



## Unveiling the enigmatic and ambiguous: A new *Frullania* species from New Caledonia

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### Abstract

*Frullania* is a large and taxonomically complex genus with over 300 accepted species. A new liverwort species, *Frullania thouvenotiana* sp. nov. from New Caledonia, is described and illustrated. The new species, and its placement in *Frullania* subg. *Microfrullania*, is based on morphology with support from previously published sequence data. Diagnostic characters associated with the leaf, especially the leaf margin, distinguishes it from all other species of *Frullania*, including similar species with a distribution comprising Fiji and New Zealand. A brief comparison is made with morphologically allied species, and an artificial key is provided. *Frullania neocaledonica* is also proposed to be a synonym of *F. chevalieri*.

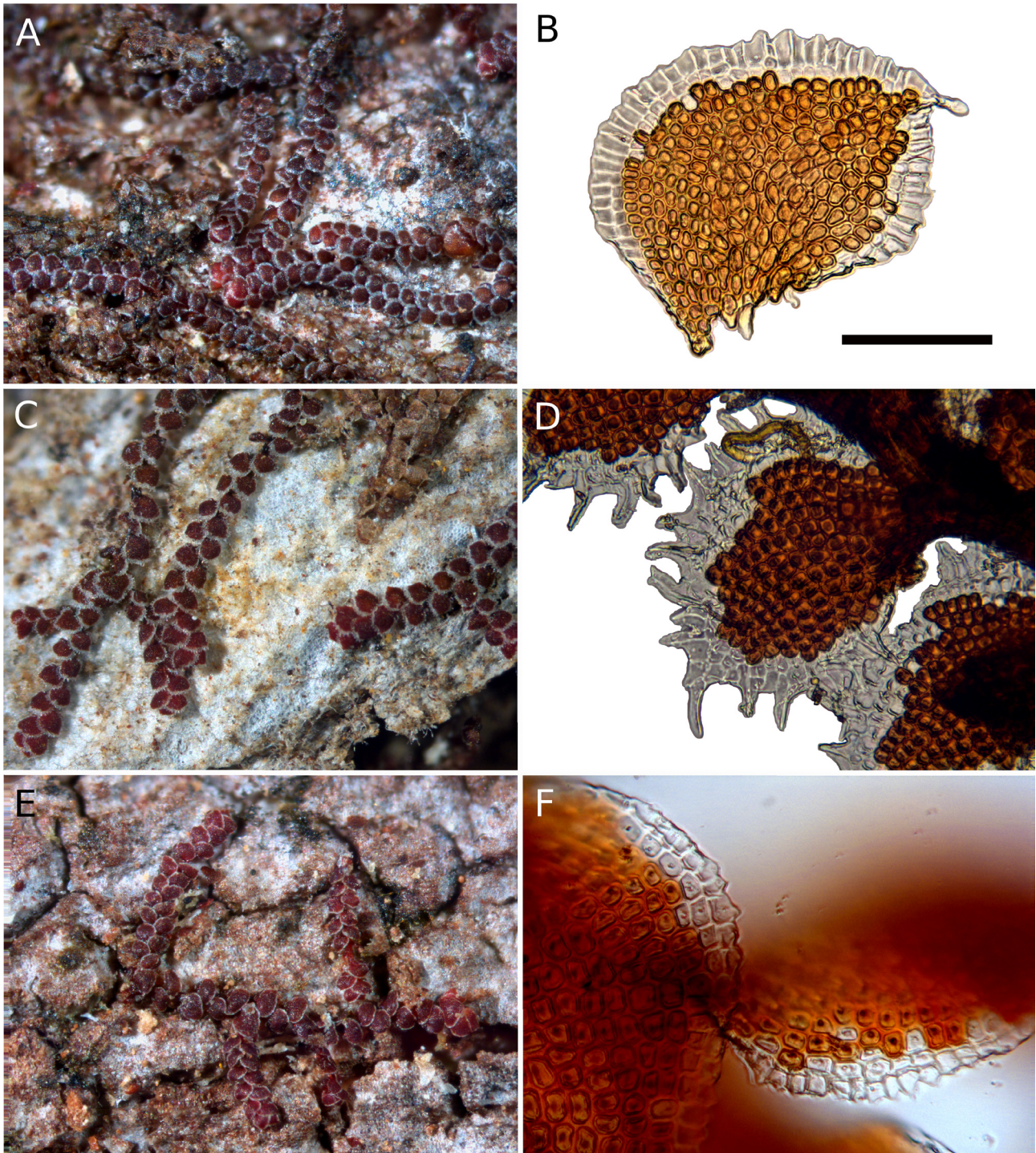
**Keywords:** Cryptic speciation, liverworts, *Microfrullania*, New Caledonia, plant diversity, plant taxonomy

### Introduction

*Frullania* Raddi (1818:9) (Frullaniaceae) is a large, cosmopolitan, and complex liverwort genus with over 2000 validly published binomials (Yuzawa 1991; von Konrat *et al.* 2010), and is present on all continents except Antarctica. Current estimates of the accepted number of species for the genus suggest there are between 300–375 accepted species (e.g., Schuster 1992; Gradstein *et al.* 2001). Söderström *et al.* (2015) included 682 accepted species as part of their worldwide checklist for liverworts and hornworts, although a significant number are of doubtful status. Von Konrat *et al.* (2012) noted that it was clear there is urgent need of more species-level phylogenies with extensive population sampling to approximate the actual diversity of *Frullania*, and to elucidate speciation processes and distribution range formation (Bombosch *et al.* 2010, Heinrichs *et al.* 2010, Ramaiya *et al.* 2010).

