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New records of *Frullania* Raddi (Frullaniaceae, Marchantiophyta) from Peru including notes on *F. tetraptera* Nees & Mont. and its synonyms

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ABSTRACT
Nine *Frullania* Raddi species are reported new for Peru, belonging to *F.* subg. *Chonanthelia* Spruce (*F. beauverdii* Steph., *F. cuencensis* Taylor, *F. holostipula* S.Hatt. & D.G.Griffin, *F. pluricarinata* Gottsche, *F. winteri* Steph.), *F.* subg. *Homotrophanta* Spruce (*F. nodulosa* (Reinw., Blume & Nees) Nees), *F.* subg. *Meteoriopsis* Spruce (*F. intumescens* (Lehm. & Linden.) Lehm. & Lindenb. var. *intumescens*, *F. lobatohastata* Steph.) and one *incertae sedis* species (*F. pyricalycina* Steph.). Androecia are newly described for *F. beauverdii* Steph., a species previously considered endemic to Bolivia. Original material of *F. tetraptera* Nees & Mont. as well as additional Peruvian specimens of this species are dioicous and deviate from earlier published circumscriptions. *Frullania conferta* Spruce, formerly considered a synonym of *F. tetraptera* Nees & Mont., is reinstated as a distinct species based primarily on differences in its monoicous sexual condition as well as lobule, styli and gynoecial bract morphology. Another prior synonym of *F. tetraptera*, *F. semiconnata* Lindenb. & Gottsche, is newly proposed as a synonym of *F. mexicana* Lindenb. *Frullania mexicana* differs from *F. tetraptera* and *F. conferta* in its gynoecial bract morphology and number of perianth keels. Lectotypes are designated for *F. conferta*, *F. cuencensis*, *F. semiconnata* and *F. tetraptera*.

KEY WORDS
Andes,
Amazonia,
Peru,
distribution,
Frullania Raddi,
new record,
lectotypifications.

RÉSUMÉ

Nouveaux signalements de Frullania *Raddi (Frullaniaceae, Marchantiophyta) au Pérou, y compris des notes sur* F. tetraptera *Nees & Mont. et ses synonymes.*

Neuf espèces de *Frullania* Raddi sont nouvellement signalées pour le Pérou, appartenant à *F.* subg. *Chonanthelia* Spruce (*F. beauverdii* Steph., *F. cuencensis* Taylor, *F. holostipula* S.Hatt. & D.G.Griffin, *F. pluricarinata* Gottsche, *F. winteri* Steph.), *F.* subg. *Homotrophanta* Spruce (*F. nodulosa* (Reinw., Blume & Nees) Nees), *F.* subg. *Meteoriopsis* Spruce (*F. intumescens* (Lehm. & Linden.) Lehm. & Lindenb. var. *intumescens*, *F. lobatohastata* Steph.) et une espèce *incertae sedis* (*F. pyricalycina* Steph.). Les androcées sont nouvellement décrits pour *F. beauverdii* Steph., une espèce antérieurement considérée comme endémique de la Bolivie. Le matériel original de *F. tetraptera* Nees & Mont. ainsi que des spécimens péruviens supplémentaires de cette espèce sont dioïques et dévient des circonscriptions publiées antérieurement. *Frullania conferta* Spruce, un synonyme antérieur de *F. tetraptera* Nees & Mont., est rétabli en tant qu'espèce distincte sur la base de différences dans sa condition sexuelle monoïque ainsi que dans la morphologie du lobule, des styles et de la bractée du gynécée. Un autre synonyme antérieur, *F. semiconnata* Lindenb. & Gottsche, est nouvellement proposé comme synonyme de *F. mexicana* Lindenb. *Frullania mexicana* diffère de *F. tetraptera* et *F. conferta* par la morphologie de sa bractée du gynécée et le nombre de carènes du périanthe. Les lectotypes sont désignés pour *F. conferta*, *F. cuencensis* Taylor, *F. semiconnata* et *F. tetraptera*.

MOTS CLÉS
Andes,
Amazonie,
Pérou,
distribution,
Frullania Raddi,
signalement nouveau,
lectotypifications.

INTRODUCTION

Frullania Raddi is a widespread genus with more than 600 accepted taxa worldwide (Söderström *et al.* 2016; Brinda & Atwood 2024). The genus is readily recognized by its reddish-brown color as well as its incubously inserted leaves that are conduplicate-trilobed with generally saccate ventral lobules and usually bifid underleaves (Gradstein *et al.* 2001; Crandall-Stotler *et al.* 2009) illustrations and keys to the 595 genera and 120 families of bryophytes (hornworts, liverworts, mosses. Menzel (1984) listed 43 taxa from Peru, however, several of these have now been placed into synonymy. New distribution records for the country have since been published by Romanski *et al.* (2011), Graham *et al.* (2016), Atwood *et al.* (2018), Ellis *et al.* (2020) and Pócs *et al.* (2022). The number of *Frullania* species documented from Peru currently stands at 46 taxa. In addition, three taxa dubiously occur in Peru and eight more were excluded from the country (Söderström *et al.* 2025). However, many *Frullania* species remain incompletely known or have fragmented distributions within the country. For example, 38 taxa are known from four or fewer departments, whereas species like *F. madothecoides* Spruce and *F. mutilata* Steph. remain known only from their type localities. Other species are known in Peru from historical collections only (including type material), whereas their distributions appear to be better known in other countries, such as *F. curviramea* Steph. in Bolivia (Churchill *et al.* 2009), *F. jelskii* Loitl. in Colombia (Gradstein & Uribe-Meléndez 2011; Gradstein 2021), *F. moritziana* Lindenb. & Gottsche in Colombia, Jamaica (Stotler 1969) and Venezuela (Hentschel *et al.* 2009) and *F. triquetra* Lindenb. & Gottsche in Mexico, Guatemala and Bolivia (Stotler 1969; Churchill *et al.* 2009). Nevertheless, large holdings of *Frullania* specimens are stored in Peruvian herbaria, some of which are of historical significance or represent taxonomic novelties and interesting distribution records. Of the several taxonomic revisions that have been conducted on *Frullania* subgenera (Stotler 1969; Hattori 1980; Yuzawa 1991; Uribe-Meléndez 2008), none have utilized specimens from these herbaria, relying instead on specimens deposited in herbaria outside of the country for which duplicates may or may not exist in Peru.

A diverse array of suitable habitat types for *Frullania* occur in Peru, ranging from areas near sea level to up to altitudes reaching 4 000 m, in coastal areas (Lomas vegetation), Andes (montane forests, dry forests, dry cloud forests, shrublands, *páramo-jalca* and puna) and Amazonia (Fig. 1). Interestingly, most of the collecting effort in Peru has focused on the Andes (since Eduard Friedrich Poeppig during 1829-1831), although many of these collections were made in exposed areas along roads (e.g. Hegewald & Hegewald 1977). Recent bryological explorations were carried out in more conserved areas in montane forests, *páramo-jalca*, puna and Amazonia resulting in new records as well as new species for liverworts (Graham *et al.* 2016, 2023; Ellis *et al.* 2020, 2023; Pócs *et al.* 2022; Pócs 2019a, 2019b). Future collecting should target ecosystems like mangroves (Tumbes) as well as regions in the Andes at the south-western side, for which there are no or few reports of *Frullania*. Furthermore, the examination of specimens from Peruvian herbaria not visited for this study (MOL, HSP, HUSA) could yield potentially interesting discoveries.

The findings here are the result of several years' study of herbarium specimens and fieldwork in Peru, and demonstrate how a thorough and critical assessment of specimens of a genus can translate into increased knowledge about organismal diversity and distribution within a country.

MATERIAL AND METHODS

The new distribution reports are based on revised specimens from Peruvian herbaria (CPUN, CUZ, HUT, USM), as well as other herbaria outside of the country (BM, G, F, LSU, MO,

Fig. 1. — General views and vegetation types of visited localities: **A**, dry shurbland with rocky outcrops, Cajabamba, Cajamarca; **B**, seasonal dry forest, La Mar, Ayacucho; **C**, humid grassland surrounded by elfin forests, Unchog, Huánuco; **D**, fragmented montane forest, Leimebamba, Amazonas; **E**, "Aguajal" in Amazon basin, Urarinas, Loreto; **F**, montane forest, Puyu Sacha forest, Junín. Photo credits: A, B, D, F, Bryan Espinoza-Prieto; C, Diego Paredes-Burneo; E, Elluz Huamán.

NY, PC, PMA, S, STR). In addition, fieldwork conducted by the first author between 2018-2022 at many localities in Ayacucho, Amazonas, Cajamarca, Huánuco, Junín, Lima and Loreto (Fig. 1) resulted in numerous specimens deposited in USM (primary) with duplicates in CPUN, CUZ, HSCH (Peru) and F, MHA, MO (outside the country). Specimens were determined using subgeneric revisions (Stotler 1969; Hattori 1980; Yuzawa & Koike 1989; Yuzawa 1991), and

floras from adjacent countries (Gradstein 2021), as well as from morphological comparisons made with selected type specimens. The subgeneric classification follows Hentschel *et al.* (2015).

The distribution maps were made using QGIS3. Since numerous specimens had erroneously been assigned coordinates or lacked this data altogether, most specimens were georeferenced using Peruvian maps and Google Earth. These *post-facto* coordinates are given in brackets. All specimens examined are organized by department followed by provinces and lower administrative ranks.

Distribution of species outside of Peru were obtained from the literature, which are cited in each species listed.

RESULTS

The following nine species are reported here as new for Peru: *F. beauverdii* Steph., *F. cuencensis* Taylor, *F. holostipula* S.Hatt. & D.G.Griffin, *F. intumescens* var. *intumescens* (Lehm. & Lindenb.) Lehm. & Lindenb., *F. lobatohastata* Steph., *F. nodulosa* (Reinw., Blume & Nees) Nees, *F. pluricarinata* Gottsche, *F. pyricalycina* Steph. and *F. winteri* Steph., bringing the total number of Peruvian *Frullania* to 55 taxa. *Frullania* is now the third taxonomically largest liverwort genus in Peru after *Plagiochila* (Dumort.) Dumort. and *Lejeunea* Lib. Most of the *Frullania* species documented from Peru occur elsewhere in the mountainous areas of tropical America (Mexico, Central America, tropical Andes, Guyana Highlands and Southeastern Brazil) (Gradstein 2021), but two species (*F. caulisequa* (Nees) Mont. and *F. griffithsiana* Gottsche) occur as disjuncts between the Andes and southeastern Brazil (Graham *et al.* 2016; Pócs *et al.* 2022). Several other species (*F. ecklonii* (Spreng.) Gottsche, Lindenb. & Nees, *F. ericoides* (Nees) Mont., *F. nodulosa*, *F. obscura* var. *obscura* (Sw.) Nees ex Mont. and *F. riojaneirensis* var. *riojaneirensis* (Raddi) Ångstr.) are pantropical and widespread (Hattori 1980; Yuzawa 1991; Gradstein 2021). There are three *Frullania* species endemic to Peru (*F. heinrichsii* Gradst., Espinoza-Prieto & J.J.Atwood, *F. rigescens* Spruce and *F. madothecoides* Spruce), excluding *F. mutilata* Steph. which has not been reevaluated since its 1911 description by Stephani.

SYSTEMATICS

Family Frullaniaceae Ordway
Genus *Frullania* Raddi
Subgenus *Chonanthelia* Spruce

Frullania beauverdii Steph.
(Figs 2; 3)

Bibliotheca Botanica 87: 241 (Stephani 1916). — Lectotype (designated by Bonner 1965: 244): **Bolivia** • Corani; *Herzog 4727*; G[G00060662]!; isolectotype: S[B22590]. — Syntypes: **Bolivia** • Altamachi; 3 400 m alt.; *Herzog 370*; G[G00264777]!; JE[JE04000969]. **Bolivia** • Corani; *Herzog 5071*; G[G00264778]!

