

The species of *Frullania* subgen. *Trachycolea* (Frullaniaceae) in Australia

Tamás Pócs 

Herbarium, Institute of Biology, Eszterházy Károly Catholic University,
Eger, H-3301 Pf 43, Hungary

Correspondence: pocs.tamas33@gmail.com

Abstract

A taxonomic revision of *Frullania* subgen. *Trachycolea* Spruce (Frullaniaceae) is presented based on specimens housed at the Australian National Herbarium (CANB) and additional collections made during four field expeditions to Australia between 1999 and 2004. Of the 29 previously recognized species, eight are reduced to synonymy, while *Frullania eymae* S.Hatt., previously known only from New Guinea, is newly reported for Australia. An artificial key, detailed species descriptions, and illustrations are provided to facilitate identification. Of the 21 species recognized here, eight are endemic to Australia, and nine are shared between Australia and New Zealand.

Introduction

The genus *Frullania* Raddi (Frullaniaceae) is represented by 63 taxa in Australia, variously placed in four or five subgenera; subgen. *Australes* (Verdoorn) Hattori, subgen. *Diastaloba* Spruce, *p.p.*, subgen. *Frullania*, subgenus *Microfrullania* (R.M.Schust.) R.M.Schust., and subgen. *Trachycolea* Spruce (see Hentschel et al. 2009). *Frullania* subgen. *Trachycolea* was established by Spruce (1884), but not without precedent. Gottsche et al. (1845) in their 3rd part of *Synopsis Hepaticarum* distinguished, as their 1st group of species, those having '*Auriculae foliorum galeatae cucullatove-rotundae*', that is, 'with round-hooded galeate lobules'. Spruce (1884) characterised subgenus II *Trachycolea* by i) the cordate-ovate leaves with round apex, ii) the rotund lobules close to the stem and more or less parallel to it, not longer than wide, with a truncate base (not prolonged along the stem), usually exceeding in length the half of leaf, and iii) the emergent, trigonous perianth having one postical and two lateral keels, sometimes with supplementary ridges and in most cases covered by tubercles, papillae or leafy scales.

Frullania falciloba Lehm. was the first species of this subgenus described from Australia, in 1844, although *F. scandens* Mont. was described a year earlier from New Zealand. A few species, as *Frullania clavata* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, *F. deplanata* Mitt., *F. monocera* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, *F. squarrosula* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees) were described before Stephani then described 13 new species from Australia between 1894 and 1910 in his *Species Hepaticarum* 4. Stephani (1910) followed Spruce's circumscription of *Trachycolea*, but renamed the subgenus to *Galeiloba* Steph., arguing that the lobule shape was a more stable character than the perianth appendices, because many species in the group have smooth perianth. While this is true, it was inconsistent with nomenclatural rules, and *Trachycolea* has priority. A more significant change was when Hattori (1976) elevated the sect. *Australes* (Verdoorn 1930) to subgeneric rank, separating the former *Trachycolea* species with campanulate perianths (wherein the perianth is constricted just above the smooth mouth). This arrangement was later discussed by molecular studies (Hentschel et al. 2009), showing that species of the subgenus or section *Australes*, which are distributed mostly throughout SE Asia and Australasia, form a strongly supported

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subclade, and warrant recognition as a subgenus distinct from subgen. *Trachycolea*. The Australian species all belong to one part of the otherwise biphyletic subgen. *Trachycolea*. Currently, 28 species of *Frullania* subgen. *Trachycolea* are recognised in Australia (McCarthy 2003; Renner et al. 2024).

Stephani, as many authors in his time, described species primarily from one or two specimens, sometimes all that was available to him, and did not deal with intraspecific variation. This is one reason why he described certain species several times under different names. When Hattori (1979a, 1979b, 1983) revised the Australasian *Frullania* species, he tried to redescribe and illustrate precisely Stephani's types, only putting under synonymy a few of them. As a result, there is some confusion among the synonyms of these species. Reinvestigation of many specimens and reconsideration of the species circumscriptions presented by Taylor in Lehmann (1844) and by Stephani (1910) suggested new synonymisations were necessary.

Sinske Hattori, a leading Japanese hepaticologist, reinvestigated and illustrated the previously described Australasian *Frullania* species, including the revision of specimens held by the Australian National Herbarium (CANB) of the Centre for Australian National Biodiversity Research (Hattori 1979a, 1979b, 1982, 1983, 1984a, 1984b, 1987a, 1987b, 1988a, 1988b; Hattori and Piippo 1986). His studies resulted in the description of more than 10 new species from subgen. *Trachycolea*. In addition, he provisionally flagged a few specimens suspected to be new to science. These require further investigations, here pursued as part of a broader investigation of intraspecific variation and species circumscription in Australian *Frullania* subgen. *Trachycolea*.

Material and methods

The late Heinar Streimann, curator of the bryophyte collection at the Australian National Herbarium (CANB) in Canberra encouraged the author to undertake a revision of *Frullania* species for the *Flora of Australia* project. The Australian Biological Resources Study Participatory Program and Hungarian Academy of Sciences provided financial supported for field collection trips in 1999, 2000 and 2001. The field work continued in 2004 on the partial support of the Leó Szilárd Award. During these trips thousands of *Frullania* specimens were collected and more were borrowed from CANB (formerly CBG) for study.

The unidentified specimens of the CANB material and all collections of subgen. *Trachycolea* made by the author were identified. Voucher specimens from his 1999 collections were deposited in CANB and in EGR, while the 2000, 2001 and 2004 collections were divided among the Australian herbaria of BRI, NSW, NT, PERTH, JCU and also EGR. In the description of species, only Australian synonyms are enumerated. Picture plates with original micrographs were made from all species available by the author (apart from three taxa).

Taxonomic Treatment

Frullania subgenus *Trachycolea* Spruce (1884)

Frullania subgen. *Trachycolea* species have shoots 1–6 (–10 cm) long and 0.5–2 mm wide, green, olive or brown to reddish brown colour. Stem 0.15–0.25 mm in diameter, usually brownish, regular or irregular pinnate branching, with different *Frullania*-

type initial appendages (von Konrat and Braggins 2001). Leaf insertion J-shaped, incubous, arrangement \pm imbricate, rarely contiguous. Leaf lobes ovate, cordate or auriculate, never much longer than wide, distally always round. Cells \pm isodiametric, only at lobe base elongate. Cell walls often sinuose, with strongly nodose trigones. Lobules galeate, from symmetric helmet or cup shape to asymmetric, bird head-like rostrate or with an elongate beak or falciform, rarely rotundate, gibbose, never longer than 1.2 \times the width. The aperture is oriented toward the stem base. Sometimes, towards the shoot apex, the lobes are explanate, lanceolate or canaliculate. Lobule attachment to lobe is very short. Stylus usually filiform or narrow triangular, 3–6 cells long, tipped by a hyaline papilla. Underleaves contiguous or imbricate, wider than the stem, with cuneate or auriculate base, insertion straight or sinuose. Often with a distinct, convex rhizoid initial area above the base. In most cases apex bilobed as U- or V-shaped, sometimes \bar{U} -shaped incision of various length. The margins entire or dentate, flat or involute.

All Australian species are dioicous, often fertile. Androecia on short lateral branches, button like, consisting only of 4 or 5 pairs of bracts, or spicate, consisting of 6–20 pairs. Two antheridia develop in each bract. Gynoecia usually terminal on side branches with one or repeated subfloral innovations, which often influence the branching pattern. Female perichaetia in 2 or 3 whorls. The innermost bracts often fused with each other and one or both sides with the bracteole. Bract lobes and bracteole with marginal dentition typical for the species. Perianths usually trigonous or triolate (sometimes with additional ridges), with smooth or tuberculate or spinose surface or keels. Sporophyte with translucent seta consisting of numerous cells in cross section. Capsule globose with two layered wall, dehiscing into 4 valves, each with different number of elaters. Spori globose with rosette like ornamentation.

Etymology. The subgenus name *Trachycolea* comes from the Greek *trachys* (rough) + Latin *coleus* (sheath), in reference to the often tuberculate or spinose perianth.

Diagnostic features of *Frullania* subgenus *Trachycolea*: The helmet shaped or rostrate (but not campanulate) leaf lobule, not longer than 1.2 \times its width, distinguishes *Trachycolea* members from other subgenera of *Frullania*. Lobule position is typically close to the stem on a very short stalk. Underleaves are wider than the stem. For a better understanding, three basic types of lobule shapes were established for use in the identification key and in the description of species: *helmet shaped*, *rostrate* and *globose* (see Fig. 1). The helmet shaped lobule can be more or less symmetric or asymmetric, without or with a short beak. The rostrate lobule is more asymmetric with a beak on its adaxial side, reminiscent of a bird's head (ornithocephal). Within this type there are three species with very elongate, cucullate, piliferous beak. There are transitions between the basic types. Within the rostrate type occur cultriform (sickle-shaped) lobules. The globose lobule is inflated, nearly spherical with narrowed mouth and involute margin, and among Australian species occurs only in *Frullania ferdinandi-muelleri* Steph.

Habitat: The species of *F.* subgen. *Trachycolea* are mostly epiphytic or rupicolous. Among epiphytes, most are on the bark of trees or shrubs, while some species (e.g. *Frullania seriata* Gottsche ex Steph.) occur preferably on tiny twigs. The

rupicolous species occur both on open and on shaded rocks. Most species occur in different forest or woodland types, from montane rainforest to sclerophyllous, dry forests or woodlands. They also occur on cultivated trees.

Distribution: The subgenus includes c. 200 species worldwide, of which at least 22 occur in mainland Australia and Tasmania. Eight species are endemic and an additional nine also occurring in New Zealand. Some other species occur on Lord Howe and

Norfolk Islands, which are not treated here. The distribution and diversity of all *Frullania* species in Australia is very disjunct. The greatest species diversity is found in the Great Dividing Range along the eastern coast from Queensland to New South Wales. Victoria and Tasmania are somewhat poorer as the tropical species are lacking, while Western Australia and the Northern Territory are poor in species due to their drier climatic conditions. No subgenus *Trachycolea* species are known from South Australia.

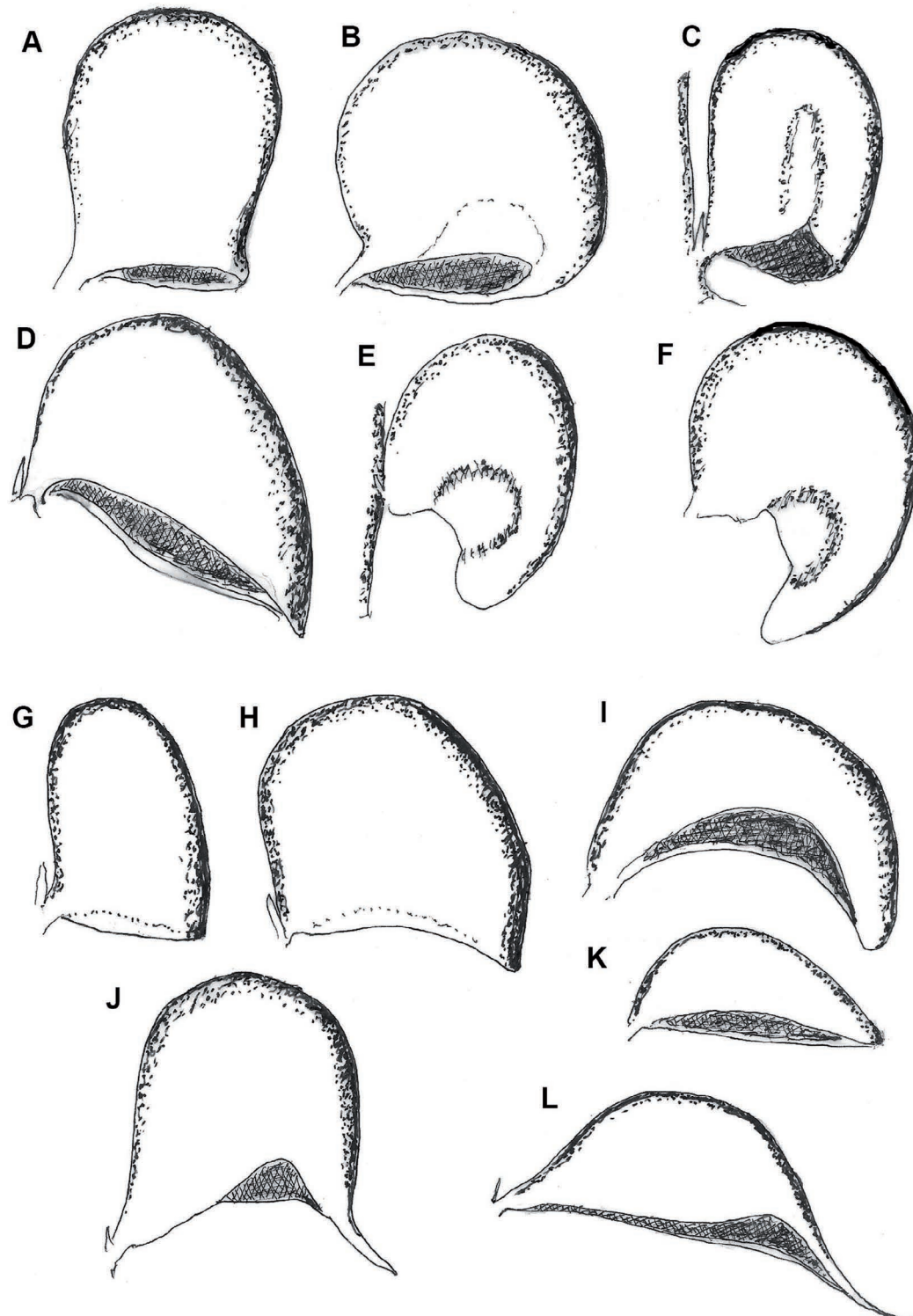


Figure 1. Terms of different lobule forms applied to *Frullania* species in this paper. A: Campanulate (only in subgen. *Austroales*). B: Globose. C: Symmetric helmet shaped. D: Asymmetric helmet shaped. E and F: Rostrate with obtuse, short and longer beak. G: Sub-symmetric, helmet shaped. H: Wide helmet shaped. I: Rostrate, cultriform (falcate). J: Helmet shaped with piliferous beak. K: Rostrate, ensiform. L: Rostrate with elongate, piliferous beak.

Artificial key to the Australian species of subgenus *Trachycolea* based primarily on vegetative characters

1. Flagelliform branches with caducous leaves present.
Lobule globose with involute margin *F. ferdinandi-muelleri*
- 1: No combination of the above properties..... 2
2. Underleaves entire or slightly retuse, almost reaching the size of side leaves, not bilobed. Lobule small, less than 1/5 of lobe length, falcate-rostrate with blunt apex. All cell walls very strongly incrassate with nodulose triangles and intermediate thickenings. Robust wet rainforest plants, widespread in New Guinea and rare in Australia..... *F. ornithocephala* var. *intermedia*
- 2: Underleaves obviously bilobed. Lobule not as above..... 3
3. Leaves squarrose, especially in wet state..... 4
- 3: Leaves usually not squarrose (but *F. seriata* can be in wet state) 6
4. Underleaf base cuneate, lobe cells with triangles and intermediate thickenings, lobule asymmetric helmet shaped, often explanate, perianth tuberculate *F. ericoides*
- 4: Underleaf base wider than the stem, lobe cells flexuose, lobules rostrate, perianth tuberculate or smooth 5
5. Lobules small, shorter than half lobe length, covered by the auriculate underleaves, perianth 3-keeled, smooth *F. squarrosula*
- 5: Lobules large, well exceed half lobe length with only their base is covered by the underleaves. Perianth densely spinose-tuberculate *F. pycnantha*
6. Underleaves small, not wider than 1–3× stem width, cover only small part of lobules 7
- 6: Underleaves larger, much wider than 3× stem width, usually cover almost all parts of lobules..... 12
7. Underleaves with entire sides..... 8
- 7: Underleaves with dentate sides 9
8. Lobe cells flexuose including the margin, lobule small, helmet shape. Lateral underleaf margins narrowly recurved in their whole length. Perianth tuberculate *F. rubella*
- 8: Lobe cells evenly incrassate at the margin, lobule rostrate, near half lobe length, exceeding the ventral lobe margin. Lateral underleaf margins nearly flat, recurved only towards their base. Perianth smooth *F. falciloba*
9. Lobule small, symmetric or asymmetric helmet shaped or explanate. Underleaves with 1 tooth along each side. Lobe cells flexuose. Perianth 3-keeled, tuberculate *F. rubella*
- 9: Lobule rostrate. Underleaves with more than one tooth along each side. Lobe cells not flexuose. Perianth with 3 or more wings, tuberculate or smooth..... 10
10. Lobule large, more than half lobe length, with obtuse beak. Perianth 4-alate, with 2 dentate ventral keels *F. scottiana*
- 10: Lobule smaller, with acute, sometimes pilose beak..... 11
11. Underleaf margins plane, with few or no teeth. Lobe marginal cells evenly thickened. Female branches develop lateral on stem. Perianth with paraphyll-like outgrowths *F. monocera* varieties
- 11: Underleaf margins recurved and strongly and irregularly dentate. Lobe marginal cells with nodulose triangles. Perianth with 3–5, spinose-tuberculate keels. Repeated one sided innovation on the stem apex results in a series of perianths near each other *F. seriata*
12. Underleaves with shallow and wide incision, which approach or exceed the stem width. Underleaf lobes with flat and entire margin 13
- 12: Underleaves with incisions deeper and narrow, usually narrower than the stem 14
13. Yellowish-brown plants in herbaria. Lobes with deeply cordate bases due to strongly appendiculate dorsal base and amplate ventral base. Style well visible, narrow triangular..... *F. queenslandica*
- 13: Yellowish-red plants in herbaria. Lobes with basal appendage only on its dorsal side, ventrally not appendiculate. Style hardly visible *F. hicksiae*
14. Lobules rostrate 15
- 14: Lobules helmet shaped 28
15. Lobules largely inflated, large, at least 1/3 of lobe width, underleaf incision usually U-shaped (see also *F. scandens* with flat perianth) 16
- 15: Lobules not or slightly inflated, their width never reaching 1/2 lobe width. Underleaf incision U or V shaped..... 17
16. Underleaf orbicular, auriculate. Lobe cells smooth. Style length up to half lobule height. Perianth cylindric, pedicellate, smooth, only the keels are minutely angulate-crispate..... *F. clavata*
- 16: Underleaf oval. Median lobe cells with one low dorsal mammilla. Style very large, exceeding the length of the lobule. Perianth obpyriform, the keels towards the apex hirsute-dentate..... *F. hamaticoma*
17. Underleaves multidentate or serrate. Perianth keels with spiny protrusions..... *F. monocera*
- 17: Underleaves entire or few-dentate, perianth keels smooth or with low protrusions in upper part 18
18. Lobules cucullate, with long, piliform, cuspidate apex. Lobe cells, at least at the margin, without trigones 19
- 18: Lobules asymmetric falcate, with blunt, never piliform beak. Lobe cells flexuose, with large, nodulose, often confluent trigones..... 21
19. Plants large, reddish-brown. Underleaves with wide, U-shaped incision and a few spinose side teeth. Innermost female bracteole connate with the bracts. Perianth elongate with sharp keels with blunt protrusions in their upper part *F. monocera* var. *streimannii*
- 19: Plants smaller, pale green, glaucous or olive. Lobules often explanate, linear. Underleaves with narrow, V-shaped incision and entire margin or with obsolete teeth. Innermost female bracteoles not connate with bract 20
20. Lobules about half lobe width, underleaves with cuneate base and sub-transverse incision. Perianth obpyriform with unsharp keels..... *F. allanii*
- 20: Vegetative characters similar the above species, but it is very rare in Australia. Lobules much smaller, less than 1/4 of lobe width. The underleaves auriculate with cuneate incision. Perianth is very different, cylindric, completely smooth..... *F. spinifera*
21. Perianth triolate 23
- 21: Perianth dorsiventrally flattened, somewhat concave ventrally, obpyriform, absolutely smooth, with a distinct beak. Lobe cells relatively thin with large trigones. Lobules asymmetric falcate, expanding below the ventral lobe margin. Innermost female bracteole with narrow, V shaped incision and spinose lobules 22
22. Small to medium size plants, shoots 0.7–1.5 mm wide, lobules narrow falcate, only 1/4–1/3 of the lobe length, underleaves with about 1/3 deep incision, female perichaetium bracteole connate only on one side with one of the bracts..... *F. deplanata*
- 22: Medium to large size plants, shoots 1.2–1.9 mm wide, lobules inflated falcate, 1/2–3/4 of lobe length, underleaves with about 1/8 deep incision, female perichaetium bracteole connate on both sides with the bracts..... *F. scandens*
23. Underleaves widely obovate with recurved upper or side margin and sometimes with minutely auriculate base. Incision very small and narrow, slit like, U-shaped, about 1/9 of underleaf length. Lobes imbricate, dorsally arching beyond the stem with strongly incurved apical part. Lobe cells flexuose with large and nodulose, often confluent trigones. Perianth cylindric, triolate, smooth. Common throughout Australia and New Zealand. Very variable, described under different names *F. falciloba*

- 23: Underleaves nearly flat, orbicular, auriculate, with V-shaped incision to 1/8–1/4 underleaf length.....24
- 24: Lobule narrow falciform with its beak exceeding the ventral lobe margin. Lobe cells with flexuose walls. Innermost female bracts with fimbriate, spinose lobule. Perianth triolate, densely and spinose-tuberculate*F. setchellii*
- 24: Lobule helmet shaped25
- 25: Vivid green or rust red in herbarium specimens. Lobe cells thin with small nodulose trigones and intermediate thickenings. Lobules asymmetric helmet shaped. Underleaves orbicular or wider than long, with plane margin. Rare Western Australian plant.....*F. latogaleata*
- 25: Deep brown in herbarium specimens. Lobe cell walls thicker with larger trigones, often flexuose walls26
- 26: Lobules near symmetric, less than half the length of the lobe, without a beak. Underleaves less than 3 times wider than the stem, obovate rectangular with entire segments, auriculate at base, with a narrow incision up to 3/10 of its length. Perianth cylindric, 3-keeled, smooth. Widespread along the whole east coast*F. victoriensis*
- 26: Lobules larger, with an obtuse beak. Underleaves wider than long and more than 3 times wider than the stem, with several triangular side teeth, cuneate base and somewhat wavy and narrowly recurved margin. Perianth not seen. Very rare in Australia, near Atherton*F. eymae*

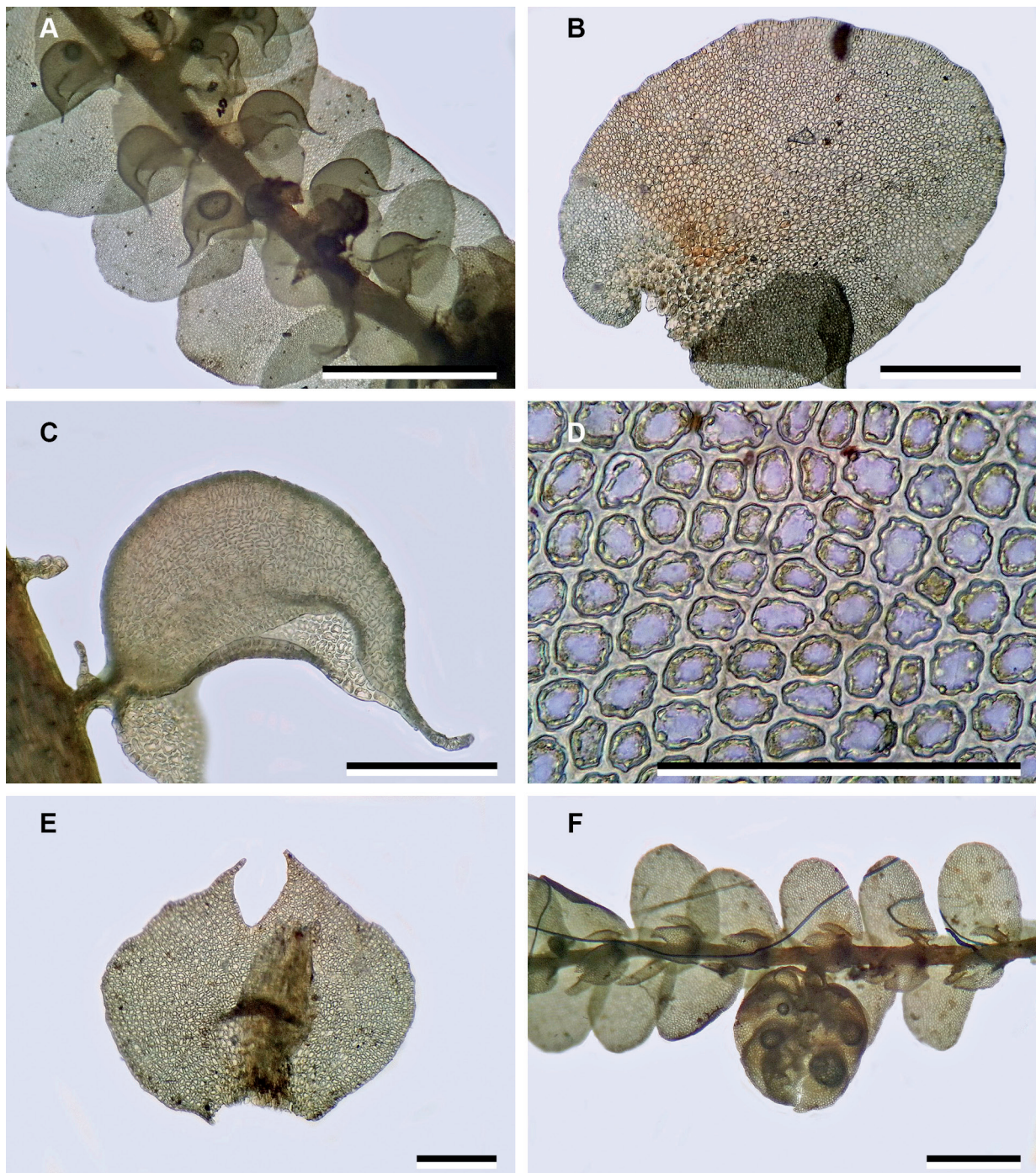


Figure 2. *Frullania allanii* E.A.Hodgs. A: Shoot, ventral view. B: Lobe with fragment of lobule. C: Lobule with style, ventral view. D: Median lobe cells. E: Underleaf. F: Branch with explanate lobules and androecium. Photographed by T. Pócs from *H. Streimann* 61332 (CANB). Scale bars: A, F = 500 µm; B–E = 100 µm.

The Australian species

1. *Frullania allanii* E.A.Hodgson, *Transactions of the Royal Society of New Zealand* 77(3): 371–372 (1949). Type: New Zealand. Wairoa, bush, on bark, Apr. 1934, *E.A.Hodgson* 3944 (Lectotype: MPN, ex Herb. Hodgson), designated by Hattori (1979b).

Etymology. Named in honour of Harry Howard Barton Allan (1882–1957), famous and versatile New Zealand botanist, after whom the Allan Herbarium in Christchurch (CHR) was named (Godley 1993, Galbreath 2000).

Illustrations. E.A.Hodgson *Transaction of the Royal Society of New Zealand* 77: 372, fig. 8 (1949); S.Hattori *J. Hattori Bot. Lab.* 46: 120, fig. 28 and 121, fig. 29 (1979b).

Description. Plants small to medium size, pale green, in herbarium dull green or olive, forming 5–8 cm large patches or intermixed among other bryophytes on tree bark. Shoots 8–50 mm long and 1–1.6 mm wide. Stem yellowish green to brownish, 150–160 µm thick, irregular pinnately branching. First branch appendage with two flat, acute segments often with a tooth. Leaves imbricate, widely spreading. Lobe elliptic, 0.7–1.5 × 0.6–0.8 mm, with rounded apices and semicircular basal auricles. The dorsal auriculate appendage extends well beyond the stem. Marginal lobe cells quadrangular, 10 µm wide. Median lobe cells 12–20 µm, isodiametric or somewhat elongate with evenly incrassate, sometimes sinuose walls with moderately nodulose trigones and intermediate thickenings. Basal lobe cells 20–28 × 15–20 µm, with nodulose trigones. Leaf lobules rostrate with a very elongate, piliferous beak or more often explanate, narrow lanceolate with acute apex. Cell walls similar to that of the median lobe. Stylus on two celled base filiform, 4–6 cells long. Underleaves nearly orbicular, 3–4 × stem width, with flat and entire margins (sometimes with 1 or two side teeth), acute lobes with V-shaped incision and cuneate base. Rhizoid initial area slightly convex with hyaline or pale brown rhizoid bundles. Asexual reproduction not known.