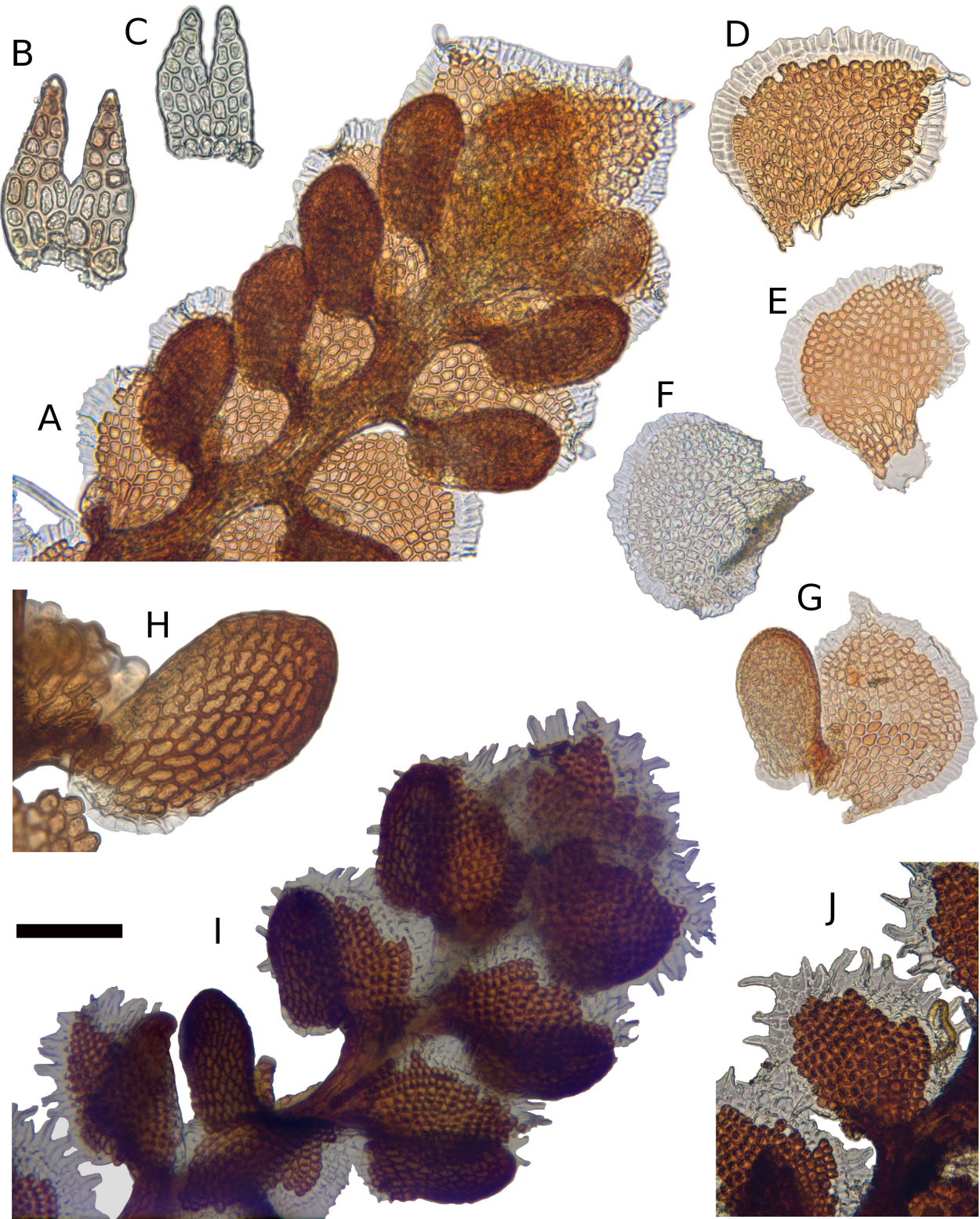
In a recent molecular investigation of species delimitation and biogeography of *Frullania* subg. *Microfrullania* (Schuster 1970:280) Schuster (1992:34), a clade of ca. 15 liverwort species occurring in Australasia, Malesia, and southern South America, Carter *et al.* (2017) uncovered a new species occurring in New Caledonia. They noted, based on combined nuclear and chloroplast sequence data, specimens representing *Frullania microscopica* Pearson (1922: 33) formed two supported sister clades and that upon re-examination were morphologically distinct. We hereby formally describe this new species that Carter *et al.* (2017) previously annotated and discussed as ‘Species A’.

In New Caledonia, the current number of accepted *Frullania* species is ca. 44, although many species are poorly known and/or taxonomically uncertain, or have not been studied critically in the framework of a recent revision or monograph (see the checklist of Thouvenot *et al.* 2011). New Caledonia is the smallest of the 35 global biodiversity ‘hotspots’ (Mittermeier *et al.* 2005) and as with other oceanic islands of rich biodiversity, extinctions would contribute disproportionately to global biodiversity decline (Pouteau & Birnbaum 2016). This study supports the value of population molecular investigations and helps unravel species estimates in critical biodiversity hotspots.



