

Hawaiian Liverworts and Hornworts: A Bryologists' Notebook, Vol. 2 of 5

Leafy Liverworts (*Diplasiolejeunea-Metacalypogeia*)

A. Virginia Freire and Emmet J. Judziewicz, July 2026

**With photographs by the authors, Zach Pezzillo, Daniel Tucker, Kevin Faccenda,
Miles K. Thomas, Larry Jensen, Randal Mindell, W. Cuyler Bleecker,
Martin H. Hutten, Graham Steinruck, and Brooke Fleischman**



Hawaiian Liverworts and Hornworts, a Bryologists' Notebook:
Vol. 2 of 5: Leafy Liverworts (*Diplasiolejeunea* to *Metacalypogeia*)

July 2026

A. Virginia Freire and Emmet J. Judziewicz
(authorship is alphabetical)

University of Wisconsin-Stevens Point and Bernice P. Bishop Museum

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Contact information: calypogeia@gmail.com (Virginia) and judzemmet@gmail.com (Emmet).

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Cover photos:

Top left: *Frullania meyeniana* and *F. hypoleuca* (Kevin Faccenda, Hualālai, Hawai‘i Island). Top right: Dark *Lopholejeunea nigricans* (A. Virginia Freire, Hawai‘i Volcanoes National Park, Hawai‘i Island), with a few light green plants of *Lophocolea hawaica*.

Bottom left: *Herbertus* aff. *helleri* (Zach Pezzillo, Maui). Bottom center: *Leptoscyphus baldwinii* (Emmet J. Judziewicz, Hawai‘i Island). Bottom right: *Fuscocephaloziopsis connivens* subsp. *sandwicensis* (Zach Pezzillo, Maui).

Below: *Liochlaena subulata*, Hawai‘i Island. Photo by E.J. Judziewicz



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Introduction

Volume 2 of “Hawaiian Liverworts and Hornworts, a Bryologists’ Notebook” covers the leafy liverworts from genera *Diplasiolejeunea* through *Metacalypogeia*. We again stress that this notebook is an attempt to focus research attention, additional field work, and popular interest, on Hawaiian liverworts. It is not a flora, and important aspects of the species’ biology – such as sexuality, perianth structure, branching morphology, and molecular systematics – are lightly if at all touched on for some taxa. The remaining volumes will cover the leafy liverwort genera *Metalejeunea* to *Vitalianthus* (Vol. 3); the thalloid liverworts and hornworts (Vol. 4); and the results of field surveys (Vol. 5). In this volume we have added thumbnail photos following the keys for those genera with more than one species. Please note that these thumbnails within genera are *not* at the same scale. For introductory material, including a glossary, refer to Volume 1, available here:

Google Drive:

https://drive.google.com/file/d/14R2peYhhx42fltOT2Owszw1Xi2OnXeB/view?usp=drive_link;

Research Gate:

https://www.researchgate.net/publication/391739828_Hawaiian_liverworts_Freire_Judz_Vol_1_A-C_May_2025;

Laukahi: Hawai‘i Plant Conservation Network:

<https://laukahi.org/wp-content/uploads/2025/07/Hawaiian-liverworts-Freire-Judz.-Vol.-1-A-C-May-2025-2.pdf>;

Plants of Hawai‘i, Bishop Museum:

https://editedimages.s3.us-east-1.amazonaws.com/Volume1_IntroA-C_10_May_2025.pdf



We wish to acknowledge the efforts of several more recent collectors (in addition to the ones discussed and illustrated in Vol. 1: 35-37) who are helping to document the liverwort and hornwort flora of Hawai‘i: Susan Fawcett (left), a research associate at the National Tropical Botanical Garden, explores Kaua‘i, while Mike Ross (right), a professor at Kapiolani Community College, explores the Ko‘olau Range on O‘ahu. We want to reiterate our gratitude and admiration for recent high elevation forays made by Kevin Faccenda, Zach Pezzillo, Miles K. Thomas, and James R. Shevock on Kaua‘i, O‘ahu, Moloka‘i, and Maui. We also thank Barbara Kennedy and Tim Gallaher of Bishop Museum for their steadfast support. They have all helped to make the last few years a “Golden Age” for liverwort exploration in Hawai‘i.

Studying these plants has been a succession of humbling experiences, as we gradually realized the magnitude of the work remaining to be done. The completion of a comprehensive floristic study of Hawaiian hepatics is, in our opinion, decades away. Nevertheless, we hope that our efforts will alert researchers and naturalists to the many challenges awaiting those who study Hawaiian hepatics and hornworts.

REVISED KEY TO THE GENERA OF LEAFY LIVERWORTS OF HAWAII

If a genus has just one species in Hawai'i, or if the species needs to have a separate entry other than the couplet to genus, then the species epithet is given in this key. Among several revisions in this key we have added *Odontoschisma fluitans*, a species recently collected on Kaua'i.

- 1. Leaves complicate-bilobed (with dorsal lobe and ventral lobule) **KEY 1**
- 1. Leaves simple, not complicate-bilobed (not folded into a lobe and lobule) **2**
 - 2. Underleaves present and well-developed **KEY 2**
 - 2. Underleaves absent or rudimentary **KEY 3**

KEY 1 (Leaf complicate-bilobed, folded so that a lobe and lobule are present)

- 1. Underleaves present **2**
 - 2. Plants (5)6-8 mm wide; leaves longitudinally ridged; dorsal lobes much smaller than the ventral lobules; rhizoids purple; rare or perhaps extirpated *Schistochila*
 - 2. Plants < 5 mm wide; leaves smooth, not ridged; dorsal lobes larger than the ventral lobules; rhizoids pale; common to rare **3**
 - 3. Lobules and underleaves ligulate (tongue-shaped); underleaves never bifid *Porella*
 - 3. Neither lobules nor underleaves ligulate; underleaves bifid or entire (except *Frullania sandvicensis*, with some ligulate lobules intermixed, but then always with bifid underleaves) **4**
 - 4. Lobule attached to the lobe's lower margin, along its length, by a fold or keel (not free, hornlike in *Colura*) **LEJEUNEACEAE (see KEY 4)**
 - 4. Lobule attached at the lobe's lower margin, not forming a fold or keel, free from it **5**
 - 5. Lobule attached near the base of the lobe's lower margin, close to the stem, connected to it by a short, thick keel, galeate (helmet-shaped) or cylindrical, some with occasional ligulate (tongue-shaped), flattened lobules intermixed; lobe apiculus (if present) always single and very short (1-3 cells long); leaf cell walls conspicuously trigonous; underleaf insertion line not or only shallowly arched; common *Frullania*
 - 5. Lobule attached on the lobe's lower margin, away from the stem, without a noticeable keel, always cylindrical; lobe apiculi 1-3, the central one usually over 3 cells long; leaf cell walls not conspicuously trigonous; underleaf insertion line conspicuously arched; rare *Jubula*
- 1. Underleaves absent **6**
 - 6. Plants julaceous, large and robust, erect or semi-erect, resembling a stonecrop; reddish to reddish-purple (green when in shade); lobules inflated, vertical and prominent *Pleurozia* (keyed here for convenience; actually a thalloid liverwort)
 - 6. Plants not julaceous, tiny to large, prostrate, procumbent or occasionally erect, but not resembling a stonecrop; lobules flat or inflated, horizontal, tiny or prominent, if vertical, tiny and not inflated **7**
 - 7. Lobule smaller than the lobe; margins entire; plants always green, never reddish **8**
 - 8. Stems robust; leaves with a single large oil body in each cell; rhizoids originating from the lobules *Radula*
 - 8. Stems weak; leaf cells with several to many oil bodies; rhizoids originating from ventral side of Stem **9**
 - 9. Lobule at most ½ as long as the lobe *Cololejeunea* (see Lejeuneaceae)
 - 9. Lobule nearly as long as the lobe *Myriocoleopsis minutissima* (see Lejeuneaceae)
 - 7. Lobule larger than the lobe; margins sometimes ciliate-dentate or denticulate; plants green or often reddish (both Scapaniaceae) **10**
 - 10. Leaves with lobe and lobule narrowly elliptical, the lobule with a central band of elongated cells

- (a vitta); rare, Maui and Hawai'i Island *Diplophyllum*
 10. Leaves with lobe and lobule $\pm$ round, the cells of lobe and lobule homogenous, lacking a central band of elongated cells; widespread *Scapania*

KEY 2 (Leaves not complicate-bilobed; underleaves well-developed)