Dioicous. Androecia on short lateral branches, button shaped, consisting of 3–4 pairs of bilobed male bracts. Gynoecia terminal or on side branches, often innovating. Perichaetial leaves in three whorls. The innermost bract lobe acuminate, 1–1.5 mm long, with a 2/5, connate, lanceolate lobule and entire margins. The bracteole 3/5 bifid, with a few spinose teeth. Perianth pyriform, 1.8 mm long, triolate or with double or triple ventral keels. The alae are obtuse and have minute protrusions and tubercles. Beak short and wide. (Fig. 2)

Diagnostic features. Differs from *Frullania monocera* by its much larger, entire underleaves, by its perianth appendices and by its female perichaetial bracteole not connate with the bracts. In other vegetative characters similar to *F. spinifera*, which has much smaller lobules, underleaves with auriculate base and completely smooth, cylindric perianth without keels. The three species seem to be closely related. Apart from these species there are no others in Australia with such elongated, piliferous lobules.

Biostatus. Native.

Habitat. The species thrives in the wetter types of forests and woodlands, usually on tree bark, between sea level and 1000 m elevation.

Distribution. Widespread in New Zealand and along the Great Dividing Range of Australia from northern Queensland to New South Wales and the Australian Capital Territory.

Representative specimens. Qld: Carnarvon National Park, Hellhole Gorge, 93 km NNW of Injune, *H.Streimann* 52113 (CANB); Clarke Range, 46 km SSW of Proserpine, *J.A.Curnow* 1097 (CANB, BRI). N.S.W.: Southern Tablelands, Tallaganda Shire, c. 1.5 km SE of Major's Creek, *L.G.Adams* 1975 (CANB, TNS, JE); Mt Warning National Park, Corumbryn Creek below the Picnic Area, *S. and T.Pócs and E.A.Brown* 0032/F (EGR, NSW).

2. *Frullania clavata* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, *Syn. Hepatic.* 3: 428 (1845). *Jungermannia clavata* Hook.f. & Taylor, *London J. Bot.* 4: 88 (1845). Type: Tasmania. Gunn (holotype: Herbarium Lehmannianum, HUH; isotype: S).

Frullania cinnamomea Carrington & Pearson, *Proceedings of the Linnean Society, New South Wales*, ser. 2, 2: 1035 (1888). Type: New South Wales: *Whitelegge* 66 (Holotype: ?BM; isotype G, ex Herb. Pearson).

Etymology. From the Latin *clavata* (club shaped), referring to the widening shoot, having leaves increasing in size towards the apex.

Illustrations. S.Hattori: *J. Hattori Bot. Lab.* 45: 327, fig. 3 (under *F. cinnamomea*); 328, fig. 4 (1979a); G.A.M.Scott: *Southern Australian Liverworts* 182–183, figs 119, 121 (1985).

Description. Plants medium size, pale, sometimes bluish green, other times with brownish or reddish tinge, parchment like, forming wefts on tree bark in large patches. Shoots relatively short, widening upwards, 5–13 mm long and 0.5–1.8 mm wide, Stem dull green to purplish brown, 150–200 µm thick, strongly and irregularly branching due to repeated subfloral innovations. Leaves imbricate, widely spreading. Lobes roundish, very concave, the larger towards stem apex 1.3–1.6 mm long and wide, with round and incurved apices and semicircular basal auricles. The dorsal auricle well exceeds the opposite stem side. The smaller lobes towards the stem or branch base are only 0.5–0.7 mm in diameter. Marginal cells with sub-equally thickened walls. Median lobe cells 20–28 µm, isodiametric or somewhat elongate, with moderate trigones and intermediate thickenings. Basal lobe cells 40–50 × 25–30 µm, with larger trigones. Leaf lobules asymmetric falcate with very inflated body, incurved margin and subacute beak, usually expanding below the ventral lobe margin. Cell walls similar to those of the median lobe, but slightly sinuose. Stylus narrow triangular, up to 10 cells long. Underleaves nearly orbicular, 3–5 × stem width, with flat and entire margins, acute lobes with narrow or wide, ∩-shaped incision where hooked lobe apices turn towards each other. Rhizoid initial area slightly convex with a few hyaline rhizoids. Asexual reproduction not known.

Dioicous. Androecia on short lateral branches, ellipsoid, consisting of 4–6 pairs of bilobate male bracts. Gynoecia terminal or on side branches, in most cases innovating. Perichaetial leaves in three whorls, much larger than normal leaves, up to 2.5 mm length and 1.5 mm width. The innermost bract lobe elliptical, acuminate, lobule half connate, with lacerate spinose margins. The bracteole about half of the bract length, 1/3 bifid

with lacerate teeth. Perianth cylindric or obovate, 2.2–2.8 mm long, sharply triolate, dorsally flat, with minutely crispate keels and short beak. (Fig. 3)

Diagnostic features. Differs from most Australian *Frullania* subgen. *Trachycolea* species by its very inflated lobules, upwards widening (clavate) shoots due to the increasing size of leaves and by the $\bar{\cup}$ -shaped incision of underleaves. This combination occurs only in the closely related, rare *F. hamaticoma* Steph., but the latter has very large (up to 0.4 mm long) stylus and dorsal mammillae on the lobe cells. Interestingly, female specimens in *F. clavata* are much common than males and usually have many perianths.

Biostatus. Native.

Habitat. Usually occurs on tree bark, forming pale green or in dry state whitish patches in the forested belts. In Queensland and New South Wales between 600–1400 m, in Victoria and Western Australia from sea level to 1000 m elevation, in any type of woody vegetation.

Distribution. The species is an Australian endemic, occurring from Queensland, becoming more common southwards from New South Wales to Tasmania, less common in the southernmost part of Western Australia and rare in the Northern Territory (Atlas of Living Australia, 2024).

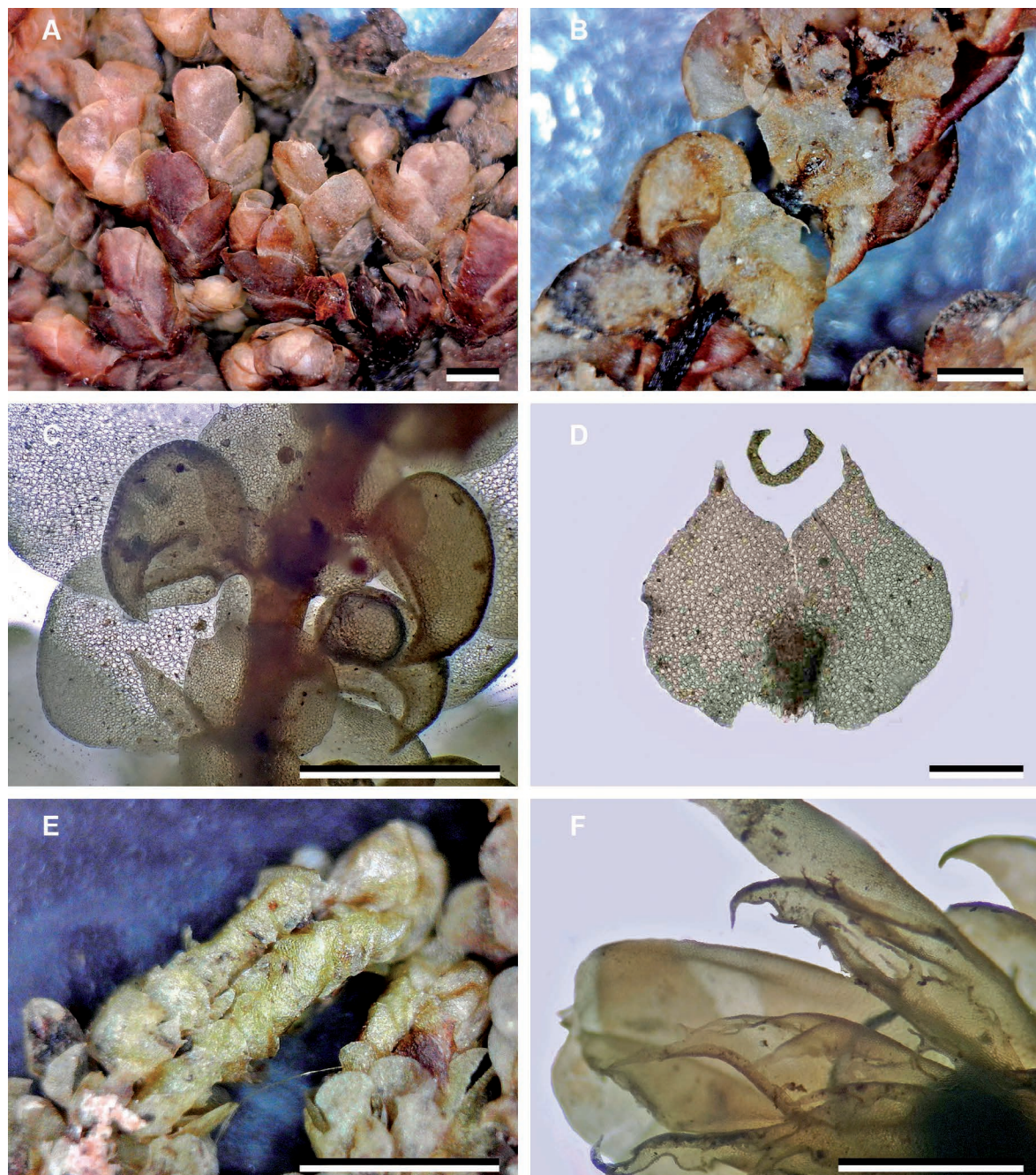


Figure 3. *Frullania clavata* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees. A: Habit with perianths and a sporophyte. B: Shoot, ventral view. C: Lobules, ventral view. D: Underleaf, showing two types of incision. E: Male branches, ventral view. F: Female perichaetium, ventral view. Photographed by T.Pócs from J.A.Curnow 772 (CANB). Scale bars: A, E, F = 1 mm; B–D = 250 µm.

Representative specimens. W.A.: Warren National Park 6–7 km SSW of Pemberton, in the valley of Warren River, *S. and T. Pócs 04154/G* (EGR, PERTH); Mt Frankland National Park, NE foot of Mt Frankland *S. and T. Pócs 04163/A* (EGR, PERTH). N.T.: Melville Island. Atlas of Living Australia, 2024. Qld.: Coochin Creek, 4 km W of Beerwah, *H. Streimann 6014* (CANB); Moreton distr., Lamington National Park, Darlington Range, *J.A. Curnow 4970* (CANB). N.S.W.: Northern Tablelands, Cattle Creek State Forest, Briggavale 12 NNE of Dorrigo, *D. Verdon 3844A* (CANB); Plantation Road 25 km WSW of Woodenbong, *H. Streimann 60958* (CANB). Vic.: Bendoc–Orbost Road, 13 km SW of Bendoc, Result Creek, *J.A. Curnow 715* (CANB, DUKE, HO, HSC, PRE, RNG); Sabine Road 16 km N of Apollo Bay, *H. Streimann 58850* (CANB, H). Tas.: Warners Sugarloaf, 18.5 km S of Deloraine, *J.A. Curnow 1912* (CANB, HO); King Solomon Cave, 34 km WSW of Deloraine *J.A. Curnow, 2159* (CANB).

3. *Frullania deplanata* Mitt. in J.D. Hooker, *Bot. Antarctic Voy. II. Flora of New Zealand* 161 (1855). Type: New Zealand: Northern Island, *W. Colenso s.n.* (syntype: E); near Wellington, 1843, *W. Stephenson s.n.* (syntype: MEL).

Frullania curnowii Steph., *Sp. Hepatic.* 4: 409 (1910).

Frullania grayana Steph., *Sp. Hepatic.* 6: 539 (1924), *nom. illeg., non* Mont. (1856).

Frullania scandens auct. *non* Mont.: *S. Hattori, Miscellanea Bryol. Lichenol.* 8(3): 46 (1978).

Etymology. From the Latin *planus* (flat, smooth), referring to the flat perianth with completely smooth surface.

Illustrations. W. Mitten in J.D. Hooker, *The botany of the Antarctic voyage. II. Flora Novae Zealandiae. Part II. Flowerless plants:* page CIV, fig. 3; F. Stephani, *Icon. Hepatic. Jard. Bot. Genève*, fig. 3681 (1985); S. Hattori, *J. Hattori Bot. Lab.* 54: 141–142, figs 53, 54 (1983).

Description. Plants typically of medium size, olive-green to brown in herbaria, with silky shine, forming wefts on living or dead tree bark. Shoots uni- or bipinnately branching, up to 20 mm long and 0.7–1.4 mm wide, Stem dull green to dark brown, 80–120 µm thick. Leaves imbricate, widely spreading. Lobes elliptic, concave, 0.5–0.7 mm long and 0.35–0.5 mm wide, with round and incurved apices and auriculate dorsal base extending beyond the stem. Marginal cells with sub-equally thickened walls. Median lobe cells 25–32 × 17–20 µm, isodiametric or elongate, with moderate trigones. Basal lobe cells 28–32 × 15–20 µm, with somewhat larger and sometimes confluent trigones. Leaf lobules asymmetric falcate or ensiform with obtuse or truncate beak, usually extending below the ventral lobe margin. Cell walls of lobule sinuose. Stylus minute, composed by 3–4 uniseriate cells. Underleaves reniform, flat, 3–4 × stem width, with 1/3 deep, U- or V-shaped incision and acute or sub-obtuse lobe apices. Rhizoids not commonly developed. Rhizoid initial area slightly convex with a short, dense bundle of blackish brown rhizoids. Asexual reproduction not known.

Dioicous. Androecia on short lateral branches, ellipsoid, consisting of 4–8 pairs of bilobate male bracts. Gynoecia terminal or on side branches, often innovating. Perichaetial leaves in three whorls, not much larger than normal leaves. The innermost bract

lobe elliptical, acuminate, up to 1.3 mm length and 0.8 mm width. lobule 1/3–1/2 connate, lanceolate, acute, with spinose or entire lower margin. The bracteole about 1 mm long, 1/3 bifid with spinose teeth, usually at one side, the base connate to the bract lobule. Perianth 1/3–1/2 exerted, dorsiventrally appressed, pyriform, completely flat and smooth, ventrally concave, without beak 1.4–2.5 mm long and near the truncate apex 0.8–1.4 mm wide. Beak 0.15 mm (3 cells) long and 0.09 mm (6–8 cells) wide. Perianth cells similar to the midlobe cells. (Fig. 4).

Diagnostic features. This species differs from all other Australian *Frullania* species, except the larger *F. scandens*, with its dorsally ventrally flat perianth. However, *F. deplanata* can easily be distinguished from *F. scandens* by its large and robust size, much larger leaf lobes and lobules.

Biostatus. Native

Habitat. The species inhabits forested areas, usually occurring on tree bark at 300–850 m elevations.

Distribution. Known from south-eastern Australia (incl. Tasmania) and in New Zealand (Atlas of Living Australia, 2024).

Representative specimens. N.S.W.: Rutherford Creek, 11 km SE of Nimmitabel, *H. Streimann 16707* (CANB, NICH, H, L). Vic.: Dinah Divide Track, 9 km SE of Club Terrace *H. Streimann 39242* (CANB, H); Arte River, 30 km NE of Orbost, *H. Streimann 43755* (CANB, H). Tas.: Great Western Tiers, track to Westmoreland Falls, 24.5 km SW of Deloraine, *J.A. Curnow 2138* (CANB).

Taxonomic Notes. There is an East African – Madagascan species, *Frullania bullata* Steph., that has a morphologically similar perianth and vegetative body (see Vanden Berghen 1976: 186–190, figs. 45, 46). Further investigation is required to establish the relationship between these taxa. However, morphologically *F. bullata* is much larger in size and ventrally, the perianth is not concave, which together distinguishes the African taxon from *Frullania deplanata*.

4. *Frullania ericoides* (Nees) Mont., *Ann. Sci. Nat. Bot.* (ser. 2) 12: 51 (1839). *Jungermannia ericoides* Nees in Martius, *Fl. Brasil.* 1(1): 346 (1833). Type: Brasil: Morro de Villa Rica in Sierra los Orgãos, *Maximilian I Joseph of Bavaria* (STR).

Taxonomic synonyms: *Jungermannia squarrosa* Reinw., Blume and Nees, *Nova Acta Acad. Caes. Leop.* 12: 219 (1824) *nom. illeg.*; *Frullania squarrosa* Dumort., *Rec. d'Obs. Jungerm.* 13 (1835) *nom. inval.*; *Frullania ericoides* var. *squarrosa* Nees ex Mont., *Ann. Sci. Nat.; Bot.*, sér. 2, 12: 51 (1839). *Frullania squarrosa* (Nees ex Mont.) Nees, *Syn. Hepatic.* 3: 416 (1845).

Uncertain synonym: *Frullania variabilis* Steph., *Sp. Hepatic.* 4: 420 (1910).

Etymology. Probably named after its imbricate and semi-convolute leaves rolled around the stem, when dry, reminiscent of some Ericaceae with scale-like leaves.

Illustrations. M. Kamimura, *J. Hattori Bot. Lab.* 24: 18, fig. IV: 1–8 (1961); C. Vanden Berghen, *Bull. Jard. Bot. Nat. Belg.* 46 (1/2): 162, fig. 39 (1976); R. M. Schuster, *Hepaticae & Anthocerotae N. America.* V: 228, fig. 811 (1992).

Description. Dioicous, often sexually dimorphic, the female specimens being larger and more ramified, than males. Plants often in extensive mats not tightly adnate to the substrate. The pale or olive green to brown shoots are irregular pinnately branched, 2–8 cm long and 0.7–1.6 mm wide. Stem yellowish green to brownish, 150–200 μm thick. First branch appendage with three segments, one of them galeate or also explanate. Leaves imbricate, semi-convolute when dry and usually very squarrose when wet, quite fragile. Lobe ovate to almost round, 0.7–1.1 \times 0.6–0.8 mm, with rounded apices and sometimes cordate with large basal auricles, dorsally spreading beyond the stem. Marginal lobe cells quadrangular, 12–14 \times 10–12 μm wide. Median lobe cells penta- or hexagonal with 18–28 μm diameter, with triangular trigones and with intermediate thickenings. Basal lobe cells more elongate, up to 36 μm . Leaf lobules asymmetric helmet shaped to rostrate, up to 0.5 mm long, apically inflated and

compressed at mouth, with an obtuse, sometimes incurved beak or are often explanate, lanceolate. Cell walls similar to that of the median lobe cells, mostly quadrangular. Stylus narrow triangular, 4–6 cells long, the uppermost 2–3 cells uniseriate. Underleaves nearly orbicular, 2–4 \times stem width, with flat, entire margin or with 1–2 low side teeth and with cuneate base and straight insertion. Underleaf lobes acuminate with 1/3 deep U-shaped incision. Rhizoid initial area in its lower part, convex, often with a rhizoid disc with brownish cell walls. Asexual reproduction by fragmented leaves or rarely by subglobose, brownish gemmae born at the lobe margin.

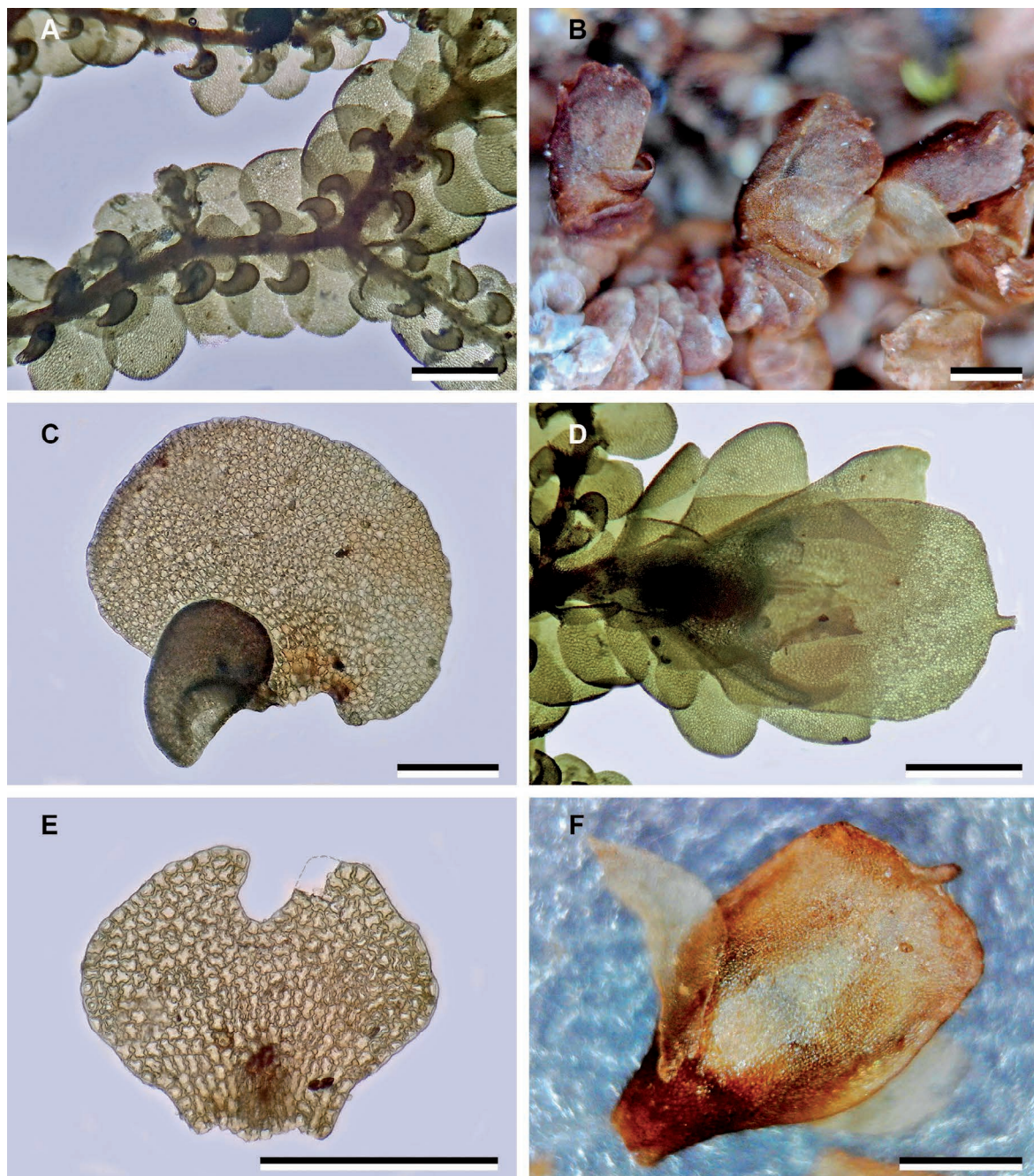


Figure 4. *Frullania deplanata* Mitt. in Hook.f. A: Habit, ventral view. B: Shoot with perianths, dorsal view. C: Leaf, ventral view. D: Female perichaetium, ventral view. E: Underleaf, dorsal view. F: Perianth, dorsal view. Photographed by T.Pócs from *H.Streimann 16707* (CANB). Scale bars: A, B, D, F = 500 μm ; C, E = 200 μm .

Androecia globose or spicate on short lateral branches, consisting of 3–12 pairs of male bracts. Gynoecia also on side branches. Perichaetial leaves in three whorls. The innermost bract unequally bilobate with acuminate lobes, 1–1.2 mm long, with a 1/2–3/5, connate, lanceolate lobule and dentate inner margins. Bracteole connate to the bracts on both sides in its lowermost part, have a few spinose teeth, apex bilobed. Perianth exserted, pyriform, 1.2–1.5 mm long, trialate or with double or triple ventral keels, somewhat flattened. Especially its lower part or the whole surface covered by many scattered tubercles and flat, scale like, spinose outgrowths. Beak cylindric or a bit expanded, up to 200 μ m long. (Fig. 5)

Diagnostic features. The squarrosity of leaves is visible mostly in a wet state. The widely opening, strongly asymmetric or explanate lobules and the cuneate underleaf bases, the fragility of leaves, combined with the spinose perianths are good distinguishing characters.

Biostatus. Native.

Habitat. *Frullania ericoides* is an extremely xero-tolerant species, occurring on tree bark or on rocks, also on artificial substrates, in drier habitats, like open woodland or sclerophyllous forest, savanna or even on plantation trees. But it occurs also in wet forests on the higher branches, or in well illuminated, disturbed openings. It occurs at all elevations with woody vegetation.

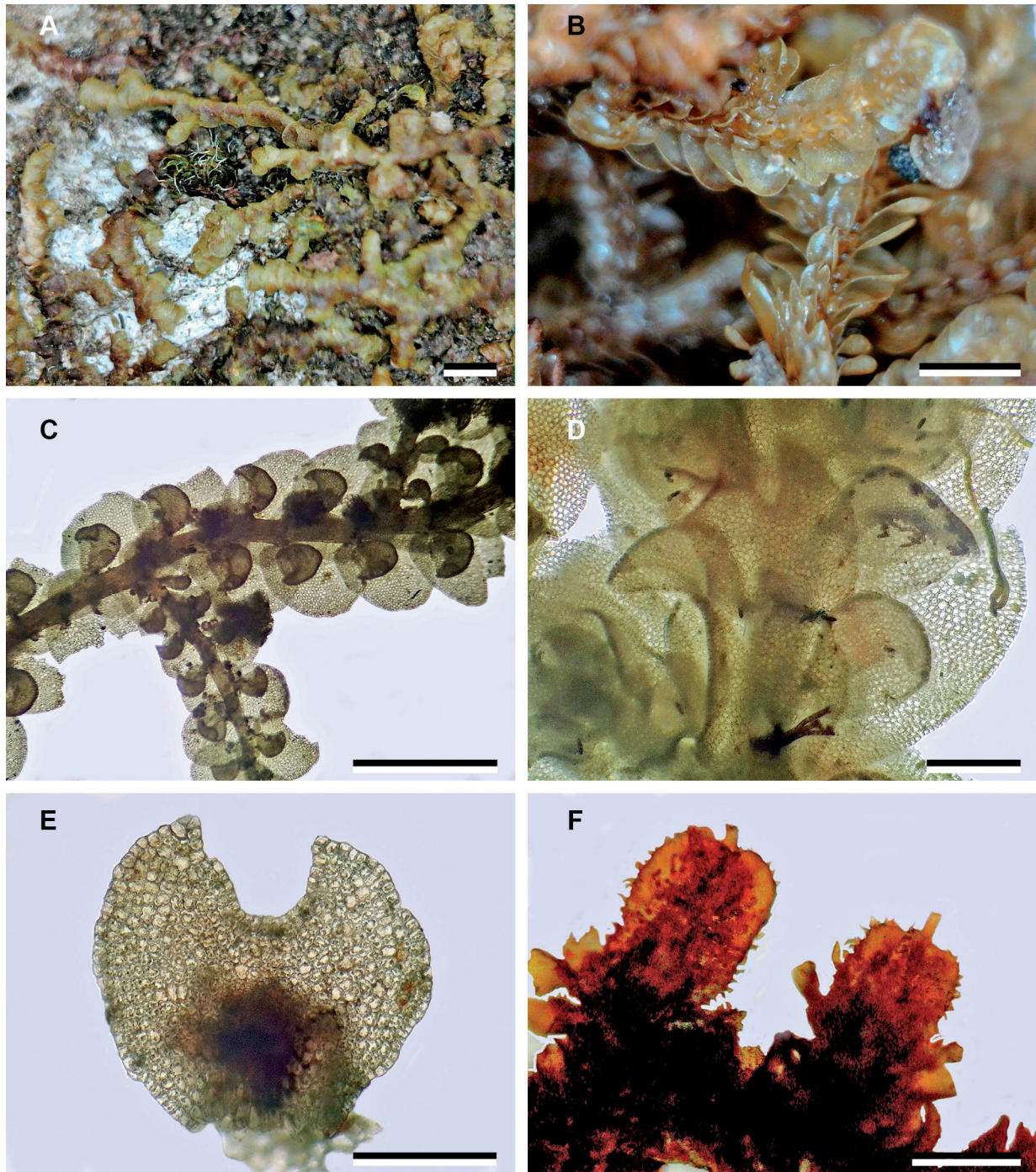


Figure 5. *Frullania ericoides* (Nees) Mont. A: Habit, dorsal view in dry state. B: Habit, ventral view in wet state. C: Shoot with branch, ventral view. D: Shoot with lobules and underleaves. E: Underleaf, dorsal view. F: Perianths, ventral view. Photographed by T.Pócs; A, B: from H.Streimann 9850 (CANB). C–E: from H.Streimann 42851 (CANB) and F: from H.Streimann 16707 (CANB). Scale bars: A–C, F = 1 mm; D, E = 200 μ m.

