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The taxonomic position and lectotypification of
Frullania diversitexta Steph. (Frullaniaceae,
Marchantiophyta) and its synonyms, with
notes on the placement of *F. ignatovii*
Sofronova, Mamontov & Potemkin

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The taxonomic position and lectotypification of *Frullania diversitexta* Steph. (Frullaniaceae, Marchantiophyta) and its synonyms, with notes on the placement of *F. ignatovii* Sofronova, Mamontov & Potemkin

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ABSTRACT

Frullania diversitexta Steph. currently occupies its own subgenus, subg. *Diversitextae* (Kamim.) S.Hatt., although its taxonomic placement is somewhat enigmatic. The habit of the species, as well as the position and shape of the lobules, are morphologically comparable to species in subg. *Diastaloba* Spruce and subg. *Frullania* Spruce, whereas its tuberculate perianth ornamentation is reminiscent of species in subg. *Trachycolea* Spruce. Here, molecular sequence data resolves *F. diversitexta* within subg. *Trachycolea* in a relationship with *F. plana* Sull. (sect. *Planae* R.M.Schust.). *Frullania diversitexta* and *F. plana* have a similar branching pattern, leaf lobe shape, leaf cell areolation, stylus, lobule position, underleaf shape and primary branch appendages that often have two saccate lobules. Differences in their lobule shape, sexuality, position of the gynoeceia and perianth ornamentation, however, decidedly warrant the placement of *F. diversitexta* in its own section, sect. *Diversitextae* (Kamim.) J.J.Atwood, Vilnet & Mamontov, *stat. nov.* Lectotypes are designated for *F. diversitexta* and its three synonyms: *F. abducens* Steph., *F. sendaica* Steph. and *F. tosana* Horik. (replaced synonym of *F. tenella* Steph., *hom. illeg.*). *Frullania ignatovii* Sofronova, Mamontov & Potemkin, having obovoid, skull shaped lobules with an unusual bilabiate mouth, is also resolved within subg. *Trachycolea*, in a sister relationship with *F. davurica* Hampe and *F. jackii* Gottsche.

KEY WORDS

Frullania subg.
Diversitextae,
Frullania subg. *Trachycolea*,
liverworts,
lectotypification,
new status.

RÉSUMÉ

Position taxonomique et lectotypification de Frullania diversitexta Steph. (Frullaniaceae, Marchantiophyta) et ses synonymes, avec des notes sur la place de F. ignatovii Sofronova, Mamontov & Potemkin.

Frullania diversitexta Steph. est actuellement la seule espèce du sous-genre *Diversitextae* (Kamim.) S.Hatt., bien que sa place taxonomique soit quelque peu énigmatique. Le port de l'espèce, ainsi que la forme et l'angle des lobules, sont morphologiquement comparables aux espèces du sous-genre *Diastaloba* Spruce et du sous-genre *Frullania* Spruce, tandis que l'ornementation du périlanthe tuberculé rappelle les espèces du sous-genre *Trachycolea* Spruce. Ici, les données de séquençage moléculaire permettent de placer *F. diversitexta* dans le sous-genre *Trachycolea* en couple avec *F. plana* Sull. (sect. *Planae* R.M.Schust.). *Frullania diversitexta* et *F. plana* ont un modèle de ramification similaire, ainsi que la forme du lobe foliaire, l'aréole des cellules foliaires, le stylet, la position du lobule, la forme de la sous-feuille et les appendices de branche primaire qui ont souvent deux lobules sacciformes. Cependant, les différences de la forme des lobules, de la sexualité, de la position du gynécée et de l'ornementation du périlanthe justifient clairement la place de *F. diversitexta* dans sa propre section, sect. *Diversitextae* (Kamim.) J.J.Atwood, Vilnet & Mamontov, stat. nov. Des lectotypes sont désignés pour *F. diversitexta* et ses trois synonymes: *F. abducens* Steph., *F. sendaica* Steph. et *F. tosana* Horik. (synonyme remplacé de *F. tenella* Steph., *hom. illeg.*). *Frullania ignatovii* Sofronova, Mamontov & Potemkin, ayant des lobules obovoïdes en forme de crâne et une ouverture bilabée inhabituelle, est également inclus dans le sous-genre *Trachycolea*, dans une relation sœur avec *F. davurica* Hampe et *F. jackii* Gottsche.

MOTS CLÉS
Frullania subg.
Diversitextae,
Frullania subg. *Trachycolea*,
hépatiques,
lectotypification,
statut nouveau.

INTRODUCTION

The genus *Frullania* Raddi, with some 675 currently accepted taxa (Söderström *et al.* 2016), has historically been divided and subdivided on a mostly morphological basis into about 15 subgenera and nearly 50 sections (Spruce 1884; Verdoorn 1928, 1929, 1930; Kamimura 1961; Hattori 1972, 1975, 1976a, b, 1977, 1981, 1983, 1986; Hattori & Lin 1985; Schuster 1985, 1991, 1992; von Konrat *et al.* 2011; Hentschel *et al.* 2015). Revisionary studies on the genus have mostly modified the ranks within this infrageneric classification (Yuzawa 1991; Schuster 1992; von Konrat *et al.* 2011), while molecular phylogenetics have reinforced the recognition of morphologically well-circumscribed groups (e.g. subg. *Chonantheria* Spruce, subg. *Thyopsiella* Spruce synonym of subg. *Frullania*, see Lima *et al.* 2020) or illustrated the need for narrower circumscriptions (e.g. subg. *Diastaloba* Spruce) (Hentschel *et al.* 2009). Perhaps the most dramatic results produced by molecular topologies have been the alignment of species in seemingly discordant relationships that challenge their former morphological classifications and require re-interpretation. For example, the southeast Asian *F. orientalis* Sande Lac., a species with a pendent habit, leaves convolute around the stem when wet and dry, and clavate to cylindrical lobules has been assigned to subg. *Meteoriopsis* Spruce (Verdoorn 1930; Hattori 1977; Schuster 1992), subg. *Trachycolea* (Uribe-M 2011; Hattori 1972) and placed within its own subgenus (subg. *Orientales* (Verd.) S.Hatt.) (Hattori 1976a), depending on which morphological characters are emphasized as taxonomically important. In a molecular phylogenetic study, Hentschel *et al.* (2009) found *F. orientalis* to be nested in subg. *Trachycolea* (as subg. *Frullania*), sister to the Australian endemic *F. ferdinandi-muelleri* Steph., a species with a creeping habit that has densely imbricate leaves as well as nearly

spherical lobules. As noted by Hentschel *et al.* (2009), the relationship of these species is justified by their nearly identical narrowed lobule mouths. Furthermore, the two species share a dioicous sexuality, dilated lobe bases on both the dorsal and antical side, filiform styli and pyriform, 3-keeled perianths. Similarly, Yuzawa (1991) treated the Neotropical *F.* (subg. *Chonantheria*) *holostipula* S.Hatt. & D.G.Griffin, a species with undivided underleaves, in sect. *Chonantheria* due to the similarity of its lobules with other species in that section that also have short laminal keels. *Frullania holostipula* was later resolved in a molecular phylogeny with species such as the pantropical *F. obscura* (Sw.) Nees ex Mont. (sect. *Cladocarpicae* Spruce) that have lobules with long laminal keels (Hentschel *et al.* 2009: as *F. arecae* (Spreng.) Gottsche). The recent discovery of the Peruvian *F. heinrichsii* Gradst., Espinoza-Prieto & J.J.Atwood, a species in sect. *Cladocarpicae* that also has undivided underleaves, lobules with long laminal keels and is morphologically similar to *F. obscura*, strengthens this initially peculiar alignment (Atwood *et al.* 2018).

