

## AUSTRAL HEPATICAE 53. UNRAVELING HIDDEN DIVERSITY: A NOVEL SPECIES OF *FRULLANIA* RADDI FROM NEW ZEALAND

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**Abstract:** *Frullania crassissima* J.J.Engel, von Konrat and Glenny, a member of the genus *Frullania* Raddi, is described and illustrated. It is morphologically most similar to *F. setchellii*, *F. svihlana* and *F. falciloba*, of New Zealand and *F. vittiana* of Lord Howe Island. The new species is also sister to *F. squarrosula*, *F. nicholsonii*, *F. vittiana* and *F. falciloba* in a previously published phylogenetic analysis. It shares with those species a falcate asymmetrical leaf lobule that is truncate at its apex. It differs from those species principally in the surface ornamentation of the perianth and leaf cell wall thickenings. It is currently only known from the type material, but is likely to be more widespread.

**Keywords:** liverworts, *Frullania*, Frullaniaceae, taxonomy, New Zealand

### INTRODUCTION

*Frullania* Raddi is a large, widely distributed, taxonomically complex leafy liverwort genus of the family Frullaniaceae, with over 1300 validly published binomials (A. Hagborg, pers. comm.). 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. A growing number of molecular investigations to elucidate speciation processes and distribution ranges are significantly contributing to our understanding of *Frullania* diversity (e.g., Bombosch *et al.* 2010; Heinrichs *et al.* 2010; Ramaiya *et al.* 2010; Vilnet *et al.* 2014; McCarter *et al.* 2017; Mamontov *et al.* 2020).

During the course of investigations on *Frullania* in connection with the Liverwort Flora of New Zealand project (Engel and Glenny 2008, 2019a, 2019b), a specimen collected by Jan-Peter Frahm in New Zealand was re-examined and evaluated. The specimen was



included in the molecular study of Hentschel *et al.* (2009) and served as the voucher listed as *Frullania falciloba* Taylor *ex* Lehm. III in *Table 1* in that study. Also listed as vouchers in *Table 1* are two other specimens from New Zealand, *Frullania falciloba* I and *Frullania falciloba* II. Hentschel *et al.* (2009) noted that *F. falciloba* was not monophyletic. The voucher of *Frullania falciloba* III is the subject of this paper.

In the topology in figure 1 of Hentschel *et al.* (2009) *Frullania crassissima* (labelled as *Frullania falciloba* III) is sister to a clade that includes *F. falciloba*, *F. squarrosula* (Hook.f. *et* Taylor) Gottsche, Lindenb. *et* Nees, *F. nicholsonii* E.A.Hodgs. and *F. vittiana* S.Hatt. There is 91% bootstrap support for its placement outside of that clade. Two samples of *F. falciloba* (labelled *Frullania falciloba* I and II in that study) sit within that clade with 98% bootstrap support.

This new species is a tribute to Prof. Tamás Pócs in recognition of his vast contributions to bryology, including *Frullania* in the South Pacific, particularly Fiji and Australia (e.g. Pócs 2008).