Specimens examined. — **Peru** • Region Cajamarca, Prov. Cutervo, Cutervo, Al NE 1.20 km del centro poblado Chipuluc; Bosque montano impactado en borde de carretera; 6°18'50.48"S, 78°49'46.08"W; 2 642 m alt.; 28.IV.2021; *B. Espinoza-Prieto, S. Riva & P. Arista 2202*; MHA!; MO[MO-7048680]!; USM! • Region Cajamarca, Prov. Cutervo, Cutervo, Al NE 1.20 km del centro poblado Chipuluc; Bosque montano impactado en borde de carretera; 6°18'50.48"S, 78°49'46.08"W; 2 642 m alt.; 28.IV.2021; *B. Espinoza-Prieto, S. Riva & P. Arista 2205-A*; CPUN; MO[MO-7048684]!; USM! • Region Cusco, Prov. Quispicanchis, between Marcapata and Achubamba; [13°35'16.04"S, 70°57'38.20"W]; ±2 700 m alt.; 13.IX.1984; *H. Inoue s.n.*; F[C0071641F]!; MO[MO-3348848]! • Region Cusco, Prov. Urubamba, Aguas Calientes bei Macchu Picchu; [13°9'24.87"S, 72°31'54.63"W]; 2 100 m alt.; 26.VI.1977; *P. Hegewald & E. Hegewald* 8717; MO[MO-5237937]! • Region Pasco, Prov. Oxapampa, Chontabamba, La Suiza, on road towards Cascada La Suiza; 10°39'39.4"S, 75°27'8.6"W; 2 190 m alt.; 19.V.2016; *M. von Konrat 20017*; F!.

Distribution. — Tropical Andes, subalpine regions of Bolivia, 2 300-2 600 m alt. (Yuzawa 1991).

Distribution in Peru. — Montane forests of western (Cajamarca) and eastern slopes (Cusco, Junín), 2 100-2 700 m alt.

Additional illustrations. — Stephani 1916: 241-243, fig. 188a-c (as *F. ovistipula*), fig. 190a-c (as *F. barbeyana*), fig. 191 (as *F. beauverdii*); Yuzawa & Koike 1989: 352, fig. 7 (as *F. barbeyana*); Yuzawa 1991: 272-273, fig. 46 (as *F. beauverdii*), fig. 47 (as *F. ovistipula*).

Discussion

Frullania beauverdii was previously known only from the Bolivian Andes (Yuzawa 1991; Churchill 2009; Churchill *et al.* 2009), but its presence in the Peruvian eastern Andes extends its distribution up to 6°S. Superficially, *F. beauverdii* could be morphologically confused with *F. obscura* (Sw.) Mont. based on its undulate underleaf and leaf lobe ventral margins, minute 1-celled styli and pluriplicate perianths. However, *F. obscura* has dentate-laciniate bract lobe margins whereas the bract lobe margins in *F. beauverdii* are entire. Moreover, the sexual condition is different, being monoicous in *F. obscura* and dioicous in *F. beauverdii*. The androecia are additionally capitate in *F. obscura* whereas they are spicate in *F. beauverdii*. Yuzawa & Koike (1989) and Yuzawa (1991) described the underleaves of *F. beauverdii* (including its synonyms *F. barbeyana* Steph. and *F. ovistipula* Steph.) as widely ovate. However, Stephani (1916) described the underleaves of *F. ovistipula* as broadly ovate and those of *F. barbeyana* and *F. beauverdii* as orbicular. All this variation exists in the examined specimens (see Fig. 3F-I). Also, Yuzawa (1991) describes the bract lobe apices of *F. beauverdii* as subapiculate, whereas Stephani (1916) describes the bract lobe apices of *F. barbeyana* as acute-acuminate, but acute for *F. ovistipula* and *F. beauverdii* (based on illustrations). Bolivian (*Churchill et al. 23109*, *23373-A*) and Peruvian specimens (*Hegewald & Hegewald 8717*) show the bract lobe apices to be acuminate, suggesting that the historical specimens revised by Yuzawa (1991) could have had broken bract lobe tips. Perianths of *F. beauverdii* are also similar in shape to *F. obscura*. However, in cross-section, four main keels and additional plications are present in *F. beauverdii* (see Fig. 3L-N) as noted and described by Stephani (1916). Yuzawa (1991) described the perianth as simply pluriplicate, yet four main keels are depicted in his

FIG. 2. — Distribution of *Frullania beauverdii* Steph. (**diamonds**), *F. intumescens* (Lehm. & Lindenb.) Lehm. & Lindenb. var. *intumescens* (**stars**), *Frullania lobato-hastata* Steph. (**square**) and *F. nodulosa* (Reinw., Blume & Nees) Nees (**triangles**).

illustration. Furthermore, the perianth beak of *F. beauverdii* is longer and relatively wider with a flaring mouth (see Fig. 3K) in comparison to the shorter perianth beak of *F. obscura*, that lacks a flaring mouth. Androecia have not been previously described for *F. beauverdii*, but are present in both the Peruvian (*Espinoza-Prieto et al. 2202, 2205-A*; *Hegewald & Hegewald 8717*) and Bolivian specimens (*Churchill et al. 23109, 23373-A*). The androecia are lateral on the stem and spicate, up to 3.6 mm long and having up to 12 pairs of bracts. Occasionally, some androecia are branched and give rise to another series of shorter spicate androecia (Fig. 3A). Within *F.* subg. *Chonanthelia*, only *F. riojaneirensis* var. *megalostipa* (Spruce) Gradst. and *F. tunguraguana* L.Clark & Frye have similarly long androecial branches. By comparison, *F riojaneirensis* is a monoicous species with a 4-keeled perianth (Yuzawa 1991), whereas *F. tunguraguana* has 2-celled styli and bluntly dentate innermost bract lobes near the apex (Clark & Frye 1952; Yuzawa 1991). The dioicous *F. beauverdii* has undulate underleaf and ventral leaf lobe margins, minute 1-celled styli and entire innermost bract lobes.

FIG. 3. — *Frullania beauverdii* Steph.: **A**, portion of male plant showing androecia; **B**, portion of female plant showing terminal gynoecium; **C**, **D**, stem leaves; **E**, stylus; **F**-**I**, stem underleaves; **J**, perianth; **K**, perianth beak; **L**-**N**, perianth cross sections: **M**, medial portion; **L**, **N**, above and below the medial portion respectively). All from *Hegewald & Hegewald 8717* (MO). Scale bars: A, B, J, L-N, 1.25 mm; C, D, F-I, 0.5 mm; E, K, 125 µm. Credits: Bryan Espinoza-Prieto.

FIG. 4. — Distribution of *Frullania cuencensis* Taylor (**diamonds**) and *F. pyricalycina* Steph. (**stars**).

Frullania cuencensis Taylor
(Fig. 4)

London Journal of Botany 5: 406 (Taylor 1846). — Lectotype here designated: [**Ecuador**] • Hab. Cuenca; *Prof. E. Jameson s.n.*; BM[BM000891049]!; isolectoypes: NY[NY04504233]!; MICH.

SPECIMENS EXAMINED. — **Peru** • Region Áncash, Prov. Áncash, Pampas Grande, Wiñapajatum, cerca al campamento, Bosque MBT; 9°41'S, 77°52'W; 2 660 m alt.; 29.XI.1985; *B. León, N. Valencia & A Cano 751*; USM! • Region Áncash, Prov. Yungay, Unterhalb der Laguna Llanganuco; [9°5'17.69"S, 77°39'47.02"W]; 3 900 m alt.; 17.X.1973; *P. Hegewald & E. Hegewald 7621*; MO[MO-5246801]!, [MO-5246817]! • Region Ayacucho, Prov. Cangallo, Zwischen Chumbis und Orcos, 2 km vor Orcos; [13°24'4.03"S, 73°54'4.06"W]; (3 020 m alt.); 4.VII.1977; *P. Hegewald & E. Hegewald 8979*; MO[MO-5237816]!) • Region Cajamarca, Prov. Cajamarca, Am Rio Chucsen zwischen Matara und Namora; [7°13'58.90"S, 78°16'3.66"W]; 2 675 m alt.; 23.V.1973; *P. Hegewald & E. Hegewald 6135*; MO[MO-5237641]! • Region Cajamarca, Prov. Cajamarca, Quebrada Gavilán (Cerro Huayllaconga) zw, San Juan u. Cajamarca; [7°15'3.60"S, 78°28'1.20"W]; 3 150 m alt.; 29.VIII.1973; *P. Hegewald & E. Hegewald 6557*; MO[MO-5237645]! • Region Cajamarca, Prov. Contumazá, 2 km südlich Contumazá; [7°22'25.14"S, 78°48'16.87"W]; 2 600 m alt.; 16.IX.1973; *P. Hegewald & E. Hegewald 7297*; MO[MO-5246811]! • Region Cusco, Prov. Calca, Bei den Inkaruinen von Pisac; [13°25'4.43"S, 71°50'41.91"W]; ±3 270 m alt.; 25.VI.1977; *P. Hegewald & E. Hegewald 8643*; MO[MO-5237944]! • Region Cusco, Prov. Calca. Huarán, A lo largo de la quebrada Huarán; 13°17'8.12"S, 72°1'51.12"W; 3 120-3 450 m alt.; 25.X.1994; *N. Salazar Allen, G. Ortiz H., W. Galeano & A. Tupayachi Herrera 15564*; PMA[PMA-00026165]! • Region Cusco, Prov. Calca. Huarán, A lo largo de la quebrada Huarán;

Fig. 5. — Distribution of *Frullania holostipula* S.Hatt. & D.G.Griffin (**diamonds**), *F. pluricarinata* Gottsche (**stars**) and *F. winteri* Steph. (**triangles**).

13°17’8.12”S, 72°1’51.12”W; 3 120-3 450 m alt.; 25.X.1994; *N. Salazar Allen, G. Ortiz H., W. Galeano & A. Tupayachi Herrera 15585*; PMA[PMA-00026167]! • Region Cusco, Prov. Calca. Huarán, A lo largo de la quebrada Huarán; 13°17’8.12”S, 72°1’51.12”W; 3 120-3 450 m alt.; 25.X.1994; *N. Salazar Allen, G. Ortiz H., W. Galeano & A. Tupayachi Herrera 15610*; PMA[PMA-00026164]! • Region Cusco, Prov. Calca, Huarán; [13°17’8.12”S, 72°1’51.12”W]; 3 400 m alt.; 27.III.1996; *A. Tupayachi Herrera 7B-A*; CUZ! • Region Cusco, Prov. Paucartambo, Ticacancha, Huaisampilla; [13°13’22.80”S, 71°29’24.00”W]; 1 800-2 000 m alt.; 7-8.XII.1950; *C. Vargas C. 9886A*; CUZ! • Region Cusco, Prov. Urubamba, Chupani; [13°14’36.92”S, 72°6’52.34”W]; 3 300 m alt.; 5.IV.1956; *C. Vargas C. 11137*; CUZ!, F!, MO[MO-7048444]! • Region Cusco, Prov. Urubamba, Pumawanca; [13°16’19.20”S, 72°7’55.20”W]; 3 150 m alt.; 10.III.1963; *C. Vargas C. 14257*; CUZ!, F!, MO[MO-7048445]! • Region Cusco, Prov. Urubamba, Huayllabamba, Yanacocha; 13°16’20”S, 72°1’23”W; 3 800 m alt.; 19.VII.2009; *R. Sierra, Á. Ramírez & P. Núñez 65A*; CUZ! • Region Huancavelica, Prov. Acobamba, Andabamba, Vegetación de matorral; 12°37’35.70”S, 74°42’6.81”W; 3 931 m alt.; 17.VIII.2019; *B. Espinoza-Prieto 1981*; MO[MO-7048494]!, USM! • Region Huancavelica, Prov. Acobamba, Andabamba, Vegetación con dominancia de *Barnadesia*, cerca de cultivos; 12°40’5.57”S, 74°39’38.54”W; 3 972 m alt.; 17.VIII.2019; *B. Espinoza-Prieto 1985*; MO[MO-7048490]!, USM! • Region La Libertad, Prov. Bolívar, Uchumarca, Collpacucho; Sandstone cliffs and wind exposed plateaus, grassy paramo with large lichen covered or exposed rock; 7°4’17”S, 77°48’43”W; 3 850 m alt.; 7.XI.2013; *R. W. Bussmann 17980*; MO[MO-7038959]! • Region La Libertad, Prov. Otuzco, Usquil, an der Strasse nach Otuzco; [7°49’37.61”S, 78°24’57.35”W]; 3 100 m alt.; 22.IV.1973; *P. Hegewald & E. Hegewald 5295*; MO[MO-5237647]!; [MO-5245136]! • Region La Libertad, Prov. Otuzco, Eucalyptus-Wäldchen bei Otuzco in Richtung Usquil; [7°52’49.59”S, 78°32’15.31”W]; 2 700 m alt.; 9.IX.1973; *P. Hegewald & E. Hegewald 7238A*; MO[MO-7038958]! • Region