Distribution. It is a pantropical species common in all tropical, subtropical or even in some warm temperate parts of the world. Being very widespread and variable, the species has been re-described many times under different names (Schuster 1992).

Representative specimens. N.T.: Black Jungle, 42 km ESE of Darwin, *H.Streimann* 48636 (CANB); Litchfield National Park. Wangi Falls, S. and T.Pócs 01043/J (DNA, EGR). Qld: Burnett Highway, 16 km SSW of Monto, *H.Streimann* 9850 (CANB); Ingham, town park, S. and T.Pócs 01105/A (BRI, EGR). N.S.W.: Richmond Range State Forest, Cambridge Walk, 34 km SW of Kyogle, *H.Streimann* 61430 (CANB); Brunswick Head Nature Reserve N of Ballina town, S. and T.Pócs and E.A.Brown 0041/C (EGR, NSW).

Taxonomic note: *Frullania ericoides* is a species complex with at least two lineages (Hentschel et al. 2009).

5. *Frullania eymae* S.Hatt., *J. Hattori Bot. Lab.* 39: 284, f. 142 (1975). *Type:* Indonesia: Prov. Papua in Western New Guinea, Wissel Lake Region, Omgewing Post, Boebeiro, 1750 m, Dr. P.J.Eyma 4915 (holotype: L, isotype: NICH).

Frullania eymae var. *dentistipula* S.Hatt., *J. Hattori Bot. Lab.* 44: 527, f. 202 (1978), synonymized by Hattori (1982: 527).

Etymology. Named after its collector, Dr. Pierre Joseph Eyma, Dutch botanist (born 1903, Maarssen, died 1945 in a Japanese P.O.W. camp in Sumatra). Educated in Utrecht and collected a lot, mostly phanerogams in Surinam and Indonesia and studied local agriculture in New Guinea's highlands. In 1940 appointed to Assistant of the Buitenzorg Herbarium (<https://www.nationaalherbarium.nl/FMCollectors/E/EymaPJ.htm>, accessed 2024).

Illustrations. S.Hattori, *J. Hattori Bot. Lab.* 39: 285, fig. 142 (1975); 44: 528, fig. 202 (1978); S.Hattori & H.Streimann, *J. Hattori Bot. Lab.* 59: 104, fig. 2 (1985); T.Pócs, *Acta Biol. Pl. Agriensis* 12(1): 25–34 (2024).

Description. Medium to large size, pale olive, in herbarium ochre-brown, ascending from tree bark. Shoots 20–40 mm long, 1.2–2.0 mm wide, irregularly bipinnate. Stem 120–200 µm thick, olive brown. First branch appendage bi- or trilobed, one of the lobes galeate. Leaves imbricate, obliquely spreading. Lobe elongate-ovate or ovate, densely imbricate, 0.96–1.6 mm long and 0.8–1.5 mm wide, apex round, narrowly incurved, margin slightly undulate, base strongly auriculate with a large dorsal appendage exceeding the stem to about 2× stem width. Lobe cells hexagonal with nodulose, sometimes confluent trigones and intermediate thickenings, at the margin 15–18, middle 20–25 µm diameter. The basal cells more elongate, 30–55 × 25–30 µm. Stylus 10–12 cells long, 2–3 cells wide at base, continuing in 3–6 uniseriate cells and tipped by a hyaline papilla. Lobules asymmetric helmet shaped, 320–480 µm long, inflated above and flattened at mouth, with a truncate beak. Underleaves contiguous to imbricate, round or reniform, 3–5× stem width, with recurved-undulate, crispate margin sometimes developed into triangular side teeth. Rhizoid initial area at the middle, here and there with short, dense bundle of dark brown rhizoids. Insertion sub-transverse. Asexual reproduction not known.

Dioicous. The Australian specimens are sterile. In New Guinea according to Hattori (1975, 1982), Hattori and Streimann (1985), the male plants usually smaller than female, androecia on short lateral branches, short to long spicate, consisting of 5–10 pairs of male bracts, often innovating. Gynoecia terminal or on robust upper branches, often with fertile innovations. The innermost bract lobe acuminate-acute, 2 mm long, strongly recurved along margin. The bracteole, together with the inner sides of bracts, strongly laciniate. Perianth 2/3 exserted, cylindric, 3.4 mm long, triolate. Keels with scattered tubercles in their upper half. Apex obtuse, with narrow beak. (Fig. 6)

Diagnostic features. Among the Australian *Trachycolea* species is unique with its very large, undulate margined lobes and undulate-crispate underleaves.

Habitat. Notophyll vine-fern forest in the wet tropics.

Distribution. The species is quite widespread in the mountainous area of West New Guinea and Papua New Guinea (Hattori and Piippo 1986). Hitherto known only from two localities in Australia.

Representative specimens. Qld: Yungaburra Road 2 km SE of Atherton, *H.Streimann* 16836 (CANB; labelled as *Frullania dentella* S.Hatt. sp. nov. in sched., but this name was never published); Paluma Range, Crystal Creek National Park, McClelland's Lookout at the edge of the plateau, at the E side of Paluma village, Pócs, 01109/J (CNS, EGR).

6. *Frullania falciloba* Lehm., *Nov. cogn. stirp.* 20 (1844). *Jungermannia falciloba* (Lehm.) Hook.f. & Taylor, *London J. Bot.* 3: 581 (1844). *Type:* Van Diemen's Land [Tasmania]. *Gunn* (?isotype: S).

Frullania crassitexta Steph. *Sp. Hepatic.* 4: 423 (1910), *syn nov.* *Type:* Queensland: Brisbane, F.M.Bailey (G 18201).

Frullania mooreana Steph., *Sp. Hepatic.* 4: 422 (1910).

Frullania asperifolia Steph. in Stephani and Watts, *J. Proc. Roy. Soc. New South Wales* 48: 105 (1914).

Frullania knightiana Steph. *Sp. Hepatic.* 6: 542 (1924).

Frullania binominata Steph. *Sp. Hepatic.* 6: 545 (1924).

Etymology. From Latin *falci-lobus* = sickle-lobe, because of its sickle shaped lobule.

Illustrations. F.Stephani, *Icon. Hepatic. Jard. Bot. Genève*, fig. 3814, as *F. falciloba* (1985); S.Hattori, *J. Hattori Bot. Lab.* 45: 337, fig. 10, as *F. falciloba*; 347: fig. 17 as *F. knightiana* Steph. (1979a).

Description. Plants medium to large size, dark green to olive or reddish-brown, in herbarium often blackish brown. Shoots uni- or bipinnately branched, 4–6 cm long and 0.8–1.5 mm wide, branches obliquely spreading, forming large patches on tree bark. Stem olive green to reddish brown, 100–200 µm thick. First branch appendage with one bilobed ventral and one saccate dorsal or with three flat, acute segments. Leaves imbricate, widely or obliquely spreading. Lobe orbicular or ovate, 1–1.2 mm long and 0.8–1.1 mm wide, concave, with rounded and strongly incurved apices. Dorsal base with semicircular appendage, well exceeding the stem. Marginal lobe cells near quadrangular, 10

μm wide, with trigones or evenly incrassate (in former *Frullania crassitexta* Steph.). Median lobe cells $25\text{--}30 \times 15\text{--}20 \mu\text{m}$, somewhat elongate with sub-nodulose, sometimes confluent trigones and sinuose walls. Basal lobe cells $35\text{--}45 \times 30\text{--}35 \mu\text{m}$, with nodulose and often confluent trigones. Lobules $0.3\text{--}0.4 \text{ mm}$ long, cucullate, asymmetric falcate-rostrate with inflated abaxial part and obtuse beak elongating beyond the ventral lobe margin. Cell walls sinuose, smaller than those of the median lobe. Stylus triangular lanceolate, $6\text{--}7$ cells long tipped by a hyaline papilla and $4\text{--}5$ cells wide at base. Underleaves widely obovate, contiguous or distant, erect-patent, $3\text{--}4\times$ stem width, with flat and entire margins, sometimes with narrowly incurved apex, with short, U- or V-shaped incision no deeper than $1/20\text{--}1/8$ of

underleaf length. Base cuneate, insertion sub-straight. Rhizoid initial area convex, below the middle, often with brownish rhizoid bundles. Asexual reproduction not known.

Dioicous. Androecia on short lateral branches, button shaped or ellipsoid, consisting of $2\text{--}7$ pairs of bilobate male bracts with dentate margin. Gynoecia terminal on stem, often innovating. Perichaetial leaves in three whorls. The innermost bract lobe widely ovate with obtuse apex and with entire or minutely toothed margins. The bracteole $3/5$ bifid, with pilose apex, entire margin or with $1\text{--}2$ teeth. Perianth semi-exserted, cylindric, 2.5 mm long, triolate, dark brown, smooth, shiny. Ventral keel inflated. Apex rounded with a very short beak. (Fig. 7)

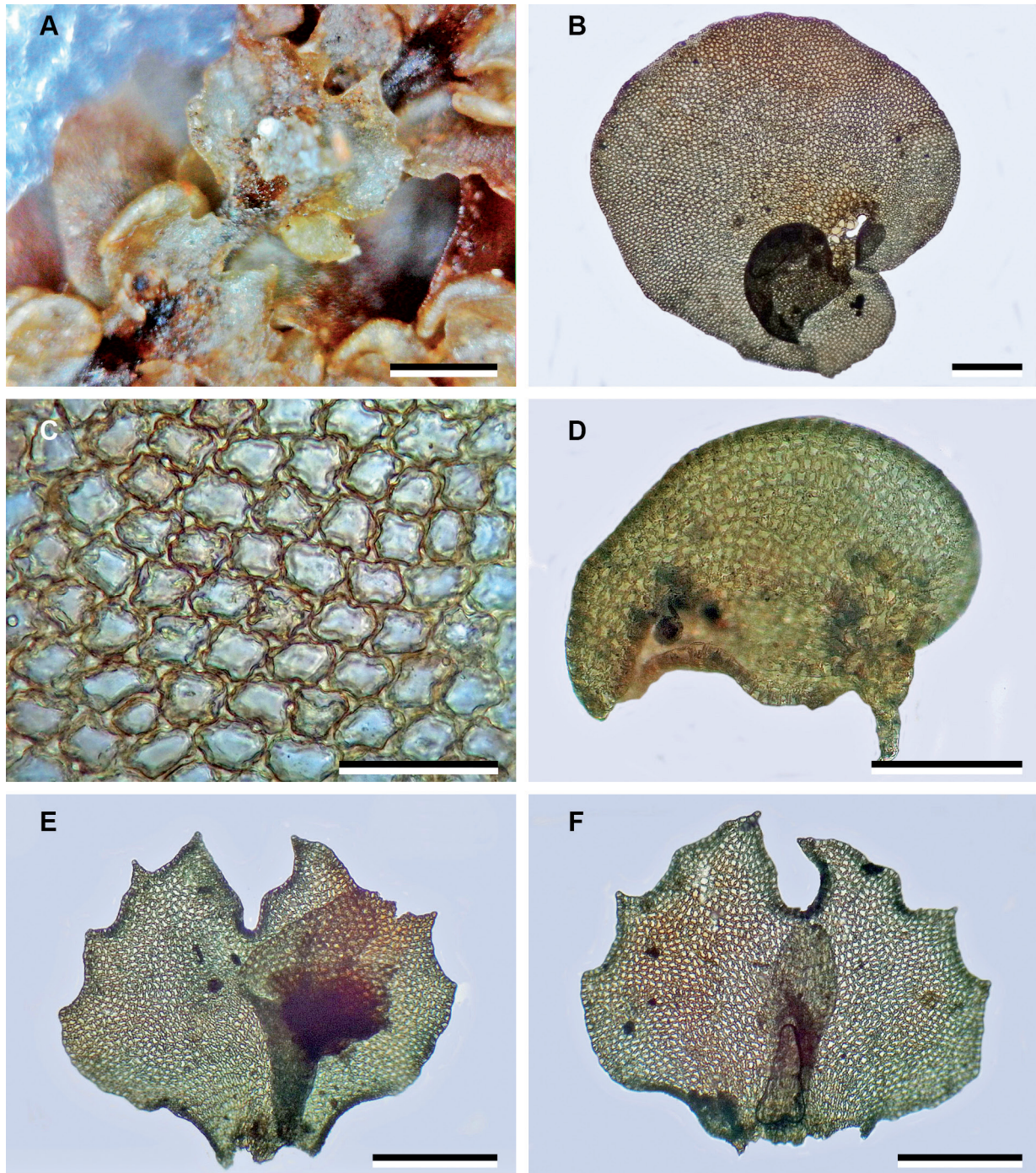


Figure 6. *Frullania eymae* S.Hatt. A: Shoot with underleaves, ventral view. B: Leaf, ventral view. C: Median lobe cells. D: Lobule, ventral view. E: Underleaf with rhizoid bundle, ventral view. F: Underleaf, dorsal view. Photographed by T.Pócs from *H.Streimann 16836* (CANB). Scale bars: A = $500 \mu\text{m}$; B, D–F = $200 \mu\text{m}$; C = $50 \mu\text{m}$.

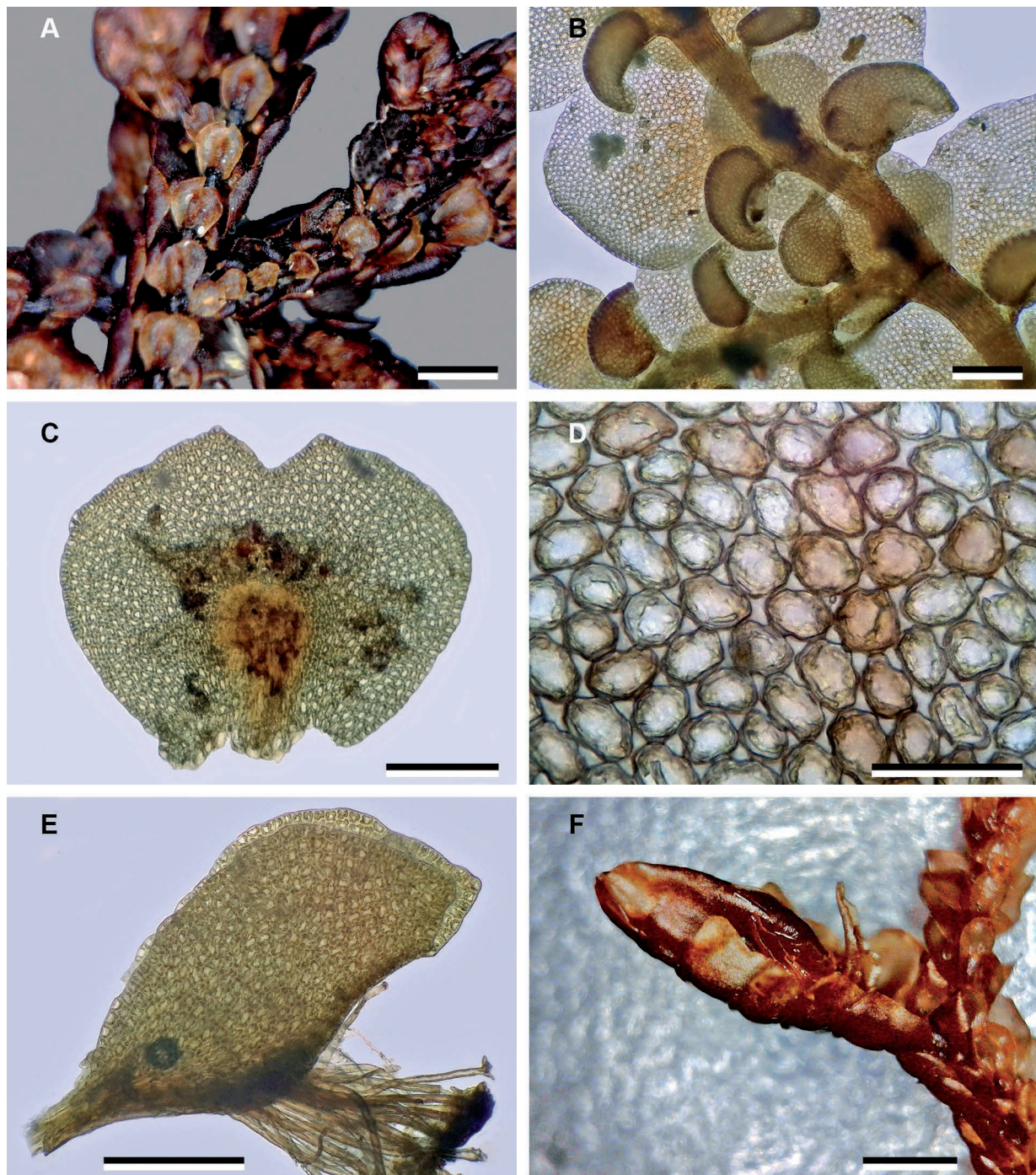


Figure 7. *Frullania falciloba* Lehm. A: Habit, ventral view. B: Shoot, ventral view. C: Underleaf, dorsal view. D: Median lobe cells. E: Erect to patent underleaf, side view. F: Shoot with perianth. Photographed by T. Pócs from *H. Streimann* 16707, 44376 and 54333 (CANB). Scale bars: A, F = 500 µm; B, C, E = 200 µm; D = 50 µm.

Diagnostic features. The concave lobes, large asymmetric, falcate lobules exceeding the lower lobe margin together with the cuneate underleaves with a very short, U-shaped incision and large, smooth, shiny perianth distinguish it from the other species of subgen. *Trachycolea*.

Biostatus. Native

Habitat. It is the commonest Australian species of subgen. *Trachycolea*, widespread in all wet, semiwet or sometimes even semidry habitats, occurring mostly on tree trunk, base and branches, rarely on rocks. Morphologically very variable, therefore described under many synonym names.

Distribution. Widely distributed in Australia except for the driest central part of the continent. Common in New Zealand and in the neighbouring islands. In addition, it is indicated also from Papua New Guinea (Consortium of Bryophyte Herbaria, 2024).

Representative specimens. W.A.: Mt Chudalup, 17 km SSE of Nortcliffe, *H. Streimann* 54318 (CANB, JE, NICH, PERTH), Warren National Park 6 km SSW of Pemberton, *S. and T. Pócs* 04153/E (EGR, PERTH). N.T.: (Renner et al. 2024). Qld.: Clarke Range, 46 km SSW of Proserpine, *J.A. Curnow* 1090 (BRI, CANB); N outliers of Mt Finlayson Range, Rossville at “Home Rule” lodge, *T. Pócs and H. Streimann* 9996/C (CANB, EGR). N.S.W.: Barrington Tops State Forest, Polblue Swamp. 50 km WNW of Gloucester, *H. Streimann* 44344 (CANB); Border Ranges National Park, Bar

Mountain picnic area at the outer caldera rim, S. and T. Pócs and E.A. Brown 0036/A (EGR, NSW). A.C.T.: Trunbilla Nature Reserve, Hurdle Creek 23 km SW of Capital Hill, Canberra, H. Streimann 55701 (CANB, EGR, H, NICH, NY, TGA); Australian National Botanic Gardens, 3.6 km NW of Capital Hill, Canberra, J.A. Curnow 4961A (CANB). Vic.: Skene Creek – Colac Road, 13 km ENE of Apollo Bay, H. Streimann 49825 (CANB, NICH, NY); East Gippsland: Eastern Strelecki Ranges, Tarra Bulga Nat. Park, Balook, E from Tarra-Bulga Visitors Centre, on the Lyrebird Ridge, T. Pócs and H. Streimann 99176/B (CANB, EGR). Tas.: Waterfall Bay track, 4 km SSE of Eaglehawk Neck, H. Streimann 40038 (CANB); Lyell Highway, 15 km ESE of Queenstown, H. Streimann 59544 (CANB).

Notes. *Frullania crassitexta* differs only by the even thickness of the lobe marginal cell walls, yet this character is within many transitional forms and the variability of *F. falciloba*, so it is not considered distinct here.

7. *Frullania ferdinandi-muelleri* Steph., *Sp. Hepatic.* 4: 417 (1910). Type: New South Wales: Tintenbar, Richmond River, on tea tree bark, 2 Aug. 1900, W.W. Watts 153 (holotype: G 18211 (herb. Levier 2628); isotype: MEL 61663).

Etymology. Named in honour of Ferdinand Jacob Heinrich von Müller (born 1825 in Rostock, Germany and died 1896 in Melbourne). He lived in Australia from 22 years old and became a government botanist, founded the National Herbarium of Victoria (1853) and later (1857–1873) became the director of Melbourne Botanic Gardens (Frahm and Eggers 2001).

Illustrations. S. Hattori, *J. Hattori Bot. Lab.* 45: 338 (1979a). J. Colloff and A. Cairns, *Australian Journal of Entomology* 50: 76, fig. 2 (2011).

Description. Plants robust size, pale green, green olive to dark purplish-brown, forming 5–9 cm large round patches with radially growing shoots or continuous weft. Shoots 2–6 cm long and 1–1.8 mm wide, adhering to the substrate. Stem 70–160 µm thick, shortly bipinnately branching. Neither Stephani (1910), nor Hattori (1979) notified in their description, that the plant often has bipinnate flagelliform microphyllous branches with narrower (up to 100 µm thick) stems, caducous leaves and much shorter internodes. Normal leaves imbricate, widely spreading, elliptic, 0.8–1.2 × 0.7–1.1 mm, with rounded apex and narrowly incurved margin and a semicircular dorsal auricle extending about stem width behind the opposite side of the stem. Marginal lobe cells quadrangular, 16–20 µm wide. Median lobe cells 18–20 × 25–32 µm, somewhat elongate with nodulose, often confluent trigones, sometimes with intermediate thickenings. Basal lobe cells 35–40 × 20–25 µm, with nodulose, confluent trigones. Leaf lobules globose, inflated, near spherical with 320–450 µm diameter, with a narrowing base and narrowed, involute mouth, completely without beak. Cells subquadrate, 10–12 × 16–20 µm, walls similar to those of the median lobe or sinuose. Stylus narrow triangular, up to 7 cells long. Underleaves widely obovate- orbicular, 4–5 × stem width, with 1/4 U-shaped incision and obtuse lobes, entire or slightly sinuose, sometimes narrowly incurved margin, slightly sinuate insertion. Rhizoid initial area near the base, convex, with radially arranged, pale brown rhizoids.

Asexual reproduction by the small, caducous leaves and underleaves of the flagelliform, pinnate, microphyllous branches.

These reduced, round leaves have no or only very small lobules, are of 400–500 µm diameter, with flat margin, producing brown, 1–3 celled gemmae with cells of 20 µm diameter. Hyaline rhizoids often grow out from the marginal cells. The whole vegetative reproduction system is very similar to that of *Frullania bolanderi* Austin of the boreal temperate zone, described and illustrated well by Schuster (1992: 168, fig. 799), except, that *F. bolanderi* does not produce extra gemmae on the margin of caducous leaves. In the presence of these tiny gemmiferous branches, it is easy to recognize *Frullania ferdinandi-muelleri* even by naked eye in the field. Although their presence or absence is a good specific character, flagelliform branches for vegetative reproduction are known in very different liverwort groups by homoplasy without meaning relationship.

Dioicous. Androecia not yet seen. Gynoecia rare, terminal on side branches, usually innovating. Perichaetial leaves in three whorls. The innermost bract lobe acuminate, ca. 1.15 × 0.6 mm, with minutely acuminate apex, entire margins with a 1/2 connate, lanceolate lobule with recurved margin. Bracteole narrow, 0.9 mm long, 1/3 bifid, with spinose apex and one lateral tooth. Perianth slightly exerted, pyriform, 1.65 mm long, triolate with truncate apex and short, spinose outgrowths scattered on its surface. Beak very short. (Figs 8, 9)

Diagnostic features. Differs from all Australian members of the subgenus by its globose lobuli and the flagelliform, microphyllous branches.

Biostatus. Native.

Habitat. *Frullania ferdinandi-muelleri* occurs from wet to semidry habitats, on tree bark and on rocks, rarely on decaying wood, between the sea level and 900 m elevation.

Distribution. It is endemic on the Great Dividing Range and on its eastern foothills down to sea level in Australia, from Queensland to the southern part of New South Wales (Atlas of Living Australia 2024).

Representative specimens. Qld: Mt Archer Environmental Park, 8 km NE of Rockhampton, H. Streimann 52321 (CANB, JE, NICH, NY); Great Sandy National Park, Fraser Island, Central Station – Eurong Road, T. Pócs and H. Streimann 9961/L (CANB, EGR). N.S.W.: Higgins Creek, 19 km NE of Batemans Bay, H. Streimann 5738 (CANB, NICH); Wilson River Flora Reserve in Mt Boss State Forest, 35 km WSW from Kempsey, S. and T. Pócs and E.A. Brown 0047/N (EGR, NSW). A.C.T.: Jervis Bay, 34 km SE of Nowra, J.A. Curnow 3205 (CANB).

Taxonomic notes. Bipinnate flagelliform microphyllous branches occur only on about 20% of Australian *Frullania ferdinandi-muelleri* specimens, therefore Stephani (1910) and Hattori (1979a) probably could not see them on the type. *Frullania hainanensis* S. Hatt. & P. J. Lin, *Journal of Japanese Botany* 61: 307, fig. 1 (1986) from southern China is similar in many aspects, but while the microphyllous branches of *F. ferdinandi-muelleri* are bipinnately branching and have also reduced, round, mostly unlobed leaves, the microphyllous branches of *F. hainanensis* are unbranched and have only underleaves. *Frullania kitagawana* S. Hatt., *J. Hattori Bot. Lab.* 57: 417–419, fig. 6 (1984b) from New Caledonia also has many similarities, has smaller leaves and no basal auricles, both are very similar, as it was pointed out by Hattori and Lin (1986).

Hattori (1977: 416) proposed a new subgenus *Huerlimannia* for the few Australasian species with this special globose type of lobuli, but according to the molecular investigations of Hentschel *et al.* (2009), *Frullania ferdinandi-muelleri* nests well among the other members of subgen. *Trachycolea*.

8. *Frullania hamaticoma* Steph., *Hedwigia* 28(3): 158 (1889).
Type: Victoria: Upper Ovens River, Mrs. MacCann 1882 (G 18214 ex Hb. Müll.Hal.).

Etymology. As it is written in the protologue by its author (Stephani 1889a) the female perichaetial leaves are four times longer than stem leaves, comate and with their hooked ends protecting the gynoeceum.

Illustrations. F.Stephani, *Hedwigia* 28(4): Tab. IV, figs 8–13 (1889); F.Stephani, *Icon. Hepatic., Jard. Bot. Genève* fig. 003624 (1985); S.Hattori, *J. Hattori Bot. Lab.* 45: 344, fig. 15 (1979).

Description. Medium sized, pale brown in herbarium. Shoot 2–5 cm long, 1.2– 1.5 mm wide, irregularly, shortly pinnately branched. Leaves densely imbricate, dorsally extended beyond the stem to its 0.5–1.0 width. Lobe oval, 0.60–0.65 × 0.45–0.50 mm, slightly concave with apically narrowly incurved margin. Towards the gynoeceia becoming much larger. Marginal lobe cells 10–15 × 10, median 15–20 × 10–13 µm with sub-equally thick walls and with a low dorsal mammilla. Basal cells 23–30 × 15–20 µm, with large, nodulose trigones. Lobule large, 0.20–0.25 mm long, asymmetric falcate with very inflated body and elongate, pilose apex extending below the ventral lobe margin. Towards the gynoeceia they become explanate. Stylus very long, up to 0.4 mm, well exceeding the lobule height, narrow triangular, 3–4 cells wide at base continuing in a 1 or 2 cells wide pilous apex. Underleaves imbricate, oblong-ovate to elliptic, with 1/4–1/3 deep, U-shaped slit and with cuneate base. Insertion sub-transverse.