There are numerous other species within *Frullania* that have unusual suites of morphological characters, and whose taxonomic position has yet to be clarified. *Frullania diversitexta* Steph. and *F. ignatovii* Sofronova, Mamontov & Potemkin are two more examples. Stephani (1897) described *F. diversitexta* from a single specimen collected by Tomitaro Makino (1862-1957) in Japan. The species was characterized as having 2-3 cm long stems; irregularly pinnate and bi-pinnate branches; slightly imbricate, ovate to orbicular and concave leaves with rounded apices and appendiculate bases; inflated and clavate to cylindrical lobules; large, sub-rotund and shallowly bifid underleaves; and a dioicous sexuality. The distribution of *F. diversitexta* has since been expanded to include stations in Korea, the Japanese Islands of Honshu, Shikoku, Kyushu and Yakushima (Kamimura 1961), China

TABLE 1. — Comparison between the morphological characters of *Frullania diversitexta* Steph. (sect. *Diversitextae* (Kamim.) J.J.Atwood, Vilnet & Mamontov), *F. orientalis* Sande Lac. (sect. *Orientalis* Verd.) and *F. plana* Sull. (sect. *Planae* R.M.Schust.).

Species	<i>F. diversitexta</i>	<i>F. orientalis</i>	<i>F. plana</i>
habit	creeping, sometimes pendent	pendent	creeping
branching	irregularly 1-2-pinnate	irregularly 1-pinnate	irregularly 1-2-pinnate
leafy shoot width (mm)	1.0-1.3	1.7-2.0	1.2-1.4
initial branch appendages	with two saccate lobules	with two saccate lobules	polymorphic, sometimes with two saccate lobules
dorsal lobe shape	broadly ovate to orbicular	narrowly ovate to subrotund	broadly orbicular
dorsal lobe apices	rounded, incurved	rounded to acute, plane	rounded, incurved
dorsal lobe bases	dilated on both sides, auriculate to appendiculate	dilated on both sides, auriculate to appendiculate	dilated on both sides, cordate to auriculate
dorsal lobe aerolation	with intermediate thickenings and conspicuous trigones	with intermediate thickenings and conspicuous trigones	with intermediate thickenings and conspicuous trigones
lobule position	remote, with mouth sharply inclined towards stem	contiguous, erect with mouth parallel to stem	contiguous, erect or with mouth slightly inclined towards stem
lobule shape	inflated and clavate to cylindrical, or explanate	inflated and clavate to cylindrical	inflated and galeate, cap-like, or clavate, or explanate
styli	minute, uniceriate	minute, uniceriate	minute, uniceriate
underleaf shape	sub-rotund	sub-rotund	sub-rotund
underleaf margins	plane	somewhat recurved	plane
underleaf bases	cordate to auriculate	auriculate to appendiculate	cordate to auriculate
sexuality	dioicous	dioicous	autoicous
gynoecia position	terminal	lateral	lateral
perianth	trigonus, tuberculate	trigonus, tuberculate	trigonus, smooth

(Hattori & Lin 1985; Pippo 1990; Zhao & Cui 2002) and Russia (Gambaryan 1990, 1992).

When Stephani (1910) described the perianth of *F. diversitexta* as pyriform, trigonous and tuberculate, he placed *F. diversitexta* in subg. *Frullania* (as subg. *Thyopsiella*) and emphasized the similarities in habit and lobule morphology over its perianth ornamentation. Species in subg. *Frullania*, by comparison, have a smooth perianth ornamentation (Stotler 1969; Schuster 1992). The intermediate taxonomic position of *F. diversitexta* was again highlighted when Hattori (1952) expanded the circumscription of the species to include several Japanese synonyms such as *F. abducens* Steph. and *F. tosana* Horik. (replaced synonym of *F. tenella* Steph., *hom. illeg.*), which Stephani (1910) assigned to subg. *Gaileiloba* Steph. (synonym of subg. *Trachycolea*), as well as *F. sendaica* Steph., which Stephani (1924) assigned to subg. *Diastaloba*. In a monograph of Japanese Frullaniaceae, Kamimura (1961) erected a new subsection within subg. *Frullania* (as subg. *Frullania* sect. *Diastaloba* (Spruce) Kamim.) to accommodate *F. diversitexta* based on morphology and karyological data. Subsect. *Diversitextae* Kamim. was subsequently elevated to subgeneric rank by Hattori & Lin (1985), who regarded it as monospecific. *Frullania* subg. *Diversitextae* (Kamim.) S. Hatt. is currently accepted by Hentschel *et al.* (2015), although these authors note its ambiguous and provisional status. This subgenus is one of two monospecific *Frullania* subgenera, the other being *F.* subg. *Steerea* (S.Hatt. & Kamim.) R.M.Schust., for which their sole species have not been included in a molecular phylogenetic study.

Frullania ignatovii, somewhat recently described from Russia (Sofronova *et al.* 2013), is a small, dioicous species that has slightly longer than wide, obovoid and skull-shaped lobules, with an unusual bilabiate mouth. Morphologically, the species is similar to the Japanese *F. amplifolia* Steph.,

the European *F. fragilifolia* (Taylor) Gottsche, Lindenb. & Nees. and the western North American *F. chilcootensis* Steph. (in synonymy *F. hattoriana* J.D.Godfrey & G.Godfrey, see Atwood & Mamontov 2020). Hentschel *et al.* (2009) found *F. amplifolia* to be placed in subg. *Trachycolea* (as subg. *Frullania*), although its relationships to other species in that subgenus have yet to be resolved. *Frullania fragilifolia* and *F. chilcootensis* (as *F. hattoriana*) are conversely resolved within subg. *Frullania* (Hentschel *et al.* 2009; Mamontov *et al.* 2020: as subg. *Thyopsiella*). The placement of *F. ignatovii* remains in question. Here, molecular sequence data is used to assess the taxonomic position and phylogenetic relationships of *F. diversitexta* and *F. ignatovii*.

MATERIAL AND METHODS

MORPHOLOGICAL STUDY

The specimens included in the molecular phylogenetic analysis were morphologically compared to the type specimen of *F. diversitexta*, as well as the types of its three synonyms: *F. abducens*, *F. sendaica* and *F. tosana*. The specimens were studied using light microscopes equipped with digital cameras. To better illustrate the three-dimensional objects, photomicrographs were combined using the stacking software HeliconFocus and then reconstructed into line drawings (Figs 2-5).

