          | <i>Liede &amp; Meve 3473</i> (UBT) <sup>m</sup>        | Ecuador: Pichincha        | HE611744 <sup>f</sup> | (HE611794 <sup>f</sup> , HE611833 <sup>g</sup> ) | HE611876 <sup>f</sup> | HE611939 <sup>f</sup> | OM128421  | OM032798  |
| <i>Scyphostelma</i> aff. <i>microphyllum</i>                          | <i>Liede &amp; Meve 3474</i> (UBT) <sup>m</sup>        | Ecuador: Pichincha        | HE611745 <sup>f</sup> | HE611760 <sup>f</sup>                            | HE611877 <sup>f</sup> | HE611940 <sup>f</sup> | OM128422  | OM032799  |
| <i>Scyphostelma</i> aff. <i>microphyllum</i>                          | <i>Liede &amp; 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 &amp; Meve 3484</i> (UBT) <sup>m</sup>        | Ecuador: Carchi           | ON571760              | ON571808   | ON571859              | ON571951              | ON571994  | ON571908  |
| <i>Scyphostelma quitense</i> (K. Schum.) Liede, Meve & Y. M. Pineda   | <i>Céron &amp; Mortesdesca 16008</i> (MO) <sup>m</sup> | Ecuador: Pichincha        | ON571761              | ON571809   | ON571860              | ON571952              | ON571995  | ON571909  |
| <i>Scyphostelma serpyllifolium</i> (Kunth) Liede & Meve               | <i>Liede &amp; Meve 3482</i> (UBT) <sup>m</sup>        | Ecuador: Carchi           | ON571762              | ON571810   | ON571861              | ON571953              | ON571996  | ON571910  |
| <i>Scyphostelma serpyllifolium</i>                                    | <i>Liede &amp; Meve 3553</i> (UBT) <sup>m</sup>        | Ecuador: Bolívar          | ON571763              | ON571811   | ON571862              | ON571954              | ON571997  | ON571911  |
| <i>Scyphostelma</i> sp. <i>Cajanuma</i>                               | <i>Liede &amp; Meve 3462</i> (UBT)                     | Ecuador: Loja             | ON571764              | ON571812   | ON571863              | ON571955              | ON571998  | ON571912  |
| <i>Scyphostelma</i> sp. <i>indet. c</i>                               | <i>Liede &amp; Meve 3551</i> (UBT) <sup>m</sup>        | Ecuador: Bolívar          | ON571765              | ON571813   | ON571864              | ON571956              | ON571999  | ON571913  |

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



| Species  | Voucher                              | Geographic origin   | trnT-trnL | trnL-trnF            | rps16    | trnD-trnT | psbA-trnH | trnS-trnG |
|--|--------------------------------------|---------------------|-----------|----------------------|----------|-----------|-----------|-----------|
| <i>Scyphostelma unguiculatum</i>                     | Wood 15800 (LPB) <sup>m</sup>        | 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) <sup>m</sup> | Ecuador: Chimborazo | HE611747  | (HE611796, HE611835) | HE611879 | HE611942  | OM128426  | OM032800  |
| <i>Scyphostelma wurdackii</i> (Morillo) Liede & Meve | Liede 3342 (UBT) <sup>m</sup>        | Ecuador: Cuenca     | HE611743  | (HE611793, HE611832) | –        | HE611938  | –         | OM032801  |

<sup>a</sup> in GenBank under *Jobinia* sp. SLS-2015

<sup>b</sup> in GenBank under *Orthosia scoparia*

<sup>c</sup> in GenBank under *Orthosia* sp. Wood 15994 (K)

<sup>d</sup> in GenBank under *Orthosia ellemannii*

<sup>e</sup> in GenBank under *Orthosia kunthii*

<sup>f</sup> in GenBank under *Orthosia bonplandiana*

<sup>g</sup> in GenBank under *Orthosia scoparia* (no subspecies indicated)

<sup>h</sup> in GenBank under *Orthosia pearcei*

<sup>i</sup> in GenBank under *Scyphostelma* sp. Wood 10297 (K)

<sup>j</sup> in GenBank under *Scyphostelma* sp.