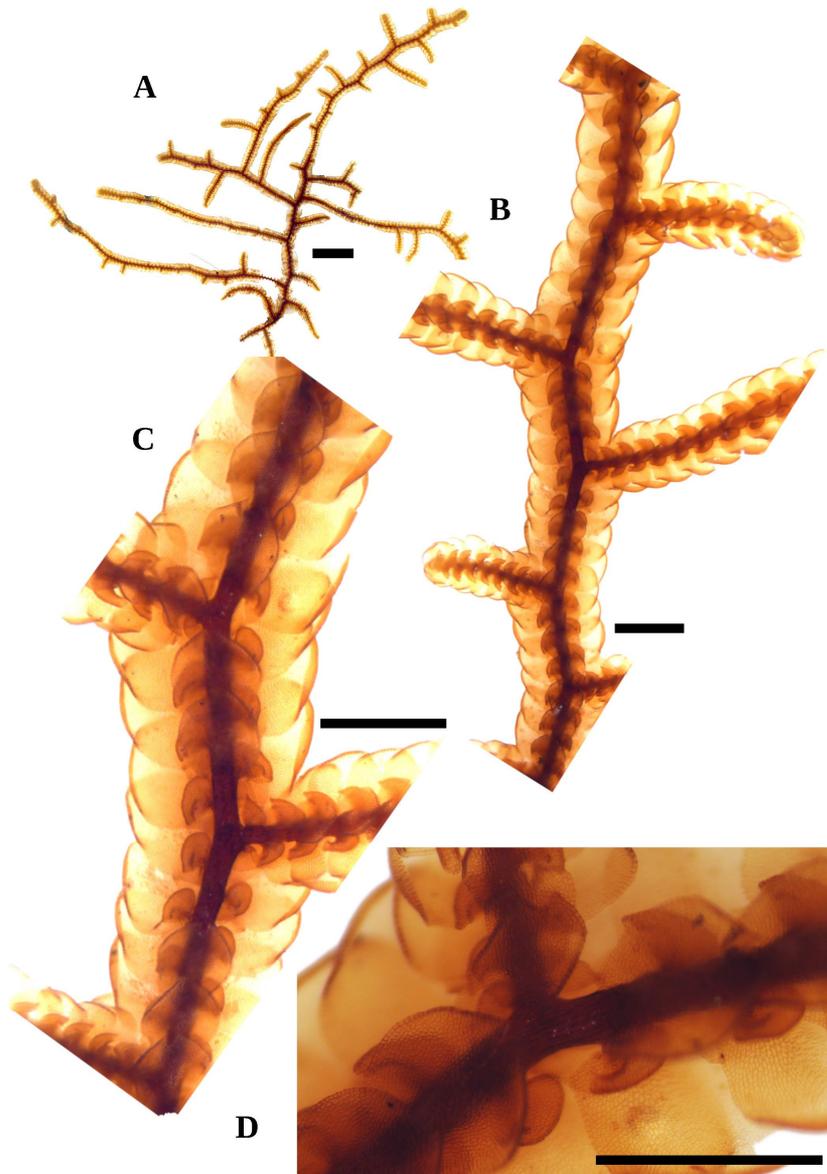
## RESULTS

### Taxonomy

***Frullania crassissima*** J.J. Engel, von Konrat & Glenney, sp. nov.  
(*Figures 1–4*)

**Diagnosis.** Similar to *Frullania setchellii* but differs in the markedly thick-walled median leaf lobe cells, with thin-walled areas (pits) totally lacking or, at most, with 1–2 pits per cell; leaf lobe margins distinctly crenate by bulging septa together with incurved intervening exposed tangential walls; concave underleaves with their margins recurved; ovate-trapezoid innermost bracteoles with a cordate base and lamina margins each with an entire-margined lobuliform process, the lamina margins otherwise entire or with a subhemispherical protrusion at the base; a sharply flared rostrum mouth, the mouth, at least in part, denticulate to lobulate; the perianth keel surface with rather sparse processes ranging in shape from verrucate, dome-like swellings, to conoidal, to acute and at times hook-like, or lamelliform.

**Holotype.** New Zealand, South Is., Nelson Lakes Natl. Park, St. Arnaud, St. Arnaud Range track, 800 m, 8 Mar. 1998, *J.-P. Frahm* 27-2 (GOET—c. per. + ♂); isotype: (F).



**Figure 1.** *Frullania crassissima* plant habit and branching detail. **A.** Sterile plant showing the main stem and branching pattern; note the somewhat indeterminate growth of some primary branches and others remaining short. **B.** Shoot with primary branches. **C.** Shoot showing two *Frullania*-type branches, the branch base at upper left at greater magnification (Fig. D), note the lobules almost all or nearly covered by the underleaves. **D.** Sector of main shoot with a *Frullania*-type branch (ventral view), an underleaf of main shoot removed for clarity, some of the underleaves of main axis removed; note saccate first branch leaf; note the red brown pigmentation of the plant. Scale bars: A = 2 mm; B, C, D, = 500 μm (All from type).

**Etymology.** The epithet "*crassissima*" was used in the superlative to call attention to the notable thickness of the cell walls of the leaf lobe.