TAXA SAMPLING

To clarify the phylogenetic affinity of *F. diversitexta* and *F. ignatovii*, the combined ITS2+trnL-F dataset was produced based on nucleotide sequences of 45 key *Frullania* species published previously by Hentschel *et al.* (2009) and *F. chilcootensis* (as *F. hattoriana*) from Mamontov *et al.* (2020). The nucleotide sequence data for two specimens of *F. diversitexta* and the holotype

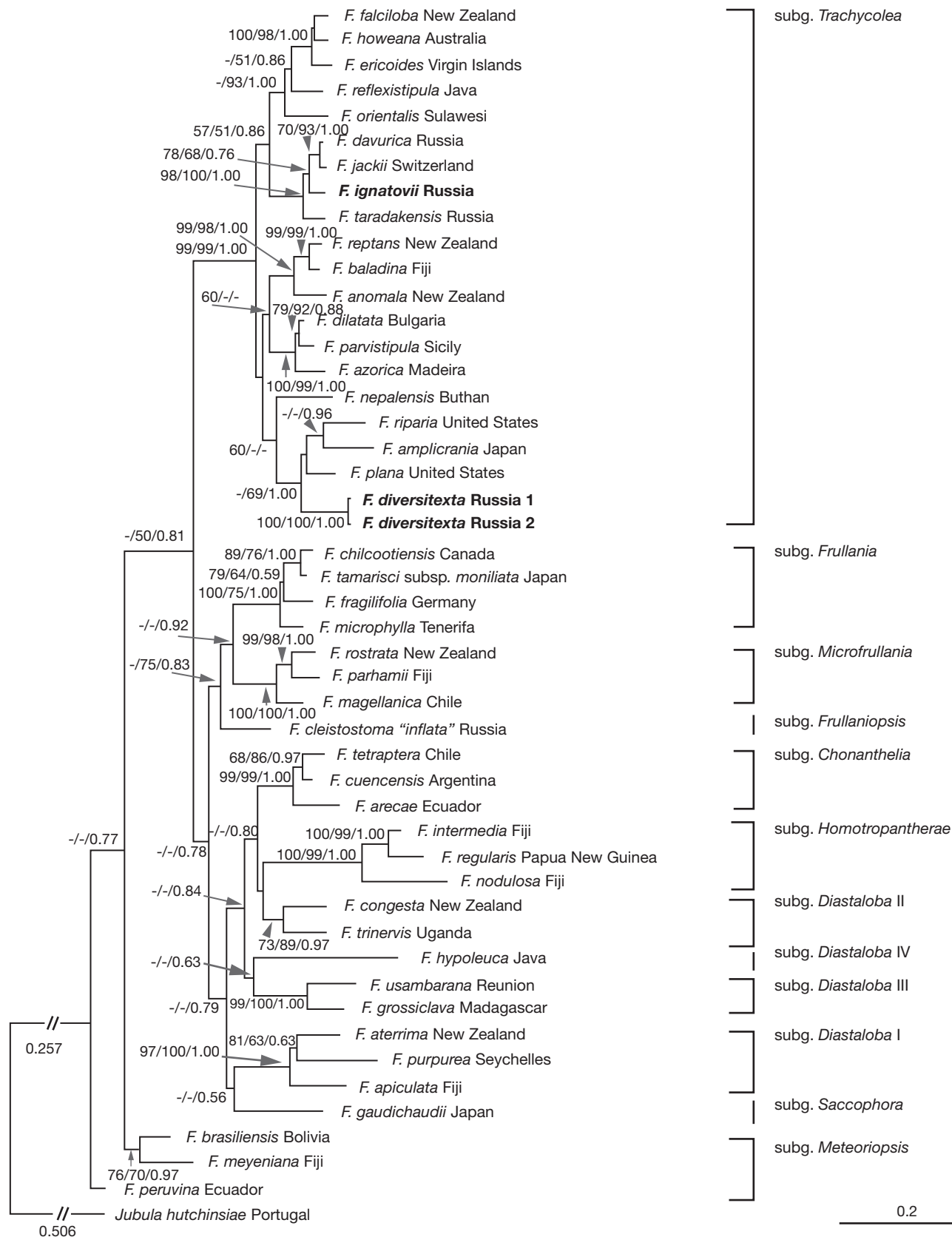


FIG. 1. — BA tree for 44 specimens from Hentschel *et al.* (2009) and single specimen from Mamontov *et al.* (2020) with the inclusion of two *Frullania diversitexta* specimens and the holotype specimen of *Frullania ignatovii*. Indication of bootstrap support values achieved in MP/ML calculations and values of Bayesian posterior probabilities more than 50%/0.50 are shown above branches. The length of cut branches is marked.

TABLE 2. — Comparison between the morphological characters of *Frullania davurica* Hampe, *F. ignatovii* Sofronova, Mamontov & Potemkin and *F. jackii* Gottsche (all of sect. *Integristipulae* Verd.).

Species	<i>F. davurica</i>	<i>F. jackii</i>	<i>F. ignatovii</i>
habit	creeping	creeping	creeping
branching	irregularly 1-2-pinnate	irregularly 1-2-pinnate	irregularly 1-2-pinnate
leafy shoot width (mm)	1.2-1.5	1.2-1.7	0.5-0.7
initial branch appendages	mostly with two galeate lobules	mostly with two galeate or explanate lobules	with a galeate and an explanate lobule
dorsal lobe shape	orbicular to broadly ovate	orbicular to broadly ovate	broadly ovate to reniform
dorsal lobe apices	rounded, incurved	rounded, incurved	rounded, incurved
dorsal lobe bases	auriculate	auriculate	auriculate
dorsal lobe aerolation	with intermediate thickenings and conspicuous trigones	with intermediate thickenings and conspicuous trigones	with intermediate thickenings and conspicuous trigones
	contiguous, mostly erect with mouth	contiguous, mostly erect with mouth	contiguous, mostly erect with mouth
lobule position	parallel or inclined towards stem	parallel or inclined towards stem	parallel or inclined slightly away from stem
lobule shape	inflated and galeate	inflated and galeate	inflated and galeate, skull-shaped
styli	filiform to subulate	filiform to subulate	filiform to subulate
underleaf shape	sub-orbicular	reniform	obovate
underleaf margins	emarginate	emarginate	entire to obtusely toothed on one or both sides
underleaf bases	cuneate	cuneate	cuneate
sexuality	dioicous	dioicous	dioicous
gynoecia position	lateral	lateral	terminal
perianth	trigonous, tuberculate	trigonous, tuberculate	unknown

of *F. ignatovii* were obtained in the current study and included in the analyses. *Jubula hutchinsiae* (Hook.) Dumort. was chosen as the outgroup taxon according to the topology constructed by Hentschel *et al.* (2009). The sequences of *F. inflata* reported from Russia in Hentschel *et al.* (2009) is now considered to belong to *F. cleistostoma* from recently established subg. *Frullaniopsis* (Mamontov *et al.* 2020) and provided in the phylogenetic tree (Fig. 1) and Appendix 1 as *F. cleistostoma* “*inflata*”. The list of specimens with voucher information and GenBank accession numbers is provided in Appendix 1.