1. Leaves divided to at least 1/2 of their length 2
 2. Segments triangular, irregular; rare, bogs, Moloka'i and West Maui *Protolophozia perssoniana*
 2. Segments regularly filiform 3
 3. Filiform segments radiating from a distinct and round blade; leaf star- or hand-shaped; rare, Kaua'i and West Maui *Temnoma setigerum* var. *hawaiiicum*
 3. Filiform segments arising near the leaf base, the blade absent or very small 4
 4. Leaves compoundly dissected into numerous fringed segments; rare, Maui *Trichocolea gracillima*
 4. Leaves simply dissected into 2-4 segments 5
 5. Leaf segments 10-13 cells long; rare, Kaua'i, West Maui, and Hawai'i *Blepharostoma trichophyllum*
 5. Leaf segments 4-7 cells long; common 6
 6. Lobes 75-150 μ m long, 2-3 cells wide at the base, usually concave; stem hyalodermis absent *Kurzia*
 6. Lobes 150-250 μ m long, 2 cells wide at the base, not concave; stem hyalodermis present *Telaranea nematodes*
 1. Leaves undivided, or divided to much less than 1/2 their length 7
 7. Leaves succubous 8
 8. Underleaves bifid, with parallel lobes 9
 9. Leaves very distant, 0.3-0.6 mm long; rare, Kaua'i *Odontoschisma fluitans*
 9. Leaves contiguous to slightly imbricate, 0.5-1 mm long 10
 10. Leaves bifid; rare *Geocalyx*
 10. Leaves entire, rounded to slightly retuse, never bifid; common *Notoscyphus lutescens*
 8. Underleaves quadrifid (occasionally 6-8-fid), the lobes often divergent (all Lophocoleaceae) 11
 11. Leaf margins with 7-10 ciliate teeth; plants tending to turn yellowish-brown with age; perianth bucket-like *Leptoscyphus baldwinii*
 11. Leaf margins with 0-5 teeth or cilia; plants remaining greenish with age; perianth tubular, or rarely broad and bucket-like 12
 12. Leaves inrolled, opposite; underleaves fused to both adjacent leaves; trigones present; leaf teeth 2-3 *Cryptolophocolea*
 12. Leaves flat, not inrolled, opposite or alternate; underleaves fused to both adjacent leaves or not; trigones present or absent; leaf teeth 0-5 13
 13. Trigones prominent, nodular 14
 14. Leaves always rounded and entire (without teeth); underleaves with 6-8 teeth; leaf margins often gemmiferous *Chiloscyphus laceratus*
 14. Leaves rounded to truncate, entire to irregularly 1-4-toothed; underleaves with 4 teeth; leaf margins never gemmiferous *Leptoscyphus species 1*
 13. Trigones small or absent; underleaves usually with 4 unequally-sized teeth (6 similar-sized in *Chiloscyphus skottsbergianus*) 15
 15. Leaves with 3-5 teeth, not bilobed; rare *Heteroscyphus*
 15. Leaves consistently with 0-2 teeth, bilobed or not 16

- 16. Leaves alternate; perianth 3-keeled; underleaves fused to just one of the adjacent leaves, or unfused to either leaf..... *Lophocolea*
- 16. Leaves opposite or subopposite; perianth round in cross-section; underleaves fused to both adjacent leaves 17
- 17. Leaves bilobed or not, but if bilobed then the lobes lacking additional teeth ...
..... *Chiloscyphus*
- 17. Leaves bilobed, the lobes often with several smaller teeth; Hawai'i Island; Mindell & Tucker: <https://www.inaturalist.org/observations/255995034>.
..... **Lophocoleaceae indet.**
- 7. Leaves incubous or transversely inserted 18
- 18. Leaves 0.3-0.4 mm long 19
- 19. Leaves 3-4-lobed *Lepidozia sandvicensis*
- 19. Leaves bilobed 20
- 20. Leaf lobes acute *Cephaloziella heteroica*
- 20. Leaf lobes rounded; rare, Kaua'i *Odontoschisma fluitans*
- 18. Leaves 0.5-1.5 mm long..... 21
- 21. Leaves transversely inserted 22
- 22. Leaves entire, unlobed *Acromastigum*
- 22. Leaves 2-4-lobed 23
- 23. Leaves 3-4-lobed *Lepidozia*
- 23. Leaves bilobed *Herbertus*
- 21. Leaves incubous 24
- 24. Plants with ventral microphyllous branches (both Lepidoziaceae) 25
- 25. Leaves often 2-3(4) dentate to much less than ½ their length (occasionally without teeth); underleaves rounded to erose *Bazzania*
- 25. Leaves 3-4-lobed to at least ½ their length; underleaves 3-4 lobed *Lepidozia*
- 24. Plants without ventral microphyllous branches (all Calypogeiaceae) 26
- 26. Underleaves deeply bifid (occasionally slightly quadrifid) 27
- 27. Stems with a partial hyalodermis; leaves distant, clearly decurrent, bordered
..... *Asperifolia arguta*
- 27. Stems lack a hyalodermis; leaves imbricate, not decurrent or bordered ... *Calypogeia*
- 26. Underleaves rounded or minutely retuse, not bifid 28
- 28. Underleaves 5 times as wide as the stem; plants with dark reddish-blackish pigments rare; Kaua'i *Calypogeia aeruginosa*
- 28. Underleaves at most 3 times wider than the stem; plants lacking blackish pigments
..... 29
- 29. Leaves acute at the apex; underleaves green; rare, Moloka'i (?) and Maui.....
..... *Metacalypogeia alternifolia*
- 29. Leaves rounded at apex; underleaves brown; widespread..... *Mnioloma fuscum*

KEY 3 (Leaves not complicate-bilobed, underleaves absent, or very reduced)

- 1. Leaves unlobed; some coarsely and irregularly toothed, but not consistently bifid or trifid 2
- 2. Leaves opposite 3
- 3. Leaves toothed, acute; common *Chiastocaulon combinatum*
- 3. Leaves entire (not toothed), rounded at apex; rare 4
- 4. Leaves round; plants 0.8-1 mm wide *Southbya organensis*

- 4. Leaves slightly longer than wide; plants 2-3.5 mm wide *Syzygiella eatonii*
- 2. Leaves alternate 5
 - 5. Leaves transversely inserted, distant; plants ca. 0.1 mm wide; rare, summit bogs, Kaua‘i *Marsupella stoloniformis*
 - 5. Leaves succubous, contiguous to imbricate; plants at least 1 mm wide 6
 - 6. Plants stoloniferous; leaves often with a shallow postical sinus *Acrobolbus*
 - 6. Plants not stoloniferous; leaves lacking a postical sinus 7
 - 7. Leaf margins toothed or ciliate, at least near the apex; leaves with a long J-shaped insertion (long dorsally, short and pronouncedly curved ventrally) *Plagiochila*
 - 7. Leaf margins entire, not toothed or ciliate 8
 - 8. Plants producing gemmae on reduced-leafy shoots9
 - 9. Leaves dorsally decurrent, with small or large trigones; plants never reddish *Liochlaena subulata*
 - 9. Leaves not dorsally decurrent, with large trigones; plants often reddish..... *Odontoschisma denudatum*
 - 8. Plants not producing gemmae on reduced-leafy shoots10
 - 10. Leaf trigones very large; plants often reddish (but can be green) *Cuspidatula*
 - 10. Leaf trigones absent or small; plants never reddish *Solenostoma*
 - 1. Leaves bifid or trifid 11
 - 11. Leaves mostly asymmetrically trifid; high elevation forests of Hawai‘i Island *Tritomaria exsecta*
 - 11. Leaves consistently bifid, never trifid 12
 - 12. Leaves horizontally (longitudinally) inserted or nearly so 13
 - 13. Leaves constricted at the base, not decurrent, the lobes not connivent; hyalodermis absent *Cylindrocolea*
 - 13. Leaves decurrent, the lobes connivent; hyalodermis present *Fuscocephaloziopsis*
 - 12. Leaves transversely inserted or succubous 14
 - 14. Plants 0.2-0.35 mm wide..... 15
 - 15. Leaves distant; widespread *Cephaloziella*
 - 15. Leaves densely imbricate; Haleakalā, Maui *Gymnomitron*
 - 14. Plants at least 0.5 mm wide 16
 - 16. Plants wormlike, with very densely overlapping leaves; Haleakalā, Maui and Hawai‘i Island *Isopaches bicrenatus*
 - 16. Plants not wormlike, the leaves not densely overlapping 17
 - 17. Leaves with a shallow sinus only 10-25(30)% of the leaf length 18
 - 18. Leaf lobes pointed (not rounded); stems very rigid and stout, leaves recurved at the margins; gemmae present; several islands *Anastrepta orcadensis*
 - 18. Leaf lobes mostly rounded; stems not very rigid and stout, leaves not recurved at the margins; gemmae absent; rare, East Maui *Marsupella emarginata*
 - 17. Leaves with a deeper sinus (25)30-50% or more of the leaf length 19
 - 19. Leaf cells very thick-walled (each lateral wall about ½ as thick as the cell lumen at leaf apices), or with prominent trigones; plants strongly colored, rusty orange, red, nearly black, or occasionally dark green *Anastrophyllum*
 - 19. Leaf cells thin- to only slightly thick-walled (each lateral wall much less than ½ as thick as the cell lumen at leaf apices), with small or no trigones; plants green, some with a reddish tint 20
 - 20. Hyalodermis present; leaf cell walls thin, without trigones; gemmae spherical (when present) *Cephalozia*