**FIGURE 1.** Comparison between *Frullania thouvernotiana* sp.nov. and morphologically similar taxa. A–B. *Frullania thouvernotiana* (A from holotype von Konrat 15715, B from Shaw 17624). C–D. *Frullania microscopica* (C from Shaw 16784, D from Schuster 52299). E–F. *Frullania parhamii* (both from von Konrat 13353). Scale bar: A, C, E (1 mm); B, D, F (100  $\mu$ m)

A brief comparison is made with another species of similar morphology: *Frullania microscopica*, also of New Caledonia, and *Frullania parhamii* (Schuster 1963:243) R.M.Schust. in Söderström *et al.* (2011:407), that is apparently endemic to Fiji.



**FIGURE 2.** *Frullania thouvenotiana* sp.nov. (A–H) and the morphologically similar and sympatric *Frullania microscopica* (I–J). *Frullania thouvenotiana*: A. Habit, ventral view, wet (from Shaw 17630); B–C. Underleaves (B from Larraín 36100, C from Shaw 17097); D–F. Leaf lobes (D from Shaw 17624, E from Shaw 17628, F from Shaw 17097); G. Leaf lobe with attached lobule (from Shaw 17628); H. Detail of leaf lobule (from Shaw 17097). *Frullania microscopica*: I. Habit, dorsal view, wet (from Schuster 52299); J. Detail of leaf lobe margin (from Schuster 52299). Scale bar: A, D–G, I (100  $\mu$ m); B, C, H (50  $\mu$ m)

## Materials and methods

**Microscopy:**—For the production of microscopic images an Olympus BX51 microscope was used, equipped with both a QICAM Fast1394 camera from QIMAGING (Surrey, Canada), and a slide scanner (moving platform stage attached between the objectives and the condenser) from Objective Imaging Ltd. (Cambridge, UK). The software “Surveyor” from the latter company was used for the digitally rendered images. The images were prepared using the focus stacking software, Zerene Stacker. Measurements were captured using ImageJ2 (Rueden *et al.* 2017).

**Specimens examined:**—In addition to the new species (listed below), material of two morphologically similar species was also examined. *Frullania microscopica*. NEW CALEDONIA. Grande Terre, Province Sud: Commune de Boulouparis, just below the summit of Mont Do, 21° 45.455' S, 166° 00.040' E, 950 m, *Araucaria montana* and *Nothofagus* forest, with tree ferns and palms, on trunk of *Nothofagus*, 27 Sept. 2012, von Konrat 14833 (F, PC); “Réserve Spéciale Botanique du pic Ningua”, at “Mine du Camp des Sapins” 21° 45.004' S 166° 09.419' E, 1150 m, *Dacrydium* forest, with *Cyathea*, *Lycopodium*, etc., at margin of exposed forest, on 5 cm dbh young *Dacrydium*, 29 Sept. 2012, von Konrat 14929 (F, PC, AK). Commune de Dumbéa, “Reserve Naturelle integrale de la Montagne des Sources”, summit of Montagne des Sources, 22° 07.900' S, 166° 36.337' E, 750 m, *Araucaria muelleri* forest, canopy 4–5 m, on 5 cm dbh trunk of small tree, 28 Sept. 2012, von Konrat 14873 (F, SUVA), 14883 (F); summit of Montagne des Sources, 22° 09.128' S, 166° 35.651' E, 530 m, *Araucaria muelleri* forest, with *Araucaria* emergent, on 5 cm dbh trunk of small tree, 28 Sept. 2012, von Konrat 14907 (F). *Frullania parhamii*. FIJI. Vanua Levu, Cakaudrove Province: S of Labasa, Mount Delaikoro, just below summit area along the access road below the telecommunication buildings, 16° 36' 15.15" S, 179° 14' 29.56" E, ca. 800 m, on bark of W-facing trunk of tree at margin of forest on small ridge, May 2012, von Konrat 13353 (F, SUVA).