DNA ISOLATION, AMPLIFICATION AND SEQUENCING

The DNA isolation, amplification and sequencing were the same as that described in Mamontov *et al.* (2018).

PHYLOGENETIC ANALYSIS

The newly sequenced loci were assembled and an ITS2+*trnL*-F dataset was automatically aligned in BioEdit 7.0.1 (Hall 1999) using the ClustalW tool and then manually corrected. All positions of final alignments were included in the phylogenetic analyses. Absent data at the ends of regions and unsequenced loci were coded as missing.

The MP analysis involved a New Technology Search with a search for the minimum-length tree by five reiterations and 1000 bootstrap resamplings; the default settings were used for other parameters; gaps were treated as missing. The program ModelGenerator (Keane *et al.* 2004) determined the TN+I+G model as the best-fit evolutionary model of nucleotide substitutions. The stopping frequency criterion (FC) for bootstrapping procedure (Pattengale *et al.* 2010) for the dataset revealed that 300 replicates are enough for reaching BS convergence with Pearson average $Q_{100} = 0.994821$ realized in RAXML v7.2.6 (Stamatakis 2006). In the ML

analysis TN+I+G model was used and the rate heterogeneity among sites was modelled using a gamma distribution with four rate categories, resampling procedure with 500 replicates was assessed for Bootstrap support (BS) for individual nodes. For the Bayesian analysis, ITS2 and *trnL*-F partitions were separately assigned the GTR+I+G model, incorporated in MrBayes v. 3.2.1 and suggested by its authors; gamma distributions were approximated using four rate categories. Two independent runs of the Metropolis-coupled MCMC were used to sample parameter values in proportion to their posterior probability. Each run included three heated chains and one unheated chain, and the two starting trees were chosen randomly. The number of generations was ten million, and trees were saved every 100th generation. The software tool Tracer (Rambaut & Drummond 2007) reveals effective sample size (ESS) 13556.9474 and auto-correlation time (ACT) 1327.7473 for our data. The 25 000 trees as determined by Tracer were discarded in each run, and 150 000 trees from both runs were sampled after burning. Bayesian posterior probabilities were calculated from trees sampled after burn-in.

RESULTS

Altogether, the ITS2 for three specimens of both tested *Frullania* species, and the *trnL*-F only for two specimens of *F. diversitexta* were sequenced in this study and included in the newly produced alignment using accessions from Hentschel *et al.* (2009) and Mamontov *et al.* (2020).

The combined ITS2+*trnL*-F alignment for 48 specimens consists of 1328 sites, of which 677 sites belong to ITS2, and 651 sites belong to *trnL*-F. The number of conservative positions in ITS2 and *trnL*-F is 268 (39.58%) and 395

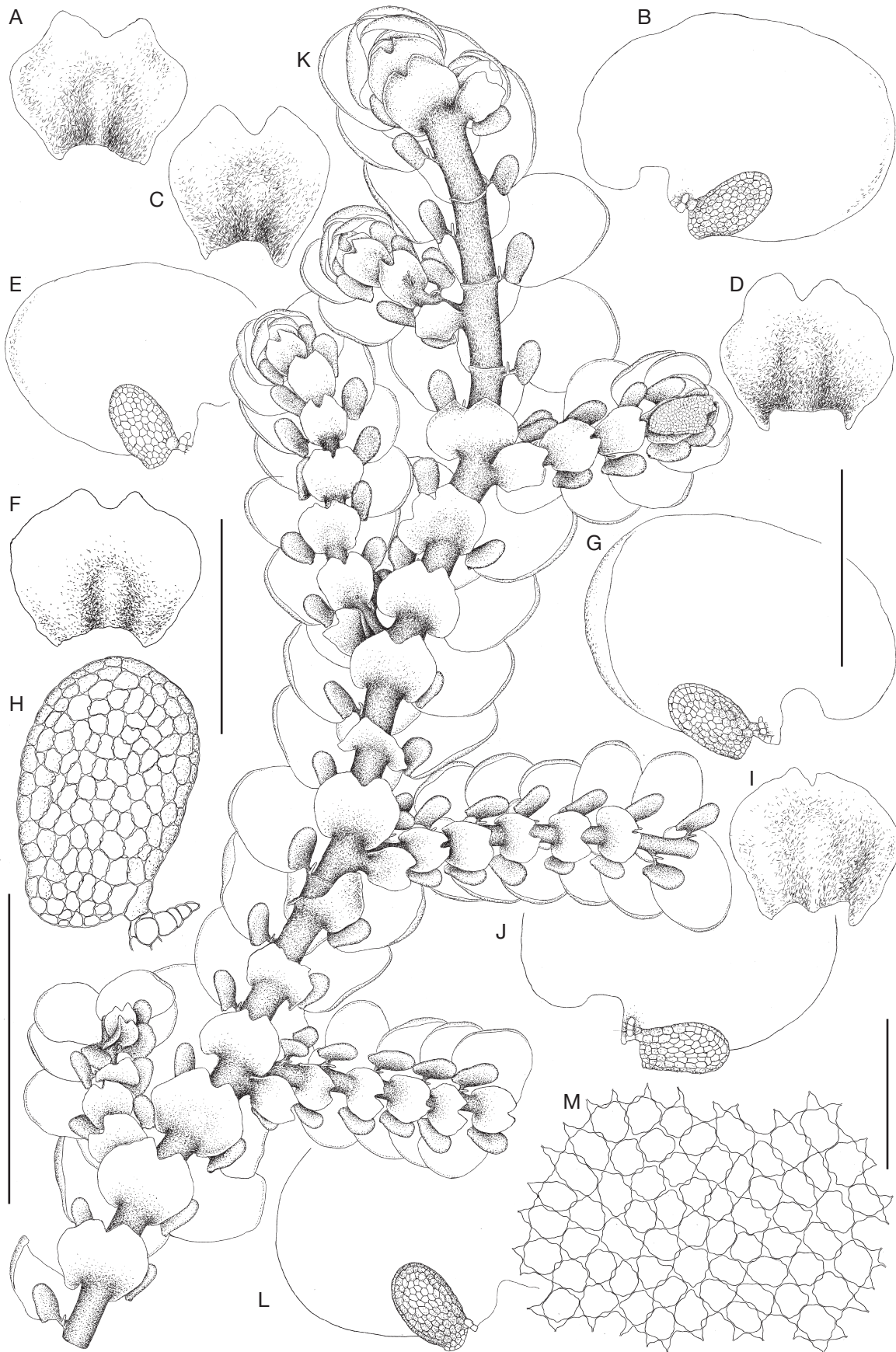


FIG. 2. — *Frullania diversitexta* Steph. **A, C, D, F, I**, underleaves; **B, E, G, J, L**, leaves; **H**, enlarged leaf lobule; **K**, sterile plant; **M**, cells of the lobe middle. Scale bars: A-G, I, J, L, 0.5 mm; H, 0.2 mm; K, 1.5 mm; M, 100 μ m. All from YuSM-805-3-1 (MHA).