20. Hyalodermis absent; leaf cell walls thin to slightly thickened, with trigones; gemmae angular **21**
21. Plants 1-2 mm wide, the lobes acuminate; plants green; moist high elevation forests, Kaua'i, Maui and Hawai'i Island ***Lophozia silvicola***
21. Plants 0.7-0.9 mm wide, the lobes acute; plants orange-brown; rare, high elevation heathlands, Haleakalā, Maui ***Sphenolobus minutus***

KEY 4: Lejeuneaceae

1. Underleaves absent or very reduced **2**
2. Leaf cells not inflated; lobules much shorter than the lobes ***Cololejeunea***
2. Leaf cells inflated; lobules nearly as long as the lobes ***Myriocoleopsis minutissima***
1. Underleaves present **3**
3. Lobules ending in an elongate, hornlike, inflated sac ***Colura tenuicornis***
3. Lobules not ending in an elongate, inflated sac **4**
4. Underleaves undivided (holostipous) (examine carefully, the notches can be inconspicuous) **5**
5. Plants blackish, blackish-green or green; stem hyalodermis present ***Lopholejeunea***
5. Plants green (blackish in rare *Marchesinia brachiata*); stem hyalodermis absent **6**
6. Underleaves with a very deeply arched insertion; rare, historical ***Marchesinia brachiata***
6. Underleaves with insertion shallowly or not at all arched **7**
7. Leaves more-or-less toothed at the apex ***Spruceanthus***
7. Leaves entire **8**
8. Leaves < 1 mm long; summit of Kaua'i ***Cheilolejeunea* species 2**
8. Leaves 1-2 mm long; widespread, mostly at low elevations **9**
9. Leaf trigones cordate, well-defined (although small); perianths occasionally produced; leaves always entire; plants yellowish-green..... ***Acrolejeunea sandvicensis***
9. Leaf trigones absent/poorly defined, never cordate; perianths usually abundantly produced; leaves sometimes with 1-2 small teeth; plants dark green.....
.....***Spruceanthus planiusculus***
4. Underleaves bifid (schizostipous; watch for small, inconspicuous notches) **10**
10. Underleaves bordered by large cells; rare, tiny epiphyll reported from O'ahu ... ***Leptolejeunea***
10. Underleaves not bordered by large cells **11**
11. Underleaves antenna-like, each lobe a series of single cells; leaf cell walls strongly sinuous; rare, Hawai'i Island..... ***Diplasiolejeunea* species 1**
11. Underleaves not antenna-like; each lobe at least two cells wide at the base; leaf cell walls not at all sinuous **12**
12. Leaves conspicuously acute; ocelli present..... **13**
13. Plants with large underleaves about three times as wide as the stem; ocelli scattered throughout lobes and lobules; rare, historical ***Lepidolejeunea involuta***
13. Plants with small underleaves not much wider than the stem; ocelli few, scattered or arranged in a row along the middle of the lobe **14**
14. Ocelli grayish, scattered; common ***Drepanolejeunea***
14. Ocelli golden orange, in a line 4-7 cells long down the middle of the lobe; rare
..... ***Vitalianthus pseudoneurus***
12. Leaves rounded to very slightly pointed; ocelli absent (except in *Microlejeunea*) **15**
15. Leaves erect to erect-spreading; plants < 0.5 mm wide **16**
16. Lobes lacking ocelli; leaves erect-spreading, with rounded lobes; stem straight;

- lobes of underleaves 3-5 cells wide at base..... ***Metalejeunea cucullata***
16. Lobes with 1-3 ocelli near base; leaves erect, with a slightly pointed apex; stem slightly zigzag; lobes of the underleaves 1-2 cells wide at base.....
.....***Microlejeunea lunulatiloba***
15. Leaves spreading; plants (0.3-) 0.5-2 mm wide **17**
17. Leaf oil bodies large, 2-3 per cell; lobules at least 1/3 as long as the lobes, often inflated; slime papillae of lobule distal (above) to lobule tooth
..... ***Cheilolejeunea***
17. Leaf oil bodies small, many per cell; lobules less than 1/3 as long as the lobes, flat; slime papillae of lobule proximal (below) to the lobule tooth ***Lejeunea***

Following pages: Thumbnails of leafy liverwort genera for each of the three volumes.

Photos by the authors except for these genera:

Kevin Faccenda - *Solenostoma*, *Spruceanthus*, *Syzygiella*

Larry Jensen - *Leptolejeunea*

Zach Pezzillo – *Acromastigum*, *Fuscocephaloziopsis*, *Lepidozia*, *Porella*

Miles K. Thomas – *Anastrepta*, *Anastrophyllum*, *Bazzania*, *Chiastocaulon*, *Chiloscyphus*, *Protolophozia*

National Tropical Botanical Garden/Ken Wood – *Acrolejeunea*, *Plagiochila*, *Scapania*, *Trichocolea*

Volume 1 (past volume): Leafy liverwort genera *Acrobolbus* to *Cylindrocolea*



Acrobolbus



Acrolejeunea



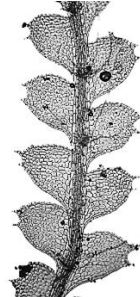
Acromastigum



Anastrepta



Anastrophyllum



Asperifolia



Bazzania



Blepharostoma



Calypogeia



Cephalozia



Cephaloziella



Cheilolejeunea



Chiastocaulon



Chiloscypus



Cololejeunea



Colura



Cryptolophocolea



Cuspidatula



Cylindrocolea

Volume 2 (present volume): Leafy liverwort genera *Diplasiolejeunea* to *Metacalypogeia*



Diplasiolejeunea



Diplophyllum



Drepanolejeunea



Frullania



Fuscocephaloziopsis



Geocalyx



Gymnomitrium



Herbertus



Heteroscyphus



Isopaches



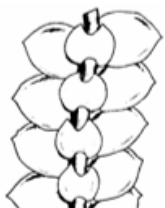
Jubula



Kurzia



Lejeunea



Lepidolejeunea



Lepidozia



Leptolejeunea



Leptoscyphus



Liochlaena



Lophocolea



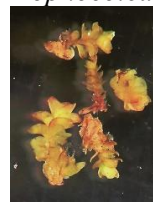
Lopholejeunea



Lophozia



Marchesinia



Marsupella

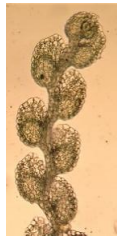


Metacalypogeia

Volume 3 (forthcoming volume): Leafy liverwort genera *Metalejeunea* to *Vitalianthus*



Metalejeunea



Microlejeunea



Mnioloma



Myriocoleopsis



Notoscyphus



Odontoschisma



Plagiochila



Pleurozia



Porella



Protolophozia



Radula



Scapania



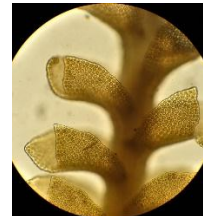
Schistochila



Solenostoma



Southbya



Sphenolobus



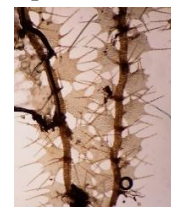
Spruceanthus



Syzygiella



Telaranea



Temnoma



Trichocolea



Tritomaria



Vitalianthus



Unknown leafies

***Diplasiolejeunea* (Spruce) Schiffn. (Lejeuneaceae)**

One species in Hawai‘i, 69 species worldwide.

***Diplasiolejeunea* species 1. Naturalized?**

Found only at Onomea, west of Hilo, Hawai‘i Island, as an epiphyte on the stem of an exotic orchid, at less than 100 ft. elevation. This is the first record of this tropical genus in Hawai‘i. We only know of it as a small fragment, mixed with *Lejeunea laetevirens* and an apparently novel species of *Cheilolejeunea* (species 3 in Freire & Judziewicz, 2025: 297). This is the first report of this genus in Hawai‘i.



This is the most intriguing leafy liverwort we discovered in Hawai‘i. The “Martian antenna” or “Peace and Love” underleaves with long, uniseriate lobes; the large, cupped leaf lobules; the sinuous leaf cell walls with prominent intermediate thickenings, and the brownish-orange plant color, are striking and distinctive.

At first sight, this tiny plant resembles a member of the genus *Myriocoleopsis*. However, the thickened leaf cell walls and the presence of underleaves (at least on the upper portion of the plant) argue against its placement in that genus. Based on photos we posted on Bryonet, Tamás Pócs and Alfons Schäfer-Verwimp, both authorities on the Lejeuneaceae, suggest that this is likely a new species of *Diplasiolejeunea* (pers. comm., 22 Dec. 2021). According to Pócs, the species bears some similarity to the Pantropical *D. cobrensis* Steph. and the Australasian *D. plicatiloba* (Hook. f. & Taylor) Grolle but is distinct enough to make it a unique species.