Plants flexuous, pale yellowish green, the main shoots large, 0.8–1 mm wide, ca. 25 mm long. Branching ± regularly 1–2(3)-pinnate, the branches (particularly primary and secondary branches) often of limited growth, but rather frequently becoming elongate, the primary branches sometimes becoming leading shoots with their own pattern of branching, the branches of the *Frullania*-type; first branch underleaf (BUL1) large and underleaf-like, bilobed, the ventral segments explanate, inserted on ventral side of branch base, ventral lobe 1 larger, +1 unlobed, much smaller dorsal segment inserted on lateral basiscopic side of branch base; first branch leaf (BL1) bifid, 1 ventral saccate segment + 1 dorsal, rather large, acute segment. Stems (leading) 9–10 cells wide, the cortical cells in a single layer of somewhat smaller, bast-like cells with markedly thickened, brownish walls and a reduced lumen; medullary cells with markedly thickened, yellow-brown walls with large, bulging corner thickenings. Leaves (main stem) loosely to rather closely imbricate; lobes weakly vertical and then with the dorsal faces regularly slightly aligned toward shoot base, incubously inclined, strongly convex, asymmetrically stoutly ovate to elliptic (when flat), the dorsal half of lobe hemispherical, the ventral margin straight or moderately arched, the apices decurved to revolute, broadly rounded (when flat), the dorsal margin at times abruptly and sharply reflexed in basal half, the margins distinctly crenate by bulging septa together with the intervening exposed tangential walls curved inward, the dorsal margin extending 0.5–1.5× the stem width beyond the opposite edge of the stem, the base distinctly auriculate to ligulate, the appendages each overlying the juxtaposed lobe insertion on dorsal side of stem, a "vortex-like" channel at the point of its insertion on the dorsal face of the stem not discernible, the ventral base rounded; lobules with the perimeter inflated, with a large concavity in median sector, strongly asymmetric, falcate-galeate, the widest part of lobule contiguous to stem to appressed to it, the lobules fairly well-covered by the underleaves, commonly with the lateral half or just the beak of the lobule exposed, occupying 25% of the exposed area of the dorsal lobe, the lobules inclined downward toward shoot base, falcate, dorsiventrally compressed and appearing pinched

inward and slightly upward along the mouth, the morphological ventral edge of mouth a little higher than the dorsal and exposing 1–4 rows of cells along the mouth on the dorsal side of the lobule, the pinched sector forming a deep, hemispherical to occasionally lunate pocket, the mouth wide, weakly to distinctly crenulate by projecting septa of cells at the mouth, the morphological ventral edge of mouth plane or inrolled and then not visible, the morphological dorsal edge of mouth  $\pm$  straight, plane or abruptly inflexed such that the margin is seen edge-on, the margins of the mouth (when both visible)  $\pm$  parallel, the upper (apical) and lateral sectors of the lobule inflated, the inflated sector gradually narrowing and in ventral view appearing subcylindrical at the outer extremity, the apex of lobule (sector closest to stem) narrowly, sharply, and hemispherically rounded, and outer margin of the lobule soon forming a gentle, smooth,  $\pm$  symmetrical, subhemispherical, arched line (in particularly robust lobules the outer margin straight in median sector and arched at either end), the inflated sector terminating in a weak beak, the arched line smooth and uninterrupted, not abruptly protracted distally and not becoming piliform, the beak oriented toward shoot base, or if the curvature of the apex and outer margin a little stronger, then the beak oriented toward the stem, the beak broadly rounded to truncate at the tip, not tapering toward tip, the beak not reaching the ventral margin of the lobes or somewhat extending beyond the ventral margin of the lobes; stylus minute, inconspicuous, a multicellular ovate base and a uniseriate row, the stylus comprised of a basal tier of 3–7 cells wide, followed by a tier of 3 laterally juxtaposed cells, then 0–2 biseriate tiers, and a terminating in a uniseriate row 2–4 cells, the tip cell with a markedly long slime papilla. Cells of lobe in distinct vertical rows; cells of median sector of lobe with trigones nodose, usually confluent with each other and with the frequent, intermediate thickenings (which are often larger than the trigones), so that the lumen is often completely surrounded by wall thickenings, with thin-walled areas (pits) totally lacking, or with all walls surrounding a given lumen totaling only 1–2 pits, the trigones and intermediate thickenings together lending the walls sinuous, the cells 11–19  $\mu\text{m}$  wide, 19–25  $\mu\text{m}$  long; basal group of cells forming a limited, local, but well-defined field of cells only a few tiers high, the cells amber, larger, often wider than those above, with walls  $\pm$  evenly thickened except for large to