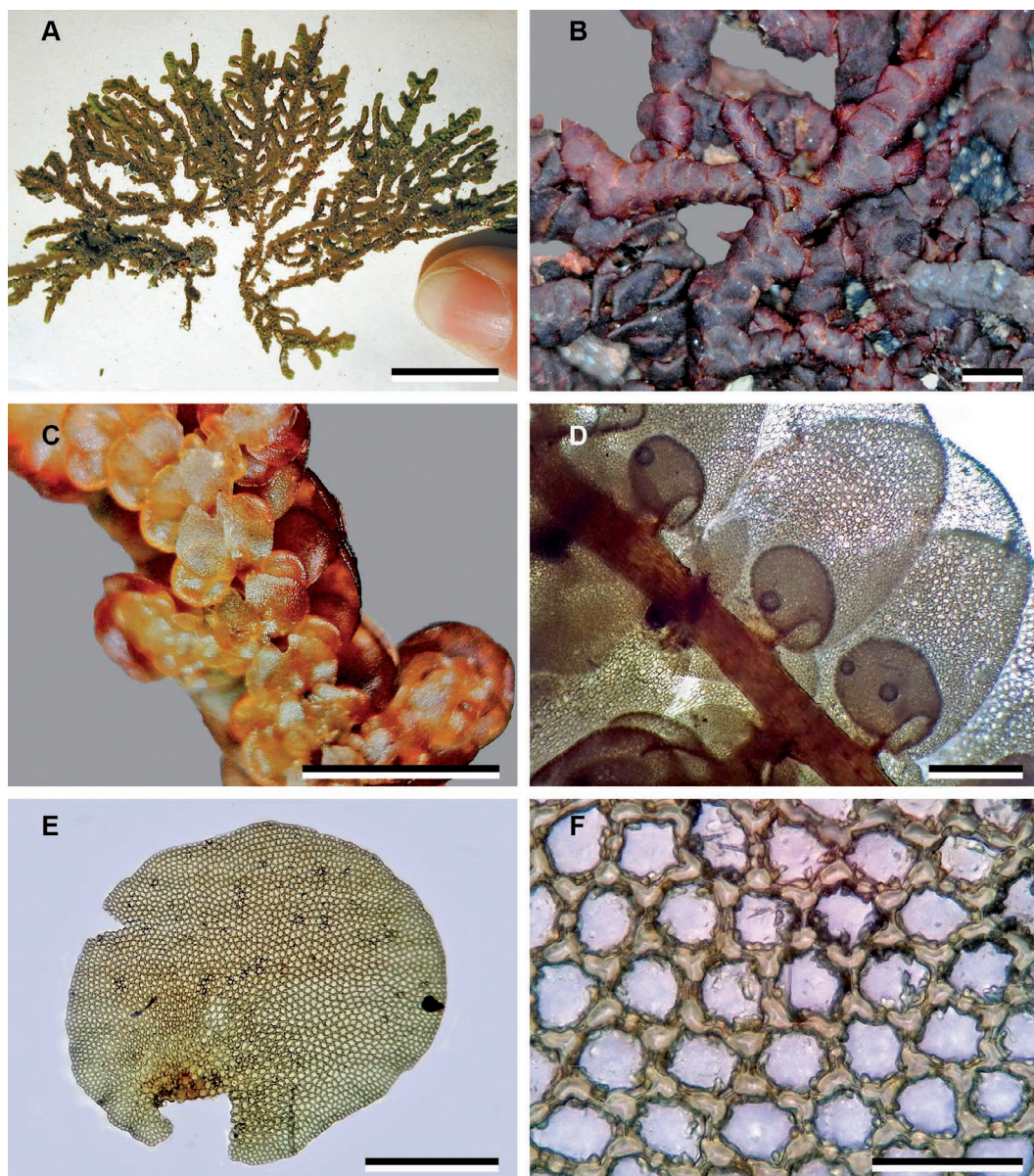


Figure 8. *Frullania ferdinandi-muelleri* Steph. A: Habit, showing the radial arrangements of shoots, ventral view. B: Habit, dorsal view. C, D: Shoot, ventral view. E: Leaf lobe. F: Median cells of lobe. Photographed by T.Pócs from J.A.Curnow 3205, from H.Streimann 28523, 43458 and 52321 (CANB). Scale bars: A = 2 cm; B, C = 1 mm; D, E = 500 µm; F = 50 µm.

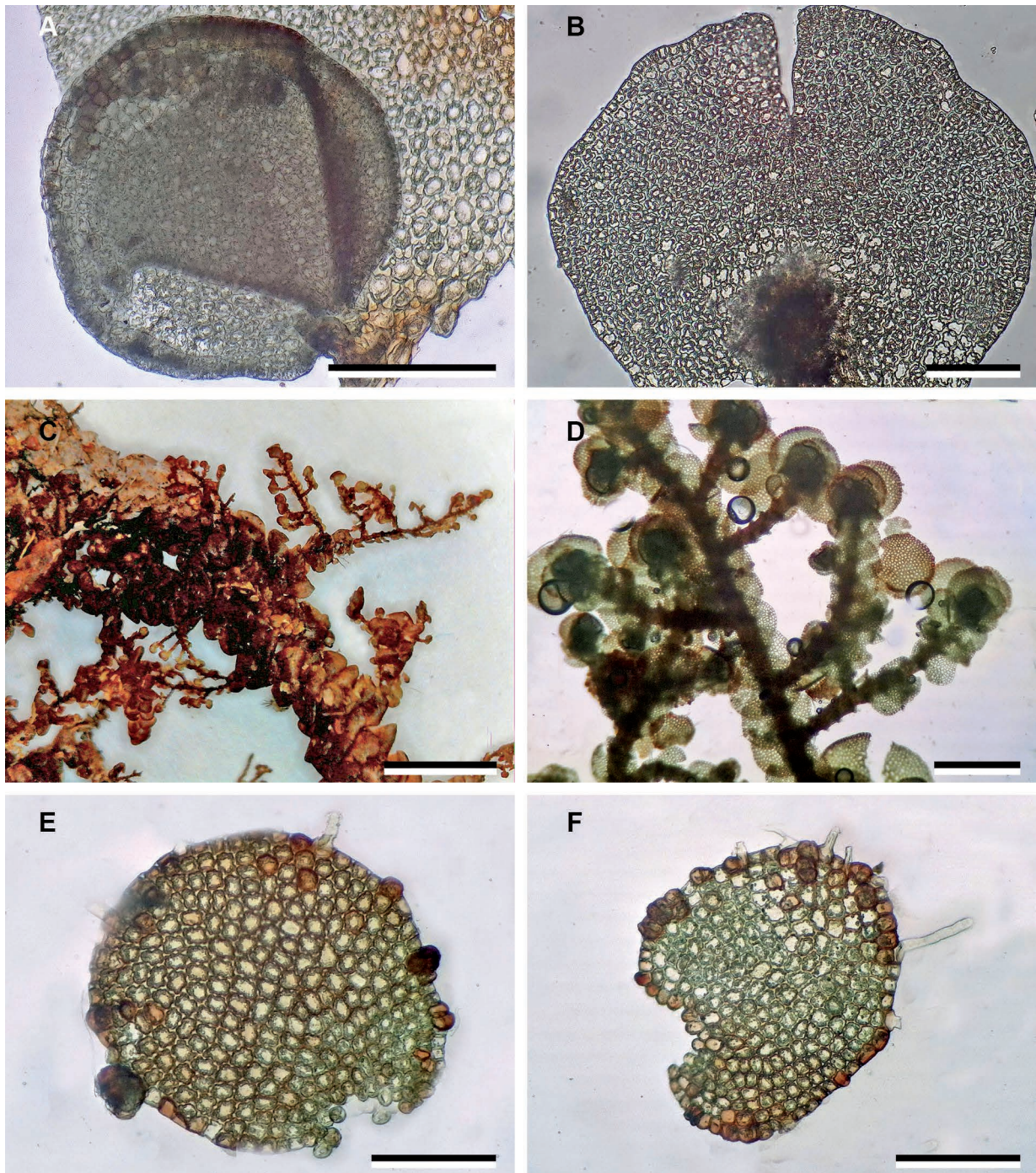


Figure 9. *Frullania ferdinandi-muelleri* Steph. A: Lobule, ventral view. B: Underleaf, ventral view. C: Flagelliform, microphyllous branches on the normal shoot, dorsal view. D: Part of microphyllous branch, ventral view. E, F: Caducous leaves of the microphyllous branch, with marginal gemmae. Photographed by T.Pócs from J.A.Curnow 3205, from H.Streimann 28523, 43458 and 52321 (CANB). Scale bars: A, B, E, F = 200 µm; C = 2 mm, D = 500 µm.

Dioicous (androecia not seen). Gynoecia terminal on stem or branches, with innovations. Perichaetial leaves in 3 whorls. Innermost female bracts up to 3 mm long, with incurved, acuminate-acute apex and shortly connate, pilose lobules. Bracteoles 2/3 bifid, strongly dissected, toothed, usually folded at the middle line. Perianth (young?) immersed in the perichaetium, obpyriform, ca. 1.5 mm long, triplicate with rugged surface and towards the apex hirsute-dentate.

Diagnostic features. The unusually long stylus combined with the inflated falciform lobuli with pilose apex, exceeding the ventral lobe margin and the mamilliose dorsal lobe surface distinguish this taxon from any other Australian *Frullania* species.

Biostatus. Native.

Habitat. As it was collected along a perennial river, probably at high altitude, the habitat supposedly was humid.

Distribution. It is known only from the type collection along the upper part of perennial Ovens River in the north-east Murray River catchment, part of the Murray-Darling basin, located in the Alpine and Hume Regions of state Victoria, where it seems to be endemic.

Representative specimen. Vic.: Upper Ovens River, Mrs. McCann, 1882. (G 18214 ex Herb. Müll.Hal.)

Taxonomic notes. Although only its type specimen is known, it has such good distinguishing characters, that there is no doubt about its taxonomic value as a valid species. Interestingly Hattori (1979a) studying the type specimen, did not mention the perianth at all, although in the protologue (Stephani 1889a) and in his *Sp. Hepatic.* (1910), it is well described and also illustrated (Stephani 1899b, 1985: 003624). It may be that the perianth was not returned to the type specimen or Hattori had seen only a part of it.

9. *Frullania hicksiae* S.Hatt. form. *hicksiae*, *Cryptogam. Bryol. Lichén.* 5(1–2): 182 (1984b). *Type:* Australia, Queensland, Devil's Thumb, W of Mossman, 1150 m, over rock outcrop, Oct. 9, 1982, M.L. Hicks 11258 (holotype: NICH; isotype: herb. M.L.Hicks (? now in F)).

Etymology. Named to honour the collector of type specimen, Dr. Marie Leach Hicks, Professor Emerita of the Appalachian State University, U.S.A. She very intensively collected during 1982 and made known a few bryophytes from Queensland between 1987 and 1992. Other results of her collections were published by several authors (e.g. Howe 2009).

Illustrations. S.Hattori, *Cryptogam. Bryol. Lichén.* 5(1–2): 183, fig. 3 (1984b).

Description. Plants small to medium size, olive green to dark purplish-brown, forming 5–10 cm large mats or continuous weft. Shoots 1–2 cm long and 0.6–1.4 mm wide. Stem 120–180 µm thick, irregularly bipinnately branching. Leaves densely imbricate, widely spreading, elliptical-obovate with incurved distal margin, 0.65–1.1 × 0.6–0.8 mm, round apex, nearly flat or with narrowly incurved margin. It has a basal auricle only on its dorsal side while its ventral base is not appendiculate, nearly straight. Lobe cells quadrangular, 18–22 µm wide. Median lobe cells 20–30 × 18–22 µm, with large, nodulose trigones and with intermediate thickenings. Basal lobe cells 30–50 × 25–30 µm, with nodulose, confluent trigones. Leaf lobules asymmetric falcate-galeate, standing parallel to the stem, 250–300 µm long and wide with unequal dorsal and ventral margin, subacute to obtuse beak, reaching the ventral margin of the lobe. Cells sub-quadrangular, smaller than those of the median lobe (18–22 µm) but with similar walls. Stylus small, 5–6 cells long. Underleaves widely obovate-orbicular with cuneate base, about 4 × stem width, 500–560 × 630–750 µm, with 1/4–1/5 deep, relatively wide V-shaped incision and subacute lobes, entire margin and straight insertion. Rhizoid initial area in the lower third, slightly convex, sometimes with a short bundle of hyaline rhizoids.

Dioicous. Androecia on short side-branches, button shape, consisting of 5–6 pairs of male bracts. Gynoecia rare, terminal on stem or on side branches, usually innovating. Perichaetial leaves in 2–3 whorls. The innermost bract lobe elliptic, ca. 1.5 × 1.0 mm, with subacute apex, entire margins. Lobule 1/2 connate, lanceolate with 1–2 distinct marginal teeth. Bracteole sub-rectangular, 0.9 mm long, 1/3 bifid, triangular with spinose apex. Perianth 1/3–1/2 exserted, 1.5–1.9 mm long, pyriform, triolate with truncate apex and short, spinose outgrowths on the wings. Beak relatively short. (Fig. 10)

Diagnostic features. The wide underleaf slit, combined with only dorsally auriculate lobe distinguish it from the related species, especially from *Frullania queenslandica* Steph.

Distribution. The species seems to be endemic to Queensland.

Representative specimens. Qld: Tully falls Road, 8 km SE of Ravenshoe, 17°40'S, 145°31'E, 940 m elev., *H.Streimann* 30101 (CANB, JE); Cardwell Range, 45 km NW of Cardwell, 18°05'N, 145°39'E, 760 m elev., *H.Streimann* 9961/L (CANB, EG).

9b. *Frullania hicksiae* form. *litoralis* S.Hatt., *Beih. Nova Hedwigia* 90: 149 (1988). *Type:* Queensland: Cook Distr., Etty Bay, adjacent to Etty Bay Caravan Park, 17°34'S, 146°E, coastal rainforest area, on bark of tree subject to salt spray at high tide, 9 July 1984, B. Thiers & R.E. Halling 2381 (holotype: NICH; isotypes: AD, NY).

Diagnostic features. It differs from form. *hicksiae* by its often explanate lobuli, obtuse underleaf lobes and by its five plicate perianths with shorter, wider beak.

Illustrations. S.Hattori, *Beih. Nova Hedwigia* 90: 150, fig. 1 (1988).

Biostatus. Native.

Habitat. While form. *hicksiae* occurs from wet to semidry montane forests, generally above 700 m elevation, form. *litoralis* S.Hatt. grows in coastal rainforests near sea level on trees subject to high tide salt spray.

10. *Frullania latogaleata* Herzog, *Trans. British Bryol. Soc.* 1(3): 189 (1949). *Type:* Western Australia: Pemberton, 34°26'S, 116°20'E, April 1946, G.G.Smith s.n. (isotype: PERTH 05940621).

Etymology. From the Latin *latus* (wide) and *galeatus* (helmet shaped), referring to the wide Greek helmet shaped lobule.

Illustrations. T.Herzog, *Trans. British Bryol. Soc.* 1(3): 189, fig. 4 (1949).

Description. Plants of medium size, vivid green, in herbarium partly rust red. Shoots 1–2 cm long and 1.28–1.92 mm wide, irregularly branching and forming radially growing, round patches. Stem 80–150 µm thick. Leaves imbricate, flat. Lobe 1 mm long and wide, orbicular. Narrowly inserted at base, cordate, widely exceeding the stem. Apical and median cells with flexuose walls, nodulose trigones and intermediate thickenings, 15–25 µm long and 12–19 µm wide, chlorophyllose. Basal cells 40 × 25 µm, subhyaline. Lobule 1/3 of lobe length, low and wide helmet shaped with truncate, parallel sided opening, not exceeding the lobe margin. Stylus indistinct. Stem underleaves large, contiguous, 0.6–0.8 mm long and 0.8–1 mm wide, rounded obovate, transversely inserted, with V-shaped apical incision. Only male plant was seen. Androecium on short side branch, button shaped, consisting of 2–3 pairs of bracts and 2–3 bracteoles. (Fig. 11)

Diagnostic features. Among the Australian *Frullania* this species is distinguished by its vivid green, round, flat leaves with wide galeate lobuli without beak and by the wide, orbicular underleaves.

Biostatus. Native

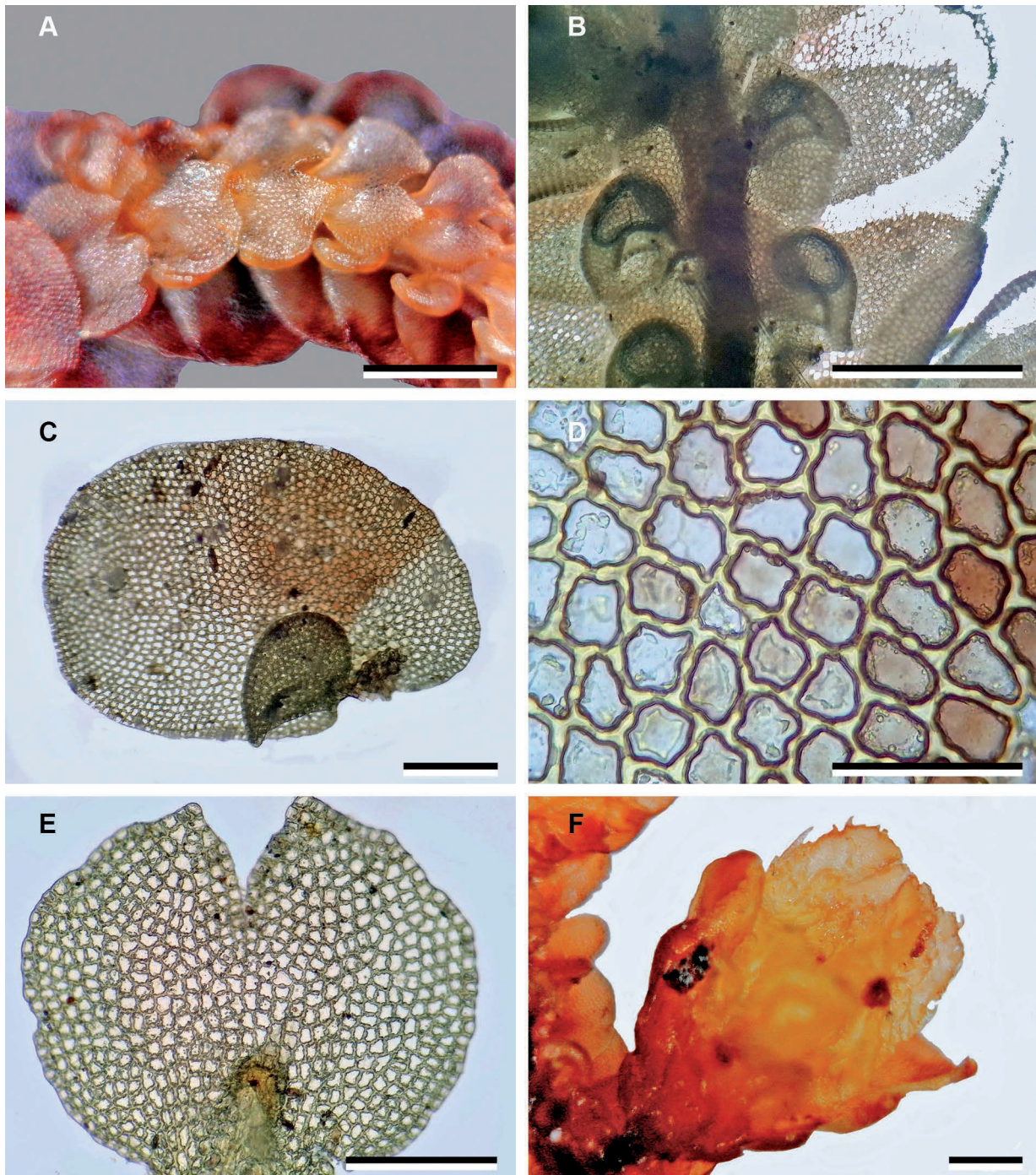


Figure 10. *Frullania hicksiae* S.Hatt. A, B: Habit, ventral view. C: Leaf lobe and lobule, ventral view. D: Median lobe cells. E: Underleaf, dorsal view. F: Gynoecium, ventral view. Photographed by T.Pócs from *H.Streimann* 30101, 30106 and 36943 (CANB). Scale bars: A, B, F = 500 µm; C, E = 200 µm; D = 50 µm.

Habitat. The species inhabits bark in karri (*Eucalyptus diversicolor*) forests and the cavities of granite outcrops.

Distribution. Apparently endemic to Western Australia.

Representative specimens. W.A.: Mt Frankland NE foot at 300 m elevation, *S.* and *T.Pócs* 04163 (EGR, PERTH).

11. *Frullania monocera* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, *Syn. Hepatic.* 3: 418 (1845). *Jungermannia monocera* Hook.f. & Taylor, *London J. Bot.* 4: 89 (1845). Type: Van Diemen [Tasmania]. misit Taylor 1847 (Herbarium Lehmannianum) (isotype: S).

Frullania hampeana Nees, *Syn. Hepatic.* 3: 426 (1845). Type: Nova Hollandia [Australia].

Frullania grossiloba Steph., *Sp. Hepatic.* 4: 424 (1910). Type: Tasmania: Carnarvon, 1 Feb. 1899, Weymouth (G).

Frullania spinigastria S.Hatt., *J. Hattori Bot. Lab.* 45: 358 (1979), *syn. nov.* Type: New South Wales: Rodriguez Pass in the Blue Mountains, *Watts 1000b* (G). Note: The number and size of teeth on the underleaves is very variable with all transitions between typical *F. monocera* and former *F. spinigastria*.

Etymology. From the Latinised form of Greek μονόκερως (*monokeros*) = one horn(-ed). Probably refers to the long acuminate, spinose beak of the lobule.

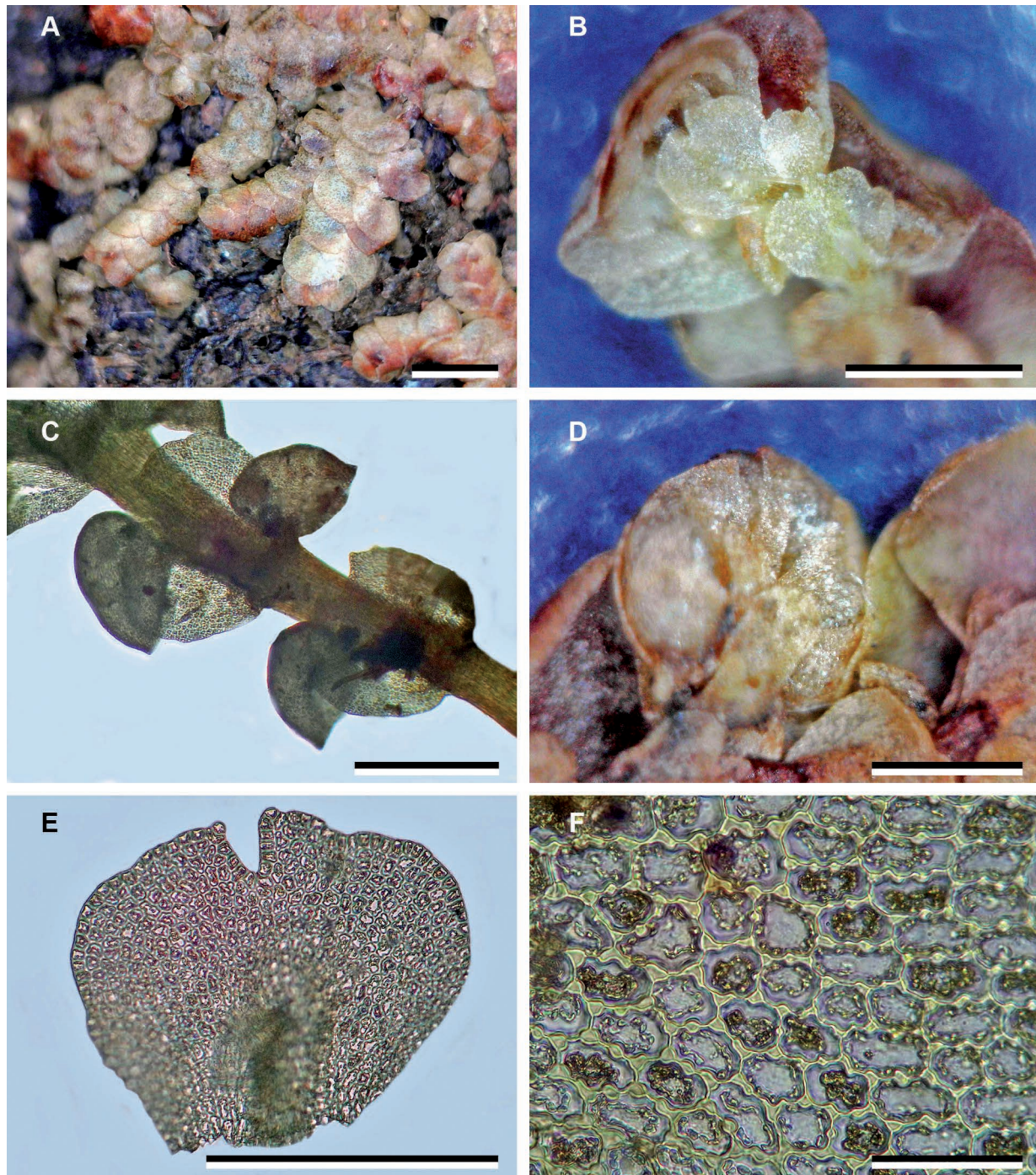


Figure 11. *Frullania latogaleata* Herzog in Hook.f. A: Habit, dorsal view. B: Habit, ventral view. C: Lobules and underleaves. D: Androecium, ventral view. E: Underleaf, dorsal view. F: Median lobe cells. Photographed by T.Pócs from S. and T.Pócs 04163 (EGR, PERTH). Scale bars: A = 1 mm; B, D = 500 μ m; C, E = 200 μ m; F = 50 μ m.

Illustrations: S.Hattori, *J. Hattori Bot. Lab.* 45: 348, fig. 18 (1979), as *F. monocera*. S.Hattori, *J. Hattori Bot. Lab.* 45: 359, fig. 25 (1979a), as *F. spinigastria*. S.Hattori, *J. Hattori Bot. Lab.* 46: 133 (1979b), as *F. hampeana*.

Notes. *Frullania monocera* is a very variable taxon. Hentschel *et al.* (2015) mention that it belongs to a not fully understood species complex. Quite a few species were described within this complex, based on the size and colour of the plant parts, the serration of the underleaves and perichaetial leaves, and the presence and size of appendages on the perianth. But after examination of more than 200 specimens, one can establish that these properties can gradually merge into each other in different

combinations, so, with a few exceptions, they can be considered only as modifications of a single protean species and cannot be distinguished at the species level (see identification key to infraspecific taxa below).

Characters distinguishing taxa formerly described as species can occur in different combinations or be variable even within one specimen (e.g. smooth and tuberclose perianths or the dentition of underleaves). Therefore, descriptions established on single type specimens many times do not work. Studying a larger population led to the synonymisation of several species, or to reduction to variety rank. The molecular examination already done on selected individuals of many species gave insight in the

subgeneric classification of the genus (Hentschel *et al.* 2009). Further molecular study on large number of specimens belonging to the same group may shed light on some cryptospecies.

Key to identify the infraspecific taxa within *Frullania monocera*

1. Shoot up to 1.3 mm, leaves 0.6–1.0 mm long. Underleaves less than 3× stem width, the plant pale to olive green, rarely has reddish tinge 2
1. Shoot up to 1.5 mm wide, leaves up to 1.2 mm long and wide, the plant usually has reddish tinge. Underleaves more than 3× stem width *F. monocera* var. *streimannii*
2. All underleaves have 1–3(–5) teeth along the lateral margin. Perianth with dense spinose outgrowths *F. monocera* var. *monocera*
2. A part or all of the underleaves entire, without teeth on their lateral margin 3
3. Underleaf margin flat, at least some underleaves dentate 4
3. Underleaf margin narrowly recurved along all its length. All underleaves with entire margin, none of them has teeth. Perianth only on the keels spinose-dentate *F. monocera* var. *pallida*
4. Perianth surface with scattered spinose outgrowth. Lobules never expanded *F. monocera* var. *acutiloba*
4. Lobules near the shoot apex all expanded. In this respect similar to *F. allanii*. But all varieties of *F. monocera* has perianths with spinose surface, the perianth of *F. allanii* completely naked, smooth *F. monocera* var. *subhampeana*

Frullania monocera var. *monocera*

Description. Small to large size, from pale to olive green sometimes with reddish tinge, or brownish, forming 5–8 cm large continuous wefts. Shoots 1–4 cm long and 0.8–1.3 mm wide. Stem 80–180 µm thick, irregularly bipinnately branching. Leaves slightly imbricate, obliquely spreading, flat, elliptic-obovate with round apex, 0.6–1.0 × 0.6–0.7 mm. A basal auricle only occurs on the dorsal side. Margin lobe cells subquadrate, 12–15 µm wide. Median lobe cells 10–15 × 13–20 µm, with sub-equally thickened walls or with small trigones and intermediate thickenings. Basal cells 20–50 × 15–25 µm, with nodulose, confluent trigones. Leaf lobules asymmetric falcate-rostrate, standing at 20–45° to the stem, 300–350 µm long and wide with unequal dorsal and ventral margin, with attenuate, hamate-spinose beak, usually exceeding the ventral margin of the lobe. Lobule cells subquadrangular, smaller than those of the median lobe (10–15 µm) with flexuose and nodulose walls. Stylus minuscule, 3 cells long and 2 cells wide. Underleaves obovate with cuneate base, less than 3(–5)× stem width, 400–520 × 310–400 µm, with 1/4–1/2 deep, narrow V-shaped incision and acute lobes, serrate with 1–4 large teeth on each side (–7 in former *F. spinigastria* S.Hatt.) and sub-transverse insertion. Rhizoid initial area absent, at the underleaf bases a few brownish rhizoids can occur.