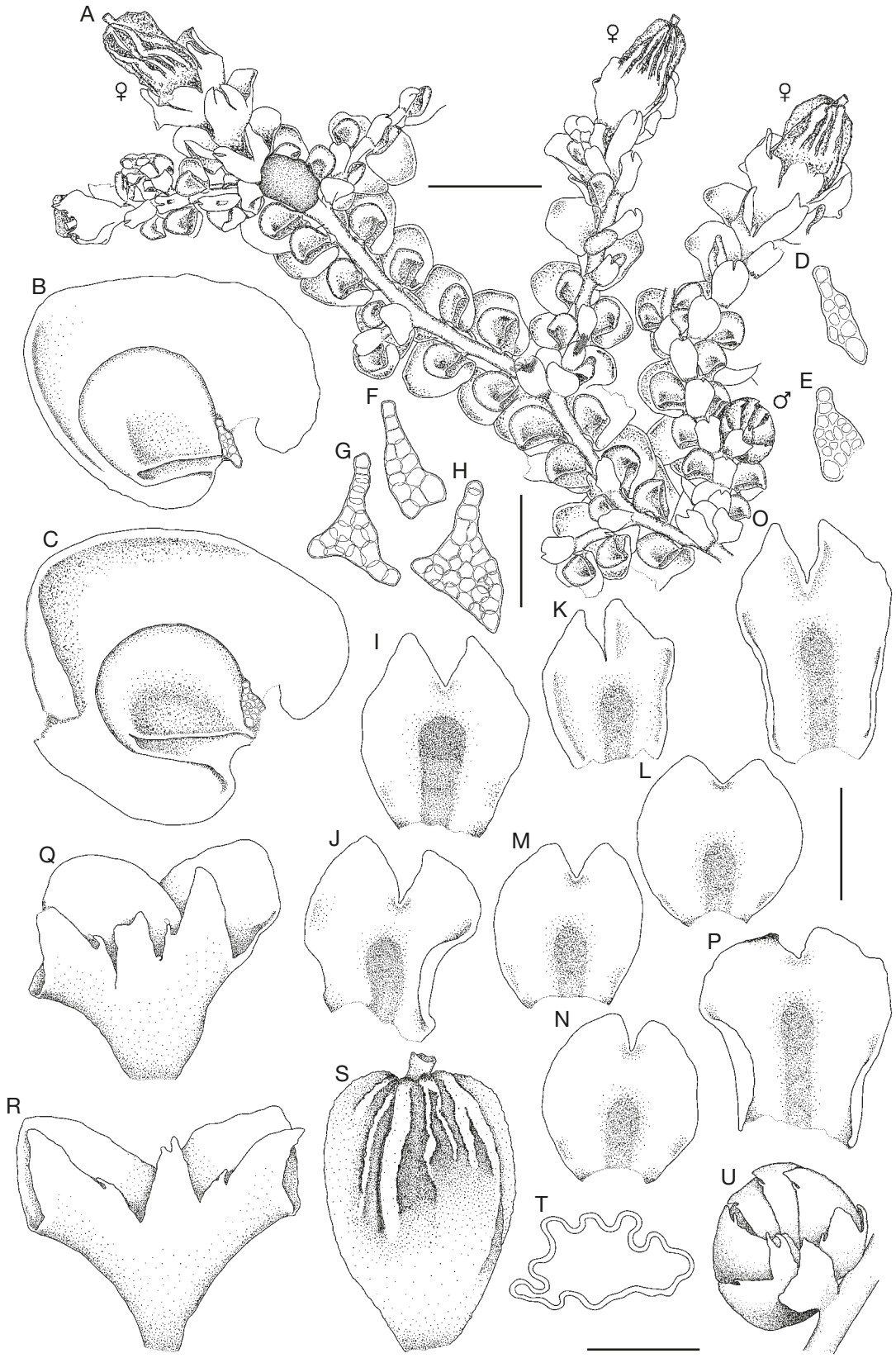

FIG. 6. — *Frullania pluricarinata* Gottsche: **A**, habit; **B**, **C**, stem leaves; **D**-**H**, styli; **I**-**P**, stem underleaves; **Q**, **R**, innermost gynoecial leaves; **S**, perianth; **T**, cross-section of perianth; **U**, androecium. A, F-H, O, P, from probable type (S-B237892); B-D, I-K, R-U, from *Espinoza-Prieto & Ccanto 2160* (MO); C, E, L-N, Q, from *Hegewald & Hegewald 8373* (MO). Scale bars: A, 1.25 mm; B, C, I-R, 0.25 mm; D-H, 125 µm; S-U, 0.5 mm. Credits: Bryan Espinoza-Prieto.

La Libertad, Prov. Otuzco, Ruta Agallapampa a Salpo, alrededores de la localidad de Chanchacap; Ladera arbustada y graminosa; 7°59'7.3"S, 78°33'44.2"W; 2 935 m alt.; 20.VIII.2017; *E. Rodríguez R., E. Alvítez I. & L. Pollack V. 4168*; HUT[HUT-60937]! • Region Lima, Prov. Huarochirí, Entrada de la Cueva I, Tres Ventanas; 12°12'23.40"S, 76°22'36.77"W; 3 800 m alt.; 5.IV.1968; *E. Cerrate, J. Gómez & B. Ojeda 4501*; USM! • Region Lima, Prov. Huarochirí, San Bartolomé, Bosque de Zárate; [11°55'27.55"S, 76°29'9.93"W]; 3 200-3 400 m alt.; V.1990; *J. Ibáñez s.n.(6)*; USM! • Region Piura, Prov. Ayabaca, Alrededores de Ayabaca; 4°38'S, 79°43'W; 2 650 m alt.; 9.IX.1976; *A. Sagástegui A. et al. 8691D*; MO[7038966]! • Region Piura, Prov. Ayabaca, Alrededores de Ayabaca; 4°38'S, 79°43'W; 2 650 m alt.; 9.IX.1976; *A. Sagástegui A. et al. 8691H*; MO[7038963]! • Region Puno, Prov. Carabaya, Ollachea (abajo); [13°47'28.09"S, 70°28'15.84"W]; 2 600 m alt.; 30.XII.1947; *C. Vargas C. 6902A*; CUZ!.

Distribution. — Widespread in high altitudes in montane forests to *páramo* in Tropical America, also in Southwestern Texas, 1 800-4 100 m alt., United States, Mexico, Dominican Republic, Panama, Venezuela, Colombia, Ecuador, Bolivia, Argentina, Brazil (Yuzawa 1991; Reiner 1992; Schäfer-Verwimp & Pócs 2009; Schäfer-Verwimp 2014; Atwood 2017; Lima 2019; Gradstein 2021).

Distribution in Peru. — Open areas along touristic paths and rivers in relative high altitudes of western to eastern Andean slopes, including dry montane forests, cloud montane forests, elfin forests, shrublands and grasslands, 1 800-4 000 m alt.

Additional illustrations. — Yuzawa 1983: 114, fig. 5 (as *F. parva*); Yuzawa 1991: 210, fig. 15a, c, f-k, m-p; Yuzawa 1991: 210, fig. 15b, d, e, l (as *F. pehlkeana*); Reiner 1992: 534-535, figs 1, 2; Gradstein 2021: 363, fig. 37c, d.

Discussion

Frullania cuencensis has a wide Neotropical distribution (Yuzawa 1991; Lima 2019; Gradstein 2021), extending into subtropical regions of the United States (Atwood 2017) as well as Argentina (Reiner 1992). The presence of this species in Peru was incorrectly reported by Yuzawa (1991) and Lima (2019) based on a specimen collected from Cuenca (*Jameson s.n.* – isotype "G"), although this locality is actually located in Ecuador. The presence of *F. cuencensis* in the central Andes is represented only by specimens from Bolivia and northern Argentina along its eastern slope. Based on the new Peruvian specimens, the presence of *F. cuencensis* in the central Andes is reported from both the eastern and western sides of this area, filling this distribution gap.

Yuzawa (1991) cites an "isotype" specimen of *F. cuencensis* from Cuenca that is supposedly deposited in G. However, the Jameson specimen of *F. cuencensis* in G that was studied and annotated by Yuzawa, is not from the type locality. Instead, this specimen was collected in Quito, located about 300 km northwards, an altogether different locality than that in the published protologue. The confusion surrounding the type citation appears to have originated with Stephani (1910: 345), where the Quito material was first cited. This error has since persisted in subsequent publications as Reiner (1992). It is therefore important to note that the description and illustrations given in Yuzawa's treatment (1991) does not correspond with original material cited in the protologue. Nevertheless, the Quito specimen of *F. cuencensis* in G does match well morphologically with the lectotype and isolectotype of that species deposited in BM and NY respectively.

Frullania cuencensis may be confused morphologically with *F. tetraptera*, and the two species are likely to be closely related. In *F. tetraptera*, however, the lobule is galeate or explanate and has a discernable beak in well-developed material, the styli are short filiform and about 3-4 cells long, and the underleaves are less bifid (up to 1/4). By comparison, the lobule of *F. cuencensis* are asymmetrically cucullate in the distal portion with a weakly developed and slightly decurrent beak and the styli are lanceolate.

Frullania holostipula S.Hatt. & D.G.Griffin (Fig. 5)

Miscellanea Bryologica et Lichenologica 8 (3): 47 (Hattori & Griffin III 1978). — Holotype: **Venezuela** • Distr. Boconó: páramo de Guaramacal above the town of Boconó, on shrub; 2 500-2 600 m alt.; VIII.1975; *D. Griffin, III et al. 994*; NICH!; isotypes: F!; FLAS; MER.

Specimens examined. — **Peru** • Region Cusco, Prov. La Convención, Santa Teresa, Camino Llactapata a Michihuañuncca, Huadquiña; [13°11'6.06"S, 72°35'20.47"W]; 8 000-10 000 ft. (±2 430-3 050 m alt.); X.1920; *C. Bües 1172*; CUZ!, MO[MO-7048426]! • Region Cusco, Prov. La Convención, Quebrada Pacchac-Jatun Ccucho, Yanama; [13°19'19.48"S, 72°50'47.39"W]; 11 000-12 000 ft. (±3 350-3 660 m alt.); X.1920; *C. Bües 1053*; CUZ!, MO[MO-7048424]! • Region Cusco, Prov. La Convención, Quebrada Pacchac-Jatun Ccucho, Yanama; [13°19'19.48"S, 72°50'47.39"W]; 11 000-12 000 ft. (±3 350-3 660 m alt.); X.1920; *C. Bües 1062*; CUZ!, MO[MO-7048425]! • Region Cusco, Prov. Paucartambo, Acjanacu; [13°11'57.18"S, 71°37'3.70"W]; 3 600 m alt.; VII.1936; *C. Vargas C. 30A*; CUZ!, F!, MO[MO-7048441]! • Region Huánuco, Prov. Huánuco, Churubamba, Unchog, Zona de Pajonal y arbustos dispersos; 9°43'54.53"S, 76°10'10.43"W; 3 600 m alt.; 7.VII.2018; *B. Espinoza-Prieto, K. Zevallos & J. Carhuapoma 1256*; HSCH!, USM! • Region Huánuco, Prov. Huánuco, Churubamba, Unchog, Zona de Pajonal y arbustos dispersos; 9°43'54.53"S, 76°10'10.43"W; 3 600 m alt.; 7.VII.2018; *B. Espinoza-Prieto, K. Zevallos & J. Carhuapoma 1257-C*; USM! • Region Junín, Prov. Huancayo, Pariahuanca, Chilifruta; [12°00'35.8"S, 74°54'6.7"W]; 3 200 m alt.; *E. Cerrate 5427*; USM!.