Hawaiian material differs from the pantropical *Diplasiolejeunea cobrensis* (Chandini et al, 2021: 289-292) in its much larger lobules and apparent absence of leaf ocelli. The Australasian species *D. plicatiloba* has globose leaves as in the Hawaiian species, but the leaf cells are thin-walled and the underleaves have a basal disk and lobes two cells wide (photo by David Tng of a Tasmanian specimen here:

<https://www.utas.edu.au/dicotkey/dicotkey/Lworts/LEJEUNEACEAE/gDiplasiolejeunea.htm>). When we compare our species with the neotropical *D. alata* Jovet-Ast (Gradstein, 2021: 468, 472-473), also a species with small underleaves and no ocelli, its lobules are much smaller than the Hawaiian species, and its underleaf lobes are 2-4 cells wide at the base, rather than 1(-2) cells wide.

Next, we provide a limited description based only on the single apical fragment available. We returned to the collection site on 20 May 2021, 30 Jan. 2022, 22 Aug. 2022, 14 Dec. 2022, and 23 Dec. 2024 and were unable to relocate it.

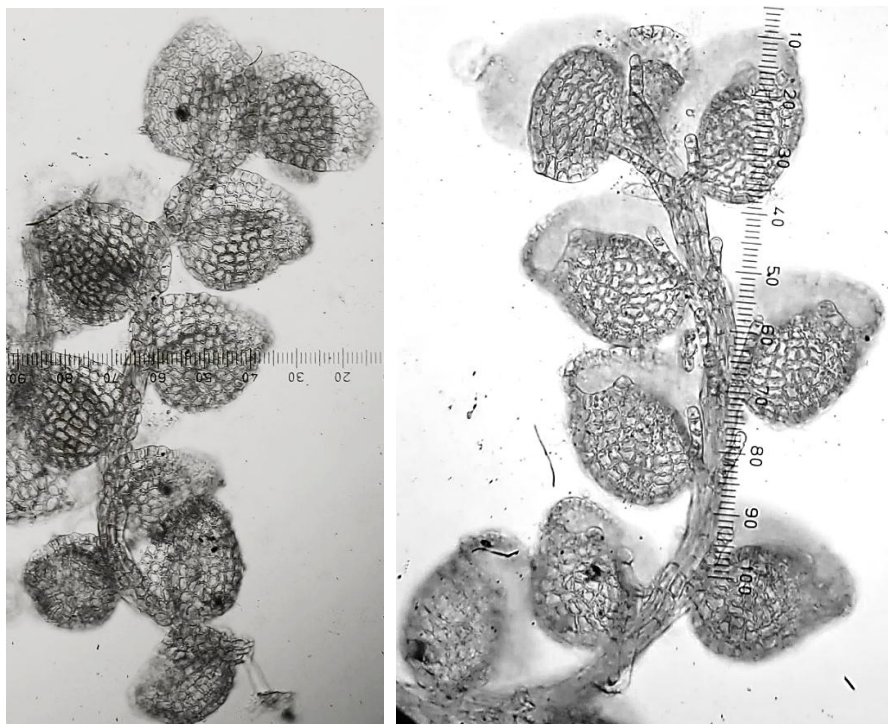
Plant small, brownish-orange, at least 1 mm long, at least 0.45–0.5 mm wide; stem fragile, 50 µm in diameter, with long rectangular cells. Leaves distant to contiguous, obliquely spreading, alternate, convex, overarching and obscuring the stem’s dorsal surface; ocelli not observed; oil bodies not observed (but fresh material not examined); leaf lobe asymmetric, broadly ovate, in dorsal view with a rounded, slightly pointed apex, slightly subcordate at base, 0.25-0.32 × 0.22–0.26 mm, both dorsal and ventral margins curved, with the dorsal margin more prominent; leaf lobules ovoid, inflated, large, 70-80% as long as the leaf lobe, 60% as broad, 0.15–0.18 × 0.13–0.15 mm, with an inrolled free margin, the apical tooth rounded and single-celled; hyaline papilla not observed. Leaf cells rectangular to quadrate, the walls orange-brown, irregularly

thickened (appearing sinuous), with trigones and prominent intermediate nodular thickenings, $25\text{--}32 \times 15\text{--}20\text{ }\mu\text{m}$; marginal cells ca. $15 \times 17.5\text{ }\mu\text{m}$, nearly quadrate, not sinuous, forming a border. Underleaves about 1.5 times as wide as the stem, $110\text{--}160 \times 20\text{--}30\text{ }\mu\text{m}$, one per leaf, produced from a (1?)2-celled merophyte, deeply bilobed nearly or to the base, the sinus V-shaped, the lobes forming a $30\text{--}40^\circ$ angle, the lobes linear, uniseriate, 4-7 cells long, some 2 cells wide at the base; underleaf lobes united by a single cell, or separate; the lobe adjacent to the leaf is associated with the lobule base and is reduced to a stylus on the lower leaves, while the second underleaf lobe becomes separated from its twin (with a gap between them) and is not apparent (perhaps aborted?) on the lower stem sector. To summarize, the underleaves are present only in the upper region of the plant but are not observed in the lower stem region, where they appear to be reduced to a stylus. Sexual and asexual reproductive structures were not seen.

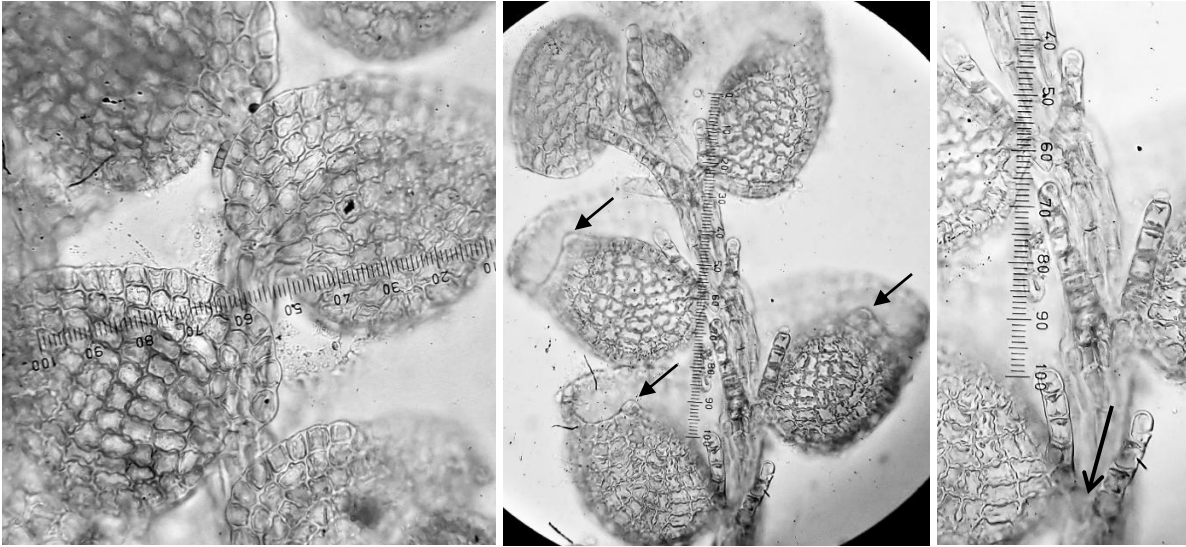
TYPE: U.S.A. **Hawai'i**. Hawai'i County. Hawai'i Tropical Botanical Garden, Onomea, $19^\circ48'35''\text{ N}$, $155^\circ05'40''\text{ W}$, el. 100 ft. Epiphyll on an exotic orchid in lush exotic forest (mostly tropical Asian species), with *Lejeunea laetevirens* and *Cheilolejeunea* (?) species 3, 20 Nov. 2019, A.V. Freire & E.J. Judziewicz 2019-154c (BISH).