Dioicous, female plants are more common (70%) while male plants are fewer (13%), the rest were sterile. In addition, the male plants are smaller with narrower shoots. Androecia on short side-branches, elongate lanceolate, formed by 6–22 pairs of male bracts. Gynoecia on short side branches, usually innovating. Bracts in 3 pairs, larger than ordinary leaves, therefore the perichaetium forms a crown-like whorl at the end of female branches. The innermost bracts have pilose apex and entire to

many-toothed margin. Lobule 2/3 connate. Bracteoles pilose, with 1 or 2 side teeth to serrately multidentate, one base connate at least to one of the bracts. Perianth 1/2–2/3 exserted, long pyriform, 1.5–2 mm long, 3 or 5 keeled, naked or verruculose or spinose or with hamate, thorn like outgrowths. Beak short to long. Sporophyte seen only once. Vegetative reproduction is not known. (Figs 12, 13)

Diagnostic features. The subquadrate, sub-equally thickened lobe cells, the asymmetric falcate-rostrate leaf lobule with attenuate, hamate-spinose beak combined in most cases with serrately toothed but flat underleaf margins distinguish *F. monocera* from the related species.

Biostatus. Native.

Habitat. It occurs in Australia from semidry sclerophyllous forests to the wet rainforests in all elevations up to 1340 m, mostly on tree bark and twigs.

Distribution. Distributed in all forested parts of the continent (including Tasmania and Norfolk Island). Widespread from India through the Malayan Archipelago to south China, Japan, New Caledonia and New Zealand (Hattori 1973, 1975, 1979a; Yuzawa and Hattori 1981; Bapna and Kachroo 2000, Hentschel *et al.* 2015; Renner *et al.* 2024).

Representative specimens: Qld.: Gordon Creek, 19 km SW of Cape Weymouth, 12°43'S, 143°18'E, 110 m elev. *H. Streimann* 56534 (CANB, EGR, H); Bunya Mts. National Park. Burtons Well, near the summit of Mt Kiangarow, 26°50'S, 151°33'E, at 1100–1140 m elev. *T. Pócs and H. Streimann* 99140/E (CANB, EGR). N.S.W.: Bangalow-Byron Bay road, 7 km SW of Byron Bay, 28°41'S, 153°34'E, 100 m elev., *H. Streimann* 43430 (CANB, NICH); Barrington Tops State Forest, 44 km WNW of Gloucester, on the ridge top. 31°55'S, 151°31'E, at 1400 m elev., *T. Pócs and H. Streimann* 99154/G (CANB, EGR).

Frullania monocera* var. *acutiloba (Mitt.) Hentschel & von Konrat, *Phytotaxa* 220(2): 136 (2015). *Frullania acutiloba* Mitt., *Proc. Linn. Soc.* 5: 120 (1860). Type: India: Nilgiri Mts, Perrottet (NY, ex herb. Montagne).

Diagnostic characters. Differs from var. *monocera* by the underleaves not wider than 3× stem width, without or with a few side teeth and by its perianth with scattered spinose outgrowths. (Fig. 13)

Illustrations: Y. Yuzawa and S. Hattori, *J. Hattori Bot. Lab.* 50: 254, fig. 1 (1981), as *F. acutiloba*.

Representative specimen: N.S.W.: Chichester State Forest, 19 km NNE of Dungog, 32°15'S, 151°44'E, 350 m elev., *H. Streimann* 38352 (CANB).

Frullania monocera* var. *pallidula (S.Hatt.) Pócs, *comb. et stat. nov.*

Basionym: *Frullania pallidula* S.Hatt., *Beih. Nova Hedwigia* 90: 152 (1988). Type: Queensland: Lamington Nat. Park, trail to Elebana Falls, 500 m, *B. Thiers* 1108 (holotype: NICH; isotype: NY).

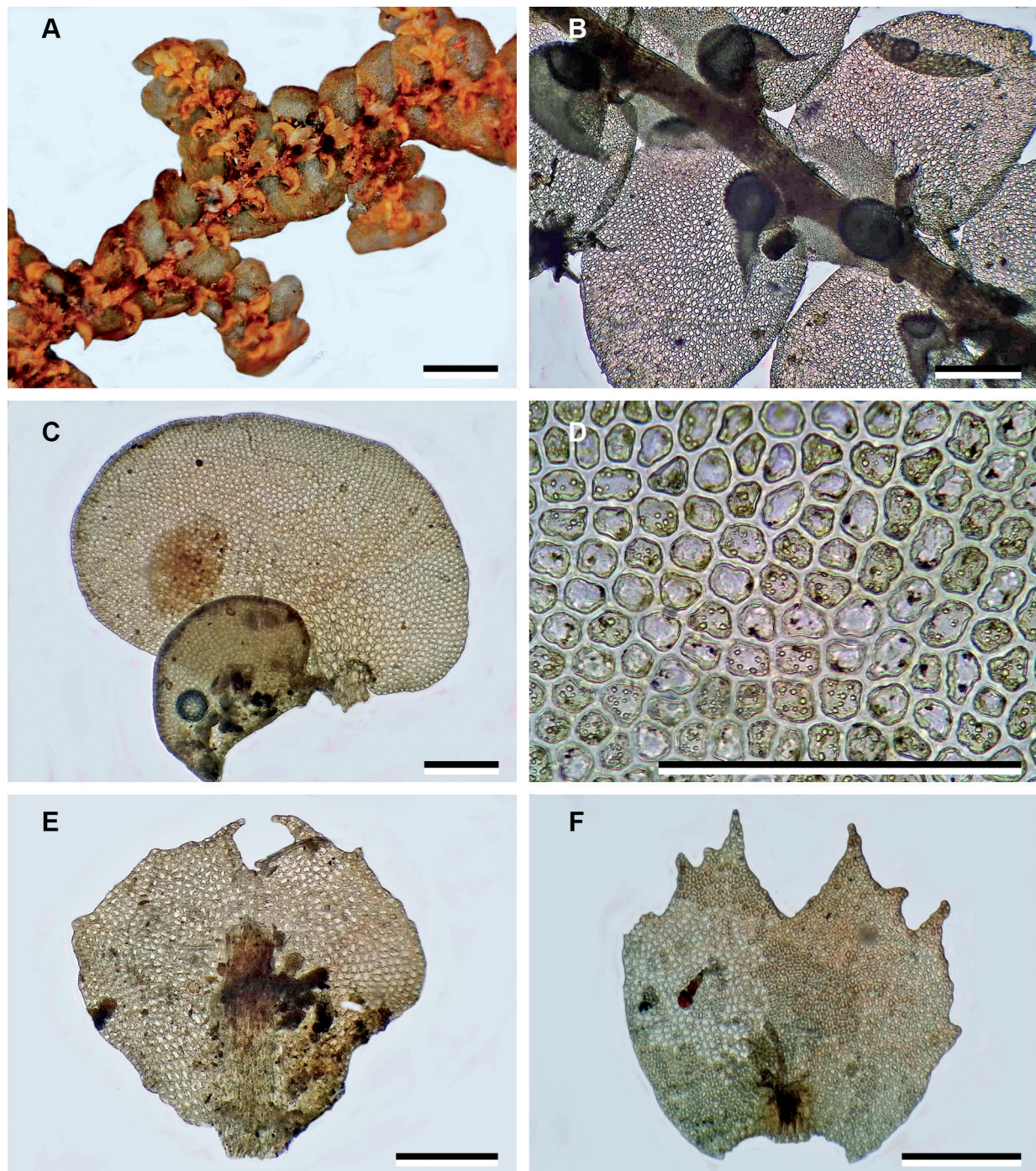


Figure 12. *Frullania monocera* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees var. *monocera* A, B: Habit, ventral view. C: Leaf lobe and lobule, ventral view. D: Median lobe cells. E: Underleaf, ventral view. F: Underleaf, ventral view. Photographed by T.Pócs, from various Australian specimens. Scale bars: A = 1 mm; B, C, E, F = 200 μ m; D = 50 μ m.

Diagnostic characters. Differs from var. *monocera* by its always entire and narrowly recurved underleaf margin.

Representative specimens: New South Wales: Border Ranges National Park, at the park entrance, on ridge, *S. and T.Pócs* and *E.A.Brown 0035H* (CANB, EGR), Mount Hyland Nature Reserve, *S. and T.Pócs* and *E.A.Brown 0015/D* (CANB, EGR).

Frullania monocera var. *streimannii* (S.Hatt.) Pócs, *comb. et stat. nov.*

Basionym: *Frullania streimannii* S.Hatt., *J. Hattori Bot. Lab.* 54: 176 (1983). Type: New South Wales: Gloucester River, 38 km

WSW of Gloucester, 32°04'S, 151°41'E, elev. 400 m, 10 Oct. 1978, *H.Streimann 6448* (holotype: NIC; isotype: CANB).

Diagnostic characters. Differs from var. *monocera* by its larger size (leaves up to 1.2 mm long and wide, perianth up to 2.2 mm long), reddish tinge, broad underleaves (3–5× stem width) with only a few (0–2) side teeth and by its female bracteole in the lower third connate on its both sides to the bracts with entire margins. (Fig. 13). There are several specimens with transitions of all combinations of characters between this variety and var. *monocera*.

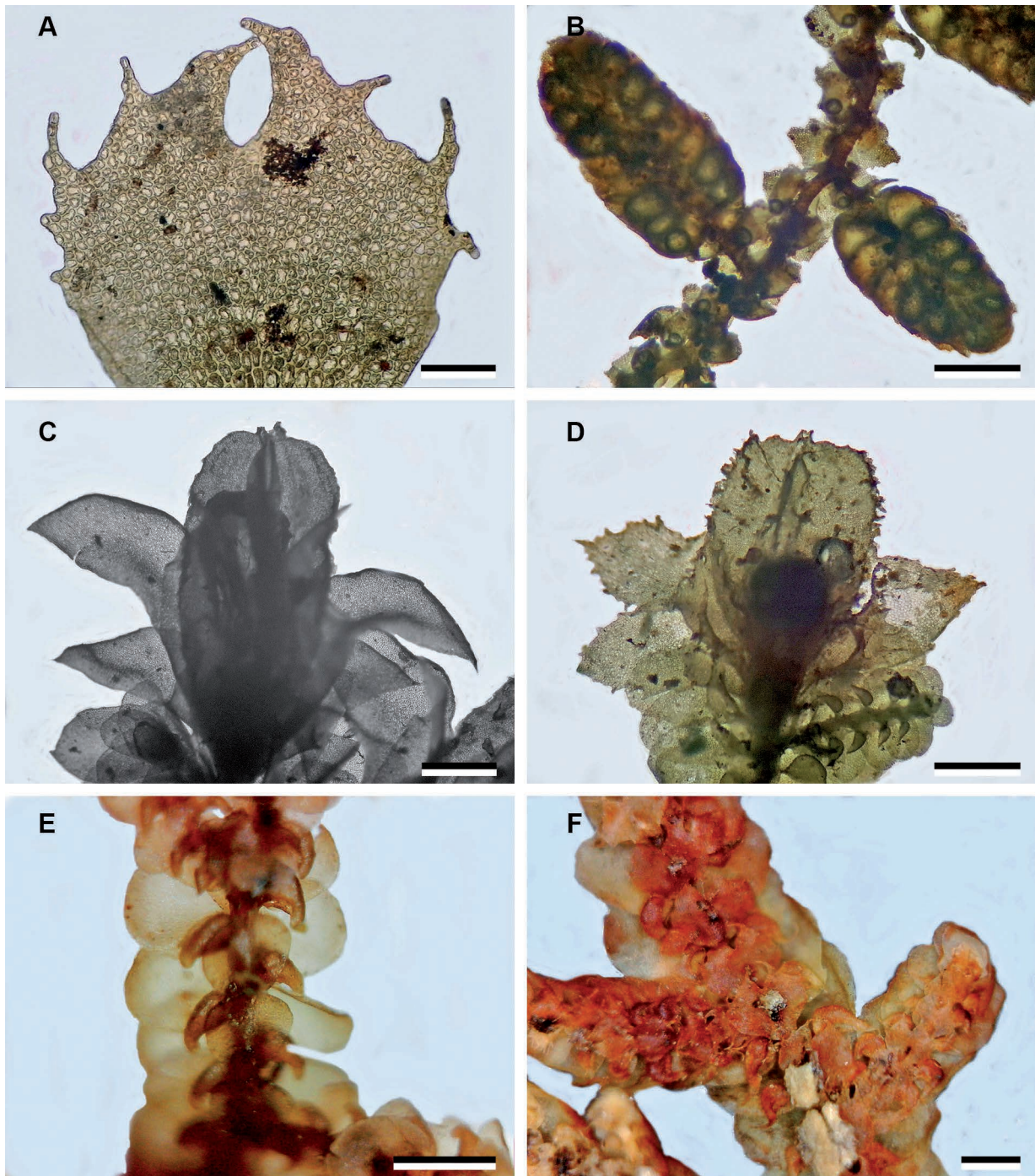


Figure 13. *Frullania monocera* and its var. *streimannii* (S.Hatt.) Pócs. A: Underleaf of former *F. spinigastria*, ventral view. B: Male branches, ventral view. C: Almost smooth perianth and entire bracts and bracteole, ventral view of var. *monocera*. D: Perianth with hamate spinules and serrate bracts on another specimen of var. *monocera*. E: *F. monocera* var. *acutiloba*, habit, ventral view. F: *F. monocera* var. *streimannii* habit, ventral view. Photographed by T.Pócs: A, from Curnow 1121 (CANB); E from Streimann 38352 (CANB); F from the isotype: Streimann 6448 (CANB). Scale bars: A = 100 μ m; B–F = 500 μ m.

Illustration: S.Hattori, *J. Hattori Bot. Lab.* 54: 177, fig. 70 (1983), as *F. streimannii*.

Representative specimens: Qld.: Balfour Range, 29 km SE of Nanango, on Brisbane Valley Highway, 26°52'S, 152°12'E, 400 m elev., *H. Streimann* 9314 (CANB); Bunya Mts. National Park, on the plateau in "Paradise" area, 26°52.5'S, 151°34–35'E, at 960–1080 m elev., *T. Pócs* and *H. Streimann* 99142/C (CANB, EGR). N.S.W.: North Coast, Barrington, 32°00'S, 151°50'E, Sep. 1941, *H. Porter* s.n. (CANB).

Frullania monocera* var. *subhampeana (E.A.Hodgs.) Hentschel & von Konrat, *Phytotaxa* 220(2): 127–142 (2015). *Frullania subhampeana* E.A.Hodgs., *Trans. Proc. Royal Soc. New Zealand* 77: 370 (1949). Type: New Zealand. Wairoa, Maunbgapoike Falls, 1937, *E.A. Hodgson* 1472 (lectotype: MPN), designated by Hattori (1979b). The complicated synonymy is described in detail by Hentschel et al. (2015).

Diagnostic characters. Differs from var. *monocera* by its mostly entire underleaves, only near the shoot apex dentate. In addition, all lobules near the shoot apex are explanate, lanceolate. In this respect similar to *F. allanii*.

Illustration: S.Hattori, *J. Hattori Bot. Lab.* 46: 145, fig. 44 (1979b); 54: 179 (1983), as *F. subhampeana*.

Representative specimens: N.T.: Melville Island, 1 km W of Snake Bay, Sandspears Jungle, 11°26'S, 130°40'E, near sea level. *J. Russell-Smith 1305* (CANB, JE, MELU). Qld.: Wyberba, junction of old highway and Eukey road, 23 km SSW of Stanthorpe, 28°52'S, 151°53'E, 770 m elev., *H. Streimann 522977* (CANB, EGR, NICH, NY). N.S.W.: Marengo Plain, Grafton Range Road 40 km NW of Dorrigo, 30°06'S, 152°24'E, 1110 m elev., *H. Streimann 47622* (CANB, JE).

12. *Frullania ornithocephala* (Reinw., Blume & Nees) Nees var. *intermedia* (S.Hatt.) S.Hatt., *J. Hattori Bot. Lab.* 39: 297 (1975). *Frullania nobilis* Steph. var. *intermedia* S.Hatt., *J. Hattori Bot. Lab.* 37: 116 (1973). *Type:* New Guinea: Wau Distr., *R.M. Schuster 67–5879* (holotype: NICH; isotypes: MASS, JE).

Etymology. *ornithocephala* is from the Greek ὄρνις (*ornis*) = bird and κεφαλος (*kephalos*) = head, referring to the bird-head shaped lobule.

Illustrations. S.Hattori, *J. Hattori Bot. Lab.* 37: 116–119, figs. 64–66 (1973); T.Pócs, *Acta Biol. Pl. Agriensis* 12(1): 31, fig. 17 (2024).

Description. Large sized, dark green, in herbarium ochre-brown, pendulous, usually hanging from tree branches. Shoots 4–20 cm long, 1.5–2.0 mm wide, remotely pinnate, branches widely spreading. Stem 120–200 µm thick, rusty to dark brown. Leaves contiguous to imbricate, obliquely spreading. Lobe suborbicular, 1.0–1.6 mm long and 0.8–1.5 mm wide with rounded, incurved apex. Dorsal base auriculate with circular or triangular appendage incurved or exceeding the stem. Lobe marginal cells quadrangular, 12 × 20 µm, with nodulose trigones and intermediate thickenings, median cells similar or with flexuose walls and confluent trigones, 25–60 × 20–35 µm, as the basal cells. Stylus lanceolate, 4–5 cells long, formed by one or two rows. Lobules asymmetric helmet shaped, relatively small, only a quarter of the lobe length, descending well below the lobe margin, with acute beak turning towards the stem. Lobule cells smaller than lobe cells, 14–22 × 8–12 µm, with nodulose trigones and intermediate thickenings. Underleaves imbricate to contiguous, wider than long (5–6 stem width), near the size of lobules, 580–640 × 880–960 µm, reniform, almost flat, with entire, round to barely retuse apex and auriculate bases.

Dioicous. The Australian and other specimens of var. *intermedia* are known only in sterile state. *Frullania ornithocephala* var. *ornithocephala*, according to Hattori (1973), has gynoecea terminal or on branches, perichaetial leaves in 2–3 whorls. The innermost bract shortly acute to obtuse, lobule 1/2 connate. Bracteole 1/2 bifid with acute-acuminate lobe apex, recurved and dentate at margins. Perianth shortly exerted, oblong, smooth, 3-keeled with indistinct ventral keel. (Figs 14, 15)

Diagnostic features. Among the Australian *Frullania* subgen. *Trachycolea* taxa this species is unique by its entire, unlobed, reniform underleaves, but in tropical and subtropical Asia there are several similar species, including *F. sabahana* S.Hatt., *F. sarawakensis* S.Hatt., and *F. cochleata* Steph. *Frullania ornithocephala* itself is a very variable plant (Hattori 1982; Hattori and Piippo 1986, as *F. nobilis*).

Biostatus. Native.

Habitat: Usually hanging epiphyte on branches of trees and treelets in notophyll vine-fern forest in the wet tropics. In Australia it occurs at an elevation between 880 m and 1240 m.

Distribution: The species is quite widespread in Indomalaysia from Sumatra to New Guinea (Hattori 1974), but *Frullania ornithocephala* var. *intermedia* hitherto known only from New Guinea and from three localities in Australia (Pócs 2024). From Queensland there is one record of *Frullania pauciramea* Steph. (Bolin and Henderson 2002: 223, but not mentioned in Windolf 1987), which differs by its underleaves with a shallow notch. This taxon was later distinguished as *Frullania nobilis* Steph. subsp. *pauciramea* S.Hatt. but finally became a synonym of *F. ornithocephala* var. *ornithocephala*. It is questionable whether this old record is really var. *ornithocephala* or belongs to var. *intermedia*.

Representative specimens: Qld: Track to Mt Finnigan Range, Cedar Bay National Park, 39 km S of Cooktown. 15°49'S, 145°16'E, at 880 m, rainforest on steep slope with large rock outcrops, on shaded treelet, *H. Streimann 57115A, 57120* (CANB); Lamb Range, near Mt Haig, 20 km SE of Mareeba, 17°05'S, 145°35'E, at 1100 m elevation, tropical forest on moderate slope, on shaded treelet stem, *H. Streimann 57656A* (CANB).

13. *Frullania pycnantha* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, *Syn. Hepatic.* 3: 411 (1845). *Jungermannia pycnantha* Hook.f. & Taylor, *London J. Bot.* 3: 566 (1844). *Type:* New Zealand (?BM).

Etymology. *pycnantha* is from the Greek πυκνός (*pyknos*) = dense and ἄνθος (*anthos*) = flower, referring probably to the densely spinose perianth.

Illustration. S.Hattori, *J. Hattori Bot. Lab.* 54: 162, fig. 64 (1983).

Description. Small to medium size, in herbarium olive green to dark brown. Shoots 2–4 cm long, main shoots 0.6–0.7 mm wide, remotely bipinnate with widely spreading long side branches. Stem 120–150 µm thick, greenish brown. Leaves contiguous to imbricate, always strongly squarrose with incurved ventral and recurved dorsal margins, semi-convolute and ± rolled around the stem when dry. Lobe ovate with rounded apex, 0.45 mm long and wide. Dorsal and ventral bases auriculate with triangular appendages. Lobe marginal cells quadrangular, 10 × 12 µm, median cells with nodulose trigones and intermediate thickenings or with flexuose walls and confluent trigones, 20–30 × 12–18 µm, the basal cells are larger, suborbicular with 25–38 µm diameter. Stylus filiform, composed of 4–5 uniseriate cells. Lobules asymmetric galeate, rostrate, large, bending down and towards the stem, well below the lobe margin. Lobule cells somewhat smaller than lobe cells, 20 × 12 µm, with thinner cell walls. Underleaves contiguous to remote, orbicular (3–4 stem width), 0.3–0.4 mm wide, bilobed 1/3–1/4 deep, V-shaped incision and auriculate bases.

Dioicous. The gynoecea terminal on short side branches, perichaetial leaves larger than normal ones, in 3 whorls. The innermost bract lobe 0.9 mm long, oblong-ovate with subacute apex. Lobules 1/2 or less connate. Bracteole 1/3 bifid with narrowly triangular to acuminate apex, irregularly dentate at margins.

Perianth exserted, obpyriform, 1.5–1.7 mm long, 3 keeled, spinose, densely covered by multicellular outgrowth at the base and becoming sparse towards the apex. Beak relatively large.

Androecia lateral on stems or branches, spicate with 4–10 pairs of bracts. Usually with two bracteoles at the base of spike. Both bracts and bracteoles have spinose-ciliate margins. (Fig. 16)

Diagnostic features. The squarrose leaves are shared by morphologically similar species such as *F. ericoides* (Nees) Mont., which also has spinose-tuberculate perianths. However, it can be immediately distinguished from that species by 1) the dorsal view of perianth surface almost absent of outgrowths

except on lateral keels, the ventral view of perianth surface sparsely covered with tubercles or more scalelike outgrowths than *F. pycnantha*, particularly the ventral and 2 lateral keels; 2) *F. pycnantha* has rostrate lobules extending well below the ventral lobe margin, while *F. ericoides* has helmet like lobules not prolonged into a rostrum and not exceeding beyond the ventral lobe margin.

The third Australian species with squarrose leaves, *F. squarrosula* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees has smooth perianth and small lobules covered by the underleaves.

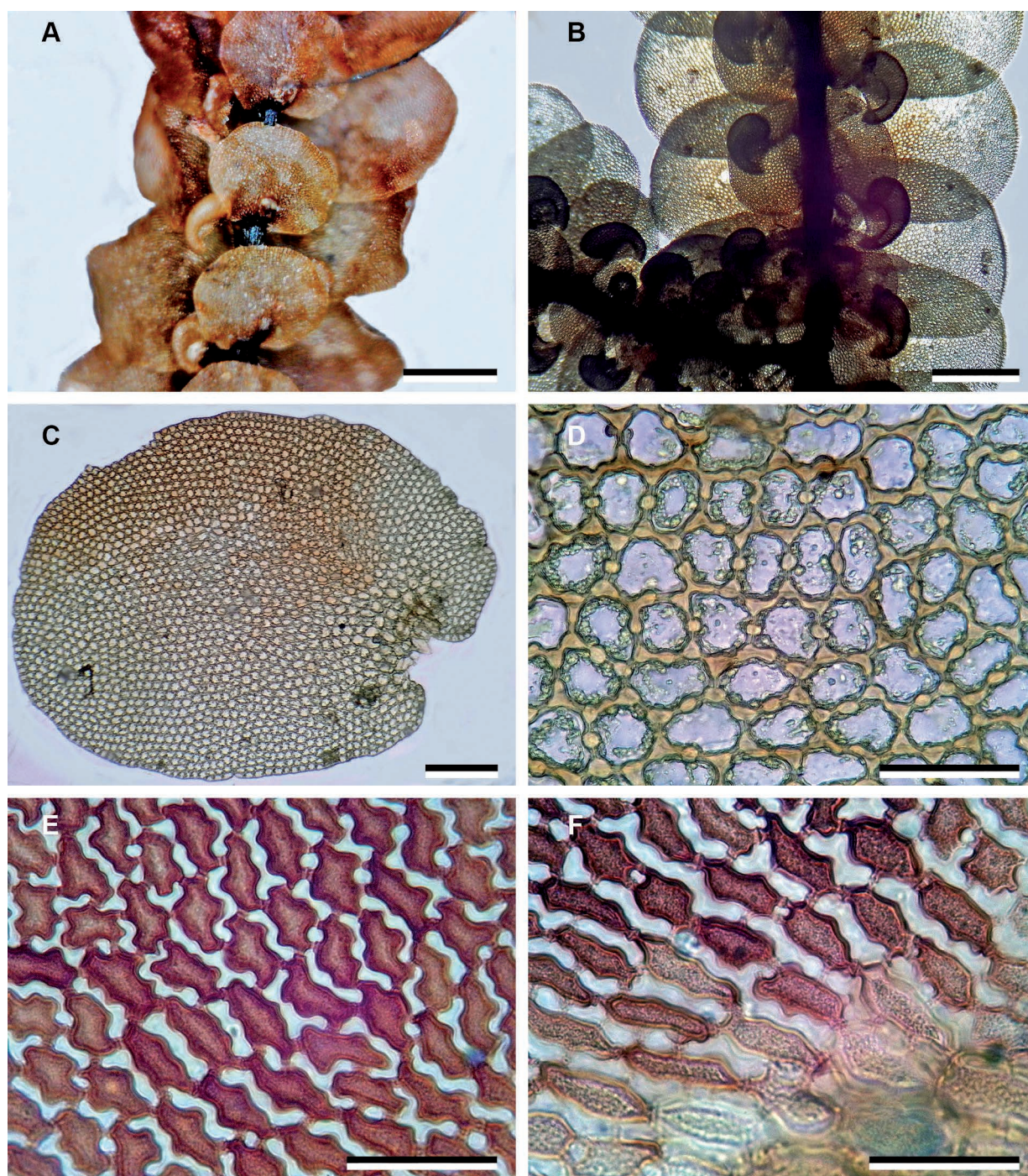


Figure 14. *Frullania ornithocephala* (Reinw., Blume & Nees) Nees var. *intermedia* (S.Hatt.) S.Hatt. A, B: Habit, ventral view. C: Lobe. D: Lobe cells near the margin. E: Median lobe cells. F: Basal lobe cells. Photographed by T.Pócs from *H. Streimann 57115/A* (CANB) and from *S. and T. Pócs 01085/B*. Scale bars: A, B = 500 μ m; C = 100 μ m; D–F = 50 μ m.