## Taxonomy

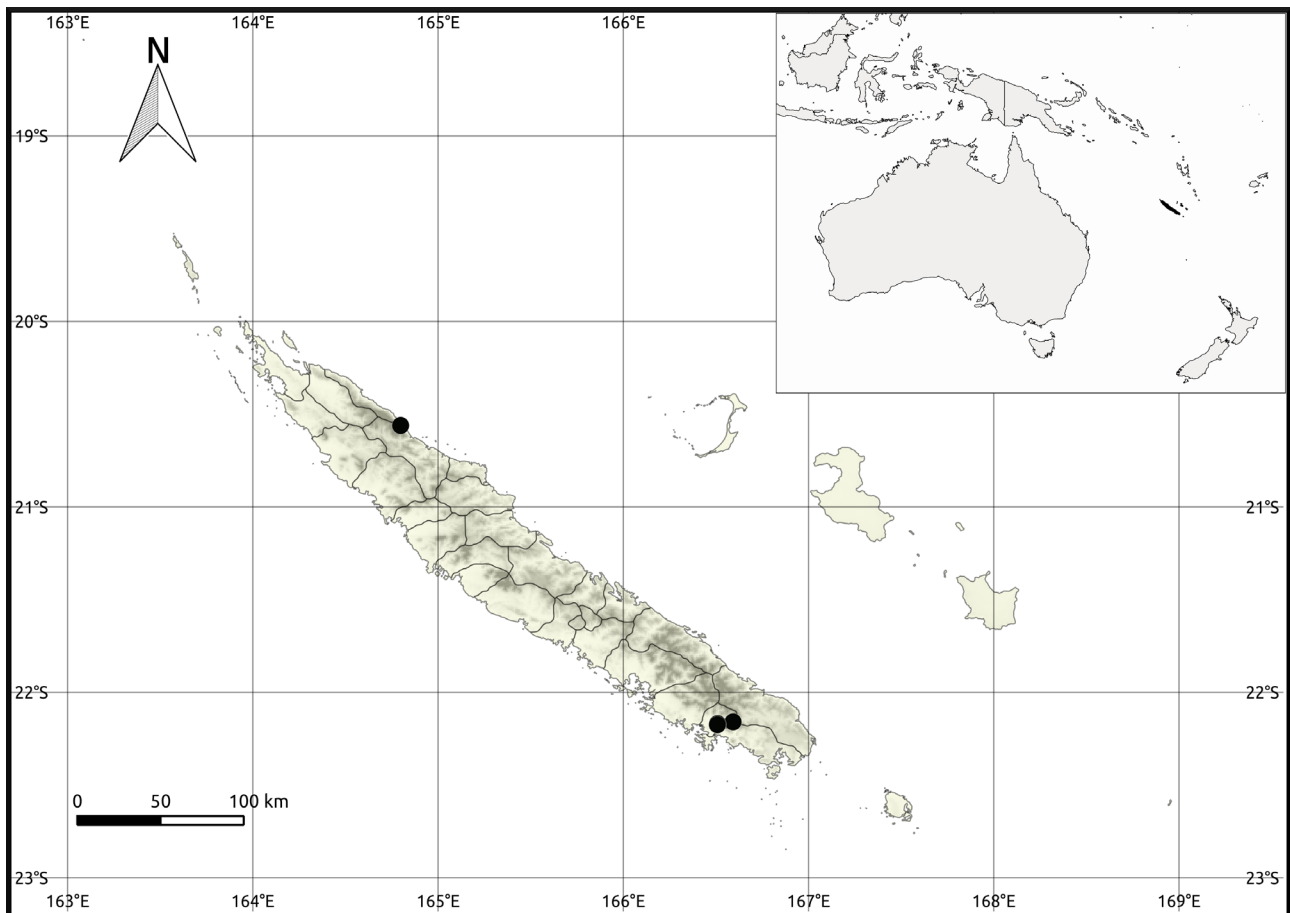
*Frullania thouvenotiana* Larrain, von Konrat, B.E.Carter & Aguero, *sp. nov.* (Fig. 1–3)

**Diagnosis:**—The new species is morphologically most similar to *Frullania microscopica*, also of New Caledonia. Both species have leaf lobes with hyaline and thin-walled marginal cells in 2–4 or more rows, but are immediately distinguished from each other with *F. microscopica* having a margin with distinct, long, spinose teeth and *F. thouvenotiana* with an entire to crenulate margin, and radially elongated marginal cells.

**Type:**—NEW CALEDONIA. Grande Terre, Province Sud: Commune de Dumbéa, Mont Koghis, along trail to the summit starting in the “auberge”, through the cascades, 22° 10' 28" S, 166° 30' 29" E, 550 m, *Agathis-Ficus* old growth forest, on trunk of 10 cm diam. at breast height of young *Agathis*, 18 Oct. 2012, von Konrat 15715 (Holotype, F; Isotypes, PC, AK, DUKE).

**Plants** small (main shoots to 400 µm wide), typically copper-brown, and closely to loosely adhering to substrate. Leading stems and branches to 3 mm long. **Branching** often irregularly to occasionally regularly pinnate. Dimorphic branching, with both *Frullania*-type (FB) and occasionally, *Lejeunea*-type (LB) branching. **Initial appendages of FB:** First branch underleaf (BUL1) always with three distinct segments, the ventral lamina divided for ca. 1/2 its length into two subequally sized lobes + 1 dorsal lobe which is usually saccate, or occasionally sulcate to explanate. First branch leaf (BL1) varies, either: reduced in size, ventral segment elobulate, and explanate to sulcate, with leaves characteristic of the main stem starting at BL2–BL3; or the appendages of BL1 ± characteristic of normal stem leaves (i.e. BL1: 1 explanate dorsal lobe + 1 saccate lobule + 1 stylus). **Initial appendages of LB:** BUL1 and BL1–BL3 are always reduced in size and lobule-free, formation of normal lobulate leaves occurring thereafter. **Stem leaves** of Stem of leading stem flat when dry and wet, slightly imbricate to contiguous, suborbicular to broadly oval, to 245 µm long × 180 µm wide, dorsal margins extending beyond the farther edge of the stem, rounded to subacute apices and non-auriculate at the base, margin with (1) 2–3 (4) rows of ± colourless cells, cells of the outermost layer distinctly radially elongated, margins entire to at most crenulate and smooth dorsal surface. **Lobules** ± remote from the stem at angles of 40–50° with the stem, so that lobules tilted outwards; cylindrically pitcher-shaped, and ca. 1.75–2.00 times as long as wide, lobules large (its area obscuring at least 1/3 of the exposed area of the dorsal lobe), to 170 µm long × 80 µm wide; somewhat dorsiventrally compressed near mouth as compared to gibbous upper third, the opening wide, extending along the abaxial lobule margin; free margin of lobular mouth crenulate-sinuate, with 1 layer of hyaline, thin-walled, radially elongated cells, such that the lobule mouth appears fan-like. **Stylus**, triangular, ± large (1/2–2/3