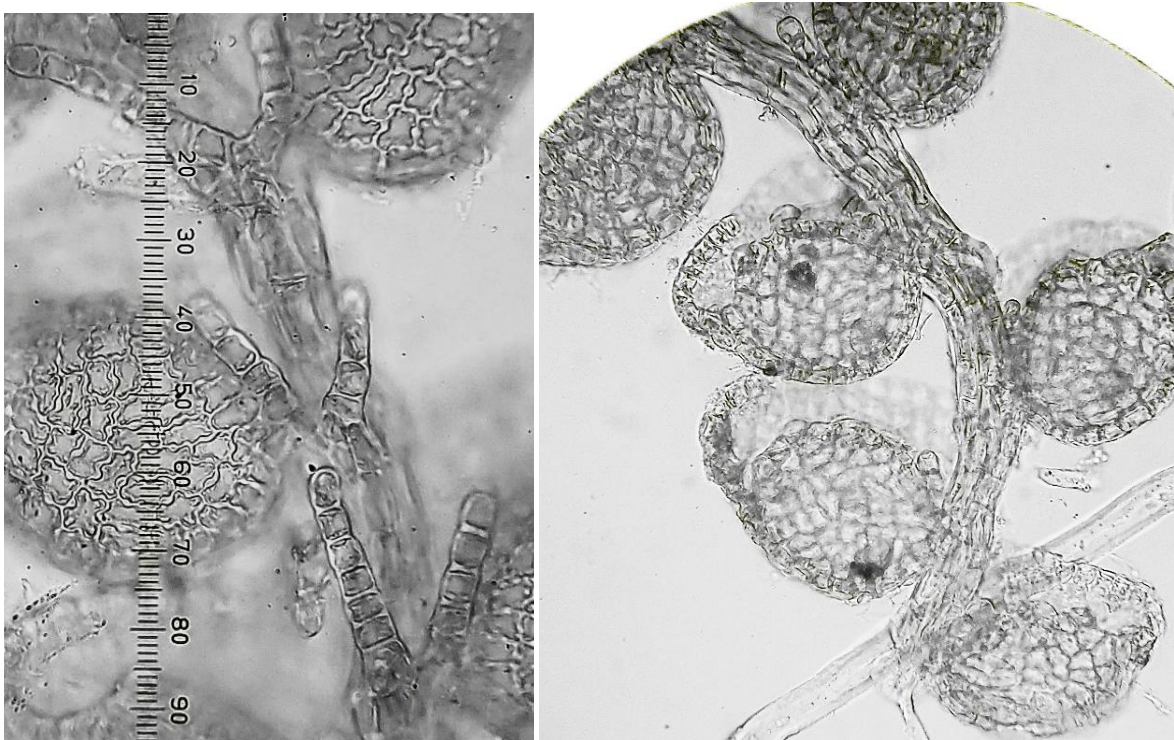
Onomea, Hawai'i Island, substrate of Freire & Judziewicz 19-154 (BISH). The dominant liverwort on this stem is *Lejeunea laetevirens*. Scale in mm.



Diplasiolejeunea species 1 (complete fragment). Left: Dorsal view. Note broadly ovate leaves with dorsal margins overarching and obscuring the stem midline. Right: Ventral view. Note the prominent cuplike, inflated lobules, each with a rounded apical tooth, and the deeply divided underleaves. Scale bar units = $10\text{ }\mu\text{m}$. Onomea, Hawai'i Island, Freire & Judziewicz 19-154c (BISH).



Left: Dorsal view showing leaves obscuring the fragile stem. Leaf lobe cells have prominent intermediate thickenings and some trigones. Note the leaf border of quadrate cells. Center and right: Ventral views. Center: Inflated lobules with rounded apical tooth (arrows). The underleaf lobe adjacent to the leaf is physically connected to the base of the lobule. Right: Note that the lower underleaf appears to have a gap between the lobes, as if they are “separating” (arrow). Scale bar units = 5 μm .

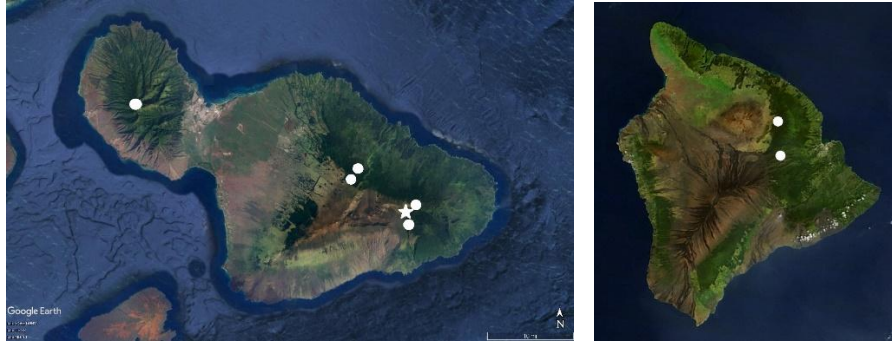


Diplasiolejeunea species 1. Left: Note the irregularly thickened leaf cell walls of the lobules, giving them a sinuous appearance. Scale bar units = 5 μm . Right: Lower portion of plant fragment. Note the styluses and lack of underleaves. Onomea, Hawai‘i Island, Freire & Judziewicz 19-154c (BISH).

Diplophyllum (Dumort.) Dumort. (Scapaniaceae)

Two species in Hawai‘i, 24 species worldwide.

This rare montane genus is found only on Maui and Hawai‘i Island. It is curious that this distinctive genus, which seems to prefer rocks in wet, shady forests and wet cliffs, has not yet been collected on the older main islands (Kaua‘i, O‘ahu, and Moloka‘i).

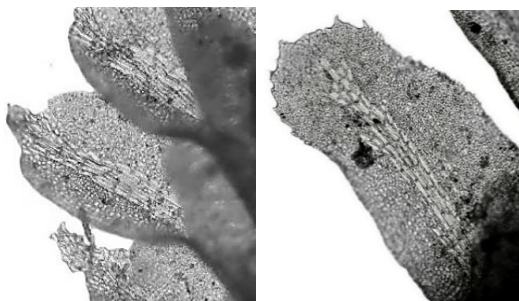


Distribution of *Diplophyllum* on Maui and Hawai‘i Island. Star = *D. albicans*. Circles = *D. exiguum*.

Diplophyllum in Hawai‘i can be green, orange-red or purplish-red. The leaves clasp the stem at their base and spread broadly; they are vittate and bilobed, with the lobes joined by a fold or keel; the ventral lobe is longer than broad and much larger than the dorsal one. Perianths are large and gemmae are frequent. *Diplophyllum* resembles *Scapania*, but in *Diplophyllum* the leaf lobes are vittate, and the ventral lobes are much narrower and longer, at least twice as long as broad, and they spread at or nearly at right angles from the stem.

Miller (1956) noted the possibility that golden plovers (kōlea) might have transported gemmae of this and other liverwort species from boreal Asia or America. We also consulted treatments of *Diplophyllum* by Amakawa & Hattori (1955; for Japan), Schuster (1974; North America), Bakalin & Vilnet (2018; for North and East Asia), and Redfearn (2023; for Flora North America). Sexuality is important in species identification; we did not observe antheridia in Hawaiian material.

1. Ventral leaf lobe with a clearly defined vittae of markedly elongated, linear cells, resembling a midvein; apical leaf margin serrulate ***D. albicans***
1. Ventral leaf lobe with a poorly defined, broad vittae of rectangular cells, not resembling a midvein; apical leaf margin slightly crenulate ***D. exiguum***

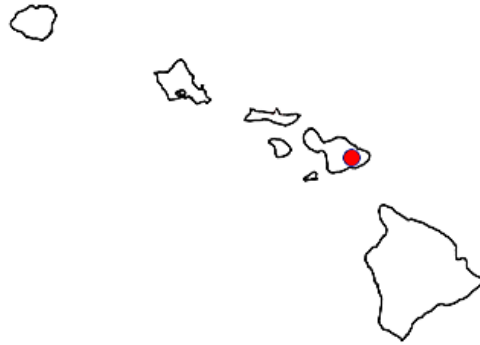


D. albicans



D. exiguum

1. *Diplophyllum albicans* (L.) Dumort. Indigenous. A widespread, mainly boreal, Asian, European, and North American species. A member of subgenus *Diplophyllum* sect. *Diplophyllum* (Söderström et al., 2016). Known only from Haleakalā, Maui (7,200-7,900 ft.): Baldwin 245 in 1876 (MU, YU), Lewis 81-388b in 1981 (F), and Pezzillo 1231 in 2025. This species grows on exposed soil at high altitudes. We did not observe this species in the field. The well-defined vittae of markedly elongate, linear cells (much longer than adjacent cells) that resembles a midvein and extends almost or to the apex, and the serrulate leaf lobe apical margins, are distinctive for this species in Hawai‘i.



Baldwin does not provide specific location or habitat description on his labels (MU, YU). Miller et al. (1983) gave East Maui as the location for Baldwin 245, following Evans (1891: 256), this perhaps (?) based on correspondence or personal communication with the collector. We found *D. albicans* (initially identified by us as *D. exiguum*) intermixed with a collection of *Gymnomitrion* cf. *laceratum* by Lewis; he provides the following collection information: Maui Island, Haleakalā National Park; Kīpahulu Ridge, 7,900 ft., on dirt bank above tree line. This was the only report for this species in Hawai‘i since Baldwin’s collection, until it was recently (2025) collected by Z. Pezzillo (no. 1231), at 7,200 ft., also on the north-south trending ridge separating the Haleakalā summit depression on the west from Kīpahulu Valley to the east.