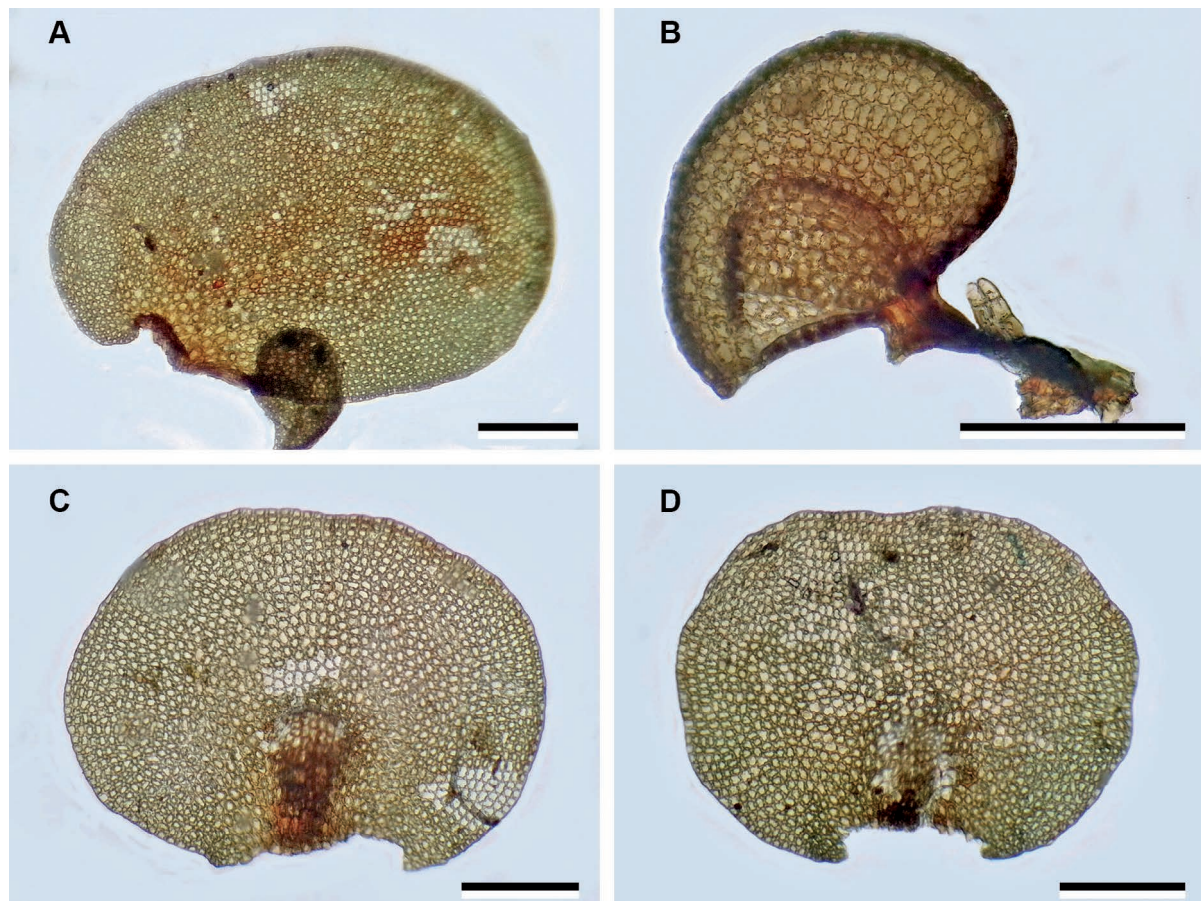


Figure 15. *Frullania ornithocephala* (Reinw., Blume & Nees) Nees var. *intermedia* (S.Hatt.) S.Hatt. A: Leaf with lobule, dorsal view. B: Lobule with style, ventral view. C: Underleaf with entire, round apex. D: Underleaf with slightly retuse apex. Photographed by T.Pócs from *H.Streimann* 57115/A (CANB) and from *S. and T. Pócs* 01085/B. Scale bars: All = 250 μ m.

Biostatus. Native.

Habitat. According to the Australian records it occurs between 150 and 700 m elevations, on rocks and rarely on bark in *Eucalyptus* dominated woodlands and in stunted monsoon forests.

Distribution. It occurs in northern and eastern Australia including Tasmania, Norfolk Island and in New Zealand (Hattori 1983, McCarthy 2003, Renner et al. 2024).

Representative specimens. N.T.: Darwin and Gulf, Headwaters of South Alligator River, 91 km E of Pine Creek township. *L.G.Adams and M.Lazarides* 3065 (CANB 251262.1). Qld: Crediton State Forest, 16 km SW of Finch Hatton, 700 m, *J.A.Curnow* 1214 (CANB 9909218). N.S.W.: Gannons Creek, 11 km SW of Wauchope, 150 m, *H.Streimann* 5959 (CANB 7811571). A.C.T.: N face of Molonglo Gorge, *N.T.Burbidge* 7139 (CANB 97356, H, NICH, NY).

14. *Frullania queenslandica* Steph., *Sp. Hepatic.* 4: 424 (1910). *Type:* Queensland: ex Herb. Brotherus 27 (syntype: G 18226); sine coll. et loc. (syntype: H).

Etymology. Named after its type locality in Queensland.

Illustrations. S.Hattori, *J. Hattori Bot. Lab.* 46: 140, fig. 40 (1979b).

Description. *Frullania queenslandica* is a relatively large species, with shoots up to 6 mm length and 0.8–1.6 mm width. In herbarium

from olive green to pale or dark brown, irregularly pinnate, with obliquely or almost perpendicular branches as wide as the main shoot. Stem 200–250 μ m thick, yellowish green. Leaves densely imbricate, widely spreading, dorsally usually reaching the opposite stem edge. Lobes ovate subtriangular to orbicular with narrowly recurved margins and cordate, strongly appendiculate bases, 0.9–1.1 mm long and wide. Marginal cells quadrangular, 18–20 \times 12–15 μ m, median hexagonal, 22–24 μ m, while the basal cells more elongate, up to 40 μ m length and 25 μ m width. Cell walls with medium to large trigones and intermediate thickenings, basal cells often with confluent trigones. Lobule small compared to the lobe, galeate, incurved with truncate beak, not reaching the ventral lobe margin. Stylus large, triangular, 3–4 cells at base, 4–5 cells high, acute, tipped by a hyaline papilla. Underleaves contiguous, 0.5–0.75 mm long and 0.8–0.96 mm wide, with very wide U- or V-shaped incision, smooth margins, strongly convex rhizoid initial area, hyaline, parallel rhizoids.

Dioicous, only sterile and female plants are known. Female bracts acute with acute lobules. Bracteole free, also with acute lobes. Perianth elongate pyriform, 3/4 exserted, tricarinate with shortly spinose keels and relatively large beak. (Fig. 17)

Diagnostic features. The cordate base with strongly developed basal appendages of leaf lobes, the strongly asymmetric, small, incurved lobule, the very wide underleaf incision and small, bulging rhizoid initial area distinguish this species from similar Australian taxa (Hattori 1979b).

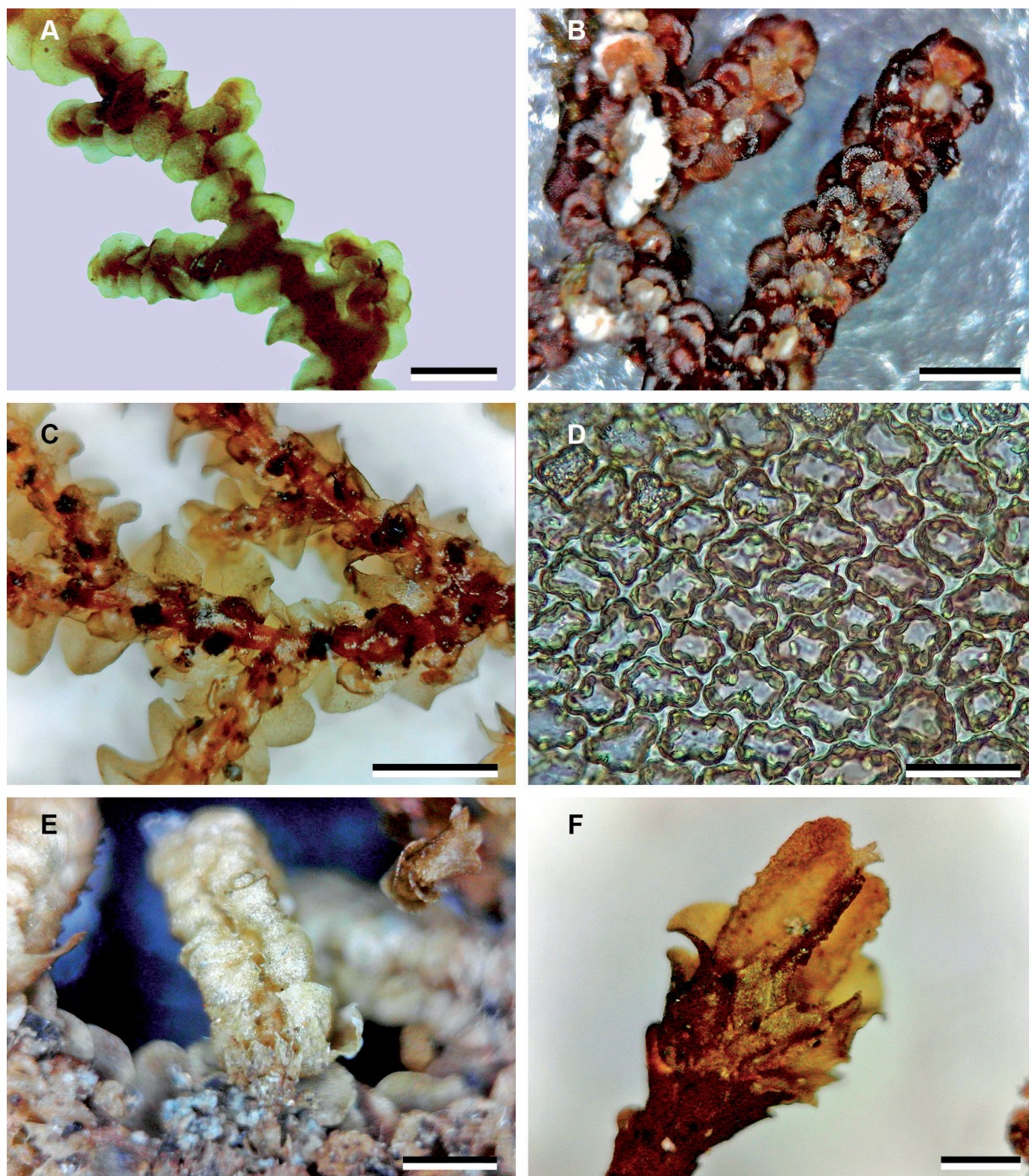


Figure 16. *Frullania pycnantha* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees. A: Habit, dorsal view. B, C: Habit, ventral view. D: Median lobe cells. E: Androecium. F: Gynoecium. Photographed by T.Pócs from J.A.Curnow 1214 (CANB) and from N.T.Burbidge 7139 (CANB). Scale bars: A–C, E, F = 500 µm; D = 50 µm.

Biostatus. Native.

Habitat. Inhabits bark or rock surfaces in semidry sclerophyllous forests and rainforests at 350–1000 m elevation.

Distribution. It was considered to be a Queensland endemic (Stephani 1910; McCarthy 2003) but became known also from the southern part of New South Wales (AVH 2025) and from Victoria (VicFlora, 2024).

Representative specimens. Qld.: Wongabel State Forest, Scrubby Creek, 5 km SSE of Atherton, 17°18'S, 145°30'E, 800 m elev., *H.Streimann* 27024 (CANB 8302775); Hugh Nelson Range, The Crater National Park, Mt Hypipamee, Barron River valley,

at 920–1050 m elev., 17°26'S, 145°29'E, *S. and T.Pócs* 01080/A (BRI, EGR, NSW). N.S.W.: Tianjara Falls, Tianjara Creek, 30 km NW of Ulladulla, 35°08'S, 150°20'E, 350 m elev., *H.Streimann* 7818 (CANB, JE).

15. *Frullania rubella* Gottsche ex Steph., *Hedwigia* 28: 159 (1889). *Type:* Queensland: Toowoomba, *Hartmann* 66 (G18227).

Frullania elongata Steph., *Sp. Hepatic.* 4: 423 (1910), *nom. illeg., non* (Lehm. & Lindenb.) Gott. in Gott. et al. 428 (1845). *Type:* New South Wales: Richmond River, Pearce's Creek *W.W.Watts in Hb. Levier* (G18203).

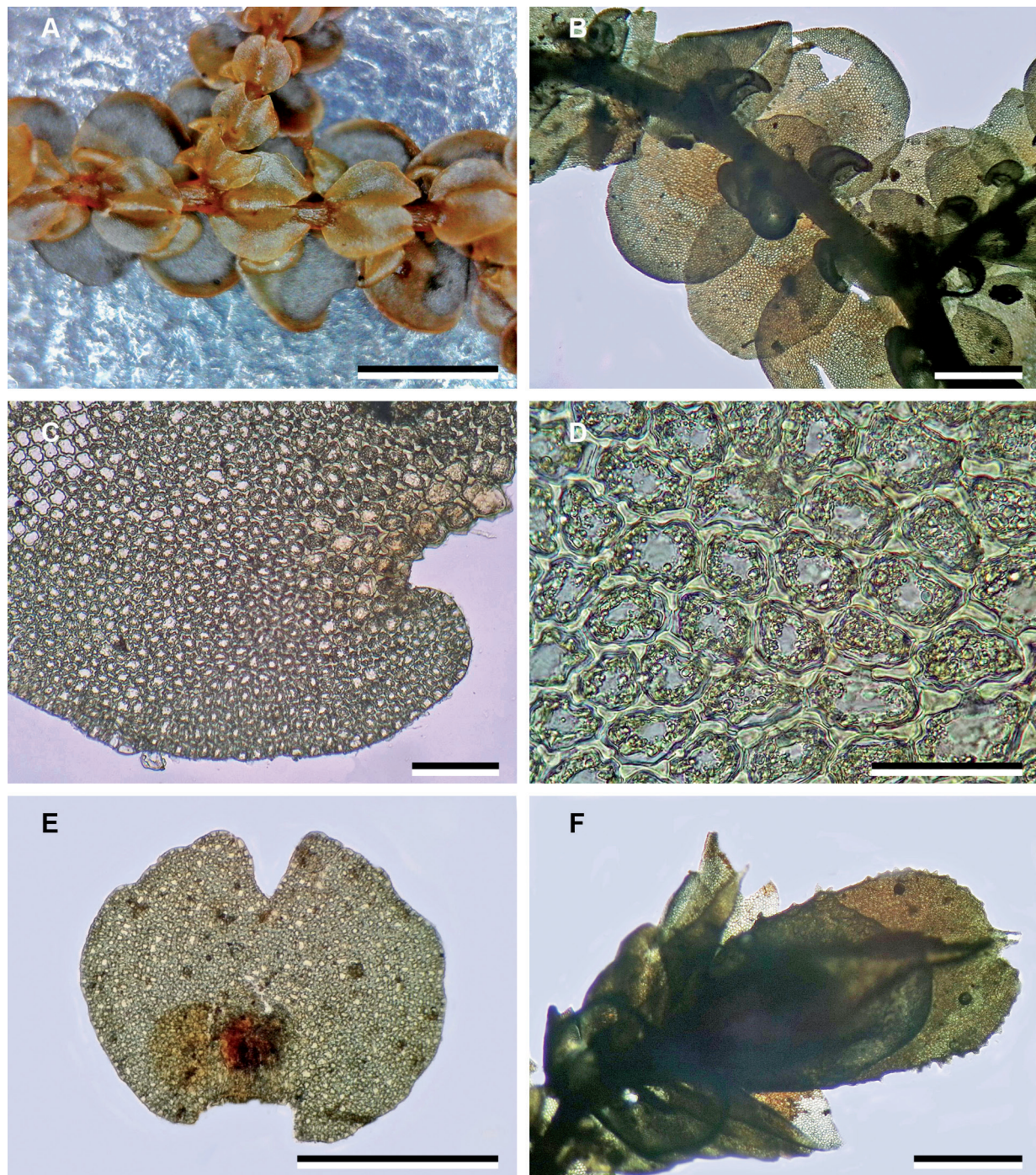


Figure 17. *Frullania queenslandica* Steph. A, B: Habit, ventral view. C: Lobe, basal auricle. D: Median lobe cells. E: Underleaf. F: Female perichaetium. Photographed by T.Pócs from H.Streimann 27024 and 7818. Scale bars: A = 1 mm; B, E, F = 500 µm; C = 100 µm; D = 50 µm.

Frullania filipendula Steph., *Sp. Hepatic.* 4: 419 (1910). Type: New South Wales: East Ballina, W.W.Watts 418 in *Hb. Levier* (G18212).

Uncertain new synonyms: ?*Frullania flexuosa* S.Hatt., *J. Hattori Bot. Lab.* 54: 146 (1983). Type: Queensland: Rockhampton, *coll. ign.* (holotype: L; isotype: NICH).

?*Frullania schusteri* S.Hatt., *Beih. Nova Hedwigia* 90: 147–158 (1988). Type: B.Thiers and R.E.Halling 2825 (holotype: NICH; isotypes: AD, NY).

Etymology. From Latin *rubellus* = reddish, referring to the partial reddish coloration of fresh plants.

Illustrations. S.Hattori, *J. Hattori Bot. Lab.* 45: 354, fig. 22; 334: fig. 8, as *F. elongata*; 340, fig. 12 as *F. filipendula* (1979a); S.Hattori, *J. Hattori Bot. Lab.* 54: 147, fig. 56, as *F. flexuosa* (1983).

Description. Plants small size, pale green with ± reddish or pinkish colouration when fresh, in herbarium mostly rusty brown. Shortly and remotely pinnately branched, shoots 1–3 cm long and 0.8–1.2 mm wide, branches widely spreading. Stem olive green to dark reddish brown, 0.10–0.14 mm thick. First branch appendage with one bilobed ventral segment, and one saccate dorsal segment. Leaves imbricate, when wet, widely or obliquely spreading, in dry state convolute. Lobe orbicular ovate, 0.55–0.61 mm long and 0.51–0.60 mm wide, strongly concave, with rounded apex. Both dorsal and ventral bases with semicircular

appendices, dorsally well exceeding the stem. Marginal lobe cells near quadrangular, $18\text{--}20 \times 12\text{--}18 \mu\text{m}$, median lobe cells $20\text{--}30 \times 11\text{--}20 \mu\text{m}$, somewhat elongate with sub-nodulose, confluent trigones. Basal lobe cells $30\text{--}50 \times 20\text{--}30 \mu\text{m}$, with nodulose and here and there confluent trigones.

Leaf lobules small compared to the lobes, 0.3 mm long, cucullate, asymmetric helmet shape or sometimes explanate. The obtuse beak never exceeds the ventral lobe margin. Cell walls sinuose, similar to those of the median lobe. Stylus minute, filiform. Underleaves contiguous or distant, obovate, with narrowly decurved margin, relatively small, 0.3 mm long and wide, only $1.5\text{--}2 \times$ stem width, with U- or V-shaped incision 1/4 deep of underleaf length. Base cuneate with sub-transverse insertion. Rhizoid initial area weakly developed, convex, with fasciculate rhizoid bundles. Asexual reproduction not known.

Dioicous. Androecia on short lateral branches, button shaped or ellipsoid, consisting of 3–4 pairs of male bracts. Gynoecial branches short, usually lateral. Perichaetial leaves in three whorls. The innermost bract lobe oblong ovate with obtuse or subacute apex and with a few marginal teeth. The bracteole 2/5 bifid, with apiculate, often pilose apex. Perianth semi-exserted, obovate pyriform, 1.5 mm long and 0.75 mm wide, tri-lobate sometimes with additional keels, surface with scattered short tuberculose outgrowths. Apex retuse with large beak. (Fig. 18)

Diagnostic features. The relatively small, helmet shape lobules, small, entire sided underleaves not wider than 2 stem width and the reddish tinge on fresh plants.

Biostatus. Native.

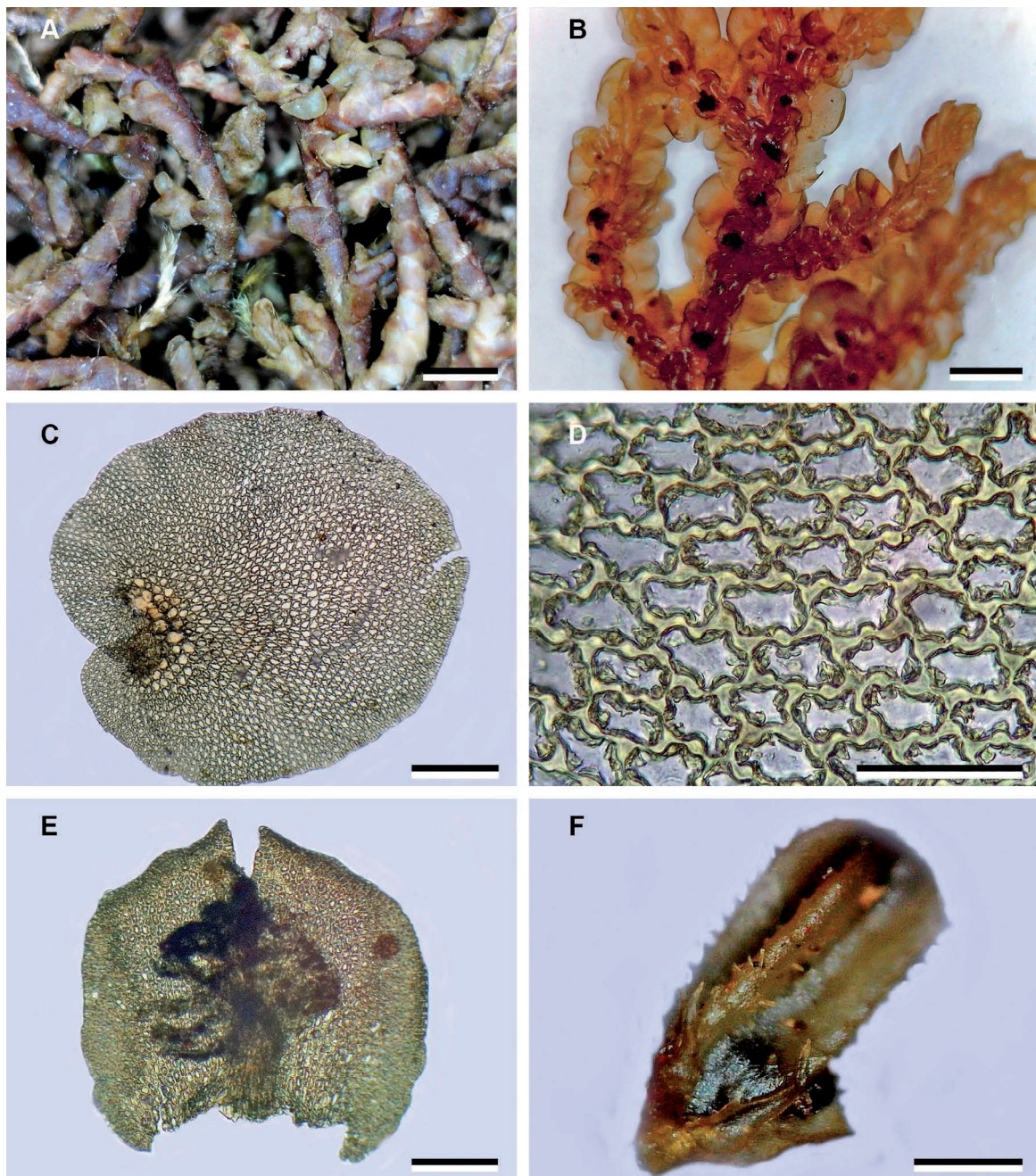


Figure 18. *Frullania rubella* Gottsche ex Steph. A: Fresh shoots in dry state, dorsal view. B: Old specimen in wet state, ventral view. C: Lobe, dorsal view. D: Median lobe cells. E: Underleaf, ventral view. F: Female perichaetium. Photographed by T. Pócs from H. Streimann 60802 and 27695. Scale bars: A, B = 1 mm; C, E = 100 μm; D = 50 μm; F = 500 μm.

Habitat. Forms small, dense patches or continuous wefts on tree or treelet bark, sometimes also on rock, boulders and cliffs between sea level and 1250 m elevation. More common at low elevation, in all kinds of forests, woodlands and solitary trees.

Distribution. Endemic, restricted to the eastern coast of Australia from northern Queensland to New South Wales (Batemans Bay) and occurs also in Victoria near Dargo.

Representative specimens. Qld.: Boonjie State Forest, 22 km SE of Yungaburra, *H.Streimann* 27572 (CANB); Yungaburra Road, 2 km SE of Atherton, *H.Streimann* 16847 (CANB); Springbrook, Purling Brook Falls, 23 km SSW of Nerang, *H.Streimann* 43514 (CANB); Border Ranges, Lions Road, 30 km WNW of Kyogle, *H.Streimann* 60862 (CANB). Vic.: Crooked River Road 12 km NNW of Dargo, *H.Streimann* 53120 (CANB), new record to the state of Victoria.

16. *Frullania scandens* Mont., *Ann. Sci. Nat., Bot. (ser. 2)* 19: 258 (1843). *Type:* New Zealand: Auckland Island, *Hombron & Jacquinot* (?holotype: PC; isotype: G 18489, ex Hb. Montagne).

Etymology. *scandens* from Latin, means climbing, referring to the type specimen creeping around a twig.

Illustrations. S.Hattori, *J. Hattori Bot. Lab.* 84: 167, fig. 65 (1983).

Description. Plants medium to large, reddish-brown in herbarium. Shoots 3–4 cm long, 1.2–1.9 mm wide, irregular pinnately branched. Stem deep brown, 0.18 mm thick. Stem leaves imbricate, widely spreading. Lobes reniform 1.1–1.2 × 1.2–1.4 mm, concave with rounded and involute apex and arched (non-appendiculate) dorsal base which extends 1–2 stem width beyond the stem. Marginal cells subquadrate, 15–18 × 12–15 µm, median cells sub-isodiametric, 22–25 × 17–20 µm and the basal ones 30–60 × 23–27 µm. Cell walls ± evenly thickened with small trigones except the basal ones with nodulose or confluent trigones. Lobules inflated, asymmetric falcate, contiguous to the stem, 1/2–2/3 of lobe length, up to 0.9 mm, with well-developed beak exceeding the ventral lobe margin. Stylus minute, filiform, in a row of 4–5 cells. Underleaves flat, wide orbicular, about 5× stem width, with a small V-shaped incision about 1/8 depth.

Dioicous. Gynoecia terminal, female perichaetia formed by 3 whorls. Innermost bracts ca. 2 mm long with ½ connate, piliferous lobules. Bracteole connate on both sides with the lobules, acute lanceolate, piliferous. Perianth flat, dorsiventrally appressed, ventrally concave with thin but distinct beak.

Diagnostic features. The flat perianth combined with in average 1.5 mm wide shoot and large, inflated falcate lobules of 1/2–2/3 lobe length.

Biostatus. Native.

Habitat. Eucalypt and other forest types between the sea level and 1250 m elevation.

Distribution. In Australia rare in New South Wales and Victoria, more common in Tasmania, widespread in New Zealand and its neighbouring islands (AVH 2025).

Representative specimens. TAS.: Kentish Municipality, above Lake Barrington near Forth Falls, *D.H.Norris* 27293 (F); Hobart

Municipality, trail from Fern Tree to Silver Falls, *D.H.Norris* 29244 (F); Esperance Municipality, seaward slope near Coal Bluff, *D.H.Norris* 30258 (F).

17. *Frullania scottiana* S.Hatt., *Mem. New York Bot. Gard.* 45: 551 (1987). *Type:* Queensland: Cardwell, Kirrama State Forest, 31 Aug. 1985, *G.A.M.Scott* s.n. (holotype: NICH 402268; isotype: MUCV 6952).

Etymology. Named after its first collector, the Australian bryologist, George Anderson MacDonald Scott (1933–1998) (Encyclopaedia of Australian Science and Innovation, 2024).

Illustration. S.Hattori, *Mem. New York Bot. Gard.* 45: 551, fig. 5 (1987).

Description. Plants small, olive green to dark rusty brown, with silky shine. Shortly irregularly branched, shoots 1.0–1.5 cm long and 0.8–1.0 mm wide, branches widely spreading. Stem olive green to dark reddish brown, 0.8–1.2 mm thick. First branch appendage with one bilobed ventral and one saccate dorsal segment. Leaves loosely imbricate or contiguous, widely spreading, extending beyond the stem up to its 1/2 width. Lobe ovate, 0.55–0.61 mm long and 0.45–0.51 mm wide, flat, with rounded apex. Dorsal base arched but never auriculate or appendiculate. Marginal cells 12–15 µm, median cells 18–25 × 12–15 µm, the basal ones 25–35 × 20–22 µm with relative thin, reddish brown walls with hyaline trigones. Intermediate thickenings rare. Lobules asymmetric helmet shaped, relatively large, with obtuse or subtruncate apex exceeding the postical lobe margin. Towards the stem or branch base, smaller and often explanate. Stylus minute, filiform. Underleaves obovate or obcuneate, 0.25–0.50 mm long and not wider than 1.5–2.5× stem width, usually with 1 or 2 marginal teeth near the apex. Incision 1/3–3/5 deep, lobes apiculate-acute. Insertion transverse. Rhizoid initial area near the base, hyaline rhizoids in one bundle.