nodulose trigones and a few intermediate thickenings, or the walls not evenly thickened and with trigones and intermediate thickenings lending the walls sinuous, the cells 19–27  $\mu\text{m}$  wide, 26–35  $\mu\text{m}$  long; median subbasal cells in several tiers, the cells longer and narrower than those of the median-basal field and with pits more frequent and well defined, and with the sinuosity more regular, especially involving the longitudinal walls that run vertically and continuously interconnecting successive tiers of cells, the walls in quite regular vertical rows, the subbasal cells rather soon grade into cells more like those in the median sector of the leaf, i.e., fewer pits between adjacent cells and sinuosity more irregular; marginal cells subquadrate, less often transversely or vertically short rectangular, the walls thickened, with nodulose trigones, often with intermediate thickenings, the trigones and intermediate thickenings lending the walls sinuous, the cells 19–27  $\mu\text{m}$  wide, 26–35  $\mu\text{m}$  long; surface smooth. Underleaves of leading stems 4.1–5.3 $\times$  stem width, slightly imbricate, the underleaves broadly concave (ventral view), the lateral sides each with a channel-like concavity on either side of a distinct, longitudinal, sharply convex rhizoid initial area, the underleaves suborbicular to suboblate, the base cordate, at times reflexed, the apex bifid to 0.12–0.2, the lobes typically concave to sulcate due to reflexed lobe margins, the lobes wide acute, the apices obtuse/narrowly rounded, less often acute, at times apiculate, the sinus narrow, acute to rounded; lamina margins recurved, often seen edge-on in median and distal sectors, broadly and evenly rounded, entire; insertion arched. Rhizoid-initial area in basal 0.35–0.5 of lamina, somewhat distal from the base, strongly convex; rhizoids short, fascicled. Asexual reproduction lacking.

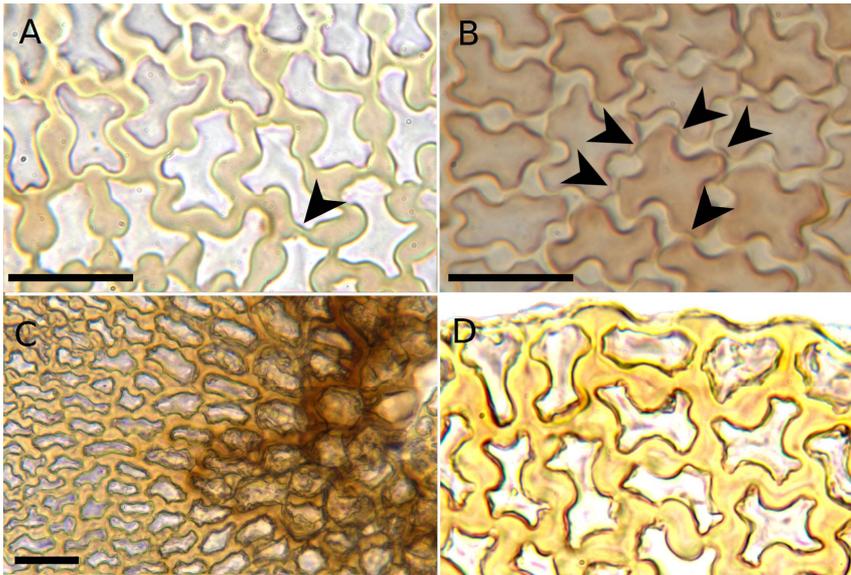
Plants dioicous. Androecia on abbreviated primary or secondary branches, with a 0–3 cycles of small leaves (with lobes + saccate or explanate lobules) at base, the androecia spicate, the bracts in 2–3 pairs, the opposing dorsal margins of bracts extending to stem midline dorsally, a distinct groove lacking. Gynoecia terminal on main shoot or short to moderately long primary or secondary branches, the gynoecial branches in same plane as subtending shoot or moderately to stiffly inclined upward; innovations often present, at times unbranched, at times with several primary branches; bracts and bracteoles in 3 closely imbricate pairs, grading to subfloral leaves; bracts and bracteoles of innermost