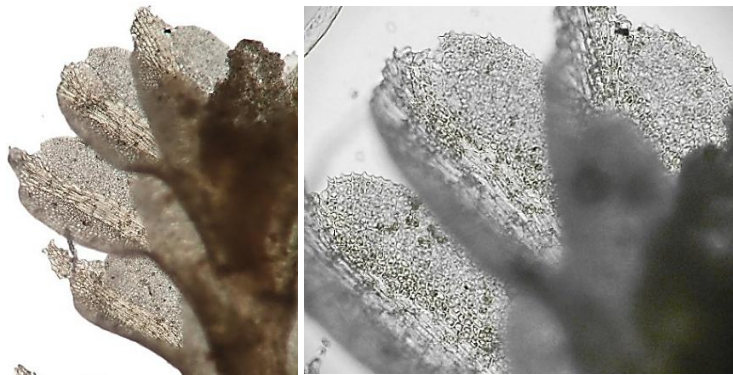
Diplophyllum albicans is reportedly a variable species (Schuster, 1974) with a well-defined vittae of markedly elongated linear cells as the distinctive identifying character. The Baldwin specimen (MU) differs from the Lewis and Pezzillo collections in the following aspects: The plants are narrower, seemingly longer (?), evenly wide (not wider above or “top heavy”), the leaves project more obliquely, are shorter and bend sharply (= “kinked”) where the basal sheath projects from the stem at the base; the ventral lobe is broader in relation to its length, the vittae are frequently exserted into an apiculum, and the dorsal lobes are more acute. We consider these collections as expressions of the variable *D. albicans*, but they are distinct enough to suggest further research to test the possibility of a species complex. The following description reflects the two morphologies combined.

Plants are flattened, some with leaves broader above than on lower parts (“top heavy”); 12-15 mm long and 1.5-2.2 mm broad. Stems robust, sparsely branched. Leaves contiguous to imbricate, sub-opposite, broadly spreading, clasping the stem (“sheathed”) at their base, not extending to its midline, flat to slightly canaliculate. Ventral lobe 2-3 times longer than the dorsal one, both lobes longer than broad, blunt to acute or apiculate at the apex and with a well-defined vittae. Ventral lobe almost squarrose, about 3 times as long as wide. Dorsal lobe spreading at 45° from the stem and about twice as long as wide. Vittae translucent (at least on dry specimens), resembling a midvein, consisting of markedly elongated linear cells in 4-8(?) rows, reaching the upper 1/3 apical portion of the leaf, or extending all the way to its apex, or sometimes exserted. Non-vittate cells quadrate and small. Leaf margins serrulate. Gemmae are present.

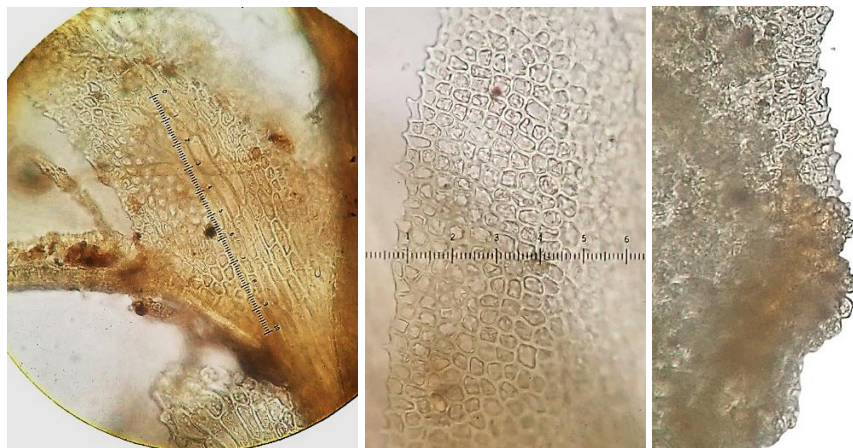
Diplophyllum albicans. All photos on this page: East Maui, Baldwin 245 (MU).



Left: Plant with robust stem. Scale in mm. Right: Detail of the “midvein-like” vittae. Note the apiculate ventral lobe apices, many with exserted vittae. The leaf ventral lobes are canaliculate (concave lengthwise). Photos by A.V. Freire and E.J. Judziewicz.



Left: Note gemmae on plant apex. Right: Vittae cells are much longer than adjacent quadrate cells. Note the serrulate apical margins of the ventral lobes. Photos by A.V. Freire and E.J. Judziewicz.

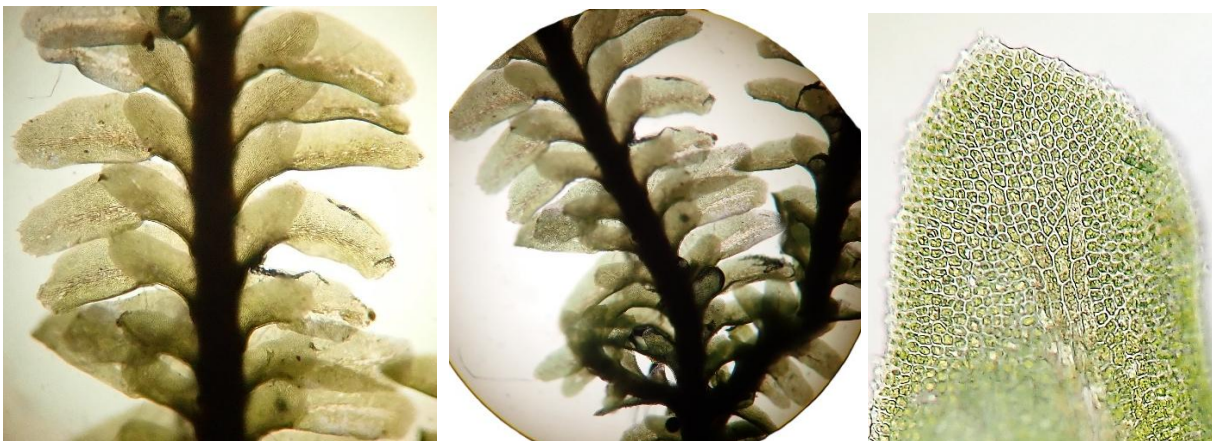


Left and center: Small (dorsal) lobe also has a vitta with markedly elongated cells and a serrulate margin. Scale subunits = 2.5 μ m. Right: Cluster of gemmae on leaf surface and margin. Photos by A.V. Freire.

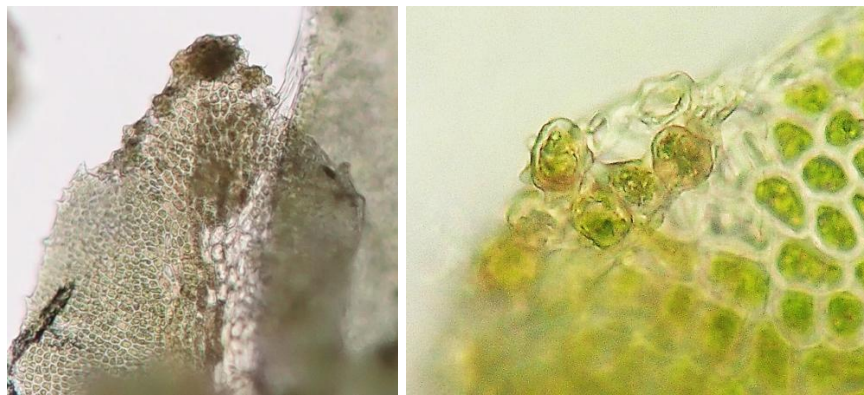
Diplophyllum albicans. All photos on this page: East Maui, Pezzillo 1231 (HALE); photos by A.V. Freire.



Population forms a dense mat, here growing with *Sphenolobus minutus*. Plants are flattened, large, with strong and dark stems. Scales in mm.

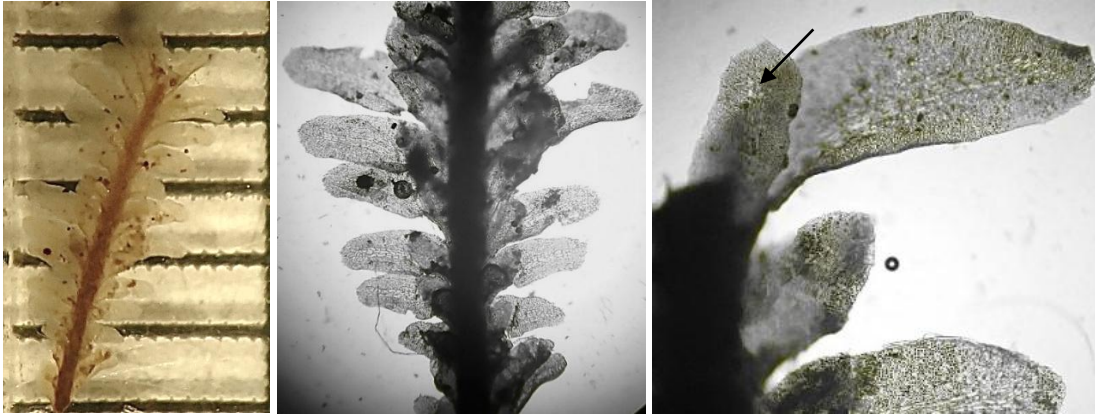


The well-defined vittae give the appearance of translucent midveins. Vittae end shortly before the longer lobe's apex.