the length of the lobule), 50–75  $\mu\text{m}$  long  $\times$  30–40  $\mu\text{m}$  wide, 5–7 cells wide  $\times$  5–9 cells high (15–25 cells in total), rarely with a slime papilla at apex. **Underleaves** of leading stems, contiguous to distant from each other, very small (ca. 0.1 times the size of leaf lobes),  $\pm$  similar to the stem in width, to 2 times as long as wide (to 110  $\mu\text{m}$  long  $\times$  55  $\mu\text{m}$  wide), broadest just below middle (4–8 cells wide), with entire lateral margins; apex of underleaf bilobed to 1/2 its length, each lobe with 2–3 cells at the base. **Microphyllous branching** absent, or with pseudo-microphyllous branches where the lobules of secondary stems  $\pm$  similar in size to main stem, but lobes and underleaves of secondary branches markedly smaller than those of leading stems. Stem leaves of branches slightly squarrose when wet. **Lobe outer marginal cells** 1.75–3  $\times$  long as wide,  $\pm$  rectangular, hyaline, with thin walls, cell cavities to 20  $\mu\text{m}$  long  $\times$  10  $\mu\text{m}$  wide; median cells  $\pm$  subquadrate, or 5-sided; cell walls subequally thickened, intermediate thickening rare to absent, cell cavities of median cells brownish red, 8–12  $\mu\text{m}$  long  $\times$  8–10  $\mu\text{m}$  wide; cells becoming gradually larger basally, cavities of the basal median group of cells to 20  $\mu\text{m}$  long  $\times$  10  $\mu\text{m}$  wide; walls of basal cells with subnodulose trigones and occasional intermediate thickenings, walls and cavities brownish red. **Dioicous**. **Androecia** subspherical to discoid, 150  $\mu\text{m}$  long  $\times$  150  $\mu\text{m}$  wide, usually with 2 pairs of closely imbricate bracts, sessile on leafless stalks or terminal on very short-stalked branches. **Gynoecia** terminal on main or leading stem. A side shoot system often occurring between bracts and perianth (subfloral innovation), or arising 2 complete leaf cycles below the gynoecia or perianth bracts i.e. a subfloral branch. Female bracts and bracteoles usually only in 2 pairs with entire margins. **Perianth** partially exerted to freely emergent, to 600  $\mu\text{m}$  long (beak omitted)  $\times$  275  $\mu\text{m}$  wide, 3 rounded keels + 2, minor, supplementary keels, oblong-ovate, tapering towards the apex into a short, distinctly discolored beak, to 75  $\mu\text{m}$  long. **Capsule** valves to 215  $\mu\text{m}$  long  $\times$  125  $\mu\text{m}$  wide. **Elaters** 12–20 in total, unispiral. **Spores** not seen.



**FIGURE 3.** Distribution map of *Frullania thouvenotiana* sp.nov. in New Caledonia, Grande Terre. Inset: location of New Caledonia in Australasia.

**Distribution and ecology:**—So far only known from New Caledonia where it has been collected from the Hienghène and Dumbéa Communes (Fig. 3). In these locations it appears to be locally common, growing between 290–700 m a.s.l. The distribution and ecology of the new species seem very similar to *Frullania microscopica*. Both appear in the North Province (Province Nord) and South Province (Province Sud), and epiphytic on several hosts, including

*Agathis*, *Nothofagus*, and shrubs. Whether there remains a microhabitat disjunction would need investigation. Hattori *et al.* (1972) and Hattori (1984, 1986) provide extensive lists of localities for *F. microscopica*.

*Frullania microscopica* is also believed endemic to New Caledonia. It was recorded for New Zealand in error by Hattori *et al.* (1972), an error later corrected by Hattori (1986). *Frullania thouvenotiana* is of note because it appears to be a narrow-range endemic, a feature which places it along with *F. microcaulis* Gola (1922:172) and *F. lobulata* (Hooker 1820:119) Dumortier (1935:13) (endemic to extreme southern Chile), *F. truncatistyla* von Konrat *et al.* (2011:63), *F. knightbridgei* von Konrat & de Lange in von Konrat *et al.* (2012:28), and *F. toropuku* von Konrat, de Lange & Larraín in von Konrat *et al.* (2013:439) (endemic to New Zealand), and the New Caledonia endemics *F. microscopica*, *F. scalaris* S.Hattori (1977:432), and *F. pseudomeyeniana* S.Hattori (1986:231) (Carter *et al.* 2017).

**Specific name etymology:**—This new species is named in honour of Louis Thouvenot (b. 1949) who is an authority of the bryophyte flora of New Caledonia. The authors, Matt von Konrat, Juan Larraín and Blanka Aguero wished to honour Louis, in recognition not only of his bryological knowledge of New Caledonia, but also for his generosity, and assistance with planning, logistics and organization of fieldwork undertaken in New Caledonia in 2012.