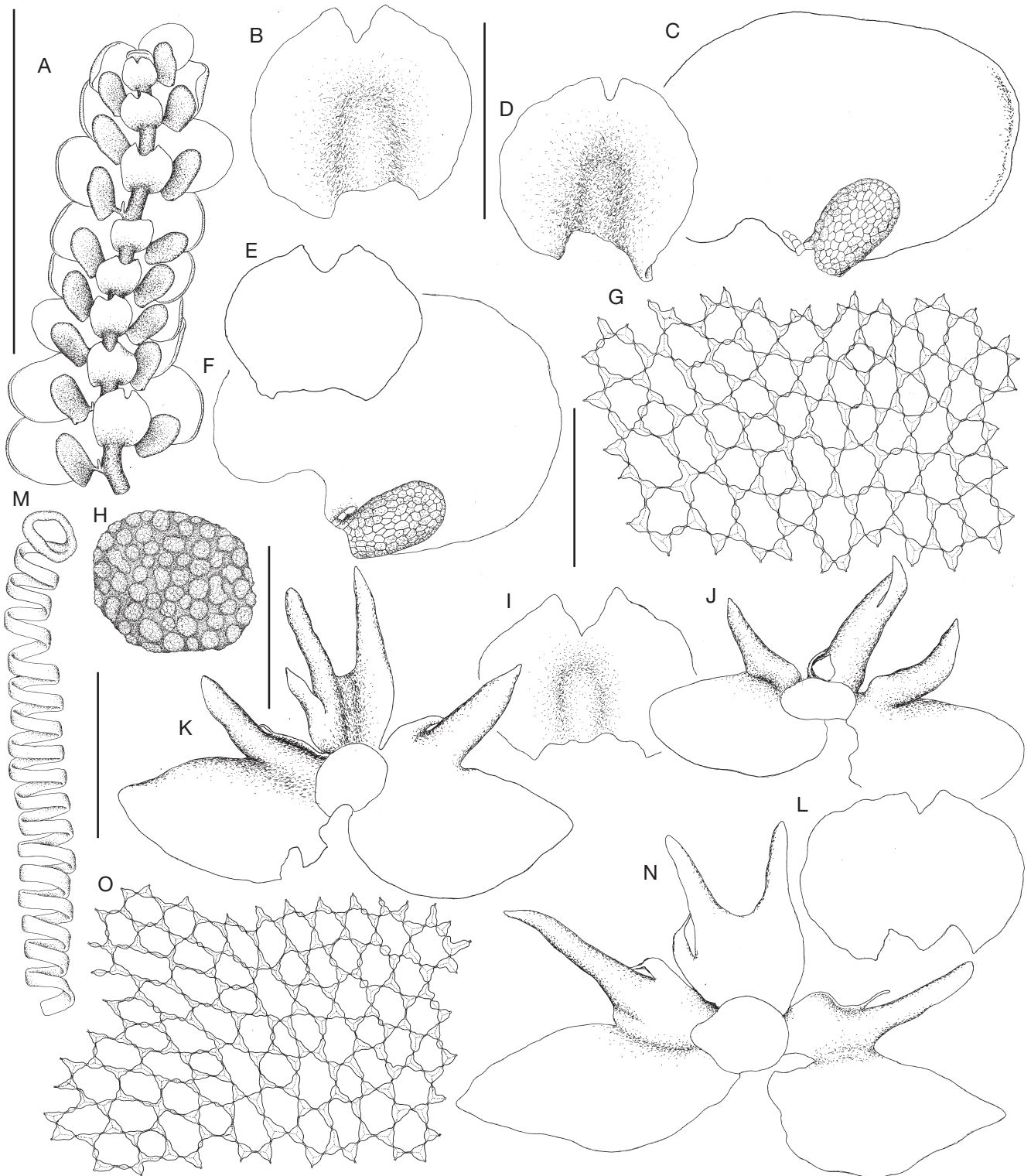


FIG. 3. — *Frullania diversitexta* Steph.: **A**, ultimate branch; **B, D, E, I, L**, underleaves; **C, F**, leaves; **G, O**, cells of the lobe base; **H**, spore; **J, K, N**, three circles of bracts with bracteoles, parts of the same gynoecium; **M**, elaters. Scale bars: **A, J, K, N**, 1.5 mm; **B–F**, 0.5 mm; **G**, 100 μ m; **H**, 50 μ m; **M**, 75 μ m. **A–G** from YuSM-805-3-1 (MHA), **H–O** from Inoue 14 (G-00066936, lectotype of *F. tosana*).

(60.68%), respectively, number of variable positions is 371 (54.80%) and 199 (30.57%), and the number of parsimony-informative positions is 267 (39.43%) and 109 (16.74%). In the combined alignment there are 663 conservative sites

(49.92%), 557 (43.45%) variable sites and 373 (28.08%) parsimony informative positions.

The MP analysis yielded the single most parsimonious tree with a length of 3382 steps, with CI = 0.452030 and RI =