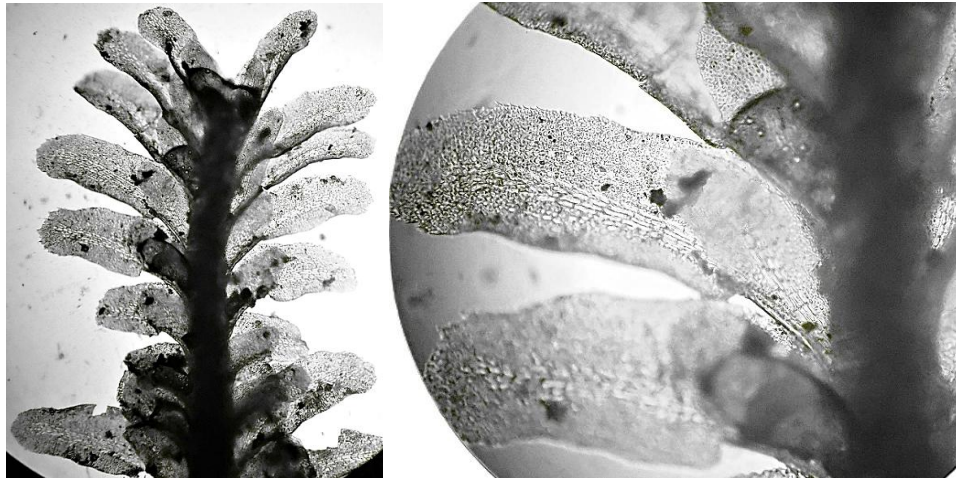


Gemmae are produced on clusters at leaf margins. The gemmae are unicellular, angular, with short, rounded projections.

Diplophyllum albicans. All photos on this page: East Maui, Lewis 81-388b (BISH, F) photos by E.J. Judziewicz.



Left: Plant with robust stem and squarrose leaves. Scale in mm. Center: Plants are “top heavy”, with longer leaves above. Right: Dorsal (small) leaf lobe with vittae (see topmost leaf pointed by an arrow).



Note the broadly spreading, elongate, narrow ventral leaf lobes. Vittae appear translucent to glistening.



Diplophyllum albicans. Left: Ventral leaf lobe. Right: Dorsal leaf lobe. Both have a well-defined vitta and serrulate apical margins. Note the quadrate and much smaller cells of the non-vittate lamina in contrast to the elongated vittae cells.

2. *Diplophyllum exiguum* Steph. Endemic. A member of subgenus *Diplophyllum* sect. *Protodiplophyllum* (R.M. Schust.) Váňa & L. Söderstr. (Söderström et al., 2016). In mixtures with other liverworts or in pure populations (3,000-6,750 ft.). Recorded from Haleakalā, Maui, including several times in Waikamoi Preserve; once on West Maui; and on Hawai'i Island in Hakalau Forest N.W.R. and in the Saddle area. The type was collected by Urbain Faurie at 2,000 m on Mauna Kea, Hawai'i Island. The broad, poorly defined vittae of rectangular cells occupying most of the leaf lobe, and the blunt lobe apices, are distinctive.



Plants are either green, orange-red, or deeply red to purple; loosely attached to the substrate, erect, sub-erect or procumbent; up to at least 6 mm long, 1.5-2.1 mm wide. Stems robust, with some lateral branching (*Frullania* type); subterminal innovations are sometimes associated with the terminal perianths. Leaves broadly spreading, squarrose, contiguous to slightly imbricate, flat, sub-opposite, bilobed, both lobes vittate. The smaller dorsal lobe is rounded, vertically or obliquely spreading, with crenulate margins. The larger ventral lobe is ribbonlike, 3-4 times longer than wide, obtuse, with a broad, poorly defined vitta of rectangular to elliptical cells, usually about 2-3 times longer than wide (but longer near the base); the vitta does not reach the apex. Non-vittate lobe cells are quadrate, thick-walled, and progressively smaller and thicker walled (and dead) towards the margins. Leaf gemmae are single-celled, angular, and produced on apical leaf margins, mainly on younger leaves. Perianths are terminal, long cylindrical, smooth, with a plicate and constricted mouth. Sporophytes are shortly emergent, the capsule dehisces in 4 valves, the elaters have two spirals, and the spores are brown, small, with a triradiate ridge.

Miller (1956) speculated that *D. exiguum* might have been derived from the widespread Holarctic species *D. taxifolium* (Wahlenb.) Dumort. However, *D. taxifolium* has more acute ventral lobes (see figure in Inoue, 1976a: 16-17) than *D. exiguum*. We wonder whether *D. exiguum* might instead be more closely related to *D. obtusifolium* (Hook.) Dumort., another Holarctic species with blunt but broader ventral leaf lobes.



Diplophyllum exiguum. Left: Dense population near small waterfall. Right: Plants with squarrose leaves. Note the ribbonlike ventral lobes with much smaller dorsal ones. Scale in mm. Honomanū Stream, Waikamoi Preserve, Haleakalā, Maui, 6,500 ft., Freire, Judziewicz, Oppenheimer & Pezzillo 23-68 (BISH).



Population of green plants. The brown to colorless plants are senescent. Scale in mm. Waikamoi Preserve, Haleakalā, Maui, 6,500 ft., Freire, Judziewicz, Oppenheimer & Pezzillo 23-155 (BISH). Photo by A.V. Freire.



Diplophyllum exiguum. Purple to orange-red plants. Left: In matrix of *Kurzia hawaica*, *Mnioloma fuscum*, and *Cephaloziella kiaeri*, Saddle area, Hawai'i Island, Freire & Judziewicz 22-924 (BISH). Right: Waikamoi Preserve, Haleakalā, Maui, 6,500 ft., Freire, Judziewicz, Oppenheimer & Pezzillo 23-68 (BISH). Photo by Zach Pezzillo.



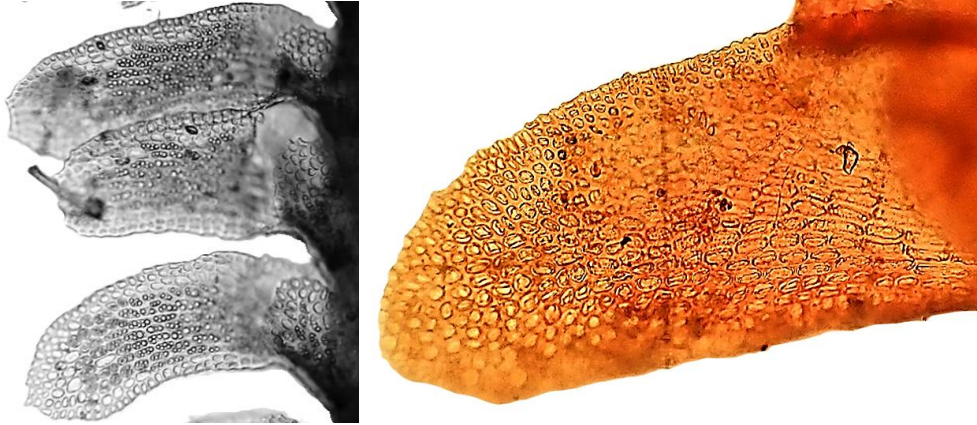
Left: Plant with distant, ribbonlike leaves and a lateral branch; scale in mm. Waikamoi Preserve, Haleakalā, Maui, 6,500 ft., Freire, Judziewicz, Oppenheimer & Pezzillo 23-155 (BISH); photo by A.V. Freire. Center: Plant with broader, imbricate leaves. Scale in mm. Right: Note squarrose leaves and abundant algal associates. Freire & Judziewicz 22-924 (BISH).