Dioicous. Androecia terminal or lateral on 1–2 reduced leaved branches, globose, with 2–4 pairs of bracts. Gynoecium terminal often with innovation. Female bracts in 3 pairs, up to 1.6 mm long, acute, with a few short teeth. Innermost bracteole 0.8 mm long, 2/3 bifid with narrow, irregularly toothed and apically pilose lobes. Perianth 2/3 exerted, obpyriform 1.2–1.5 mm long with truncate apex, 2 lateral and 2 ventral keels. Sometimes 2 dorsal keels also develop. The keels are sharp, with dentate or paraphyllium like outgrowths. (Fig. 19)

Diagnostic features. The ovate, flat leaves with relatively large helmet shaped lobules, with a tendency to become smaller towards the stem or branch base, the small underleaves with large teeth at apical margins, the male branches with a few reduced leaves and the obpyriform, 4 sharp, dentate keeled perianth.

Biostatus. Native.

Habitat. It occurs on bark, twigs and on leaves of tropical rain forests, sometimes also on garden trees, between 600–840 m elevations.

Distribution. Seems to be endemic to the high rainfall areas of Queensland.

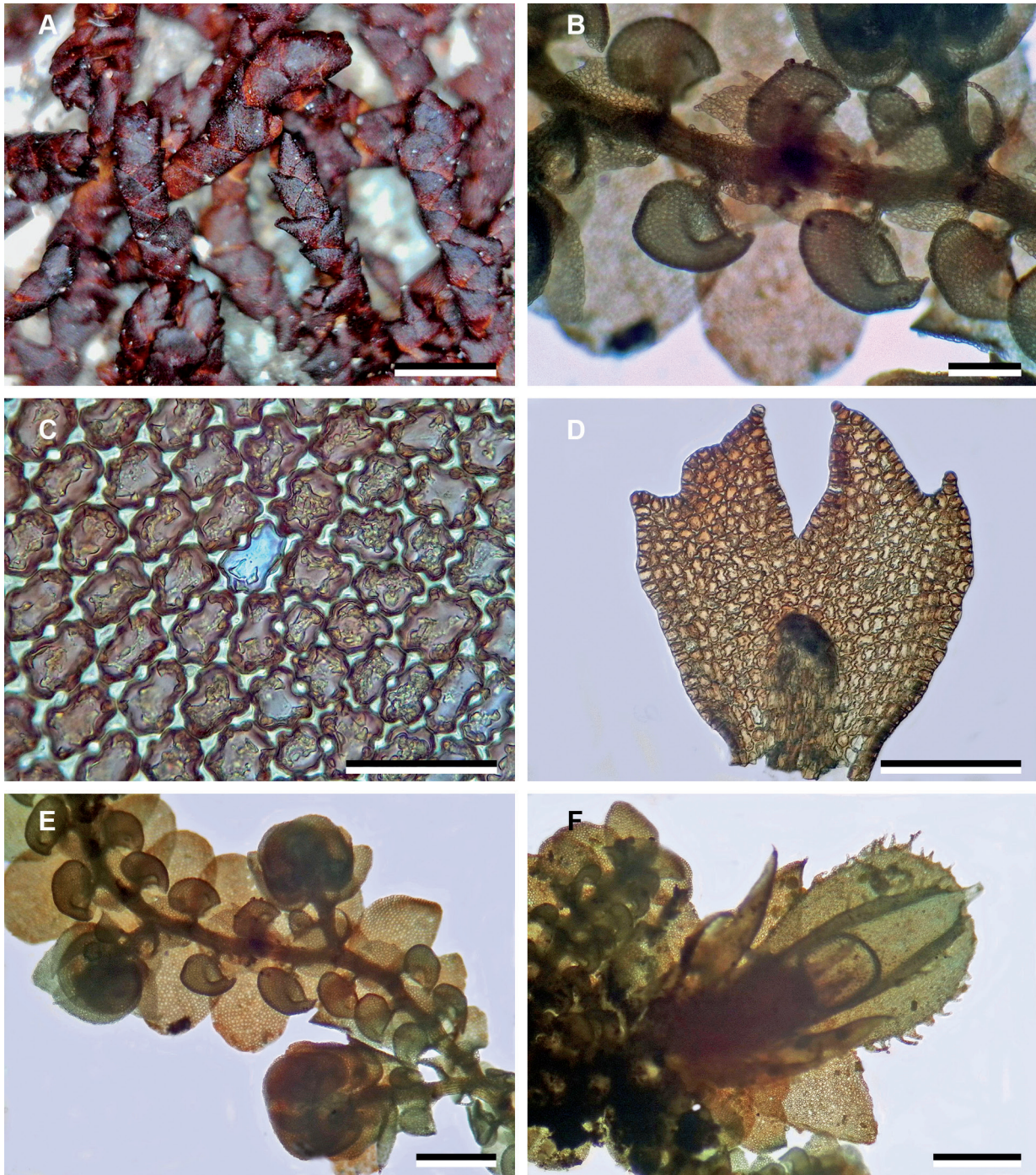


Figure 19. *Frullania scottiana* S.Hatt. A: Habit in dry state, dorsal view. B: Habit, ventral view. C: Median lobe cells. D: Underleaf, ventral view. E: Male branches, ventral view. F: Female branch, ventral view. Photographed by T.Pócs from J.A.Curnow 1190 and S.Pócs 01078/S. Scale bars: A = 1 mm; B, C = 100 µm; D = 50 µm; E, F = 500 µm.

Representative specimens. Qld.: Clarke Range, Crediton State Forest, 20 km SSW of Finch Hatton, sterile, therefore a bit uncertain identification, *J.Curnow* 1089 (CANB, H, NICH, NY); Atherton, Woodland Tourist Park, *S.Pócs* 01078/S (EGR). Before it was known only from the type and from an epiphyllous collection (Pócs and Streimann 1999, McCarthy 2003): Koombooloomba Dam Rd., 23 km SE of Ravenshoe, *H.Streimann* 28969 (CANB).

18. *Frullania seriata* Gottsche ex Steph., *Hedwigia* 28(3): 160 (1889). Type: Queensland. Toowoomba, *Hartmann* 28 (G 18228).

Frullania dietrichiana Steph., *Sp. Hepatic.* 4: 423 (1910). Type: Queensland. A.*Dietrich* 3612 (G 18207).

Frullania difficilis Steph., *Sp. Hepatic.* 4: 425 (1910). Type: New South Wales: Richmond River, Pearce's Creek, 1900, *W.W.Watts*, herb. *Levier* 2632 (G 18467).

Etymology. From the Latin *seriatus* = serial, because the perianths are arranged densely in rows, due to the repeated subfloral innovations on the same side.

Illustration. S.Hattori, *J. Hattori Bot. Lab.* 45: 355, fig. 23 (1979a); 332, fig. 7, as *F. dietrichiana*; S.Hattori, *J. Hattori Bot. Lab.* 46: 130, fig. 34 (1979b), as *F. difficilis*.

Description. Medium size, yellowish green to olive in fresh specimens, brownish in herbarium, sometimes reddish plants.

Shoots 10–25 mm long and 1.2–1.6 mm wide, uni- or bipinnately branching, often spreading in wide angle from the twig or thin branch substrate. Stem 0.18–0.22 mm thick, dark brown. Leaves imbricate, dorsally extending the stem about the distance of the stem width, embracing the stem when dry, obliquely to widely spreading in wet state. Lobes widely asymmetric ovate, 0.7–0.8 mm long and wide. Apex rounded, base gibbous, appendiculate on dorsal and semicircular on the ventral base or auriculate on both sides. Marginal cells subquadrate, with flexuose walls, 10–15 μm size. Median cells 22–26 \times 15–18 μm , the basal ones 40–50 \times 20–30 μm , with large, often confluent trigones. Lobules helmet shaped, 130–170 \times 100–110 μm , as seen from the ventral side, but flattened almost 200 μm wide. Lobule cells much smaller than the lobe cells. Underleaves cuneate with 1/3–2/5 deep, U-shaped sinus and undulate-dentate, strongly recurved margins. Insertion moderately sinuate. Underleaf cells similar to the median lobe cells.

Dioicous, both sexes are common with proliferous gametoecia. Androecia regularly and densely developed on very short side branches, spicate with obtuse apex, consisting of 6–10 pairs of imbricate bracts. Gynoecia terminal on one sided subfloral innovations (helicoid monochasial cyme), becoming sometimes densely seriate, similarly to former *Taxilejeunea* (Spruce) Steph. species. Perichaetial leaves in 3 whorls. Innermost bracts 1.2 mm long, apiculate. Lobe 1/2 connate with attenuate apex. Bract lobe and bracteole with spinose-dentate to entire margins. Perianth semi-exserted, obpyriform, 1.5–2.2 mm long, with 3 principle and often several irregular additional keels or almost without them (former *Frullania difficilis* Steph.). The perianth keels and surface are decorated with scattered or dense triangular or spinose outgrows or the surface is smooth. Different specimens show high variability with all transitions in keel differentiation and appendages. (Figs 20, 21).

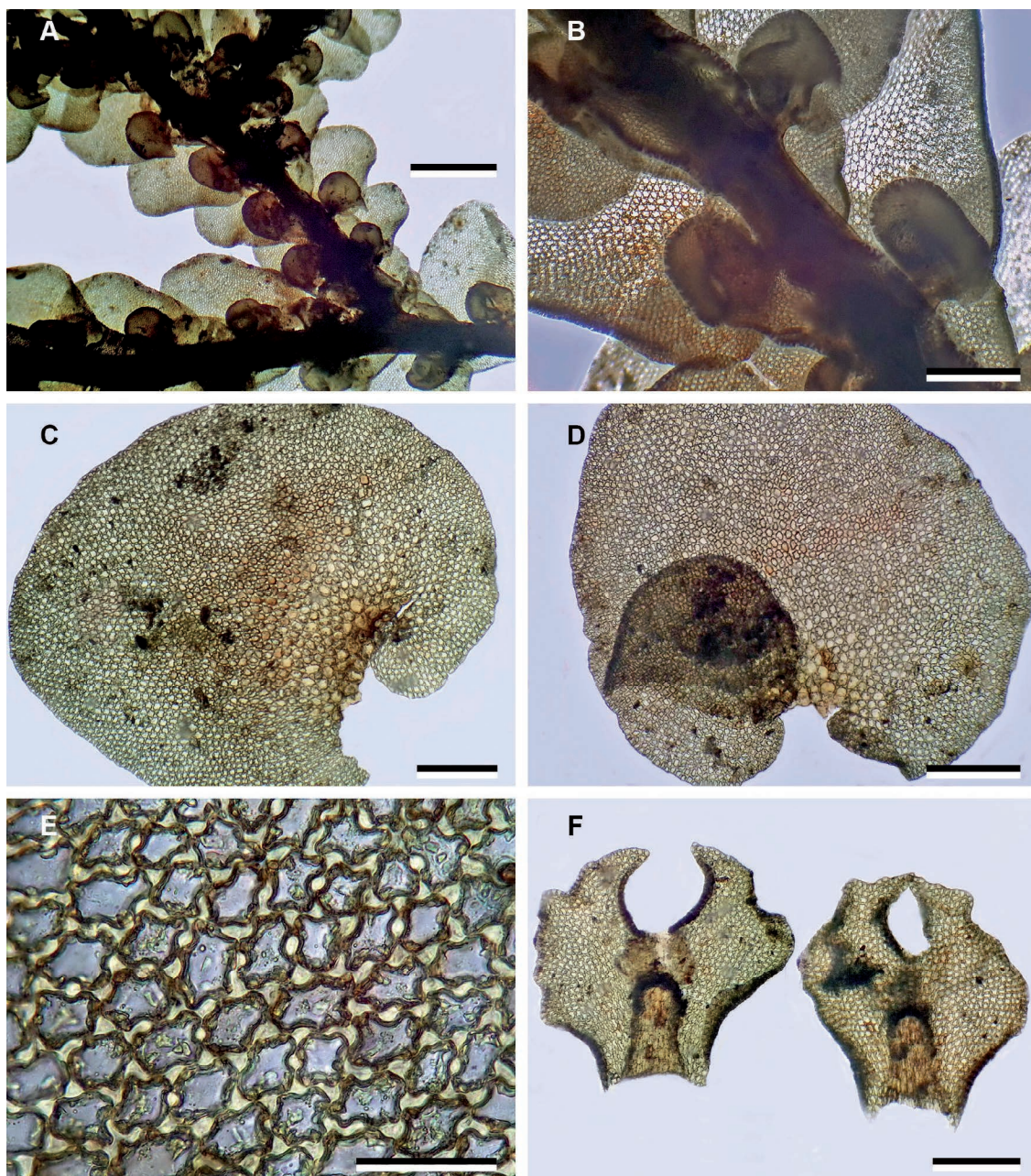


Figure 20. *Frullania seriata* Gottsche ex Steph. A: Habit, ventral view. B: Stem with lobules, ventral view. C: Lobe, ventral view. D: Leaf with lobule, ventral view. E: Median leaf cells. F: Underleaves. Photographed by T.Pócs from *H.Streimann* 6142 and *T.Pócs* 9977/F. Scale bars: A = 500 μm ; B–D, F = 200 μm ; E = 50 μm .

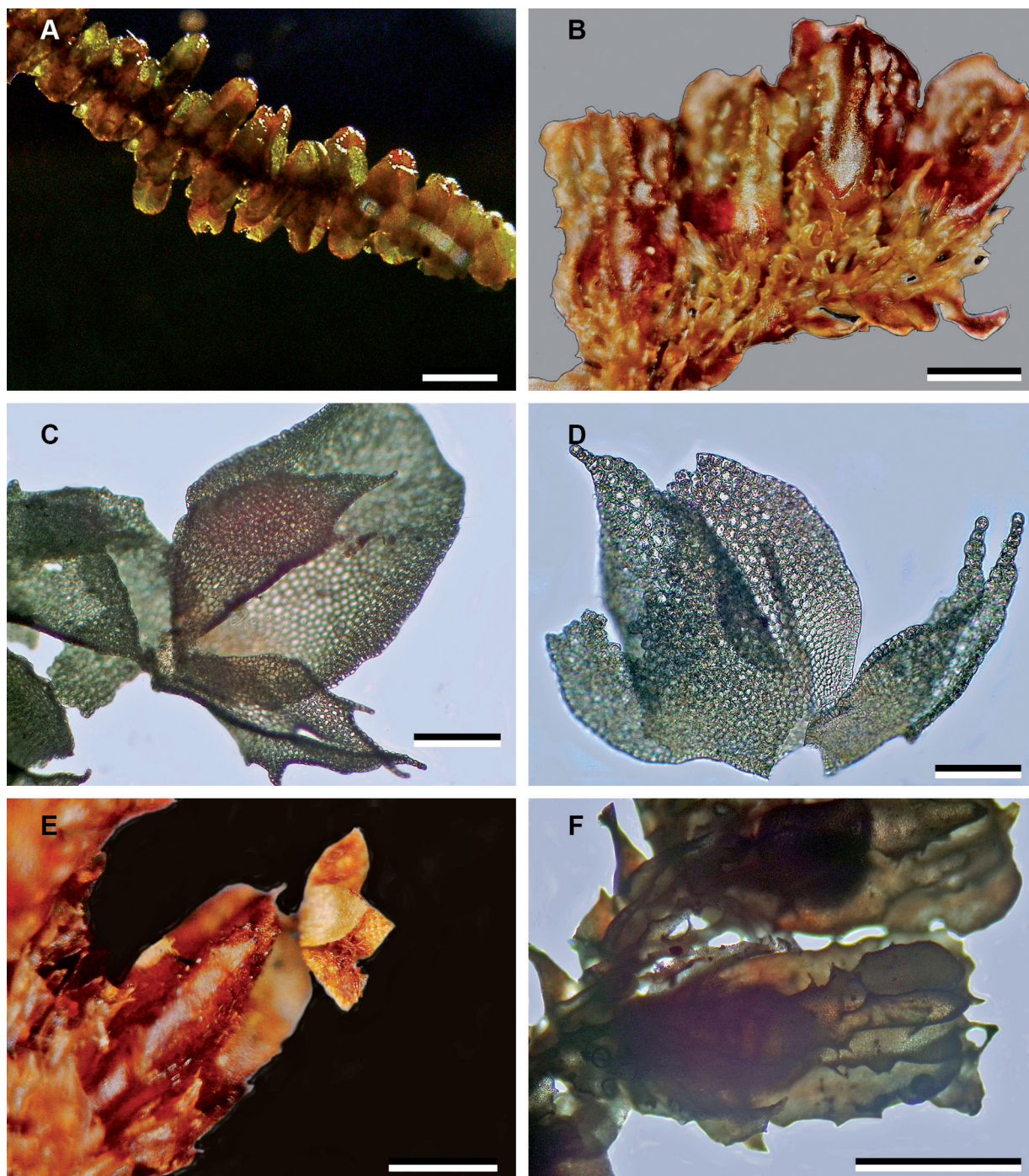


Figure 21. *Frullania seriata* Gottsche ex Steph. A: Male plant with androecia, dorsal view. B: Female plant with serial perianths, side view. C: Perichaetium with spinose bracteole. D: Perichaetium with smooth-margined bracteole. E: Perianth with mature sporophyte. F: Perianths, ventral view. Photographed by T.Pócs from *H.Streimann* 52308 and *T.Pócs* 9977/F. Scale bars: A, B, E, F = 1 mm; C, D = 100 μ m.

Diagnostic features. The cuneiform underleaves with undulate, dentate, strongly recurved margin and deep, $\bar{\cup}$ -shaped sinus, combined with seriate perianths with irregular keels distinguish *F. seriata* well from the other Australian *Trachycolea* species.

Biostatus. Native.

Habitat. Prefers twigs and treelet stems, spreading in wide angle from the substrate but also grows in wefts on bark of larger trees and on rocks. It inhabits different types of forests and other woody communities, including orchards and tree plantations in relatively high rainfall areas, from the sea level to 910 m elevation.

Distribution. It is an endemic of Queensland and New South Wales.

Representative specimens. Qld.: Black Mountain Road, 16 km NW of Kuranda, *H.Streimann* 31168 (CANB, JE. NICH, NY); Paluma Range, edge of Paluma Dam, 40 km S of Ingham, *T.Pócs* and *H.Streimann* 9977/AF (CANB, EGR); Capricorn Highway, 19 km ESE of Duaringa, *H.Streimann* 52308 (CANB). N.S.W.: Boatharbour Nature Reserve, the "Big Scrub" 7 km E of Lismore, *S. and T.Pócs*, *E.A.Brown* and *R.G.Coveny* (CANB, EGR, NSW); Richmond Range State Forest, Cambridge Walk, 34 km SW of Kyogle, *H.Streimann* 61420 (CANB, EGR); Wadbilliga National Park, Nelson Creek 14 km NE of Bomboka, *H.Streimann* 49234

(CANB), southern-most occurrence of the species at a latitude of 36°32'S.

19. *Frullania setchellii* Pearson, *Univ. California Publ. Bot.* 10(4): 326, pl. 102, figs 1–14 (1923). *Frullania falciloba* Lehm. var. *setchellii* (Pearson) E.A.Hodgson, *Trans. Roy. Soc. New Zealand* 77: 367 (1949). Type: New Zealand: Bush near Waiotapu, 1904, W.A. Setchell 159 (UC-213713).

Frullania engelii S.Hatt., *J. Hattori Bot. Lab.* 54: 143 (1983). Type: Tasmania: Florentine River, near Gordon River Road, E of S end of Lake Gordon, J.J. Engel 15080 (holotype: NICH; isotype: F).

Etymology. Named after its first collector, William Albert Setchell (1864–1943), professor at California University, Berkeley, who made large cryptogamic collections in the Pacific during early last century (Online Archive of California, 2025).

Illustrations. S.Hattori, *J. Hattori Bot. Lab.* 54: 144, fig. 55, as *F. engelii*; 169, fig. 66, as *F. setchellii* (1983).

Description. Small to medium sized, pale green or olive in fresh, pale yellowish to reddish or dark brown in herbarium. Shoots 2–4 cm long, 0.7–1.3 mm wide, irregularly pinnate, branches widely spreading. Stem blackish brown, 0.12–0.16 mm thick. First branch appendage with one bilobed ventral and one saccate dorsal segment. Leaves loosely contiguous to imbricate, widely spreading. Lobe concave with incurved, rounded apex, elliptical, sometimes slightly falcate, 0.7–0.8 × 0.6–0.7 mm. Base ventrally arched and dorsally, in most cases, strongly appendiculate, extending beyond the stem width. Cells at margin 10–18 × 8–15 µm, at middle 15–25 × 8–20 µm, at base 24–35 × 16–20 µm. The walls with trigones and intermediate thickenings, often bulging, confluent, making the cells flexuose. Lobules narrow falcate, rostrate, with elongate, truncate beak extending below ventral lobe margin. Stylus filiform, uniseriate part 4–6 cells long. Underleaves contiguous to slightly imbricate, nearly flat with smooth margin, V-, U- or ũ-shaped incision up to 1/4 depth, cuneate or auriculate base and sinuate insertion. Rhizoid initial area below middle, prominent.

Dioicous. Androecia lateral, on a stalk having only 2–3 leaves, spherical to spicate with 3–8 pairs of bracts. Bracteoles in the whole length of the androecium. Gynoecial branches short, consisting of 3–4 whorls of leaves. The innermost female bracts with obtuse apex, 1.0–1.2 mm long, lobule connate to 1/3 length, acute, laciniately toothed. Bracteole acutely bilobed with lacinate or denticulate margins. Perianth more than half exerted, obpyriform, 2.0–2.4 mm long, tri-late, spinose-tuberculate all over but more densely in its lower part and on the keels. These outgrowths are sometimes triangular, flat and paraphyllium like. Apex obtuse with a long beak. (Figs 22, 23)

Diagnostic features. The narrow, falcate lobules and spinose-tuberculate perianth distinguish it well from the related and much more widespread *F. falciloba* Lehm. with broader lobules and smooth perianth.

Biostatus. Native.

Habitat. Cool or warm temperate and subtropical rainforests, wet and dry sclerophyllous forests, shrublands, mostly at elevation

700–1350 m in mainland and down to sea level in Tasmania. Generally occurs on bark, sometimes on rocks (granite, dolerite).

Distribution. Eastern and southern Australia including Tasmania and New Zealand (McCarthy 2003; Renner et al. 2024).

Representative specimens. Qld.: Main Coast Range, SW slope of the summit of Mt Lewis W of Rumula, S. and T. Pócs 01085/B (EGR, NSW); Atherton Tableland, Cardwell Range, E slope of Mt Fischer 9 km NE of Ravenshoe, T. Pócs and H. Streimann 99114/O (CANB, EGR). N.S.W.: Northern Tablelands, Cattle Creek State Forest 12 km NNE of Dorrigo, D. Verdon 3847 (CANB, NICH); Dorrigo National Park, 8 km SE of Dorrigo, H. Streimann 47441 (CANB, JE, NICH); Barrington Tops State Forest, Moppy Lookout, H. Streimann 44445 (CANB). A.C.T.: Tower 2.5 km N of Orroral Tracking Station, 36 km SSW of Canberra, H. Streimann 39889 (CANB, H, NICH, PRE). Vic.: South Gippsland, Strelecki Range N of Thora, 2 km SSE of Gunyan Gunyah, T. Pócs and H. Streimann 99181/T (CANB, EGR). Tas.: Southwest National Park, W side of Mt Eliza towards the E coast of Lake Pedder, P.J. Dalton, S. and T. Pócs 0087/L (EGR); Maria Island National Park, on the summit of Bishop and Clark Peak, T. Pócs 0092/B (EGR).

20. *Frullania spinifera* Taylor, *London J. Bot.* 5: 407 (1846). Type: New Zealand: Auckland, Dr. Sinclair (BM ex hb. Hooker).

Etymology. *spinifera* is from the Latin *spiniferus* = spine bearing, spinose = referring probably to the elongate, piliform (many times explanate) lobules.

Illustration. S.Hattori, *J. Hattori Bot. Lab.* 54: 162, fig. 64 (1983); *Consortium of Bryophyte Herbaria* (2024).

Description. Small to medium size, olive green to dark brown. Shoots 2–4 cm long, main shoots 0.6–0.7 mm wide, remotely bipinnate with widely spreading long side branches. Stem 120–150 µm thick, greenish brown. Leaves contiguous to imbricate, even in dry state often and in wet always squarrose with strongly incurved ventral and strongly recurved dorsal margins. Lobe ovate with rounded apex, 0.45 mm long and wide. Dorsal and ventral bases auriculate with triangular appendages. Lobe marginal cells quadrangular, 10 × 12 µm, median cells with nodulose trigones and intermediate thickenings or with flexuose walls and confluent trigones, 20–30 × 12–18 µm, the basal cells are larger, suborbicular with 25–38 µm diameter. Stylus filiform, composed of 4–5 uniseriate cells. Lobules asymmetric rostrate, small, with piliferous apex, bending down and often reaching the ventral lobe margin. Underleaves contiguous, near orbicular (2–3 stem width), 0.55–0.65 mm wide, bilobed 1/3–1/4 deep, V-shaped incision and auriculate bases.

Dioicous. The gynoecia terminal on short side branches, perichaetial leaves larger than normal ones, in 3 whorls. The innermost bract lobe 1.3 mm long, oblong-ovate with subacute apex. Lobules 1 mm long, shortly connate. Bracteole 1/2 bifid with narrowly triangular to acuminate apex and narrow, slit like sinus, irregularly dentate at margins. Perianth exerted, inflated cylindric with subtruncate to retuse apex, 2.0–2.2 mm long, absolutely smooth. Beak short, 0.15 mm long.

Diagnostic features. Differs from all other Australian *Trachycolea* species by its absolutely smooth, inflated cylindric perianth.

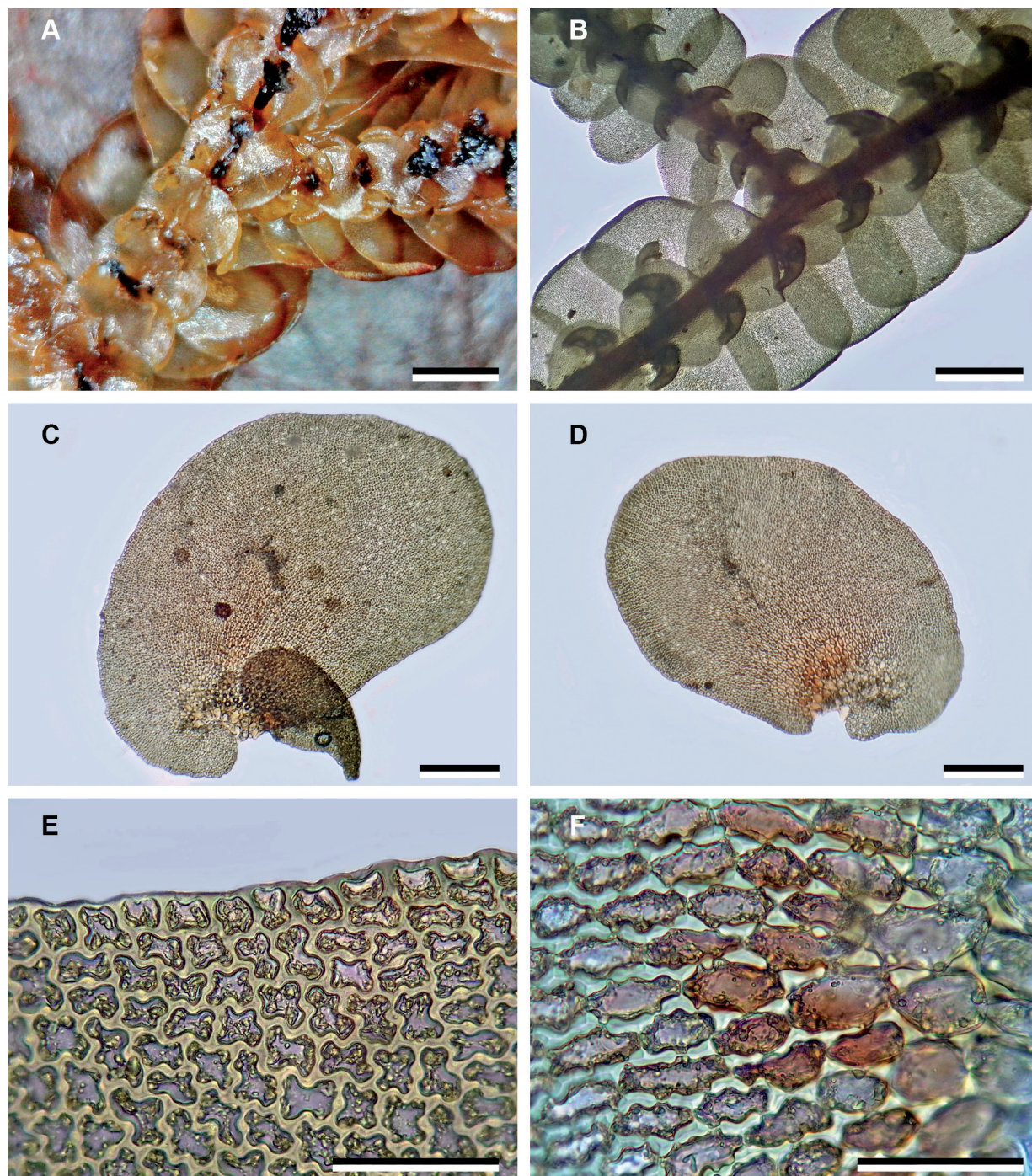


Figure 22. *Frullania setchellii* Pearson. A, B: Habit, ventral view. C: Leaf with lobule, dorsal view. D: Lobe, ventral view. E: Marginal and median lobe cells. F: Basal lobe cells. Photographed by T.Pócs from *H.Streimann* 44508, 4743 and from *Verdon* 3847. Scale bars: A, B = 500 µm; C, D = 100 µm; E, F = 50 µm.