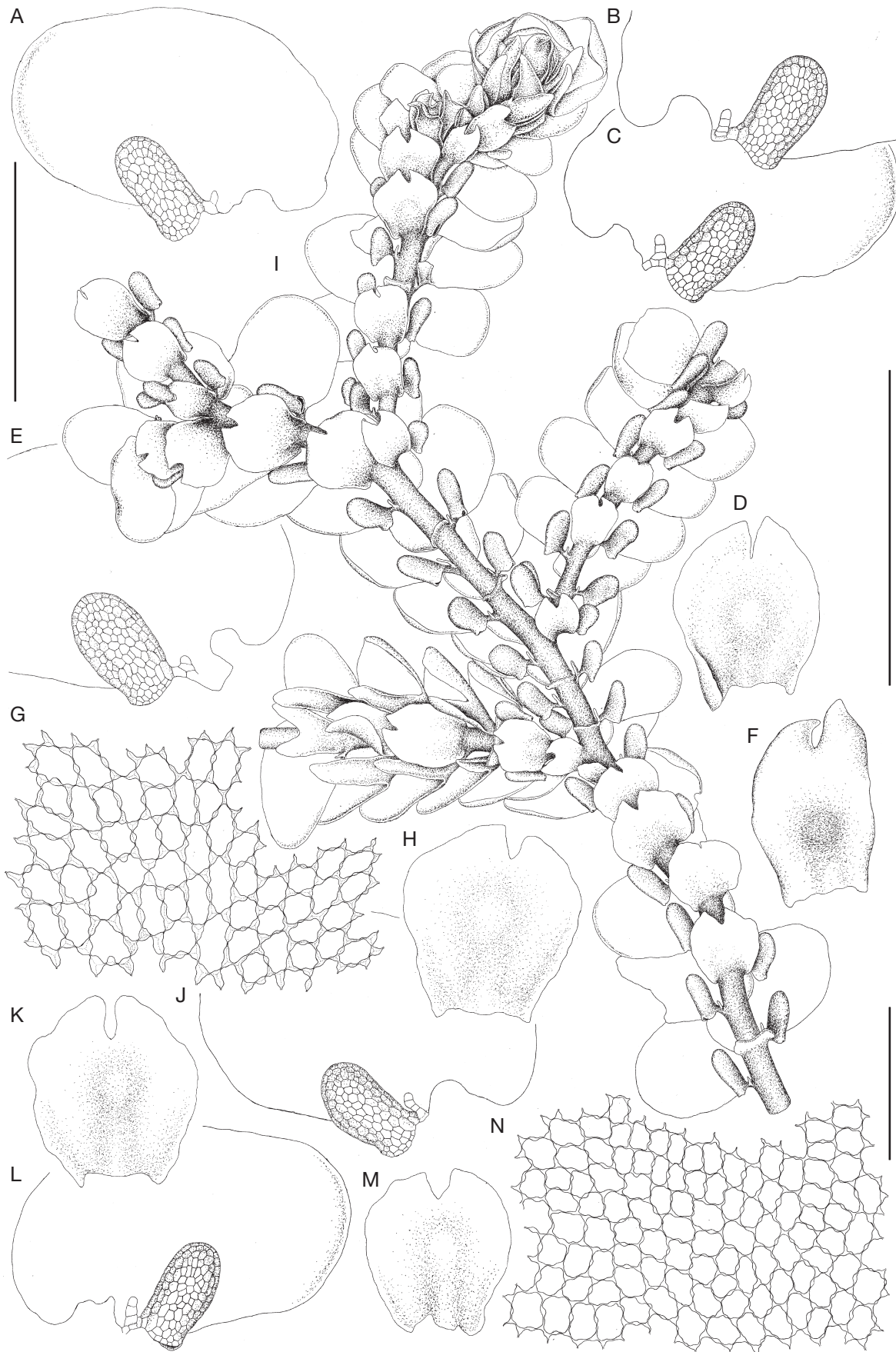


FIG. 4. — *Frullania diversitexta* Steph.: A-C, E, J, L, leaves; D, F, H, K, M, underleaves; G, cells of the lobe middle; I, female plant; N, cells of the lobe base. Scale bars: A-F, H, J-M, 0.5 mm; G, N, 100 μm; I, 1.5 mm. All from Makino s.n. (G-00067128, lectotype).

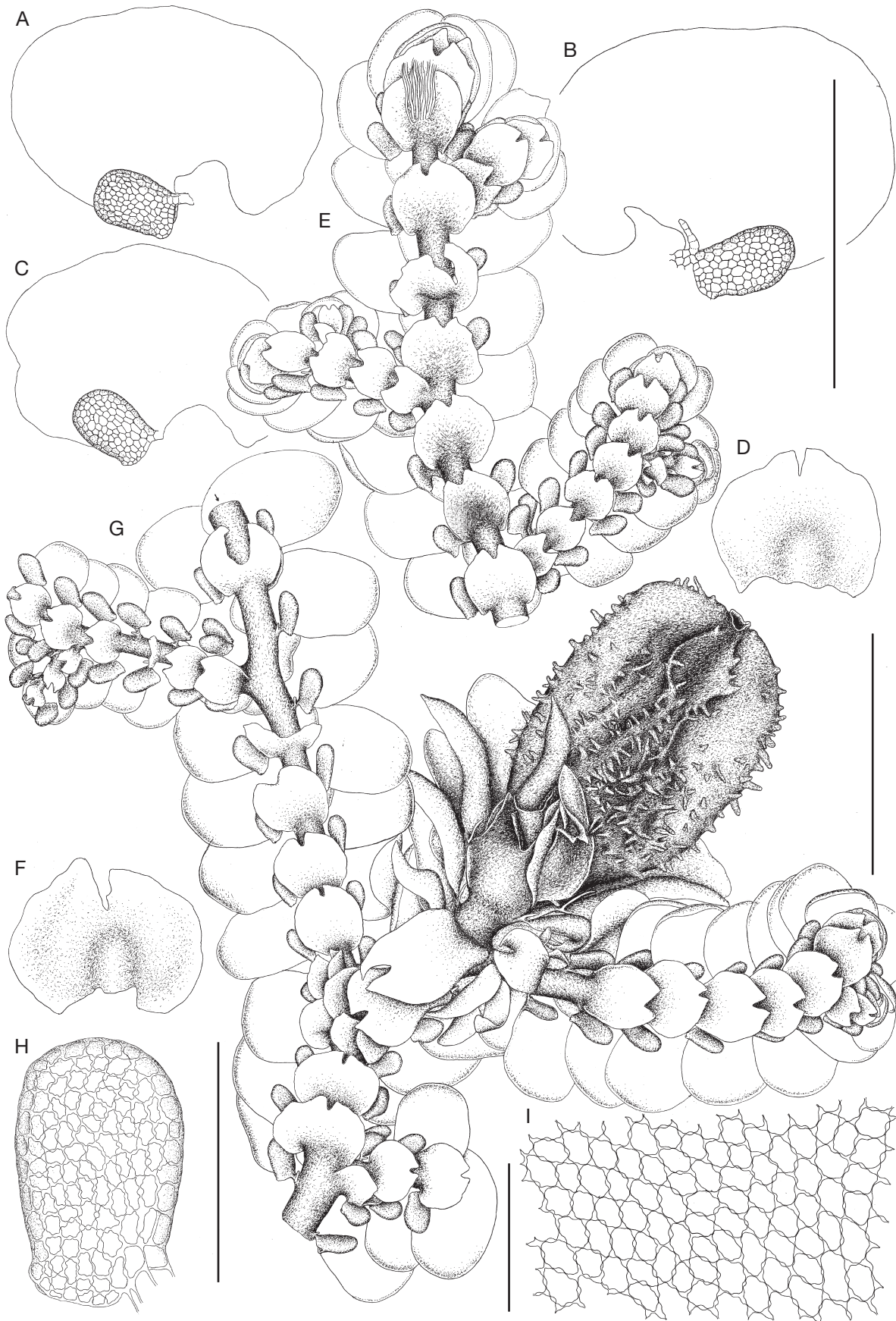


FIG. 5. — *Frullania diversitexta* Steph.: A-C, leaves; D, F, underleaves; E, G, parts of the same female plant; H, enlarged leaf lobule; I, cells of the lobe middle. Scale bars: A-D, F, 0.5 mm; E, G, 1.5 mm; H, 0.2 mm; I, 100 µm. All from *Inoue 14* (G-00066936, lectotype of *F. tozana*).

0.579618 calculated in Mega 5.1. The ML calculation resulted in a single tree, the arithmetic means of Log likelihood was -11659.83. Average standard deviation of split frequencies between the two runs in the BA analysis was 0.010116, and arithmetic means of Log likelihoods for both sampled runs were -101195.82 and -11196.99, respectively.