series not or occasionally weakly appressed to perianth, the bracts unequally bilobed, the lobes of innermost series erect to weakly spreading, with their dorsal bases strongly and broadly overlapping one another toward base, the dorsal margins soon widely spreading and delimitating a broad, V-shaped exposure of dorsal face of perianth, the lobes of innermost series erect and in same plane as the perianth or, often, somewhat ventrally secund, the lobes convex (dorsal view), asymmetrically rather narrowly elliptic, the apex narrowly rounded, the dorsal margin broadly and strongly arched, plane or sharply and abruptly reflexed in basal half, the extreme base with a 1–3 single-celled, notably thick-walled teeth, otherwise entire, the ventral margin  $\pm$  straight distally, somewhat dilated and arched toward base, entire; lobules of innermost series to ca.  $1\times$  lobe length, the basal half ca.  $0.3\text{--}0.5\times$  as wide as lobes but becoming much narrower than lobes distally, connate with lobes to  $0.2\text{--}0.4$  and forming a sharp keel, strongly canaliculate, erect or somewhat recurved at apex, narrowly acute, attenuate distally, the apex acute, terminating in a single cell, not protracted, the ventral margins of lobules on each side of innermost bracteole overlapping lateral flanks of the bracteole, the distal half entire or with a strong tooth near apex, the basal half with a prominent, sulcate to canaliculate, lobuliform process and, basal to that, a smaller, acute to lanceolate lobuliform process and, basal to that a smaller laciniiform process, the margin entire toward base, the lobule dilated at juncture of upper lobuliform process; innermost bracteole ca.  $1\times$  lobule length, free on both sides, convex (ventral view), almost folded along the longitudinal midline (in adaxial view sharply canaliculate), the adaxial faces of lobes somewhat facing one another, the bracteoles ovate-trapezoid, cordate at the base, bilobed to ca.  $0.5$ , the lobes erect, sulcate to canaliculate, acute, the apices acute to subpiliform, with margins entire or with a rounded dilation at base outer margin, the lamina margins on each side with a lobuliform process below midpoint of lamina, the process undivided or bifid, the lamina margins otherwise entire or with a subhemispherical protrusion at base. Perianth exerted to ca.  $0.2\text{--}0.5$ , stoutly clavate to elliptic, 2–3-keeled, the 2 lateral keels sharp, the ventral keel obtusely rounded or  $\pm$  flat and plateau-like, each side of “plateau” with a sharp edge at juncture with keel flanks, or the keel essentially lacking, reduced to a low, indistinct longitudinal swelling within a deep sulcus, the

dorsal face convex or with a longitudinal sulcus, the perianth totally lacking plicae, the surface of both keels and intervening sectors between keels (mature perianths) with sparse processes ranging from a simple verrucate swelling to conoidal (with length to width 1:1), grading to longer than wide and then narrowly acute, the processes at times terminating in a single cell or a uniseriate row of 2–3 cells, the processes with protracted tips at times downward projecting, hook-like, or the armature broader and lamelliform, the armature usually rather dense from at or below middle the perianth to its base, the armature shorter and more sparse toward perianth apex, the surface in young perianths sparse to nearly smooth throughout except for scattered verrucate swellings; rostrum long and rather narrow, cylindrical below and sharply flaring at the mouth, the mouth distinctly sinuate, at least in part denticulate to lobulate, the lobules 2–3 cells long, 3 cells wide at base, narrowing to 2 biseriate tiers and terminating in a single cell, the cells at the mouth isodiametric or vertically short elongate (ca. 1.5–3:1), sub-rectangular, very thick-walled cells that are variably free at the summit: at times completely free on 1 side or on both sides, at times with half of subtending cell + all of cell at mouth free, or with subtending cell and cell at mouth both completely free, at times not free (the radial walls completely fused to summit) the free end truncate or arched outward. Sporophyte not seen.