Distribution. — Andes of Venezuela and Bolivia. 2 500-3 700 m alt. (Hattori & Griffin III 1978; Yuzawa 1991; Atwood *et al.* 2018; Gradstein 2021).

Distribution in Peru. — Montane forests (Cusco) to elfin forests and humid puna (Cusco, Huánuco, Junín), 2 430-3 660 m alt.

Additional illustrations. — Hattori & Griffin III 1978: 47, figs a-f; Yuzawa 1991: 244, fig. 33.

Discussion

Frullania holostipula has been previously reported from Venezuela (Hattori & Griffin III 1978; León *et al.* 1998; Hentschel *et al.* 2009) and Bolivia (Atwood *et al.* 2018). Its presence in the Peruvian Andes partially closes the distribution gap for the species, as it is apparently only found on the western slope of the Andes. Bolivian and Venezuelan specimens show variation in their underleaves in being not consistently undivided but rather retuse to somewhat emarginate (Atwood *et al.* 2018). This character was also observed in the Peruvian specimens. However, in its beaked lobule with shallow laminar part, filiform styli, large and auriculate underleaves almost

FIG. 7. — *Frullania winteri* Steph.: **A**, habit; **B**, **C**, stem leaves; **D**, **E**, stem underleaves; **F**-**L**, styli; **M**, **N**, innermost gynoecial leaves; **O**, innermost bracteole (upper-half portion). A, F-H, M, N, from *Hegewald & Hegewald 7059* (MO); B-E, I-L, M, from lectotype (G00066922). Scale bars: A, 1.25 mm; B-E, M-O, 0.5 mm; F-L, 0.25 mm. Credits: Bryan Espinoza-Prieto.

or the same size as the leaf lobes, and its dioecious sexuality, *F. holostipula* cannot be confused with any other Neotropical *Frullania* species.

Frullania pluricarinata Gottsche
(Figs 5; 6)

Annales des Sciences Naturelles, Botanique, série 5, 1: 168 (Gottsche 1864). — Probable type: Bogota; S[B237892]!

Specimens examined. — **Peru** • Region Áncash, Prov. Huaraz, Monterrei bei Huaraz; [9°28'10.135"S, 77°31'56.543"W]; 3 100 m alt.; 16.X.1973; *P. Hegewald & E. Hegewald 7465*; MO[MO-5246816]! • Region Ayacucho, Prov. La Mar, Anco, A 2.04 km SE de Maclopampa. Cerca del río Torobamba; Bosque seco interandino; 13°7'32.34"S, 73°54'16.02"W; 2 320 m alt.; 18.XII.2020; *B. Espinoza-Prieto & E. Ccanto 2160*; CUZ, F!, MHA!, MO!, USM! • Region Cajamarca, Prov. Cajabamba, Cachachi, A 4.5 km NE de Chuquibamba; Matorral abierto con afloraciones rocosas; 7°37'29.924"S, 78°11'15.598"W; 2 600 m alt.; 10.IX.2019; *B. Espinoza-Prieto 2008*; MO[MO-7048489]!, USM! • Region Huancavelica, Prov. Acobamba, Andabamba; Plantación forestal de eucaliptos; 12°38'29.75"S, 74°39'53.82"W; 3 441 m alt.; 17.VIII.2019; *B. Espinoza-Prieto 1982*; MO[MO-7048493]!, USM! • Region Huancavelica, Prov. Acobamba, Andabamba; Plantación forestal de eucaliptos; 12°38'29.75"S, 74°39'53.82"W; 3 441 m alt.; 17.VIII.2019; *B. Espinoza-Prieto 1983*; MO[MO-7048492]!, USM! • Region Junín, Prov. Tarma, Río Yanamayo hinter Palca zw. Tarma u. San Ramon; [11°20'32.79"S, 75°33'50.12"W]; 2 700-2 750 m alt.; 10.VI.1977; *P. Hegewald & E. Hegewald 8373*; MO[MO-5237791]! • Region La Libertad, Prov. Bolívar, Uchumarca; dry forest with *Anadenanthera*, *Pseudobombax*, close to San Vicente; 7°2'14"S, 77°55'18"W; 1 873 m alt.; 26.X.2012; *R. W. Bussmann 17423 p.p.*; MO[MO-7039117]! • Region La Libertad, Prov. Huamachuco, La Cabaña (am Rio Agucasa) zw. Huamachuco u. Cajabamba; [7°44'13.085"S, 77°58'49.278"W]; ±3 000 m alt.; 22.V.1973; *P. Hegewald & E. Hegewald 6104A*; MO[MO-7041816]!.

Distribution. — Disjunct distribution in Mexico, Guatemala, Colombia, Ecuador, and central Chile. 0-3 550 m alt. (Gradstein & Cuvertino 2015; Atwood 2017; Juárez-Martínez & Delgadillo-Moya 2017; Gradstein 2021).

Distribution in Peru. — Exposed and dry areas, including forest plantations, dry shrublands, dry forests, and puna, 1 800-3 450 m alt.

Discussion

Frullania pluricarinata has a disjunct distribution, from the northern Andes, to Guatemala and southwestern North America, as well as the Mediterranean region of central Chile (Gradstein 2021). This is the first record of the species in the central Andes, suggesting that it could be found in southern Peru and Bolivia as well.

Although Yuzawa (1991) describes and illustrates the styli as filiform, the styli have also been reported as subulate for this species (Clark & Svihla 1950; Atwood 2017). However, among the examined specimens, including a probable type specimen that was cited by Yuzawa (1991) as an "isotype", the styli exhibit notable variation, ranging from subulate to widely triangular. Additionally, this variability extends to the underleaves. Some underleaves have recurved margins at the base, such as the probable type specimen (Fig. 6O, P) and recently collected specimens (*Espinoza-Prieto & Ccanto 2160*, Fig. 6I-K) but are shorter. A specimen, *Hegewald & Hegewald 8373*, by comparison, has rather ovate-elliptical underleaves (Fig. 6M, N) and lack an indentation on one side. The underleaves in all of these specimens are similarly cuneate and slightly decurrent at the base. Moreover, the description of the lobule given by Yuzawa (1991) notes it to be consistently inflated and lacking a beak. The lobule in all of the specimens examined, however, is not inflated near the mouth, giving the appearance of having a weak beak. The illustration shown in Yuzawa (1991) differs by the characters mentioned above, citing that it was drawn from type material deposited in G. The type material related to *F. pluricarinata* that was annotated by him and deposited in G is that of *F. grandiloba* Steph., a proposed synonym from Mexico. Examination of the type material of *F. grandiloba* reveals subulate styli (2 cells at base, 4-5 cells high), contrary to the filiform styli described and illustrated by Yuzawa (1984). The styli appear even wider when found alongside poorly developed lobules. In these cases, the portion closest to the stem is slightly folded upward, creating the impression that the stylus is wider than subulate. Additionally, there is some inconsistency in the depiction of the perianths. Yuzawa (1984) illustrated perianths with three keels on one side and describing them as pluriplicate. However, the lectotype has perianths with three keels on the dorsal side and five keels on the ventral side, for a total of 10 keels.

Another proposed synonym, *F. subalpina* Spruce from Ecuador, was examined during this study. Contrary to what was published in his monograph, Yuzawa did also study this specimen based on his handwritten notes on subpackets containing dissected plants, although the specimen does not bear his formal annotation label. The plants exhibit lobules similar to those of the other two species, as well as subulate styli (2-3 cells at the base, 4-5 cells high). Interestingly, we observed three gynoecia (all with pluriplicate perianths). Two of which feature the innermost bracteole being half to slightly more connate with both bracts – one with an entire, blunt apex, and the other with a retuse apex. The third bracteole displays a shallowly bifid, unequal apex. All of these bracteoles have recurved margins. Yuzawa (1991) described the innermost bracteole as shallowly bifid and illustrated this structure (Fig. 32m) with recurved margins. Consequently, at least part of the illustration most likely corresponds to *F. subalpina* rather than *F. pluricarinata*. Nevertheless, given the observed morphological variability and overall relatively few known specimens attributed to *F. pluricarinata*, a detailed morphological and molecular study of the *F. pluricarinata*-complex is warranted.

We have been unsuccessful in our attempt to locate additional type material of this species. While the S specimen cited by Yuzawa (1991) is adequate and matches the description in Gottsche (1864), the label data is sparse with only "Bogota", and lacks many of the details from the type citation. For this reason, we maintain the S specimen to be a probable type rather than the lectotype in hope that more suitable type material can be located. It would seem that Yuzawa may have also been of a similar opinion when citing the S specimen as an "isotype" rather than the "holotype" specimen, which he more frequently uses throughout his treatment.

Fig. 8. — Distribution of *Frullania tetraptera* Nees & Mont. Type (**star**), other records (**diamonds**).

Frullania winteri Steph.
(Figs 5; 7)

Species Hepaticarum 4: 338 (Stephani 1910). — Lectotype (designated by Bonner 1965: 467): **Mexico** • *Leibold s.n*; G[G00066922]!; isolectotype: BM[BM000891104].

Specimens examined. — **Peru** • Region Amazonas, Prov. Bongará, Laguna Pomacochas; 5°49'39.91"S, 77°57'42.51"W; 2 220 m alt.; 1.IX.1973; *P. Hegewald & E. Hegewald 7059*; MHA!, MO[MO-5237642]! • Region Amazonas, Prov. Bongará, Laguna Pomacochas; 5°49'39.91"S, 77°57'42.51"W; 2 220 m alt.; 1.IX.1973; *P. Hegewald & E. Hegewald 7062A*; MO[MO-7038967]! • Region Amazonas, Prov. Bongará, Laguna Pomacochas; 5°49'39.91"S, 77°57'42.51"W; 2 220 m alt.; 1.IX.1973; *P. Hegewald & E. Hegewald 7075B*; MO[MO-7039740]! • Region Amazonas, Prov. Chachapoyas, Leimebamba, A 1.47 km SE de Siogue. Bosque montano fragmentado, subiendo hacia cabaña; 6°44'25.59"S, 77°47'28.28"W; 2 627 m alt.; 16.XII.2021; *B. Espinoza-Prieto & D. Paredes-Burneo 2399*; MHA!, MO[MO-7048484]!, USM! • Region Cajamarca, Prov. Celendín, Jalca Gelig; 6°51'44.64"S, 78°6'35.33"W; 2830 m alt.; 16.VII.1993; *J. Mostacero, F. Mejía, F. Pérez, W. Zelada, E. Rodríguez, V. Quipuscoa & S. Sáenz 3227A*; HUT[HUT-35547]! • Region Cajamarca, Prov. Cutervo, Cutervo, Al NE 1.20 km del centro poblado Chipuluc; Bosque montano impactado en borde de carretera; 6°18'50.48"S, 78°49'46.08"W; 2 642 m alt.; 28.IV.2021; *B. Espinoza-Prieto, S. Riva & P. Arista 2200-D;* MO! • Region Cajamarca, Prov. Cutervo, Cutervo, Al NE 1.20 km del centro poblado Chipuluc; Bosque montano impactado

en borde de carretera; 6°18'50.48"S, 78°49'46.08"W; 2 642 m alt.; 28.IV.2021; *B. Espinoza-Prieto, S. Riva & P. Arista 2205-C*; CPUN, MO[MO-7048487]!, USM! • Region Cajamarca, Prov. Cutervo, Cutervo, Al NE 1.20 km del centro poblado Chipuluc; Bosque montano impactado en borde de carretera; 6°18'50.48"S, 78°49'46.08"W; 2 642 m alt.; 28.IV.2021; *B. Espinoza-Prieto, S. Riva & P. Arista 2206-E*; MO[MO-7048486]! • Region Junín, Prov. Chanchamayo, San Ramón, Pasando Mina Pichita; Bosque Puyu Sacha, trocha hacia la parcela PR; Bosque montano en recuperación; 11°5'40.05"S, 75°25'34.19"W; 2 212 m alt.; 14.VII.2018; *B. Espinoza-Prieto, K. Zevallos & J. Carhuapoma 1372-A*; MO! • Region Piura, Prov. Huancabamba, El Carmen de la Frontera, Rosarios bajo, entre el Tambo y Pan de Azúcar; Bosque montano húmedo disturbado. Ladera con suelo arcilloso; 4°56'23.99"S, 79°18'57.45"W; 1 935-2 250 m alt.; 25.IV.2006; *A. Cano, N. Valencia & I. Salinas 16360-B*; USM[USM-319796]!.