Biostatus. Native.

Habitat. According to the Australian records it occurs in wet montane forests.

Distribution. It is rare in eastern Australia in Queensland and New South Wales, while widespread in New Zealand (Atlas of Living Australia 2025).

Representative herbarium specimen. NSW: Macquarie Pass, 28 km SW of Wollongong, *H.Streimann* 4805 (CBG 7707714; Renner et al. 2024).

21. *Frullania squarrosula* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees Syn. *Hepatic.* 3: 412 (1845). *Jungermannia squarrosula*

Hook.f. & Taylor, *London J. Bot.* 4: 88 (1845). Type: New Zealand: *sin. coll. et loc. speciali.*

Etymology. *squarrosula* is from the Latin diminutive of *squarrosus* = squarrose, projecting outwards, referring to the leaf arrangement.

Illustration. S.Hattori, *J. Hattori Bot. Lab.* 54: 174, fig. 69 (1983).

Description. Medium to large size, in herbarium olive green to dark brown. Shoots 2–4 cm long, 1.2–1.6 mm wide and squarrose when wet. When dry, the leaves are ± rolled around the stem and the shoot less than 1 mm wide, remotely bipinnate with widely spreading long side branches. Main stem up to 200 µm thick, light brown, in branches about 100 µm thick and greenish

brown. Leaves imbricate, always strongly squarrose, when wet with incurved ventral and patent dorsal margins. Lobe ovate with rounded apex, 650–700 μm long and 550–600 μm wide. Dorsal and ventral bases auriculate with round appendages. Marginal cells of lobe quadrangular, $10 \times 15 \mu\text{m}$, median cells isodiametric of 20–28 μm diameter, with nodulose trigones, in cases becoming confluent. Basal cells suborbicular or elongate, 30–50 \times 20–28 μm . Stylus filiform, composed of 7–8 cells long,

of which the upper 2–3 are uniseriate. Lobules asymmetric galeate, 270–310 μm long and 250–300 μm wide, not exceeding the ventral lobule margin. The underleaves cover fully or partly the lobules. Underleaves \pm imbricate, orbicular, about 3 \times stem width, 500–600 μm long and wide, bilobed to 1/5 depth with U- or V-shaped incision, bases auriculate and the insertion sinuose. Rhizoid initial area at the middle, rhizoids hyaline, fasciculate.

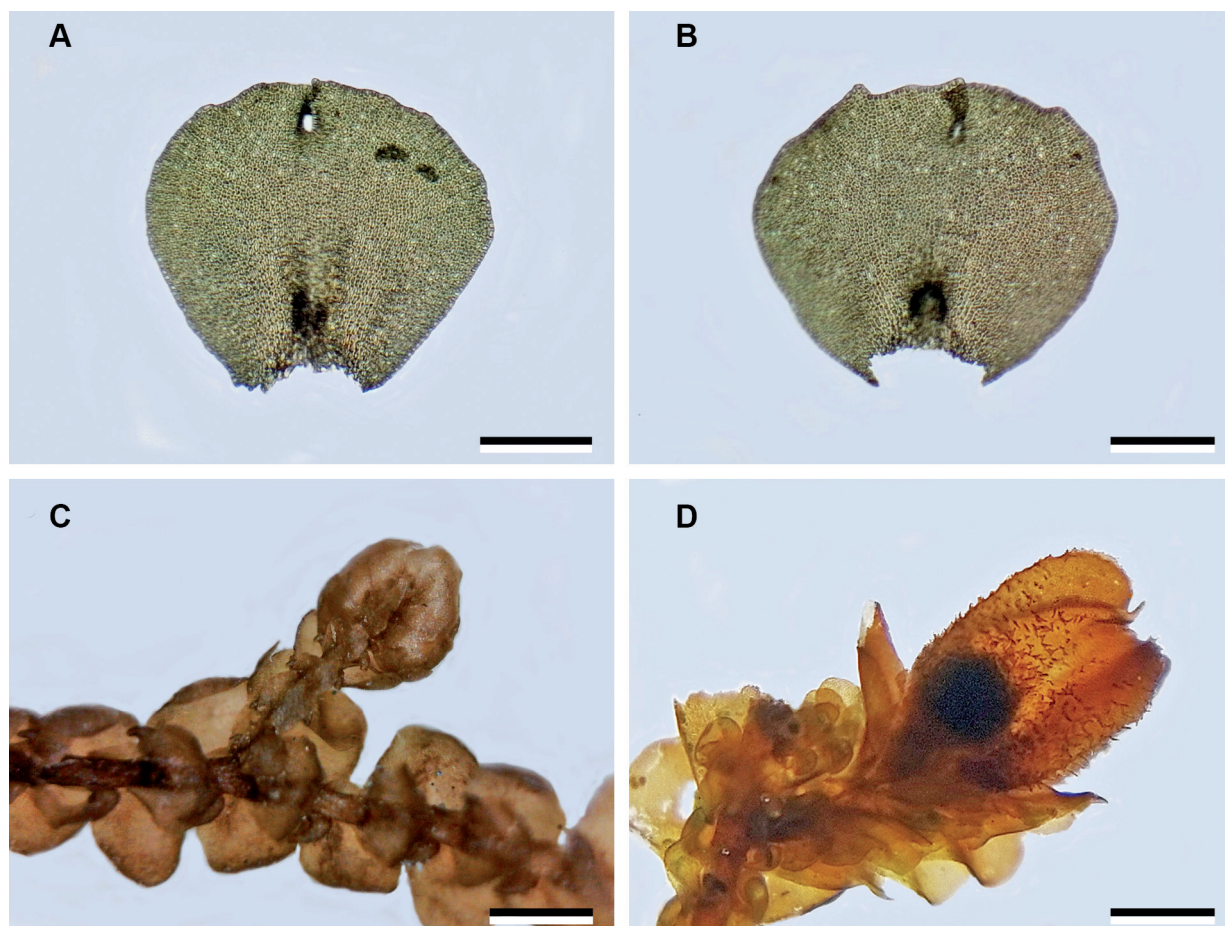


Figure 23. *Frullania setchellii* Pearson. A, B: Underleaf, ventral view. C: Androecium, ventral view. D: Gynoecium, ventral view. Photographed by T. Pócs from *H.Streimann* 4743, 44508 and 44445. Scale bars: A, B = 100 μm ; C, D = 1 mm.

Dioicous. The androecia spiciform, composed of 6–12 pairs of male bracts. Gynoecia terminal on short side branches, frequently innovating. Perichaetial leaves in 2–3 whorls, gradually diminishing to the normal leaves. The innermost bract lobe 1.5 mm long, elliptical with widely acute apex. Lobules 1/2 or less connate, 1.35 mm long. Bracteole 1/2 bifid with attenuate, pilliform apices. Perianth semi-exserted, long cylindric, 2 mm long, clearly and sharply 3 keeled, smooth. Beak relatively large, 150–200 μm long. (Fig. 24)

Diagnostic features. The squarrose leaves are shared with morphologically similar species such as *F. ericoides* (Nees) Mont. and *F. pycnantha* (Taylor) Gottsche, Lindenb. & Nees but well distinguished from both species by its totally smooth perianth surface. Differs from *F. pycnantha* by its small lobules not exceeding the lobe margin and from *F. ericoides* by the semi-orbicular shape and entire margin of underleaves with auriculate base and sinuose insertion.

Biostatus. Native.

Habitat. According to the Australian records, it occurs between the sea level and 1050 m elevation, mostly on bark, rarely on rocks, in open, *Eucalyptus* dominated forests, tropical, subtropical and temperate sclerophyllous or rainforests.

Distribution. Common and very widespread in eastern Australia from Queensland to Victoria and in New Zealand. Rare in Western Australia and also occurs on Norfolk Island (Atlas of Living Australia, 2025).

Representative herbarium specimens. Qld: Road to Mt Stuart, 10 km S of Townsville, *H.Streimann* 56221 (CANB, NICH); Queensland: Clarke Range, 70 km W of Mackay, at the corner of Dalrymple and Black Roads, 4 km ENE of Eungella, *T.Pócs* and *H.Streimann* 9968/C (CANB, EGR). N.S.W.: Cambridge Plateau Drive, near Pawpaw Skids Road, 25 km WSW of Kyogle, *H.Streimann* 61320 (CANB); Wilson River Flora Reserve in Mt Boss State Forest, 35 km WSW from Kempsey, *T.Pócs* and *E.A.Brown* 0047/F (EGR, NSW).

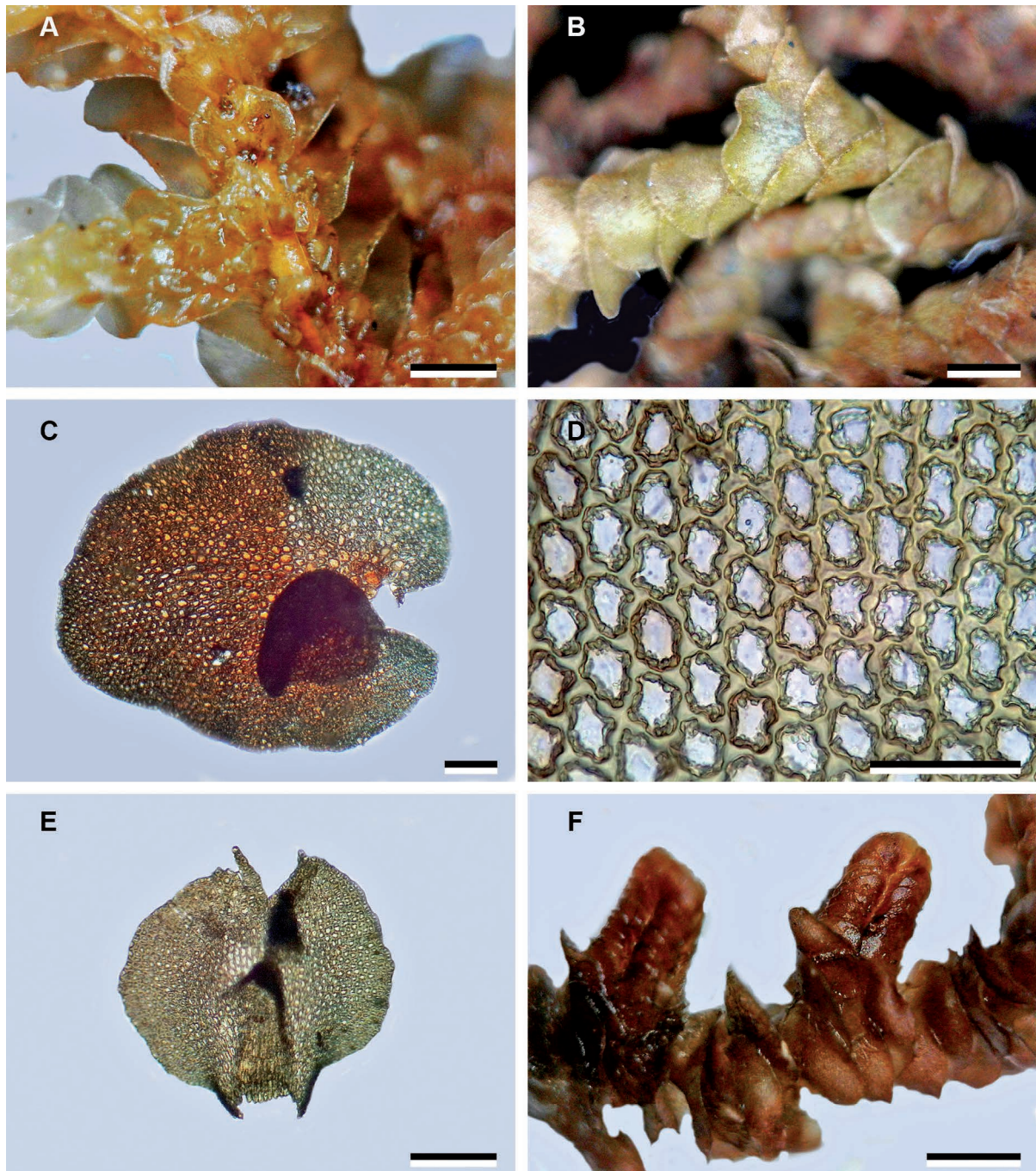


Figure 24. *Frullania squarrosula* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees A: Wet habit, ventral view. B: Dry habit, dorsal view. C: leaf with lobule, ventral view. D: Median lobe cells. E: Underleaf, dorsal view. F: Androecia, side view. Photographed by T.Pócs from *H.Streimann* 56221, 61320 (CANB); *T.Pócs* and *H.Streimann* 9958/G (CANB, EGR) and from *J.A.Curnow* 1250 (CANB). Scale bars: A, B, F = 500 µm; C, E = 100 µm; D = 50 µm.

22. *Frullania victoriensis* Steph., *Sp. Hepatic.* 4: 418 (1910).
Type: Victoria: Upper Ovens River, Mrs. MacCann 164 (G 18232).

Frullania wattsi Steph., *Sp. Hepatic.* 4: 559 (1911), *syn. nov.*
Type: New South Wales: Blackheath, Head of Neate's Glen, W.W.Watts 688 (Herb. Levier 4429 in G).

Frullania forsythiana Steph., *Sp. Hepatic.* 4: 419 (1910). *Type:*
 New South Wales: Shoalhaven River District, Forsyth 10 (G 19213).

Frullania excisula Steph., *J. Proc. Roy. Soc. New South Wales* 48: 107 (1914). *Type:* New South Wales. "Yarrowa", Mt Wilson, W.W.Watts 1071 in hb. Watts (G 18204).

All the three above synonyms were applied by Hattori (1979a) to *F. falciloba* (Hook.f. & Taylor) Lehm.

Uncertain taxonomic synonym: *Frullania binominata* Steph. *Sp. Hepatic.* 6: 545 (1924). *Type:* New South Wales: the Avenue, Mt Wilson, W.W.Watts 1094 (Herb. Watts 109 in G 18193).

Etymology. From the name of Victoria, state in Australia, where the type specimen was collected along the Upper Ovens River.

Illustrations. S.Hattori, *J. Hattori Bot. Lab.* 45: 335, fig. 9, as *F. excisula*; 341, fig. 13, as *F. forsythiana*; 360, fig. 26, as *F. victoriensis*; 361, fig. 27, as *F. wattsi* (1979a); F.Stephani, *Icon. Hepatic. Jard. Bot. Genève*, fig. 3642 (1985).

Description. Medium sized, olive green to rusty or brown in herbarium. Shoot 2–5 cm long, 1.2–1.5 mm wide, pinnately or bipinnately branched. Stem blackish brown, 0.20–0.25 mm thick. Leaves imbricate and when wet, somewhat squarrose, dorsally extended beyond the stem. Lobe elliptic, widely ovate to orbicular, 0.8–1.1 mm long and wide, concave, with incurved upper and ventral margin. Both its dorsal and ventral bases strongly appendiculate. Marginal cells subquadrate, 10–18 μm , walls with trigones. Median cells 12–22 \times 8–12 μm with nodulose trigones and intermediate thickenings, sometimes confluent with flexuose walls. Basal cells 20–40 \times 16–30 μm , with nodulose, often confluent trigones. Lobules small, symmetric or slightly asymmetric helmet shaped, not wider than the stem and contiguous to it. Their length does not exceed the half lobe width

and the ventral lobe margin. Underleaves contiguous or slightly imbricate, obovate to orbicular with 1/6–1/5 deep, V-shaped slit and auriculate base. Insertion sinuose.

Dioicous. Androecia develop on very short side branches, button shaped, consisting of 4–6 pairs of male bracts. Gynoecia at the end of main stem or branches, with innovations. Perichaetial leaves in 1–3 whorls. Female bracts 1 mm long, elongate triangular with obtuse apex and its lobule fused to 1/5 length. Bracteole almost as long as the bracts, bifid to half length, segments with acute apex with one side tooth. Perianth exserted, obpyriform to cylindric, 1.0–1.5 mm long, shiny, rust brown, with 3 or 4 obtuse keels and with completely smooth surface. Apex subtruncate or round with an obvious, up to 10 cells long beak. (Figs 25, 26)

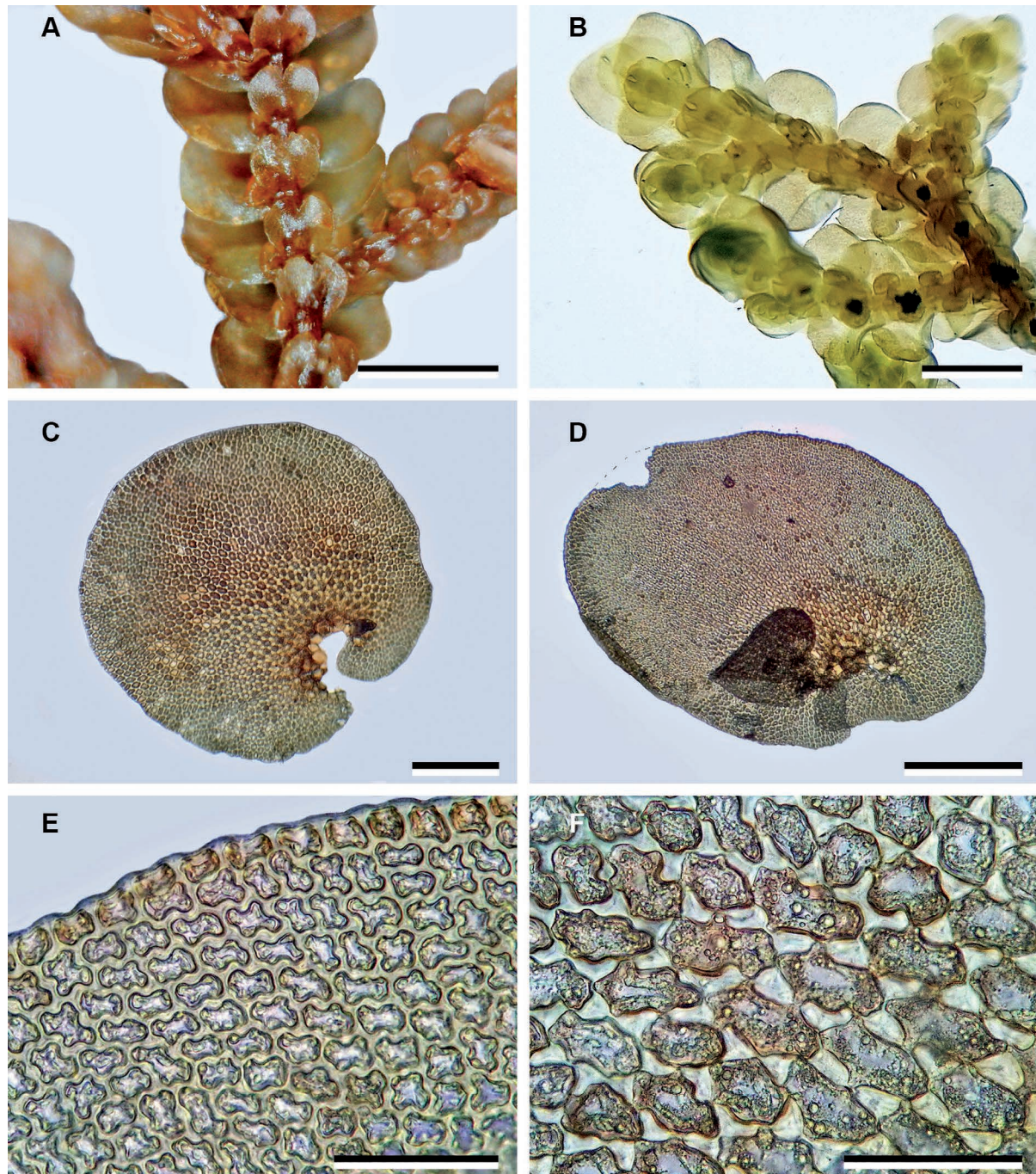


Figure 25. *Frullania victoriensis* Steph. A: Habit, ventral view in reflected light. B: Habit, ventral view in transmitted light. C: Lobe of leaf branch. D: Stem leaf with lobule. E: Marginal and median lobe cells. F: Basal lobe cells. Photographed by T.Pócs from *H.Streimann* 5750 and 31534. Scale bars: A, B = 1 mm; C = 100 μm ; D = 200 μm ; E, F = 50 μm .

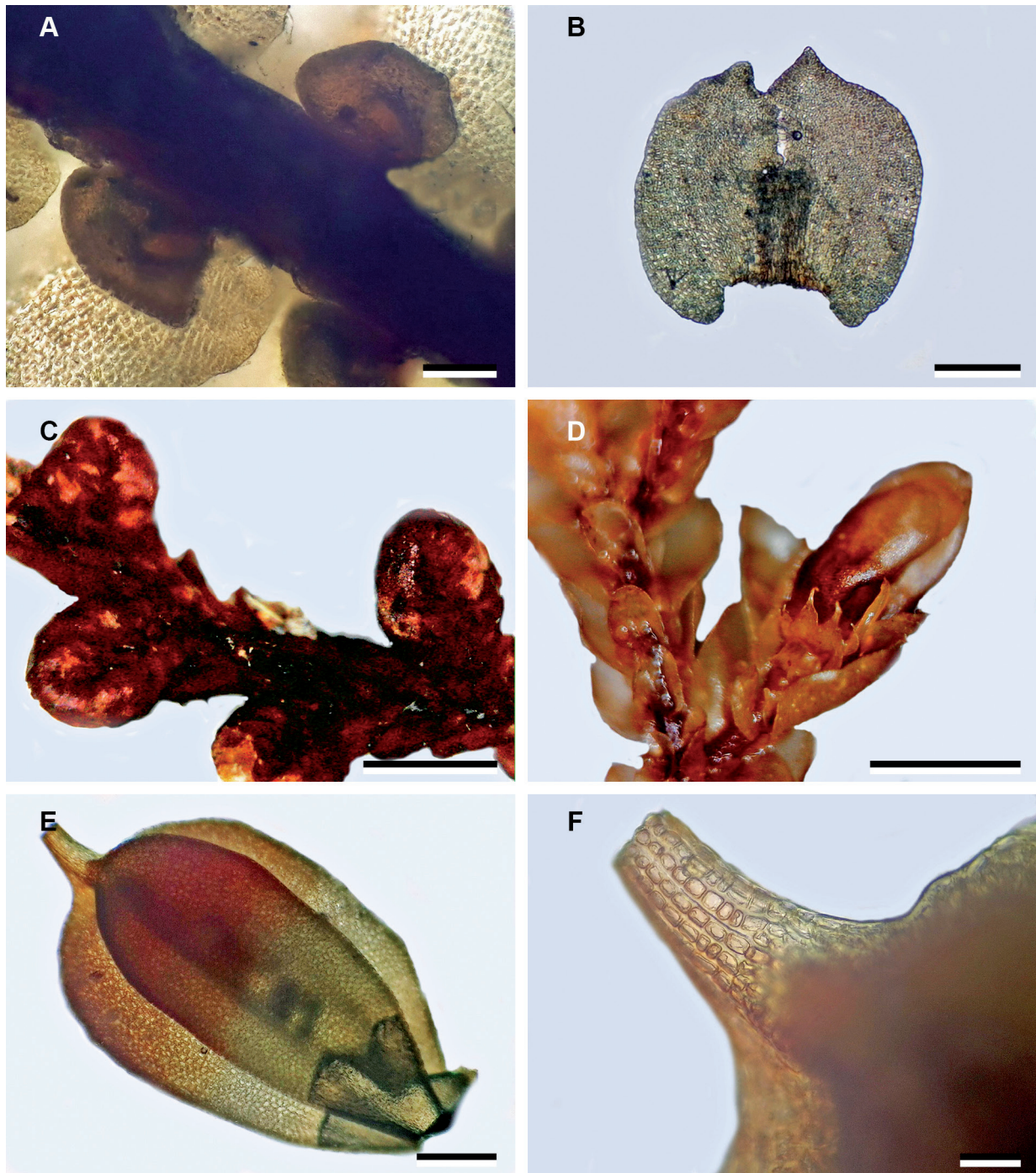


Figure 26. *Frullania victoriensis* Steph. A: Lobules, ventral view. B: Underleaf. C: Male branches with androecia. D: Female branch with gynoeceium. E: Perianth, ventral view. F: Perianth beak. Photographed by T.Pócs from *H.Streimann* 3166 and 5750. Scale bars: A, F = 100 μ m; B, E = 200 μ m; C, D = 1 mm.

Diagnostic features. The strongly auriculate lobe bases, the small, helmet shaped lobuli parallel to the stem and not exceeding the ventral lobe margin. The obovate to orbiculate underleaves with flat margin, combined with the totally smooth, tri- or quadrangular perianth distinguish well the species.

Biostatus: Native.

Habitat. Grows mostly on bark of trees, rarely on rocks, occurring in any type of woody vegetation from sclerophyllous to rainforest or on solitary trees, including palms. Elevation range from sea level to 1590 m.

Distribution. It is an Australian endemic widely distributed from northern Queensland to Victoria. Most common in New South

Wales, from where it was published under four different names. Also sporadically occurs in Western Australia (AVH 2025).

Representative specimens. W.A.: Porongurup National Park, Angwin Peak, 19 km SE of Mount Barker, *H.Streimann* 54438 (CANB). Qld.: Hugh Nelson Range 15 km S of Atherton, *H.Streimann* 29472 (CANB); Tully Falls Road 8 km SE of Ravenshoe, *H.Streimann* 30114 (CANB, JE, NICH, NY); Paluma Range, Mt Spec State Forest 6 km W of Paluma, *J.A.Curnow* 907 (CANB). N.S.W.: Sea Acres Nature Reserve 4 km SSE of Port Macquarie, *H.Streimann* 38645 (CANB); Mount Wilson, 23 km NNE of Katoomba, *H.Streimann* 31534 (CANB); Barrington Tops National Park, Thunderbolt Lookout, *H.Streimann* 47289 (CANB, JE, NY); Higgins Creek, 19 km of Batemans Bay, *H.Streimann*

5750 (CANB). A.C.T.: Jervis Bay, Caves Beach, *H. Streimann* 3602 (CANB); Mt Clear, 64 km S of Canberra, *H. Streimann* 10600 (CANB). Vic.: Trentham Galls, 16 km of Daylesford, *H. Streimann* 38993 (CANB, H, NICH, NY); Womba State Forest, Lederberg River Road, 16 km SE of Daylesford, *H. Streimann* 39070 (CANB, JE, NICH, NY); Buchan Caves, Spring Creek, 1 km W of Buchan, *H. Streimann* 39752 (CANB, H, NICH, NY).

Taxonomic notes. Since *Frullania victoriensis* was described, there was a confusion to distinguish it from the also widespread and somewhat similar *Frullania falciloba* Lehm., although Stephani in his *Species Hepaticarum* well distinguishes them, clearly describing *F. victoriensis* (1910: 418) with '*Lobulus parvus cauli aequilatus, contiguus suberectus*', while based on the type of *F. falciloba* from Tasmania, Stephani (1910: 421) describes this species with '*Lobulus magnus, cauli contiguus...rostrum longo decurvo ...cauli parallelo marginem folio superante*'. Apart from the differences in lobule structure of *F. victoriensis*, its lobe has at both its dorsal and ventral bases large appendicules, while the lobe of *F. falciloba* is appendiculate only at its dorsal base. *Frullania victoriensis* has suborbicular underleaves with an auriculate base and obviously sinuose insertion, while *F. falciloba* does not.

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