**Affinities.** As mentioned above, *F. crassissima* is sister to *F. falciloba*, *F. squarrosula*, and *F. nicholsonii* of New Zealand and *F. vittiana* of Lord Howe Island; see Hentschel *et al.* (2009, fig. 1). The species in this clade share a number of characters: leaves with the dorsal base of lobes strongly auriculate to ligulate; leaf lobules are asymmetrically falcate-galeate with the mouth smooth and entire or crenulate; the lobule apex and outer margin form a gentle, smooth, symmetrical, hemispherical to lunate, arched line terminating at a well-developed beak, the arched line is smooth and uninterrupted, and is not abruptly protracted distally, the beak does not become piliform and is neither prominent nor acute at the apex; the stylus is minute and filiform to acute; cells of the median sector of lobe have trigones that are subnodose, with intermediate thickenings lacking, or, if frequent, then the trigones and intermediate thickenings collectively lend the walls a markedly sinuous appearance; underleaves of leading stems are large with lamina margins entire or with a low rounded or angular projection;

the underleaf base is rounded to auriculate; asexual reproduction is lacking; sexuality is dioicous; gynoecia are unspecialized in position and terminate the main stem or are terminal on varyingly elongated branches; the innermost bract lobules are much narrower than the lobes and their ventral margins are armed with dentiform to lanceolate processes; the innermost bracteole is free on both sides; the perianths are smoothly trigonous and plicae are absent; the rostrum mouth is crenulate or denticulate to lobulate.



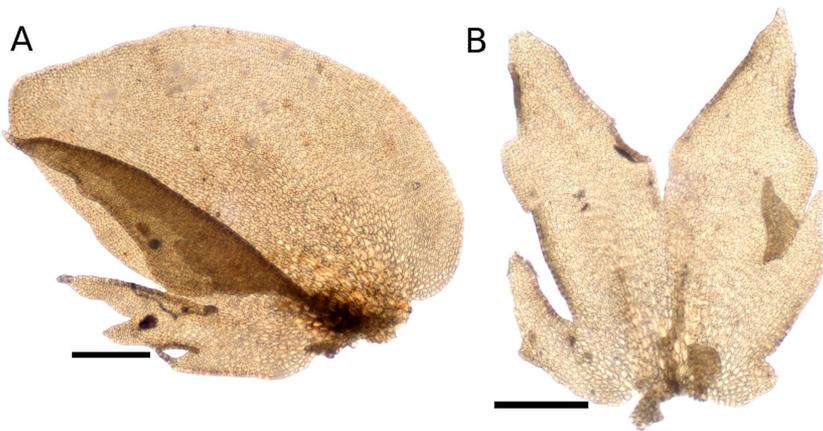
**Figure 2.** Leaf lobe cellular detail and margin. *F. crassissima*. A, C, D; *F. svihlana* B. **A, B.** Median cells of leaf lobe. Note, arrows indicating cell wall pits; only 1-2 in *F. crassissima* and **C.** Median-basal and subbasal cells of leaf lobe. **D.** Leaf lobe dorsal margin showing crenation. Scale bars: A, B, D = 20  $\mu\text{m}$ ; C = 30  $\mu\text{m}$  (All from type materials).

Vegetatively the plants in this clade appear superficially similar, yet detailed examination reveals a number of significant differences. There are also distinctive features of the leaf cell walls and also the perianths which distinguish the species represented in Hentschel *et al.* (2009) as well as other morphologically similar species that were not included as exemplars in that study, e.g., *F. setchellii* and *F. svihlana* S.Hatt. It is noteworthy that *Frullania crassissima* is distinct from this suite of species by the following features. 1) The areolation of median lobe cells (*Figure 2A*), up to 2

pits per cell versus at least 5 pits per cell in allied species (*Figure 2B*). 2) Leaf margins are crenate (*Figure 2D*) vs. entire and without bulging septa in the allied species (septae in *F. falciloba* may be at times somewhat bulging and then the margin is crenulate). 3) There is a stronger development of armature on the innermost bract lobule ventral margin (*Figure 3A*). The basal half of the margin has 3 well-developed processes: 2 prominent, lobuliform processes and, below, a laciniiform process. The allied species have weaker expression of armature where the basal half has 2 prominent processes – a large laciniiform to lobuliform process and, basal to that, a smaller lanceolate process (*F. falciloba*), or with a single process (at times in *F. nicholsonii*), or the ventral margin has merely a subhemispherical, entire-margined dilation in the basal half (*F. squarrosula*, at times in *F. nicholsonii*). 4) The perianth keel surface has sparse processes ranging from verrucate, dome-like swellings to conoidal to acute and at times hook-like, or lamelliform outgrowths (*Figures 4A and E*). In the allied species the perianth surface is smooth throughout, or has relatively few verrucate swellings (*F. svihlana*), or has dense hook-like projections (*F. setchellii*), or has  $\pm$  horizontally inserted, convex to cucullate lamellae (*F. nicholsonii*). 5) The rostrum mouth is sharply flared (*Figure 4E*) and is, at least in part, denticulate to lobulate. In allied species the rostrum mouth is not flared and is entire and smooth, or at most crenulate. Note that the gynoeceium of *F. vittiana* is unknown (Hattori 1987).