All calculations resulted in highly congruent topologies. The BA tree for 48 specimens with indication of bootstrap support values achieved in MP/ML calculations and values of Bayesian posterior probabilities are shown (Fig. 1).

The backbone phylogeny of the genus *Frullania* is similar with that published and described by Hentschel *et al.* (2009). Both specimens of *F. diversitexta* composed a clade with high support in all three estimations (BS in MP = 100%, BS in ML = 100%, PP in BA = 1.00 or 100/100/1.00) that lies in a sister relationship (-69/1.00) to a clade of *F. plana* Sull., *F. riparia* Hampe ex Lehm. and *F. amplicrania* Steph. *Frullania ignatovii*, with support 78/68/0.76, is related to *F. davurica* Hampe and *F. jackii* Gottsche (70/93/1.00). Both newly tested taxa, *F. diversitexta* and *F. ignatovii*, have robust positions within subg. *Trachycolea*.

TAXONOMIC ADDITIONS AND CHANGES

Frullania (subg. *Trachycolea*) sect. *Diversitextae*
(Kamim.) J.J. Atwood, Vilnet &
Mamontov, stat. nov.

Frullania (subg. *Frullania* sect. *Diastaloba* (Spruce) Kamim.) subsect. *Diversitextae* Kamim., *Journal of the Hattori Botanical Laboratory* 24: 80. 1961. — *F.* subg. *Diversitextae* (Kamim.) S.Hatt., *Journal of the Hattori Botanical Laboratory* 59: 154. 1985. — Type specimen: *Frullania diversitexta* Steph., *Bulletin de Herbarium Boissier* 5: 89. 1897. Type citation: [Japan] Tosa, Makino 2520. — Type specimen: Japan, Tosa, Makino (lecto-, designated here, G[G00067128]!)

Frullania abducens Steph., *Species Hepaticarum* 4: 396 (1910). — Type citation: Japonia, loco Yasui. Type specimen: Japan, Yasui, Aug. 1898, leg. Inoue 24 (lecto-, designated here, G[G00066970]!) *syn. fide* Hattori (1952)

Frullania tenella Steph., *Species Hepaticarum* 4: 397 (1910), *illeg. hom.*, non *F. tenella* Sande Lac., *Nederlandsch Kruidkundig Archief* 3: 423 (1854); *F. iosana* Horik., *Acta Phytotaxonomica et Geobotanica* 13: 213 (1943), *nom. nov.* — Type citation: Japonia, Provincia Tosa. Type specimen: Japan, Tosa, Jasui, Aug. 1898, leg. Inoue 14. (lecto-, designated here, G[G00066936]!) *syn. fide* Hattori (1952)

Frullania sendaica Steph., *Species Hepaticarum* 6: 552 (1924). — Type citation: Japonia: Sendai. (*Jishiba* legit). Type specimen: Japonia, Provinz Sendai, 1907, leg. *Ishiba* No. 52. (lecto-, designated here, G[G00069109]!) *syn. fide* Hattori (1952)

DISCUSSION

The taxonomic position of *F. diversitexta* has been somewhat controversial due to its intermediate morphology that straddles the perimeter of subg. *Diastaloba*, subg. *Frullania* and subg. *Trachycolea*. The overall habit as well as lobule position and shape are similar to species in *F.* subg. *Diastaloba* and subg. *Frullania*, whereas its tuberculate perianth ornamentation

is more similar to species in subg. *Trachycolea*. This atypical morphological combination has resulted in *F. diversitexta* being assigned to its own, monospecific subgenus, subg. *Diversitextae*. The inclusion of two *F. diversitexta* specimens (Figs 2, 3) in our molecular phylogenetic analysis, based on a representative sampling of *Frullania* from Hentschel *et al.* (2009), shows that this species is not phylogenetically isolated in its own subgenus, nor belongs to subg. *Diastaloba* or subg. *Frullania* as previously proposed. *Frullania diversitexta* is resolved in subg. *Trachycolea*, in a relationship with *F. plana*.

Frullania subg. *Trachycolea* presently contains thirteen sections (Schuster 1992; Hentschel *et al.* 2009) and three-times the taxonomic diversity that is currently attributed to other *Frullania* subgenera (Söderström *et al.* 2016). Species in this subgenus are largely characterized as having a creeping habit, mostly monopodially branched stems, frequently rounded lobe apices, galeate or campanulate lobules that are erect and contiguous, more or less with their mouths in a parallel position with the stem, vestigial styli, gynoecea mostly terminal on stem, innermost female bracteoles mostly free from the bracts, perianth with mostly 3–5 keels and a tendency to have a tuberculate perianth ornamentation (Stotler 1969; Yuzawa 1991; Schuster 1992). The subgenus nevertheless contains species whose morphology deviates from this succinct circumscription, in one or more characters. For example, the aforementioned *F. orientalis* has a pendent habit and clavate to cylindrical lobules (Hattori 1976a), the Asiatic *F. sino-sphaerantha* S.Hatt. & P.J. Lin and *F. faurieana* Steph. have bi-pinnate to tri-pinnate branching (Hattori & Lin 1985), while the lobules of the Chinese *F. parvifolia* Steph. spread at an angle of 50–70° from the stem (Hattori 1973). *Frullania* subg. *Trachycolea*, is the only subgenus to include species with a tuberculate perianth ornamentation. Therefore, a roughened perianth ornamentation may be predictive of phylogenetic position, even though it is not expressed in all taxa of the subgenus. The other subgenera including species with a non-smooth perianth ornamentation are subg. *Mammillosae* S.Hatt., which has a mamilliose surface (Hattori 1986), and some species in subg. *Diastaloba* (e.g. sect. *Inconditum* von Konrat, Hentschel & Heinrichs), which has denticulations on the surface of the keels (von Konrat *et al.* 2010).

Frullania diversitexta is morphologically aligned with subg. *Trachycolea* in its rounded lobe apices, vestigial stylus, tendency to have explanate lobules, plane underleaf margins and tuberculate perianth (Figs 4, 5). The most morphologically similar species in the subgenus is *F. orientalis* due to the previously mentioned similarities in their habit and lobule shape. The relationship of these species is also reinforced by their similar dilated bases of the leaf lobes, underleaves, styli, perianth ornamentation and development of their initial branching appendages. The relationship of species based on their initial branching appendages was emphasized by von Konrat & Braggins (2001), who found support for species with similar initial branching appendages at various taxonomic ranks. In *F. diversitexta*, the initial branching appendages are composed of two saccate lobes. The initial branching appendages of *F. orientalis* also has two saccate lobes (Uribe-M 2011). However,

an important morphological distinction separating these two species is the position of their gynoecia. In *F. diversitexta*, the gynoecia are terminal on the stem or main branch, whereas the gynoecia in *F. orientalis* are on short lateral branches (Hattori 1976a).