**Additional specimens examined (paratypes):**—NEW CALEDONIA. Grande Terre. Province Nord: Commune de Hienghène, Tao, along trail to Wé Caot river valley (NE slopes of Mt. Panié), flooded forest with palms, *Pandanus*, ferns, on bark of tree, 10 cm diam., 1 m above ground, –20.561247, 164.797919, 290 m, 6 Oct. 2012, *B. Shaw 17097* (DUKE, F). Province Sud: Commune de Dumbéa, Noumea area, Montagne des Sources, along road to Pic Buse area, edge of burned/unburned mid-elevation forest in valley on N-facing slope, –22.159535, 166.592657, 400–420 m, 28 Sept. 2012, *B. Shaw 16752* (DUKE, F); open woodland on S-facing slope along trail to ‘cascades’ (ultramafic), –22.174404, 166.508807, 530 m, 18 Oct. 2012, peeling tree bark at base, *B. Shaw 17624* (DUKE, F), rough bark of dead standing tree at base, *17625* (DUKE, F), *17627* (DUKE, F), bark of 5 cm diameter tree trunk, in filtered light, *17628* (DUKE, F), peeling bark of 15 cm diameter tree at 1.5 m height, *17630* (DUKE, F); Mt. Koghis, along trail to the summit starting in the ‘auberge’, through the cascades, in *Agathis-Ficus* old growth forest, epiphytic along the trail in open area, 22°10’28”S, 166°30’29”E, 550 m, 18 Oct. 2012, *Larraín 36100* (CONC, DUKE, F), *36102B* (CONC, DUKE, F); 600–700 m, margin of forest and exposed shrubland, epiphytic on scrub, 18 Oct. 2012, *von Konrat 15709* (F, AK); epiphytic in the forest edge, 22°10’07”S, 166°30’32”E, 670 m, *Larraín 36114* (CONC, F).

**Affinities, Differentiation & Variation:**—The new species is superficially similar to *Frullania microscopica*, as well as *F. parhamii* of Fiji. Figure 1 provides a comparison of the three species in dorsal view under low magnification (x32) illustrating the similarity in size, form and the distinctly visible pale margin of the leaf lobes. The unique pale margins are not known in any other *Frullania* species. However, there are a suite of characters associated with the margin of the leaf lobe that separate the three species (see the key below):

### Key to morphologically allied species

1. Margins of leaf lobes with long spinose teeth, i.e., leaves sharply and coarsely dentate. New Caledonia ..... *F. microscopica*
1. Margins of leaf lobes entire to weakly dentate. New Caledonia, Fiji, New Zealand ..... 2
2. Marginal cells hyaline in 2–3 (4) rows, many cells of the outermost layer radially elongated. New Caledonia ..... *F. thouvenotiana*
2. Marginal cells hyaline or similar to interior cells, if a hyaline border of 1–2 cells, then cells not radially elongated. Fiji, New Caledonia, New Zealand ..... 3
3. Surface of the dorsal lobe with cell walls raised into sharp, well-defined central tubercles or papillae; leaf-lobe with a distinct hyaline border of 1–2 cells. Fiji ..... *F. parhamii*
3. Surface of the dorsal lobe with smooth or slightly papillose cells; leaf-lobe without a distinct hyaline border. Fiji, New Caledonia, New Zealand ..... *F. chevalieri*

### Discussion

The type of *F. microscopica* (Mt. Mou, *Compton 609 p.p.*, BM!) is characterized by long ciliate lobe margins; the marginal teeth can extend to 45 µm in length, and are typically composed of two elongated and adjacent cells so that the teeth appear longitudinally septate (Fig. 1D, 2J). In contrast, *F. thouvenotiana* has entire to crenulate leaf margins (Fig. 1B, 2D–G). Previously, Carter *et al.* (2017) already noted the two species are sympatric, morphologically distinct and reciprocally monophyletic with strong posterior probability and bootstrap support, and warranted to be recognized as two distinct species.

*Frullania thouvenotiana* is part of *F.* subg. *Microfrullania* sect. *Microfrullania* that was circumscribed by

Söderström *et al.* (2015) to include *Frullania chevalieri* (Schuster 1970:289) Schuster (1992:34), *Frullania microscopica*, *Frullania neocaledonica* J.J.Engel in Engel & Smith Merrill (1999:344), and *Frullania parhamii*. However, Carter *et al.* (2017) concluded based on morphology and molecular evidence that *F. neocaledonica* is a morphological variant of *F. chevalieri*. We formally synonymize this below. Carter *et al.* (2017) also revealed that *Frullania chevalieri* and *F. parhamii* are part of a species complex, which they referred to as the *Frullania chevalieri* complex. Nomenclatural and species refinements in this section are part of a more thorough morphological investigation as part of a forthcoming monograph of the species complexes. This study as well as Carter *et al.* (2017) has also unveiled further collections of *F. parhamii* that were previously only known from sterile material and only known from a single microscopic slide. This has greatly aided species delimitation of the new species described here.