Distribution. — Mexico, Northern Andes (Colombia, Ecuador) (Yuzawa 1991; Gradstein 2021), Central Andes (Bolivia) (Churchill *et al.* 2009).

Distribution in Peru. — Northern Andes (Amazonas, Cajamarca, Piura) to Central Andes of Peru (Junín), 1 950-2 830 m alt.

Additional illustrations. — Haarbrink 1981: 53, figs 14-20 (as *F. vanderhammenii*); Yuzawa 1991: 232, fig. 26 (as *F. winteri*); Yuzawa 1991: 234, fig. 27 (as *F. winteri* var. *vanderhammenii*); Gradstein 2021: 376, fig. 39u (as *F. winteri* var. *vanderhammenii*).

Discussion

Yuzawa (1991) studied type material of *F. winteri* (*Leibold s.n.*, lectotype-G) and *F. vanderhammenii* Haarbrink (*van Hammen et al. 2482*, holotype-COL, isotype-U), and reduced the latter to a variety of *F. winteri*. *Frullania winteri* var. *vanderhammenii* (Haarbrink) Yuzawa differs from the type variety in having a filiform stylus 5-8 cells long and 1-2 cells wide, and the innermost bracteole abruptly narrowed at the apex and shortly bifid. Descriptions of both varieties reference the bract lobe apices as being subacute. Stephani (1910) and Haarbrink (1981), however, describe the innermost bract lobe as acute and acute to acuminate, respectively. The type specimens examined by Yuzawa may have had the innermost bract lobes broken in the apex, thereby explaining the description and illustrations in his treatment. Another character that is not discussed by Stephani (1910) nor Yuzawa (1991) is the shape of the stylus in the innermost gynoecial leaves. Haarbrink (1981) referred to this structure as having *"…a few blunt teeth and one lacinia near the connection with the bracteole."* Examined Peruvian specimens clearly show filiform or laminar styli, and the innermost gynoecial leaves as described by Stephani (1910) and Haarbrink (1981). Furthermore, the stylus between the innermost bract lobule and bracteole is long laciniate as described by Haarbrink (1981). In regards to the innermost bracteole of the Peruvian specimens, the apices are abruptly narrow and shortly bifid (as described by Yuzawa (1991) in *F. winteri* var. *vanderhammenii*), but with segments broken, so that these segments may be more acute or acuminate.

Another variable character observed among the examined specimens is the structure of the styli. In the original description by Stephani (1910), this feature was described as narrowly triangular and reflexed. Although the latter character state was not explicitly mentioned by Yuzawa (1991), it was depicted in his illustrations. Yuzawa (1991) provides dimensions for the styli in terms of cell count (11-13 cells long, 5-10 cells wide), culminating in a spinose apex composed of 3-5 uniseriate cells. However, deviations from these descriptions were noted in the type material, where some styli were notably longer (approaching 20 cells in length), occasionally exhibiting reflexed features on one or both sides at the base, resulting sometimes in a structure wider than it is long (Fig. 7I-L). Furthermore, a different variation in styli morphology was observed in another specimen (*Hegewald & Hegewald 7059*; Fig. 7G, H), where the shape aligns more closely with the descriptions provided by Stephani (1910) and Yuzawa (1991). However, within the same specimen, there were instances of styli that were considerably less narrow (measuring 3 cells at the base and 6-7 cells in length), reminiscent of those found in *F. winteri* var. *vanderhammenii*. Unfortunately, the type material of *F. vanderhamennii* was not available for study, but it is plausible that similar variations in styli morphology may exist within that taxon as well.

Frullania winteri is used here in the broad sense due to the observed morphological overlap in the diagnostic characters of the two varieties. We refrain from making formal synonymy due to the relatively small number of specimens known for this species. More study is needed.

Subgenus *Homotropantha* Spruce

Frullania nodulosa (Reinw., Blume & Nees) Nees (Fig. 2)

Synopsis Hepaticarum 3: 433 (Gottsche *et al.* 1845). Basionym: *Jungermannia nodulosa* Reinw., Blume & Nees, *Nova Acta Physico-Medica Academiae Caesareae Leopopoldino-Carolinae Naturae Curiosorum Exhibentia Ephemerides sive Observationes Historias et Experimenta* 12: 217 (Reinwardt *et al.* 1824). — Type (lectotypification needed, cited by Sukkharak (2018: 189) as "holotype"): **Indonesia** • Java, "Lebock", Bantam; without date; *Blume s.n.*; STR.

Specimens examined. — **Peru** • Region Loreto, Prov. Maynas, Las Amazonas, Explorama Lodge, *ca*. 80 km downstream from Iquitos; [3°26'36.86"S, 72°50'59.31"W]; 90 m alt.; 11.V.1986; *S.L. Timme & E. Mockford 6323*; MO[MO-7039738]! • Region Loreto, Prov. Loreto, Urarinas, Entre San Roque y Saramurillo, en el cauce del río Marañón, Aguajal bien abierto, con predominancia de herbáceas; 4°31'12"S, 74°41'31.20"W; 110 m alt.; 10.IX.2022; *B. Espinoza-Prieto & E. Huamán 2537*; F!; HSCH!, MO!, USM!.

Distribution. — Pantropical, lowland rainforests and on isolated trees and shrubs in savannas, 100-300 m alt. In the Neotropics it occurs in Cuba, Dominican Republic, French Guiana, Surinam, Brazil, Colombia, Ecuador (Hattori 1980; Gradstein & Costa 2003; Gradstein & Ilkiu-Borges 2009; Gradstein 2021).

Distribution in Peru. — Lowland forests in Amazon basin, 90-110 m alt.

Additional illustrations. — Hattori 1980: 209, fig. 28; Gradstein 2021: 368, fig. 38m, n.

FIG. 9. — *Frullania tetraptera* Nees & Mont: **A**, **C**, parts of the same female plant; **B**, female plant with perianth. All from isolectotype, d'Orbigny s.n. (STR). Corresponding asterisks (*) indicate where the same shoot is continued after a break in the drawing. Scale bar: 1.5 mm. Credits: Yuriy S. Mamontov.

Discussion

Frullania nodulosa is a widespread pantropical species (Hattori 1980; Gradstein *et al.* 2001; Gradstein 2021). In South America, it occurs in Amazonia (Ecuador, Colombia, Brazil, Bolivia, French Guiana, Suriname) and Mata Atlántica (Southeastern Brazil) and was expected to occur in Peru. Timme (1985) studied the bryophytes of the Amazonian region from many localities along the Amazon River in Peru, reporting two *Frullania* species (*F. crispiloba* Steph. and *F. gibbosa* Nees). His backlog of unprocessed specimens, many of which are still in their original collecting bags, was gifted to MO in 2012. A preliminary sort of these specimens by genera and initial curation into herbarium packets revealed material of *F. nodulosa* that was mixed with Lejeuneaceae and collected in Loreto near Iquitos. The first author also collected a specimen of this species from an area dominated by palms and herbs within the same department. These specimens were found as epiphytes on palm, as well as on a small branch of a fallen tree, the latter suggesting it may grow over branches or trunks of nearby living trees. *Frullania nodulosa* can be easily determined by its suborbicular leaf lobes, pendant lobules, filiform styli, large ovate-triangular underleaves with curved insertion and large auricles.

Subgenus *Meteoriopsis* Spruce

Frullania intumescens var. ***intumescens***
(Lehm. & Lindenb.) Lehm. & Lindenb.
(Fig. 2)

Synopsis Hepaticarum 3: 460 (Gottsche *et al.* 1845). Basonym: *Jungermannia intumescens* Lehm & Lindenb., *Novarum et minus cognitarum stirpium pugillus sextus*: 52 (Lehmann 1834) — Lectotype (designated by Stotler 1969: 445): **Jamaica** • *Bancroft s.n.*; NY[NY02564986]!; isolectoypes: G, S[B27790, B27791, B27792].

Specimens examined. — **Peru** • Region Amazonas, Prov. Chachapoyas, Leimebamba, A 1.47 km SE de Siogue; Bosque montano fragmentado, subiendo hacia cabaña; 6°44'25.59"S, 77°47'28.28"W; 2 627 m alt.; 16.XII.2021; *B. Espinoza-Prieto & D. Paredes-Burneo 2397*; CPUN!, MO!, USM! • Region Amazonas, Prov. Chachapoyas, Leimebamba, A 1.64 km SW de La Playa. En borde de bosque montano fragmentado colindando con pastizal de crianza de ganado; 6°45'36.95"S, 77°47'39.654"W; 3 226 m alt.; 17.XII.2021; *B. Espinoza-Prieto & D. Paredes-Burneo 2467*; CPUN!, F!, MO!, USM! • Region Cajamarca, Prov. Cutervo, San Andrés, Gruta Salomón; [6°13'45.36"S, 78°44'51.59"W]; 2 400 m alt.; 2.VII.1967; *A. López, A Sagástegui & A. Aldave s.n.*; HUT[HUT-6664]!, MO[MO-7048403]! • Region Cajamarca, Prov. San Miguel, San Miguel, Taulis Recorco (Calquis); [6°56'7.41"S, 78°59'2.33"W]; 2 650 m alt.; 3.VII.1986; *J. Mostacero L., E. Alvítez I., S. Leiva G., F. Mejía C. & F. Peláez P. 1139*; F, HUT!, MO • Region Cusco, Prov. La Convención, Echarate, localidad Papelpata; Bosque montano secundario; 12°45'29"S, 72°36'42"W; 1 656 m alt.; 21.VIII.2008; *G. Calatayud 3778a*; MO[MO-7048418]! • Region Huánuco, Prov. Leoncio Prado, Tingo María; [9°17'7.27"S, 76°1'4.71"W]; 660 m alt.; 21.X.1973; *P. Hegewald & E. Hegewald 7796*; MO[MO-5275916]!.

Distribution. — Tropical America, distribution incompletely known (Gradstein 2021). Jamaica (Stotler 1969), Ecuador (Schäfer-Verwimp *et al.* 2013).

Distribution in Peru. — Submontane to montane forests in eastern slopes, 660-3 230 m alt.

Additional illustrations. — Stotler 1969: 503, figs 101-109 (as *F. intumescens*, stylus illustrated without basal appendage); Yuzawa & Koike 1989: 356, fig. 10 (as *F. intumescens*).

Discussion

Frullania intumescens was described as having concave leaf-lobes with recurved and mucronate to apiculate apices, saccate or canaliculate leaf-lobules, filiform styli, auriculate underleaves that are bifid with segments and margins recurved, innermost bracts with few scattered teeth, innermost bracteoles with dentate margins and a 3-keeled perianth (Lehmann 1834; Gottsche *et al.* 1845; Stotler 1969). Yuzawa & Koike (1989) detected the presence of appendiculate styli in an isolectotype specimen deposited of *F. intumescens* in G, and subsequently placed the morphologically similar *F. pachoensis* Steph. into synonymy with that species. Furthermore, the authors recognized *F. closterantha* Spruce as a distinct species that differs from *F. intumescens* in lacking the stylar appendage. Although the stylar appendage was overlooked by Stotler (1969) in his description and illustrations of *F. intumescens*, it is indeed present in the lectotype specimen annotated by him and deposited in NY, which contains portions of plants he examined and clarified but with unremoved underleaves. A few of the underleaves were dissected for this study, where the styli were observed to be composed of a filiform part with a basal appendage, exactly as those described and illustrated from the G isolectotype by Yuzawa & Koike (1989) as well as from an isolectotype specimen in S[B27792] by Gradstein & Uribe-Meléndez (2011). We confirm that *F. closterantha* (synonym of *Frullania intumescens* var. *closterantha* (Spruce) Gradst. & Pócs) is indeed distinct from *F. intumescens* as noted by Gradstein & Pócs (2021).