Frullania diversitexta also shares many morphological similarities with *F. plana*, and on a molecular basis is more closely aligned. *Frullania plana* occupies a monospecific section within subg. *Trachycolea* due to its distinct morphology and endemic distribution in eastern North America (Schuster 1992). The two species share resemblance in their branching habit, broad leaf lobes with dilated bases, leaf cell areolation, vestigial stylus, angled position of the lobules, tendency to have explanate lobules and in the shape of the underleaves as well as their bases. Interestingly, the initial branching appendages of *F. plana*, although polymorphic also can sometimes have two saccate lobes (Schuster 1992). On the other hand, *F. diversitexta* and *F. plana* are immediately separated by their lobule shape, sexuality, position of the gynoecia and perianth ornamentation. Because *F. diversitexta* does not easily fit into either *F. sect. Orientales* or *F. sect. Planae*, its suite of morphological characters warrants its own section, *F. sect. Diversitextae*, stat. nov. Lectotypes for *F. diversitexta* (Fig. 4), as well as for *F. abducens*, *F. sendaica* and *F. tosana* (Fig. 5) are designated from specimens deposited in Stephani's herbarium (now G). The proposed synonymy by Hattori (1952) is accepted as these three species are indeed morphologically indistinguishable from *F. diversitexta*.

Frullania ignatovii is a small, blackish brown, dioicous species with creeping stems, imbricate and broadly ovate to reniform leaves, galeate and skull shaped lobules, and obovate underleaves that vary from entire margined to obtusely toothed on one or both sides. When Sofronova *et al.* (2013) described the species, they morphologically compared it to *F. ampicrania*, *F. fragilifolia* and *F. chilcootensis*. However, *F. ampicrania* is resolved within subg. *Trachycolea* (Hentschel *et al.* 2009: as subg. *Frullania*), whereas *F. fragilifolia* and *F. chilcootensis* (as *F. hattoriana*) are placed within *F. subg. Frullania* (Hentschel *et al.* 2009; Mamontov *et al.* 2020: as subg. *Thyopsiella*). Molecular sequence data obtained from the holotype specimen of *F. ignatovii* places the species in subg. *Trachycolea* in a sister relationship with *F. davurica* and *F. jackii*. These two closely related species have been treated within the subgenus in sect. *Integristipulae* Verd. due to their sub-orbicular to reniform underleaves that are emarginate and about four times the width of the stem. Compared to the shape and marginal dentation of the underleaves of *F. ignatovii*, the remarkable difference in underleaf morphology would initially suggest that these species seem unrelated. However, Hentschel *et al.* (2009) found evidence of homoplasy in subg. *Trachycolea* (as subg. *Frullania*) for species with holostipous underleaves, since they failed to form a monophyletic clade. *Frullania ignatovii*, *F. davurica* and *F. jackii* are similarly dioicous, share concave lobes with incurved apices and auriculate antical leaf bases, filiform to subulate styli and with dorsal lobe median cells with sinuous trigones and intermediate thickenings. The inflated and

galeate, skull shaped lobules of *F. ignatovii* are also overall similar to *F. davurica* and *F. jackii* in their shape, although the lobule mouths of *F. davurica* and *F. jackii* have a rostrate external margin and tend to be oriented towards the stem, rather than being slightly angled away from it.

Molecular sequencing offers a powerful tool for refining infrageneric relationships, especially when the results are not congruent with prior, morphology based classifications. Here, molecular sequence data were used to assess the taxonomic positions of *F. diversitexta* and *F. ignatovii*. The phylogenetic placement of both species required a reevaluation of the morphological characters that were previously emphasized as taxonomically important. Their resulting molecular topologies offer an improved understanding and insight into the evolutionary relationships within subg. *Trachycolea*.

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APPENDIX 1. — The #list of specimens used in the molecular phylogenetic analysis with the GenBank accession numbers (ITS2/*trnL*-F). Voucher specimen information is provided for the newly generated accessions.

Frullania anomala New Zealand FJ380457/FJ380297; *F. amplicrania* Japan FJ380447/FJ380285; *F. apiculata* Fiji FJ380523/FJ380371; *F. arecae* Ecuador FJ380473/FJ380313; *F. aterrima* New Zealand FJ380522/FJ380370; *F. azorica* Madeira HQ330386/HQ330422; *F. baladina* Fiji FJ380454/FJ380293; *F. brasiliensis* Bolivia FJ380538/FJ380389; *F. congesta* New Zealand FJ380485/FJ380331; *F. cuencensis* Argentina FJ380480/FJ380322; *F. davurica* Russia FJ380444/FJ380280; *F. dilatata* Bulgaria FJ380434/FJ380270; *F. diversitexta* 1, Russia: Primorye Territory, YuSM-802-2 (KPABG), MT408597/MT410977; 2, YuSM-805-3 (KPABG), MT408598/MT410978; *F. ericoides* Virgin Islands FJ380405/FJ380240; *F. falciloba* New Zealand FJ380395/FJ380229; *F. fragilifolia* Germany FJ380511/FJ380357; *F. gaudichaudii* Japan FJ380356/FJ380510; *F. grossiclava* Madagascar FJ380497/FJ380343; *F. chilcootensis* (as *F. hattoriana*) Canada KR152269/KR152283; *F. howeana* Australia FJ380409/FJ380244; *F. hypoleuca* Java FJ380483/FJ380325; *F. ignatovii* Russia: Republic of Buryatiya, YuSM-384-8 (LE, holotype), MT408599/-; *F. cleistostoma* “inflata” Russia FJ380513/FJ380359; *F. intermedia* Fiji FJ380494/FJ380339; *F. jackii* Switzerland FJ380445/FJ380281; *F. lindenbergii* Reunion -/FJ380326; *F. magellanica* Chile FJ380464/FJ380304; *F. meyeniana* Fiji FJ380532/FJ380383; *F. microphylla* Tenerifa FJ380512/FJ380358; *F. nepalensis* Bhutan FJ380430/FJ380266; *F. nodulosa* Fiji FJ380490/FJ380335; *F. obcordata* United States -/FJ380329; *F. orientalis* Sulawesi FJ380427/FJ380263; *F. parhamii* Fiji FJ380463/FJ380303; *F. parvistipula* Sicily FJ380438/FJ380274; *F. peruviana* Ecuador FJ380543/FJ380394; *F. plana* United States FJ380431/FJ380267; *F. purpurea* Seychelles FJ380515/FJ380362; *F. reflexistipula* Java FJ380422/FJ380258; *F. regularis* Papua New Guinea FJ380495/FJ380341; *F. reptans* New Zealand FJ380450/FJ380288; *F. riparia* USA FJ380446/FJ380284; *F. rostrata* New Zealand FJ380461/FJ380301; *F. tamarisci* subsp. *moniliata* Japan FJ380500/FJ380346; *F. taradakensis* Russia FJ380441/FJ380277; *F. tetraptera* Chile FJ380320/FJ380478; *F. trinervis* Uganda FJ380488/FJ380333; *F. usambarana* Reunion FJ380496/FJ380342; *Jubula hutchinsiae* subsp. *hutchinsiae* Portugal DQ987260/DQ987380.