**Diagnostic characters.** Leaf-lobe cells have a remarkable areolation, seemingly unlike any other species of the genus in New Zealand. Similarly, the perianth has distinctive features, especially those associated with surface ornamentation that is distinct for the species.

**Median lobe cells.** The cells of the median sector of the lobe have nodose trigones that are usually confluent not only with each other but also with the intermediate thickenings, which are frequent and notably large. The thickenings are so extensive that the cell lumen is often completely surrounded by wall thickenings, with thin-walled areas (pits) either totally lacking or with walls surrounding a given lumen having at most a total of only 1–2 pits (*Figure 2A*). The trigones and intermediate thickenings together lend the walls exceedingly sinuous (*Figure 2A*).



**Figure 3.** *Frullania crassissima*. **A.** Innermost bract, note ornamentation of ventral margin of lobule. **B.** Innermost bracteole, note lobuliform processes one on each side of lamina. Scale bars: A, B = 200  $\mu\text{m}$  (All from the type).

**Median basal cells.** Median basal cells form a limited, local, but well-defined field of cells only a few tiers high. The cells are larger, particularly wider, than those in the subbasal and median sectors of the lobe. The walls of the median-basal cells are either  $\pm$  evenly thickened except for large to nodulose trigones and a few intermediate thickenings, or the walls have trigones and intermediate thickenings separated by narrow, thin-walled areas, together lending the walls sinuous (i.e., the walls are not evenly thickened).

**Median subbasal cells.** Cells in this sector are quite different from those of the median-basal field. They are in several tiers, and, compared to those of the median-basal field, are longer, narrower, the pits are more frequent and well defined, and the sinuosity more regular. The sinuosity is especially evident by longitudinal walls that run vertically and that interconnect cells of the successive tiers of cells. The subbasal cells rather soon grade into cells more like those in the median sector of the leaf, i.e., fewer pits between adjacent cells and sinuosity more irregular (*Figure 2C*).

**Marginal cells.** Marginal cells also have notably thickened walls, nodulose trigones, and frequent intermediate thickenings. Like the median lobe cells, marginal cells have trigones and intermediate thickenings that collectively lend the walls sinuous.

**Perianth.** As in *F. setchellii*, the perianth surface of both keels and intervening sectors between keels is ornamented. In both species the armature is denser and larger in the median and basal sectors of the perianth but smaller, more sparse, and less well expressed toward the summit. In *F. crassissima* the ornamentation ranges from a simple verrucate swelling (Figures 4B, D, E) to conoidal and as long as wide, grading to longer than wide and then narrowly acute. The processes at times terminate in a single cell or a uniseriate row of 2–3 cells, and, when the processes are protracted, the tips are often hook-like and quite distinctive in aspect (Figures 4A, C). Perianth armature also may be broader and lamelliform. It should be noted that perianth ornamentation is optimally expressed on mature perianths. Young perianths, including those that have exerted to about half their length, have ornamentation sparsely developed and may be nearly smooth throughout except for scattered verrucae. The type specimen has both young and older, mature perianths that are likely from the previous growth season. Careful examination of several perianths should be made for presence of perianth surface armature, particularly on older perianths. A careful search should include gently teasing back the innermost bracts and bracteole, since armature at times is better represented in the lower half of the perianth.

The analysis in Hentschel *et al.* (2009) demonstrated that these species, together with *F. ericoides* (Nees) Mont., *F. pycnantha* (Hook.f. et Taylor) Gottsche, Lindenb. et Nees, and *F. howeana* Steph., form a larger clade. However, as noted by Hentschel *et al.* (2009), neither *F. ericoides* nor *F. falciloba* are monophyletic. Clearly, an extension of the sampling and detailed morphological studies are necessary to arrive at a natural circumscription of this clade and species boundaries. It is noteworthy that Hodgson (1949) reduced *Frullania setchellii* to a variety, i.e., *F. falciloba* var. *setchellii* (Pearson) E.A.Hodgs. This exemplifies the taxonomic confusion surrounding this suite of species without fertile material or without examining vegetative material in cellular detail. However, there is a suite of morphological characters that will facilitate recognition of *F. setchellii* at the species level, which will be explored in another connection.