There have been previous distribution reports of *F. intumescens* from Peru under the now synonymous names *F. longicollis* Lindenb & Gottsche and *F. cucullata* Lindenb. & Gottsche (Stephani 1911; Clark 1958; Ayala Flores 1970; Fulford & Sharp 1990; Schuster 1992; López 1993; Rodríguez Rodríguez *et al.* 2017; Costa *et al.* 2018). However, considering the current delimitation of *F. intumescens* var. *intumescens*, *F. longicollis* would seem to lack appendiculate styli following Stotler's (1969) treatment, and may instead correspond to *F. intumescens* var. *closterantha*. The other species, *F. cucullata* is based on a misdetermined specimen, *Ayala s.n.* (HUT-7189), that is actually *F. haematocysta* Spruce. Records of *F. intumescens* from Puno and cited by Menzel (1984) are based on specimens originally determined as *F. closterantha* and cited by Weberbauer (1911, 1945) as well as by Soukup (1955). It is assumed that these specimens therefore correspond to the current concept of *F. intumescens* var. *closterantha*. As suggested by Gradstein (2021), an exhaustive revision of *F. intumescens* and its synonyms is required to determine the distribution of this species and its variety.

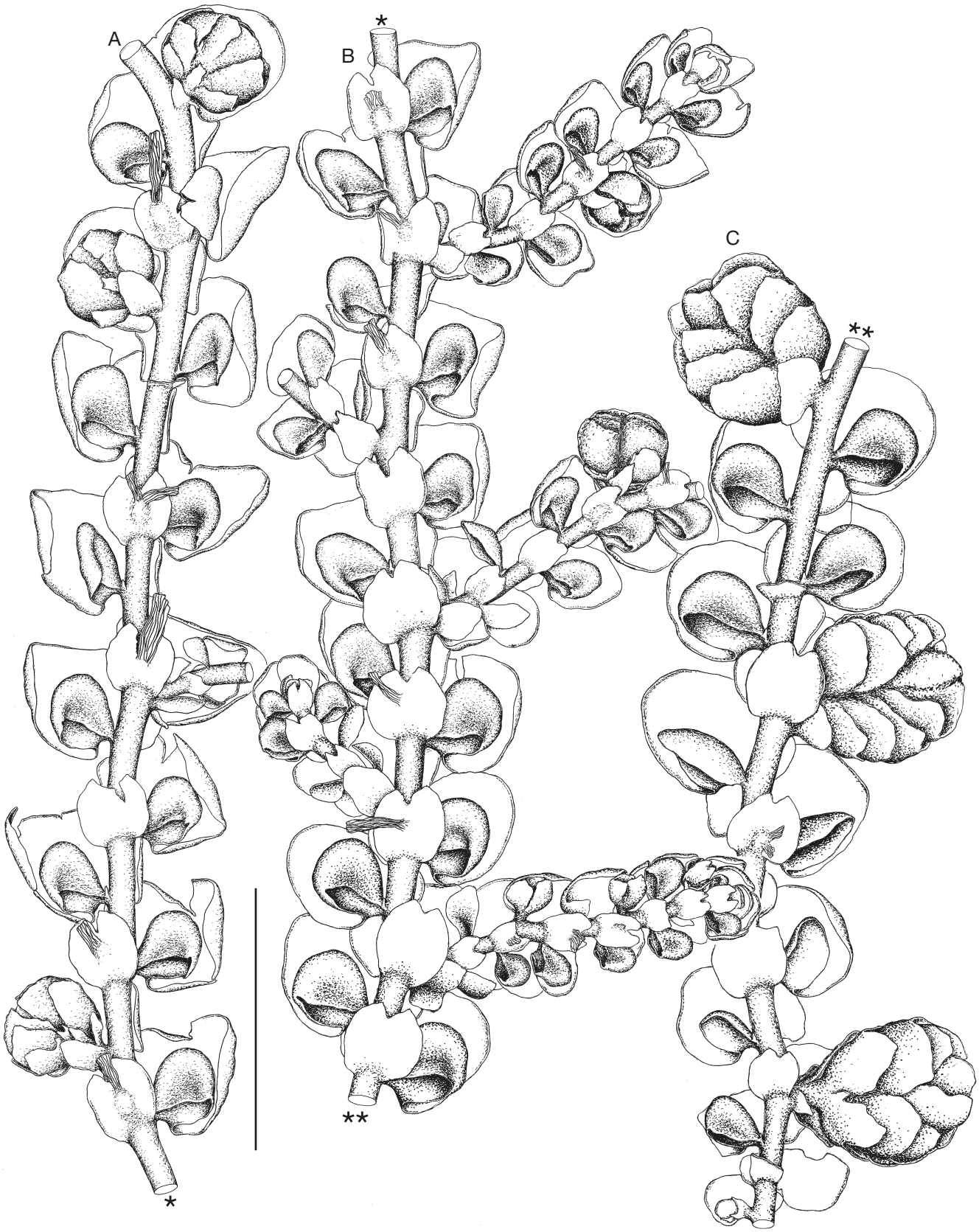

Fig. 10. — *Frullania tetraptera* Nees & Mont: **A**-**C**, shoot fragments with androecia, parts of the same male plant. All from isolectotype, d'Orbigny s.n. (STR). Corresponding asterisks (*) indicate where the same shoot is continued after a break in the drawing. Scale bar: 1.5 mm. Credits: Yuriy S. Mamontov.

Frullania lobatohastata Steph.
(Fig. 2)

Species Hepaticarum 4: 499 (Stephani 1911). — Lectotype (lectotype designated by Bonner 1965: 355): [**Colombia**] • N. Granada; *Lindig 187*; G[G00067107]!; isolectotype: BM[BM000891061].

Specimens examined. — **Peru** • Region La Libertad, Uchumarca, Paramos on Cerro Colpacuchu cerca de Quinhuahuaycu, sandstone; 7°4'17"S, 77°48'43"W; 3 950 m alt.; 29.X.2012; *R. W. Bussmann, N. Paniagua Zambrana, C. Vega Ocaña & C. Téllez 17563C*; MO[MO-7039747]!.

Distribution. — Montane forests and shrubby *páramo* in Colombia and Ecuador, 1 800-4 000 m alt. (Stotler 1969; Gradstein & Uribe-Meléndez 2011; Schäfer-Verwimp *et al.* 2013; Gradstein 2021).

Distribution in Peru. — *Páramo-jalca* in northern Peru, *ca*. 4 000 m alt.

Additional illustrations. — Stotler 1969: 543, figs 274-282; Uribe-Meléndez 2004: 91, fig. 1 (as *F. apollinari*); Gradstein & Uribe-Meléndez 2011: 387, fig. 8; Gradstein 2021: 368, fig. 38h, i.

Discussion
Frullania lobatohastata was originally described as having concave leaf-lobes with inrolled, apiculate apices; saccate leaf-lobules; filiform styli; underleaves that are 1/4 bifid with recurved segments and margins, and bases with undulate, long auricles; innermost bracts with toothed margins; innermost bracteoles with laciniate margins; and subterete perianths (Stephani 1911; Stotler 1969).

Uribe-Meléndez (2004) examined type material of *F. apollinari* Steph. and *F. villosa* Steph. and placed the latter species in synonymy with *F. apollinari*. Distinctive characters of *F. apollinari* include concave leaf-lobes with recurved and rounded apices; saccate leaf-lobules; filiform styli; underleaves 1/5 bifid, recurved near the apex, and bases with undulate, long auricles; toothed innermost bracts, and terete perianths. When Gradstein & Uribe Meléndez (2011) further recognized *F. apollinari* to be a synonym of *F. lobatohastata*, they expanded the circumscription of the species to include plants with mostly rounded leaf-lobe apices, that are occasionally short-apiculate. Schäfer-Verwimp *et al.* (2013) also reported variation within *F. lobatohastata*, based on specimens from Ecuador, that had sharply 3-keeled versus subterete perianths. In addition, Gradstein (2021) reported more variation in the bifid underleaves, noting plants that are up to 1/3 bifid. The current circumscription of *F. lobatohastata* therefore includes significant variation, and a molecular study, combined with the re-examination of type material of the proposed synonyms, is needed to confirm the extent of this morphological variability. The lectotype specimen of *F. lobatohastata* has underleaves auricles with undulate margins and blunt triangular bases. The long auricles are positioned either parallel to the stem or folded (and therefore crossed). The underleaves of the Peru specimen are similar and the plants otherwise closely match the G lectotype specimen, except for lacking perianths.

INCERTAE SEDIS

Frullania pyricalycina Steph.
(Fig. 4)

Species Hepaticarum 4: 394 (Stephani 1910). — Lectotype (designated by Bonner 1965: 408): **Bolivia** • Rio Blanco; *T. Herzog s.n.*; G[G00069123]!.

Specimens examined. — **Peru** • Region Cajamarca, Prov. San Ignacio, San José de Lourdes, A 1 km SE de Nambacasa, Transición matorral seco y bosque premontano, perturbado; En quebrada húmeda; 5°4'9.58"S, 78°56'39.34"W; 673 m alt.; 30.IV.2021; *B. Espinoza-Prieto, S. Riva & P. Arista 2261*; CPUN, MHA!, MO[MO-7048685]!, USM! • Region Cusco, Prov. La Convención, Uchumayo; [12°57'00"S, 72°40'19.20"W]; 1 200 m alt.; VI.1919; *R. A. C. Bües 1504*; CUZ!, MO[MO-7048428]!.

Distribution. — Previously only known to Bolivia (Stephani 1910; Herzog 1954; Atwood *et al.* 2021).

Distribution in Peru. — Submontane to montane forests in eastern slopes, 650-1 200 m alt.

Additional illustrations. — Atwood *et al.* 2021: 336, fig. 3.

Discussion
Frullania pyricalycina was originally described by Stephani (1910) under the subgenus *Galeiloba* Steph. (synonym of *Trachycolea* Spruce). No new information about the species has been published since its original description, resulting in Söderström *et al.* (2016) to categorize the species as *incertae sedis*. In a subsequent study, Mamontov *et al.* (2020) proposed a new combination for *F.* subg. *Trachycolea* subsect. *Inflatae* R.M.Schust. (synonym of *Frullania* subg. *Chonanthelia* sect. *Inflatae* (R.M.Schust.) J.J.Atwood, Vilnet & Mamontov), suggesting that certain species, including *F. pyricalycina* and *F. subpyricalycina* Herzog, might belong here.

Atwood *et al.* (2021) conducted molecular sequencing on recent material of *F. subpyricalycina* from central Chile and found that this species indeed belongs to the subgenus *Chonanthelia*, closely aligning with *F.* sect. *Inflatae* based on morphology. They also discussed the morphological similarities with *F. pyricalycina*; however, notable differences were observed in the bracteole (strongly connate with the bracts on both sides in *F. subpyricalycina*, whereas loosely connate on one side and nearly free on the other in *F. pyricalycina*) and the perianth (featuring two sharp lateral and two broader ventral keels with a short beak in *F. subpyricalycina*, while *F. pyricalycina* exhibits four sharp and irregularly repand keels, along with a more pronounced beak).

Based on the commonly explanate lobules and irregular branching observed, Atwood *et al.* (2021) suggested that *F. pyricalycina* may also belong to the newly described *F.* subg. *Frullaniopsis* J.J.Atwood, Vilnet & Mamontov. The placement of this species into the subgenera *Chonanthelia* or *Frullaniopsis* remains unresolved.