### Other nomenclatural changes:

***Frullania chevalieri*** (R.M.Schust.) R.M.Schust., Hapat. Anthocerotae N. Amer. 5: 34. 1992

≡ *Neohattoria chevalieri* R.M.Schust., J. Hattori Bot. Lab. 33: 289. 1970. Type: New Caledonia, Mt. Mou, *Compton 616 p.p.* (BM!) [mixed with the types of *F. microscopica* and *Neohattoria caledonica*]. ≡ *Schusterella chevalieri* (R.M.Schust.) S.Hatt., Sharp & Mizut., J. Jap. Bot. 20: 331. 1972.

≡ *Neohattoria caledonica* R.M.Schust., J. Hattori Bot. Lab. 33: 291. 1970. ≡ *Frullania neocaledonica* J.J.Engel, Novon 9: 344. 1999. (blocked by *Frullania caledonica* Gottsche ex Steph., Hedwigia 33: 156. 1894). **syn. nov.** Type: New Caledonia, Mt. Mou, *Compton 616 p.p.* (BM!) [mixed with the types of *F. microscopica* and *Neohattoria chevalieri*].

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### References

- Bombosch, A., Wieneke, A., Busch, A., Jonas, R., Hentschel, J., Kreier, H.-P., Shaw, B., Shaw, A.J. & Heinrichs, J. (2010) Narrow species concepts in the *Frullania dilatata-appalachiana-eboracensis* complex (Porellales, Jungermanniopsida): evidence from nuclear and chloroplast DNA markers. *Plant Systematics and Evolution* 290: 151–158.  
<https://doi.org/10.1007/s00606-010-0357-3>
- Carter, B.E., Larrain, J., Manukjanová, A., Shaw, B., Shaw, A.J., Heinrichs, J., de Lange, P., Suleiman, M., Thouvenot, L. & von Konrat, M. (2017) Species delimitation and biogeography of a southern hemisphere liverwort clade, *Frullania* subgenus *Microfrullania* (Frullaniaceae, Marchantiophyta). *Molecular Phylogenetics and Evolution* 107: 16–26.

<https://doi.org/10.1016/j.ympcv.2016.10.002>

- Dumortier, B.C.J. (1835) *Recueil d'Observations sur les Jungermanniacées*. Belgium, Tournay, imprimerie de J.-A. Blanquart, 27 pp.  
<https://doi.org/10.5962/bhl.title.731>
- Engel, J.J. & Smith Merrill, G.L. (1999) Austral Hepaticae. 29. More new taxa and combinations in *Telaranea* (Lepidoziaceae) and a new name for *Frullania caledonica* (Schust.) Schust. (Frullaniaceae) from New Caledonia. *Novon* 9 (3): 339–344.  
<https://doi.org/10.5962/bhl.title.744>
- Gola, G. (1922) Le epatiche raccolte dal Dott. G.B. De Gasperi nella Terra del Fuoco sud-occidentale. *Nuovo Giornale Botanico Italiano* (n.ser.) 29 (1/4): 162–173.
- Gradstein, S.R., Churchill, S.P. & Salazar-Allen, N. (2001) Guide to the bryophytes of tropical America. *Memoirs of the New York Botanical Garden* 86: 1–577.
- Hattori, S. (1977) Dr. H. Hürlimann's collections of New Caledonian Frullaniaceae. *Journal of the Hattori Botanical Laboratory* 43: 409–438.
- Hattori, S. (1984) New Caledonian Frullaniaceae. *Journal of the Hattori Botanical Laboratory* 57: 405–426.
- Hattori, S. (1986) A synopsis of New Caledonian Frullaniaceae. *Journal of the Hattori Botanical Laboratory* 60: 203–237.
- Hattori, S., Sharp, A.J. & Mizutani, M. (1972) *Schusterella*, a new genus of Jubulaceae (Hepaticae). *Journal of Japanese Botany* 20: 329–338.
- Heinrichs, J., Hentschel, J., Bombosch, A., Fiebig, A., Reise, J., Edelmann, M., Kreier, H.-P., Schäfer-Verwimp, A., Caspari, S., Schmidt, A.R., Zhu, R.-L., von Konrat, M., Shaw, B. & Shaw, A.J. (2010) One species or at least eight? Delimitation and distribution of *Frullania tamarisci* (L.) Dumort. s. l. (Jungermanniopsida, Porellales) inferred from nuclear and chloroplast DNA markers. *Molecular Phylogenetics and Evolution* 56: 1105–1114.  
<https://doi.org/10.1016/j.ympcv.2010.05.004>
- Hooker, W.J. (1820) *Musci Exotici*, vol. II. London: Longmans.  
<https://doi.org/10.5962/bhl.title.10721>
- Mittermeier, R.A., Robles, G.P., Hoffman, M., Pilgrim, J., Brooks, T., Goetsch, C., Mittermeier, J.L. & Da Fonseca, G.A.B. (2005) *Hotspots revisited: Earth's biologically richest and most threatened terrestrial ecoregions* (Conservation International: Chicago).
- Pearson, W.H. (1922) Hepaticae (in: Compton, R. H., A systematic account of the plants collected in New Caledonia and Isle of Pines by Mr. R. H. Compton, M. A. in 1914.—Part III. Cryptogams (Hepaticae-Fungi)). *Journal of the Linnean Society. Botany* 46 (305): 13–44.  
<https://doi.org/10.1111/j.1095-8339.1922.tb00474.x>
- Pouteau, R. & Birnbaum, P. (2016) Island biodiversity hotspots are getting hotter: vulnerability of tree species to climate change in New Caledonia. *Biological Conservation* 201: 111–119.  
<https://doi.org/10.1016/j.biocon.2016.06.031>
- Raddi, G. (1818) *Jungermanniografia Etrusca*. La Società tipografica, Modena, 45 pp.
- Ramaiya, M., Johnson, M.G., Shaw, B., Heinrichs, J., Hentschel, J., von Konrat, M., Davison, P.G. & Shaw, A.J. (2010) Morphologically cryptic biological species within the liverwort *Frullania asagrayana*. *American Journal of Botany* 97: 1707–1718.  
<https://doi.org/10.3732/ajb.1000171>
- Rueden, C.T., Schindelin, J., Hiner, M.C., DeZonia, B.E., Walter, A.E., Arena, E.T. & Eliceiri, K.W. (2017) “ImageJ2: ImageJ for the next generation of scientific image data”, *BMC Bioinformatics* 18: 529.  
<https://doi.org/10.1186/s12859-017-1934-z>
- Schuster, R.M. (1963) Studies on antipodal Hepaticae. I. Annotated key to the genera of antipodal Hepaticae with special reference to New Zealand and Tasmania. *Journal of the Hattori Botanical Laboratory* 26: 185–309.
- Schuster, R.M. (1970) Studies on Antipodal Hepaticae, III. *Jubulopsis* Schuster, *Neohattoria* Kamimura and *Amphijubula* Schuster. *Journal of the Hattori Botanical Laboratory* 33: 266–304.
- Schuster, R.M. (1992) *The Hepaticae and Anthocerotae of North America east of the hundredth meridian*. Volume V. Field Museum of Natural History, Chicago, 854 pp.
- Söderström, L., Hagborg, A., Pócs, T., Sass-Gyarmati, A., Brown, E., von Konrat, M. & Renner, M. (2011) Checklist of hornworts and liverworts of Fiji. *Telopea* 13 (3): 405–454.
- Söderström, L., Hagborg, A., von Konrat, M., Bartholomew-Began, S., Bell, D., Briscoe, L., Brown, E., Cargill, D.C., Costa, D.P., Crandall-Stotler, B.J., Cooper, E.D., Dauphin, G., Engel, J.J., Feldberg, K., Glenney, D., Gradstein, S.R., He, X., Heinrichs, J., Hentschel, J., Ilkiu-Borges, A.L., Katagiri, T., Konstantinova, N.A., Larrain, J., Long, D.G., Nebel, M., Pócs, T., Felisa Puche, F., Reiner-Drehwald, E., Renner, M.A.M., Sass-Gyarmati, A., Schäfer-Verwimp, A., Moragues, J.G.S., Stotler, R.E., Sukkharak, P., Thiers, B.M., Uribe, J., Vána, J., Villarreal, J.C., Wigginton, M., Zhang, L. & Zhu, R.-L. (2016) World checklist of hornworts and liverworts. *PhytoKeys* 59: 1–821.  
<https://doi.org/10.3897/phytokeys.59.6261>