**Figure 4.** *Frullania crassissima*. Features associated with the perianth. **A.** Mature gynoecium, ventral-lateral view; note ornamentation on keels as well as between keels. **B, D.** Detail of perianth surface ornamentation showing verrucate swellings on perianth keel. **C.** Detail of multicellular hook-like process oriented downwards. **E.** Mouth of perianth rostrum and note verrucate keels. Scale bars: A, E =  $100\ \mu\text{m}$ ; B =  $40\ \mu\text{m}$ ; C, D =  $40\ \mu\text{m}$  (All from the type).

*Frullania crassissima* is distinguished from all other morphologically similar species in the Australasian region by the following key.

KEY TO *FRULLANIA CRASSISSIMA* AND MORPHOLOGICALLY SIMILAR SPECIES IN THE AUSTRALASIAN REGION

- 1 Leaves distinctly squarrose and elevated when wet..... **2**
  - Leaves not squarrose, usually horizontally spreading or flat when moist or dry..... **3**
- 2 Plants medium to ± large in size; stem underleaves bifid up to 0.25, the bases auriculate or strongly cordate; perianth surface smooth..... ***F. squarrosula***
  - Plants typically medium-sized, occasionally small; stem underleaves bifid up to 0.35, the bases the bases straight or cordate; perianth surface with dense, multicellular, almost spinose outgrowths or projections..... ***F. pycnantha***
- 3 Perianth with a smooth surface..... ***F. falciloba***
  - Perianth surface variously verrucate, tuberculate or with multicellular outgrowths or projections..... **4**
- 4 Perianth with very large rounded to foliose outgrowths, transversely inserted and appearing scale-like, with the aspect of a miniature pine cone..... ***F. nicholsonii***
  - Perianth with dome-like swellings (verrucate) to conoidal to acute and at times hook-like, multicellular projections, or with spinose projections..... **5**
- 5 Multicellular projections or outgrowths very dense and closely spaced, very conspicuous and visible, the perianth surface not verrucate, without dome-like swellings..... **6**
  - Multicellular projections or outgrowths sparsely and sporadically distributed, often not very visible without peeling back bracts and bracteole at lower portion of perianth, the surface frequently also verrucate, with dome-like swellings..... **7**
- 6 Underleaves not flat, the margins very strongly recurved, undulate, irregularly repand-lobate; perianth basal portion densely covered with multicellular, spinose outgrowths, the upper surface entirely smooth..... ***F. vittiana***
  - Underleaves appearing nearly flat, the margins not recurved, entire and smoothly arched or with a broadly rounded dilation

- at about level of sinus base or a little lower, not undulate; perianth with unicellular and multicellular outgrowths, densely covered from the base and continuing on the keels toward the perianth rostrum, but mostly absent and smooth between the keels.....***F. setchellii***
- 7 Cell lumen not completely surrounded by wall thickenings, typically with 3 to 6 or more thin-walled areas (pits); perianth surface mostly smooth, with very few, scattered verrucae, no hook-like armature.....***F. svihlana***
- Cell lumen often completely surrounded by wall thickenings, with thin-walled areas (pits) totally lacking, or with only 1–2 pits; perianth with surface of both keels and intervening sectors between keels (mature perianths) with variable processes or projections ranging from verrucate, dome-like swellings to conoidal, grading to processes with protracted tips, at times hook-like, the armature usually more dense between the middle of the perianth and its base.....***F. crassissima***

This species belongs to sect. Ornithocephalae Verd.

**Distribution and Ecology.** The species is known only from the type, which occurred as an epiphyte in a *Nothofagus fusca* forest at 800 m. Although the species is only currently known from the type specimen, we predict that the distribution will be expanded after further collections and more importantly re-examination of herbarium specimens, especially those that may have been identified as *F. falciloba* or *F. setchellii*. Therefore, it is premature to make any statement regarding the species conservation.

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