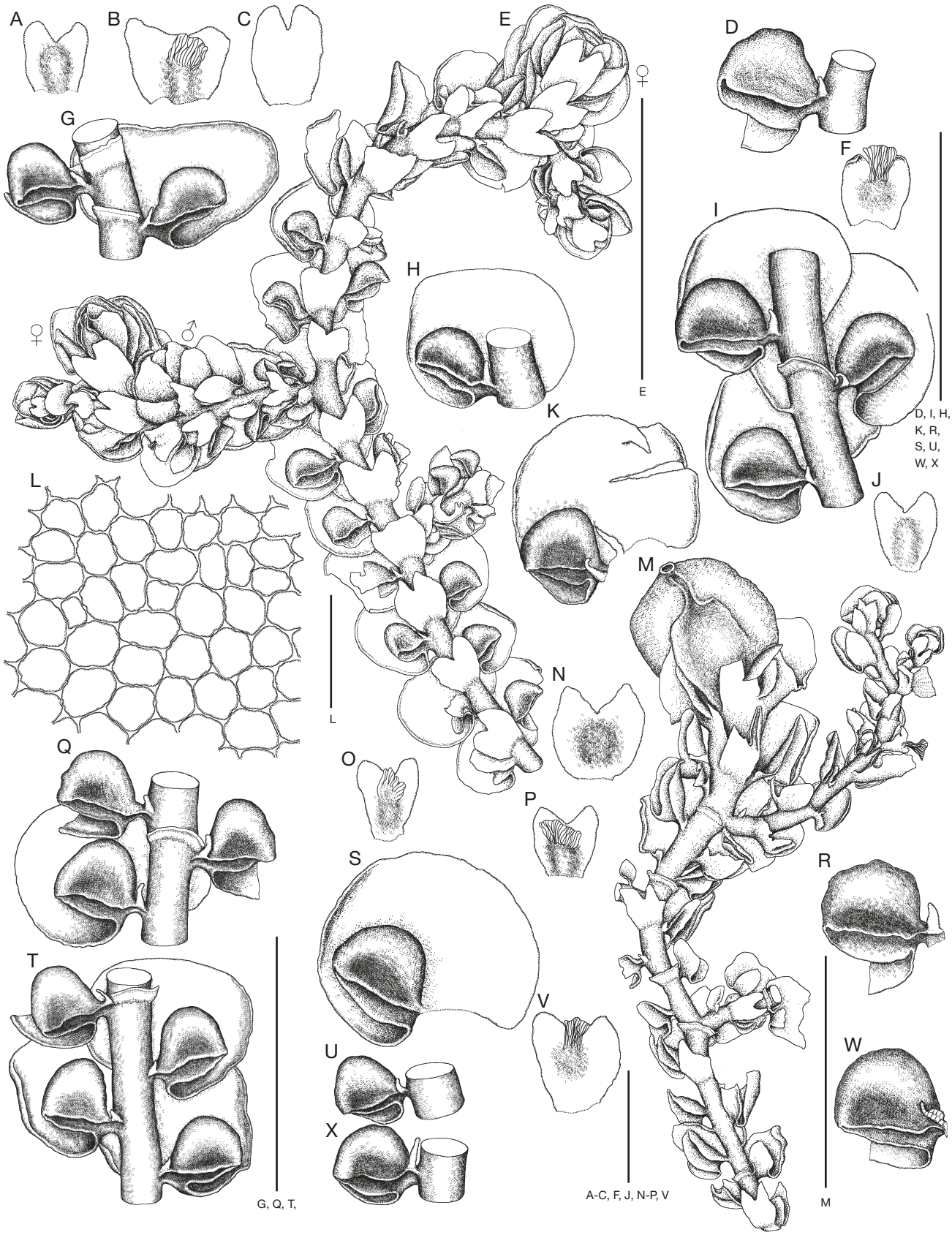

Fig. 11. — *Frullania conferta* Spruce: **A**-**C**, **F**, **J**, **N**-**P**, **V**, underleaves; **D**, **G**-**I**, **K**, **Q**-**U**, **W**, **X**, parts of shoots showing leaf lobes, lobules and styli; **E**, fertile shoot with an androecium and two gynoecia; **L**, median leaf cells; **M**, fertile shoot with a perianth. All from lectotype (G00047604). Scale bars: A-C, F, J, N-P, V, 0.5 mm; E, 2 mm; D, H, I, K, R, S, U, W, X, 1 mm; G, Q, T, 0.75 mm; L, 0.05 mm; M, 1.5 mm. Credits: Yuriy S. Mamontov.

NOTES ON *FRULLANIA TETRAPTERA* NEES & MONT. AND ITS SYNONYMS

Frullania tetraptera Nees & Mont.
(Figs 8-10)

Annales des Sciences Naturelles, Botanique, sér. 2, 9: 47 (Montagne 1838). — Lectotype (here designated): [**Peru**] • Islai Peruviae; cl. d'Orbigny 157 ad Neesium; PC[PC0094167]!; isolectotype: STR!.

Specimens examined. — **Peru** • Region Áncash, Prov. Huarmey, Lomas de Lupín, Vegetación de Loma; 10°29'24.252"S, 77°48'1.868"W; 639 m alt.; 29.IX.2018; *B. Espinoza-Prieto & K. Peña-Ramos 1641*; MO!, USM! • Region Áncash, Prov. Huarmey, Lomas de Lupín, Vegetación de Loma; 10°29'11.893"S, 77°48'1.757"W; 756 m alt.; 29.IX.2018; *B. Espinoza-Prieto & K. Peña-Ramos 1643*; F!, MO!, USM! • Region Arequipa, Prov. Caraveli, Lomas de Atiquipa; [15°46'14.412"S, 74°22'29.798"W]; 600-800 m alt.; 17.VI 1977; *P. Hegewald & E. Hegewald 8568*; MO[MO-5237870]! • Region Cajamarca, Prov. Cajamarca, Llacanora, Cerca a Catarata, rodeado de árboles de Eucalipto, camino hacia la catarata; 7°11'8.941"S, 78°25'26.414"W; 2 701 m alt.; 14.VI.2019; *B. Espinoza-Prieto, E. Cueva Infante & C. Muñoz Tavera 1941*; F!, MO[MO-7048496]!, USM! • Region Cajamarca, Prov. Cajamarca, Namora, Zona Litológica Los Sapitos; Zona de roquedales con arbustos dispersos; 7°11'23.338"S, 78°21'24.109"W; 2 42 m alt.; 14.VI.2019; *B. Espinoza-Prieto, E. Cueva Infante & C. Muñoz Tavera 1948;* MO[MO-7048431]! • Region Cajamarca, Prov. Cajamarca, Namora, Zona Litológica Los Sapitos; Zona de roquedales con arbustos dispersos; 7°11'23.338"S, 78°21'24.109"W; 2 942 m alt.; 14.VI.2019; *B. Espinoza-Prieto, E. Cueva Infante & C. Muñoz Tavera 1950*; MO[MO-7048432]!, USM! • Region Cajamarca, Prov. Chota, Llama, Pasando Izco, a 4 km W de Llama; Matorral en borde de carretera; 6°29'52.8"S, 79°9'9.24"W; 1 200 m alt.; 27.IV.2021; *B. Espinoza-Prieto, S. Riva & P. Arista 2199-A*; MHA!, MO[MO-7048488]!, USM! • Region La Libertad, Prov. Bolívar, Uchumarca; dry forest with *Anadenanthera*, *Pseudobombax*, close to San Vicente; 7°2'14"S, 77°55'18"W; 1 873 m alt.; 26.X.2012; *R. W. Bussmann, N. Paniagua Zambrana, C. Vega Ocaña & C. Téllez 17423*; MHA!, MO[MO-6769826]!• Region La Libertad, Prov. Bolívar, Uchumarca; dry forest with *Anadenanthera*, *Pseudobombax*, close to San Vicente; 7°2'14"S, 77°55'18"W; 1 873 m alt.; 26.X.2012; *R. W. Bussmann, N. Paniagua Zambrana, C. Vega Ocaña & C. Téllez 17424*; MO[MO-6894583]! • Region La Libertad, Prov. Otuzco, Casmiche; [7°58'3.907"S, 78°38'25.775"W]; 2 000 m alt.; 8.IV.1973; *P. Hegewald & E. Hegewald 5028*; MO[MO-5245133]! • Region La Libertad, Prov. Otuzco, Casmiche; [7°58'3.907"S, 78°38'25.775"W]; 2 000 m alt.; 8.IV.1973; *P. Hegewald & E. Hegewald 5047*; MO[MO-5237668]!• Region La Libertad, Prov. Otuzco, Casmiche; [7°58'3.907"S, 78°38'25.775"W]; 2 000 m alt.; 8.IV.1973; *P. Hegewald & E. Hegewald 5052*; MO[MO-5245940]! • Region La Libertad, Prov. Otuzco, Coina; [7°48'39.154"S, 78°21'59.144"W]; 2 050 m alt.; 21.IV.1973; *P. Hegewald & E. Hegewald 5211*; MO[MO-5237815]! • Region La Libertad, Prov. Otuzco, Coina; [7°48'39.154"S, 78°21'59.144"W]; 2 050 m alt.; 21.IV.1973; *P. Hegewald & E. Hegewald 5212*; MO[MO-5237673]! • Region La Libertad, Prov. Otuzco, Coina; [7°48'39.154"S, 78°21'59.144"W]; 2 050 m alt.; 21.IV.1973; *P. Hegewald & E. Hegewald 5220*; MO[MO-5237664]! • Region La Libertad, Prov. Otuzco, Coina; [7°48'39.154"S, 78°21'59.144"W]; 2 050 m alt.; 21.IV.1973; *P. Hegewald & E. Hegewald 5226*; MO[MO-5237868]! • Region La Libertad, Prov. Otuzco, Coina; [7°48'39.154"S, 78°21'59.144"W]; 2 050 m alt.; 21.IV.1973; *P. Hegewald & E. Hegewald 5251*; MO[MO-5245148]! • Region La Libertad, Prov. Otuzco, Samne zwischen Trujillo und Otuzco; [8°00'34.448"S, 78°41'28.324"W]; 1 300 m alt.; 25.VIII.1973; *P. Hegewald & E. Hegewald 6512*; MO[MO-5237801]! • Region La Libertad, Prov. Trujillo, Cerro Campana; [7°58'30"S, 79°6'29.999"W]; 550 m alt.; 26.I.1969; *F. Ayala s.n.*; HUT[HUT-7175]!, MO[MO-7048411]! • Region Lima, Lomas de Lachay; [11°21'47.279"S, 77°21'52.24"W]; 14.IX.1958; *B. Lowy s.n.*; LSU! • Region Lima, Prov. Cañete, Mala, Comunidad Campesina de Mala, Loma de arbustos, hierbas y cactáceas; 12°41'5.25"S, 76°36'3.81"W; 235 m alt.; 19.IX.2018; *B. Espinoza-Prieto 1607*; MO!, USM! • Region Lima, Prov. Huaral, Lomas de Iguanil; 11°24'19.56"S, 77°14'0.96"W; 400 m alt.; IX.2009; *J. Opisso 2150*; USM!.

Description

Leafy shoots 8-10 × 1.1-1.3 mm, dull, black to dark reddish brown, irregularly 1(-2)-pinnately branched, with obliquely spreading branches, 0.2-0.4 mm long. First branch appendage consisting of an asymmetric, ovate-lanceolate segment. Second branch appendage lateral and consisting of two, short-lanceolate, flat segments of unequal length. Stems rounded, 160-175 µm wide, light-brown, stem epidermis approximately 8 cells wide, consisting of firm- to thin-walled, rectangular cells, 40-65 × 12-15 µm, ventral merophyte 6-7 cells wide. Leaves imbricate to contiguous, becoming somewhat remote in the upper part of the stem, reflexed when moist. Dorsal lobes broadly ovate, 725-870 × 650-760 µm, concave, apices usually decurved, broadly rounded, margins entire, antical base arched and dilated, extending beyond distal edge of the stem by slightly less than the stem width. Marginal cells subquadrate, 12-20 µm, median cells regularly polygonal, 15-27 µm, with distinct to moderately bulging trigones and intermediate thickenings, basal cells more oblong, 25-32 µm, with distinct trigones; cuticle smooth; oil bodies not seen; ocelli lacking. Lobules remotely spaced, usually inflated, becoming explanate in the upper part of the shoots, when inflated, parallel to the stem or slightly inclined away from it, with distal portion galeate, 320-405 × 340-380 µm, widest near the middle, external margin mostly rostrate with beak decurrent when well-developed, proximal portion narrowly triangular, 110-160 × 300-360 µm, keel 75-110 µm, when explanate, perpendicular or obliquely angled from stem, ovate-lanceolate, 520-550 × 280-300 µm, occasionally flattened but more often with decurved margins. Styli filiform and uniceriate, 1-4 cells long. Underleaves ovate to suborbicular, 260-320(–430) × 270-300 (–450) µm, shallowly bifid for about 30-50 µm, sinus rounded or acute, lobes triangular, subacute or blunt, lateral margins plane, entire. Rhizoids sparse, light-brown, in fascicles from the base of the underleaves. Lacking specialized asexual reproduction. Sexual condition dioicous. Androecia lateral on stem or main branch, sessile or on abbreviated branches with a single pair of vegetative leaves, globose, 50-90 µm, with 2-5 pairs of bracts. Gynoecia terminal on the stem or main branch, bracts in 2 pairs, lacking subfloral innovations, unequally bifid and divided to about 0.5-0.7 their length, innermost bract lobe ovate, 960-1000 × 590-600 µm, apex obtuse to broadly acute or rounded, margins plane and entire, lobule oblong, 800 × 380 µm, apex acute, free margin reflexed, entire except for a 3-cell long, filiform, stylar tooth near the approximate middle of the leaf; bracteole ½-connate with the bract, elliptical, 580 × 360 µm, bifid for about 30 µm, sinus acute, lobes triangular, subacute, lateral margins plane and entire. Perianth exserted above the bracts for about its length, oblong-obovate,

FIG. 12. — *Frullania mexicana* Lindenb: **A**, **B**, fertile shoots; **C**, **D**, shoot fragments. A, from lectotype of *F. semiconnata* Lindenb. & Gottsche (G00114899); B-D, from isolectotype of *F. mexicana* Lindenb. (W-2014-06935). Scale bar: 1.5 mm. Credits: Yuriy S. Mamontov.