- Thouvenot, L., Gradstein, S.R., Hagborg, A., Söderström, L. & Bardat, J. (2011) Checklist of the liverworts and hornworts of New Caledonia. *Cryptogamie, Bryologie* 32: 287–390.  
<https://doi.org/10.7872/cryb.v32.iss4.2011.287>
- von Konrat, M., Hentschel, J., Heinrichs, J., Braggins, J.E. & Pócs, T. (2010) Forty-one degrees below and sixty years in the dark: *Frullania* sect. *Inconditum*, a new section of Australasian *Frullania* species including *F. colliculosa*, sp. nov., *F. hodgsoniae*, nom. and stat. nov., *F. aterrима*, and *F. hattorii* (Frullaniaceae, Marchantiophyta). *Nova Hedwigia* 91: 471–500.  
<https://doi.org/10.1127/0029-5035/2010/0091-0471>
- von Konrat, M., Hentschel, J., Heinrichs, J. & Braggins, J.E. (2011) Deep southern hemisphere connections: A revision of *Frullania* sect. *Amphijubula*. *Bryologist* 114 (1): 52–66,  
<https://doi.org/10.1639/0007-2745-114.1.52>
- von Konrat, M., de Lange, P., Greif, M., Strozier, L., Hentschel, J. & Heinrichs, J. (2012) *Frullania knightbridgei*, a new liverwort (Frullaniaceae, Marchantiophyta) species from the deep south of Aotearoa-New Zealand based on an integrated evidence-based approach. *PhytoKeys* 8: 13–36.  
<https://doi.org/10.3897/phytokeys.8.2496>
- von Konrat, M., de Lange, P., Larrain, J., Hentschel, J., Carter, B., Shaw, A.J. & Shaw, B. (2013) A small world: Uncovering hidden diversity in *Frullania*—a new species from Aotearoa-New Zealand. *Polish Botanical Journal* 58 (2): 437–447.  
<https://doi.org/10.2478/pbj-2013-0056>
- Yuzawa, Y. (1991) A monograph of subgen. *Chonantheria* of gen. *Frullania* (Hepaticae) of the world. *Journal of the Hattori Botanical Laboratory* 70: 181–291.