1.6 × 0.8 mm, composed of two compressed lateral keels and two broad ventral keels, the surface and keels smooth; beak cylindrical 115 × 100 µm, slightly flaring, mouth occluded by short, blunt, shallowly projecting papilloid cells, 10-15 µm, up to 25 µm inside the beak. Sporophytes not seen.

DISCUSSION

Frullania tetraptera has been considered to be a widespread Neotropical species occurring at high elevations from Mexico to Argentina and Chile (Yuzawa 1991). The species was characterized as having a monoicous sexuality; ovate, more or less flattened dorsal lobes; galeate and sometimes rostrate lobules with narrowly triangular proximal portions; filiform to subulate styli, obovate underleaves and 4-keeled perianths (Stephani 1910; Haarbrink 1981; Yuzawa 1991; Gradstein 2021). Stephani (1910: 342) recognized two synonyms for the species, *F. mexicana* Lindenb. and *F. semiconnata* Lindenb. & Gottsche, although a few pages later (p.344) he curiously treats *F. tetraptera* as a synonym of *F. gibbosa* Nees. *Frullania tetraptera*, however, is morphologically dissimilar to *F. gibbosa* in its non-appendiculate styli, narrower underleaves that lack auricles, and terminal gynoecia, among other characters. The Paraguayian *F. conferta* Spruce was further added as a synonym of *F. tetraptera* by Yuzawa (1991), who illustrated type material of it and *F. semiconnata* in his figure of *F. tetraptera* (Fig. 24). For his monograph of *F.* subg. *Chonanthelia*, Yuzawa (1991) did not examine type material of *F. tetraptera*, nor can we find any indication in the literature that the type has been critically examined by other authors since it was originally described.

Original material of *F. tetraptera* is deposited in J. Montagne's (1784-1866) personal herbarium in PC and in C. D. G. Nees von Esenbeck's (1776-1858) personal herbarium in STR. These specimens match the description of *F. tetraptera*, although their label information does not entirely match the type citation in Montagne (1838). The PC specimen packet, PC0033604, has the label "Islai Peruviae, cl. d'Orbigny, n. 157 ad Neesium' along with the note "ms 413 p. 155-157". The page numbers correspond to a bound volume of Montagne's illustrations and species descriptions kept at PC, with page 157 having Montagne's handwritten description of "*Jungermannia* (*Jubula*) *tetraptera* Montagne" and the note "n. 157" referencing the label of specimen PC0033604. This manuscript is also referenced in the 1838 protologue as "Nees et Montag. mss.", with the species description identically matching that published for *F. tetraptera*. Despite conflicts in the locality of the type citation, this specimen evidently was the material used for the original description. The "ad Neesium" note on the packet of PC0033604 references the duplicate specimen now deposited in STR with Nees's handwritten label noting "*Jubula tetraptera*" and "157".

In addition to these two specimens exists another specimen in PC on a sheet from É. Bescherelle's (1828-1903) personal herbarium. The sheet contains numerous *Frullania* species glued to it in a grid-like fashion. One of the specimens (PC0094167), on the lower left-hand corner on the sheet, is "#38" *F. tetraptera* with the label "Chili, d'Orbigny". Like the specimen from Montagne's herbarium, this specimen also matches the description of *F. tetraptera* and in part better matches the type citation, although it too is not complete. Bescherelle was not involved in the description of *F. tetraptera*, and while this specimen may be original material, the label data is likely based on the published type citation and is not original label information. The reasoning for this is that the numbered specimens on this sheet correspond to the numbers assigned to species in fascicle 3 of synopsis *Hepaticarum* by Gottsche *et al.* (1845), with number 38 belonging to *F. tetraptera*. Two other validly published and numbered *Frullania* specimens are glued to this sheet, all with labels in the same handwriting: #34, *F. quillotensis* (Nees & Mont.) Nees & Mont. and #36, *F. trinervis* var. *berteroana* Gottsche, Lindenb. & Nees. Both were published after *F. tetraptera* in 1845 and have similarly abbreviated label information that in part matches the original type citations. This herbarium sheet appears to be Bescherelle's reference set of specimens, compiled after 1838.

The specimen in Montagne's herbarium, PC0033604, is designated as the lectotype with the STR specimen an isolectotype. "Islai Peruviae" may refer to "Islay, Peru" a small coastal region in the southern part of the country that is also a Province, near Chile. Both PC and the STR specimens are morphologically similar in having densely ramified, 1-2 pinnate shoots that are approximately 1.3 mm wide with broadly ovate dorsal lobes, explanate or galeate and sometimes beaked lobules and suborbicular underleaves. Some shoots bear globose androecia while others have immature gynoecial bracts or perianth. These structures are not, however found together on the same shoot, although the shoots with androecia have morphologically similar lobules and underleaves to the shoots bearing gynoecia. Based on this, we conclude that the shoots belong to the same species and do not represent a mixture of two different species. Since the shoots with androecia have no traces of gynoecia, and the shoot with gynoecia have no traces of androecia, *F. tetraptera* is considered to have a dioicous, rather than monoicous sexuality as noted in some prior descriptions (Stephani 1910; Haarbrink 1981; Yuzawa 1991; Gradstein 2021) although not in the original description (Montagne 1838) where the sexuality is not described.

Several specimens of *F. tetraptera* are here confirmed from Peru, housed in both Peruvian and international herbaria (HUT, LSU, MO, USM) and all aligning with the lectotype. All of them have leaf lobules that occupy at least half of the leaf lobe, whether saccate, beaked or not, along with explanate lobules. Additionally, they all exhibit filiform styli, distant underleaves which are ovate to suborbicular and shallowly bifid, dioicous sexuality and 4-keeled perianths with short beaks. While slight variations exist among specimens – such as perianths displaying an additional dorsal keel (*Hegewald & Hegewald 5220*, *5226*, *8568*) or perianth beaks being short and cylindrical as well as flaring at the mouth (*Hegewald & Hegewald 6512*) – these differences are insufficient to warrant classification at a subspecific rank, particularly as they occur within the same specimen.

These specimens were predominantly collected in regions characterized by dry conditions, where aridity prevails over humidity or rainfall throughout the year. Notably, five additional specimens were collected from Peru's coastal areas (Arequipa, La Libertad, Lima), specifically within Lomas formations – an ecosystem nestled within a hyperarid belt that experiences increased humidity during winter months (Rundel *et al.* 2007; Dillon *et al.* 2011). While detailed collection data for the lectotype is lacking, it is presumed to have been collected from a similar environment. Additional specimens were gathered at higher elevations, amidst various types of dry vegetation, such as shrublands and forests, with minimal rainfall occurring over several months. Although most specimens were collected during periods of increased humidity or rainfall, six stand out (*Ayala s.n.*; *Bussmann et al. 17423*, *17424*; *Espinoza-Prieto et al. 1948*, *1950*; *Hegewald & Hegewald 6512*) for being collected during the dry season. This observation suggests that *F. tetraptera* exhibits a tolerance for xeric conditions – a departure from previous assertions by Haarbrink (1981) and Gradstein (2021), who characterized the species as favoring moist habitats like montane forests and *páramo*. There are also more records of this species from Peru (Amazonas) reported by Kürschner & Parolly (1998a, 1998b) as well as by Gradstein (1999). However, they are likely misdeterminations due to the previous circumscription of *F. tetraptera* by Yuzawa (1991).

Frullania conferta Spruce
(Fig. 11)

Bulletin de la Société Botanique de France 36 (suppl.): 190 (Spruce 1889). — Lectotype (first step lectotypification designated by Bonner 1965: 270, second step lectotypification here designated): **Paraguay •** Guarapi, in cortice; 1 880 m alt.; *B. Balansa 4249*; G[G00047604!]; isolectotype: G[G00047603]!.

Discussion

Yuzawa (1991) in his treatment of the subgenus *Chonanthelia*, considered *F. tetraptera* to have three synonyms: *F. semiconnata*, *F. mexicana*, and *F. conferta*. As previously discussed, *F. tetraptera* is morphologically distinct from these three species primarily in its sexuality and number of perianth keels. The three prior synonyms however are morphologically similar and form a species complex. Examination of type material of the three names revealed *F. conferta* to be a distinct species compared to the other two, which are treated here to be conspecific. The primary differences include the monoicous sexuality, and the 5-6(–7) keeled perianth.

Frullania conferta was illustrated in both Yuzawa (1991) and Reiner (1988), as having imbricate leaves, that are widely spreading and slightly concave; lobules laminar, canaliculate to galeate; styli subulate 2-cells wide at base and up to 6 cells high; bracteole almost free to low connate with the bracts, and obovate perianth with four main keels (two lateral and two ventral) with an additional plication on its ventral side and one to two additional plications on its dorsal side, and a shallow tubular bent beak with a flaring mouth (Fig. 11). Although the number of keels were not well illustrated in both illustrations, a cross section of the type was found and was the same as illustrated in Reiner (1988: fig. 2B).

Frullania mexicana Lindenb.
(Fig. 12)

Synopsis Hepaticarum 3: 425 (Gottsche *et al.* 1845). — Lectotype (lectotype designated by Atwood & Mamontov 2018: 208): [**Mexico**] • auf *Gaylussacia buxifolia*; STR!; isolectotype: W[2014-06935]!.

Frullania semiconnata Lindenb. & Gottsche, *Synopsis Hepaticarum* 5: 776 (Gottsche *et al.* 1847). — Lectotype (lectotype here designated): [**Mexico**] • Habitat in terries Mexicanis apud Chinantla; G[G00114899]!; isolectoype: BM[BM000891098] **syn. nov.**

Discussion

Frullania semiconnata and *F. mexicana* have consistently inflated and galeate lobules, subulate to triangular styli that are usually wider at their bases (two or more cells wide), bracteoles half connate on one side and low connate on the other with the bracts, and oblong perianth with four main keels with one or two additional plications at both sides (Fig. 12), and with a short, broad beak (Atwood 2017). Within this framework, *F. semiconnata* and *F. mexicana* are conspecific. *Frullania mexicana* has priority over *F. semiconnata* as the older name, and the latter is reduced here to synonymy.

There are two specimens in G that are labeled as, and correspond to, type material of *F. conferta*: specimen G00047603 and G00047604. Both specimens have mostly the same label information including the collector name and collection number, however G00047604 is from the herbarium of Benedict (Benjamin) Balansa (1825-1891), the collector of the type specimen. Bonner (1965), designated the lectotype of *F. conferta* to be deposited in G, but given that two specimens are actually present, a second-step lectotypification is needed. Specimen G00047604 from Balansa's herbarium is larger and has numerous perianths and is designated as the lectotype.

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