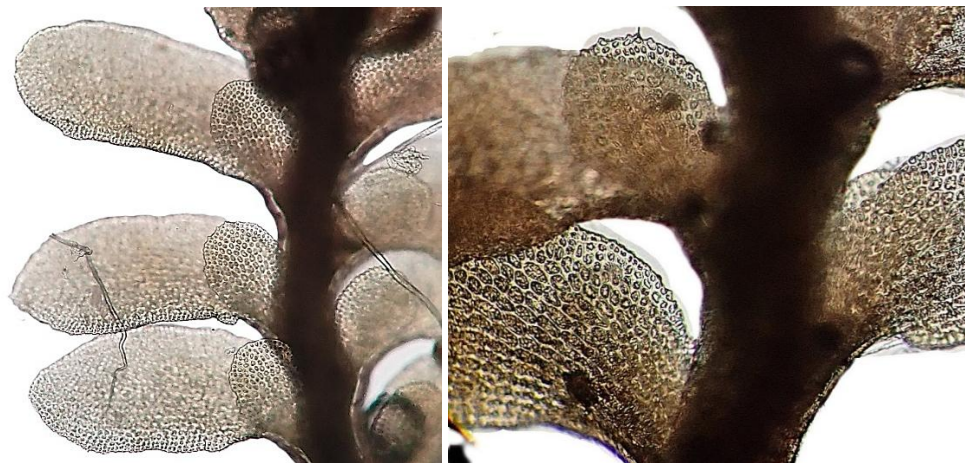
Left and right: Plant with subterminal innovations associated with the perianth. Right: Plant with lateral branching. Hakalau Forest National Wildlife Refuge, Hawai‘i Island, Freire & Judziewicz 23-191 (BISH).



Diplophyllum exiguum. Left: Squarrose leaves with crenulate margins and small, thick-walled cells enclosing the poorly developed vittae; Hakalau Forest National Wildlife Refuge, 6,500 ft., Hawai‘i Island (this population may be close to Faurie’s type locality), Freire & Judziewicz 23-191 (BISH). Right: Broad vittae with living cells. Note the thick-walled and progressively smaller non-vittate dead cells. Saddle area, Hawai‘i Island, Freire & Judziewicz 22-924 (BISH).



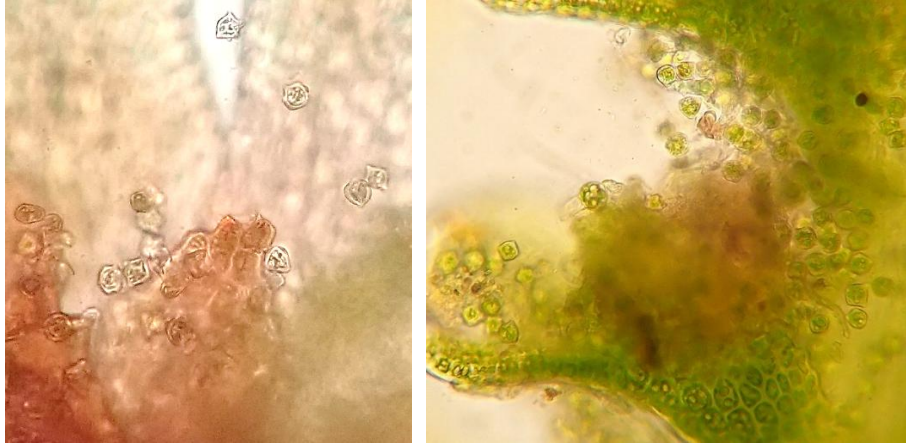
Leaf vittae are broader and more indistinct than in *D. albicans*, and do not reach to the leaf apex. Left: Saddle area, Hawai'i Island, Freire & Judziewicz 22-926 (BISH). Right: Haleakalā, Maui, Forbes 1585 (BISH). Photo by E.J. Judziewicz.



Small dorsal lobes with blunt, rounded apices, crenulate margins, and a vittate region. Hakalau Forest National Wildlife Refuge, Hawai'i Island. Freire & Judziewicz 23-191 (BISH).



Diplophyllum exiguum. Gemmae on the apical margins of younger leaves. Saddle area, Hawai'i Island, Freire & Judziewicz 22-924 (BISH).



Angular, single-celled gemmae. Left: Saddle area, Hawai‘i Island, Freire & Judziewicz 22-924 (BISH). Right: Waikamoi Preserve, Haleakalā, Maui, 6,500 ft., Freire, Judziewicz, Oppenheimer & Pezzillo 23-155 (BISH).



Left: Population with large, terminal, tubular perianths (arrows). Right: Perianth with shortly exserted and dehiscent capsule. Freire & Judziewicz 23-191 (BISH).



Diplophyllum exiguum. Tubular perianth with plicate, constricted mouth. Left: Wai‘ānapanapa, Haleakalā, Maui, Stemmermann 2461 (BISH). Photo by E.J. Judziewicz. Right: Hakalau Forest National Wildlife Refuge, Hawai‘i Island, Freire & Judziewicz 23-191 (BISH).

***Drepanolejeunea* (Spruce) Steph. (Lejeuneaceae)**

Five species in Hawai‘i, 128 species worldwide.

All named Hawaiian species are apparently members of subgenus *Drepanolejeunea* (Söderström et al., 2016: 353-358). These tiny (typically 0.3-0.7 mm wide, or occasionally up to 1 mm wide) trailing or creeping, epiphytic or epiphyllous plants are loosely attached to their substrate. The leaves are often cupped, with scattered or row-forming ocelli on the lobes; the lobules are inflated and toothed; the underleaves are small and bifid, with narrow, divergent to parallel lobes. The publication by Evans (1900) is the most recent treatment for this genus in Hawai‘i. *Drepanolejeunea pseudoneura*, formerly placed in this genus (Staples & Imada, 2006), is a member of *Vitalianthus* (Judziewicz & Freire 2023c).



Drepanolejeunea epiphytic on the moss *Pyrrhobryum pungens*. Ko‘olau Range, O‘ahu, May 2023. Photo by Miles K. Thomas, with permission.

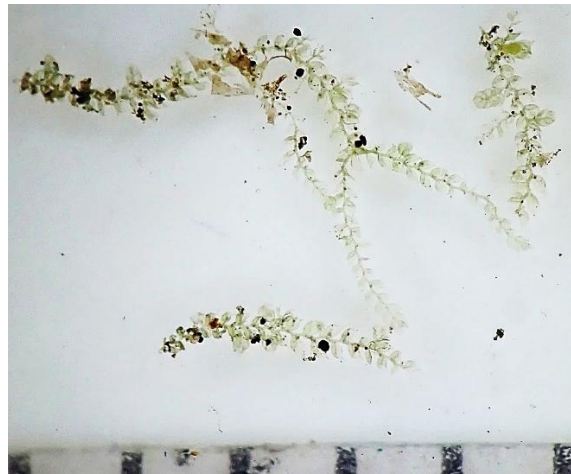
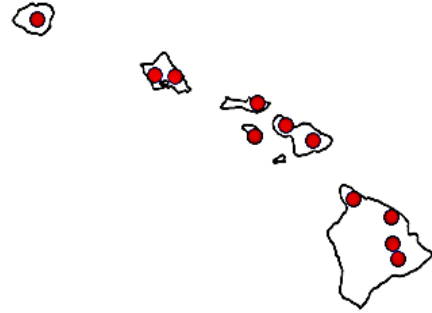
1. Leaf lobes entire or nearly so, without prominent teeth (although 1-2 small, blunt marginal teeth may be present) 2
 2. Lobes acute or some acuminate; ocelli dark and granular; common ***D. anderssonii***
 2. Lobes truncate; ocelli light and crystalline; uncommon ***D. species 1***
1. Leaf lobes with one to several prominent teeth 3
 3. Lobes with one or two large, reflexed lateral teeth; uncommon, Hawai‘i Island ***D. species 2***
 3. Lobes with teeth ascending or spreading but never reflexed 4
 4. Lobes with a clearly dominant and conspicuously falcate apical tooth that curves up; ocelli amber-colored; rare, O‘ahu ***D. pentadactyla***
 4. Lobes lacking a clearly dominant nor conspicuously falcate apical tooth; ocelli dark; widespread....
..... ***D. unguolata***



D. anderssonii* *D. pentadactyla* *D. unguolata* *D. species 1* *D. species 2

1. *Drepanolejeunea anderssonii* (Ångstr.) A. Evans.

Endemic. Found on all major islands (1,500-6,160 ft.). A common bark epiphyte, sometimes on canopy branches and phyllodes of *Acacia koa*; occasionally an epiphyll. Plants are less than 0.5 mm wide but several mm long, light green, creeping; stems are slender, long, irregularly and frequently branched. Leaves are distant to contiguous, slightly concave, ovate and acute (resembling “elves’ ears”), spreading at 45° angles, with entire margins although 1-2 small blunt teeth may be present on the lobe’s upper margin. Leaf lobes with 2-6 dark (black, gray to brown) and granular ocelli, these single or paired, scattered or forming a single, central vertical row of (2)3-5, separated vertically by 2(3) chlorophyllous cells; apical ocelli can be paired. Lobules are ovate, inflated, inrolled, more than ½ the lobe’s length, with a large and curved apical tooth. Some branch lobules may be underdeveloped. Underleaves are distant, deeply bifid, usually with divergent but sometimes parallel linear lobes. Plants are monoicous, with androecia and gynoecia produced on lateral branches. Antheridial branches are compressed, ovate, with 3-4 pairs of globose, imbricate bracts. Perianths with one basal innovation, turbinate, truncate, keeled, each keel with a distal projection, giving the perianth a “horned” look.



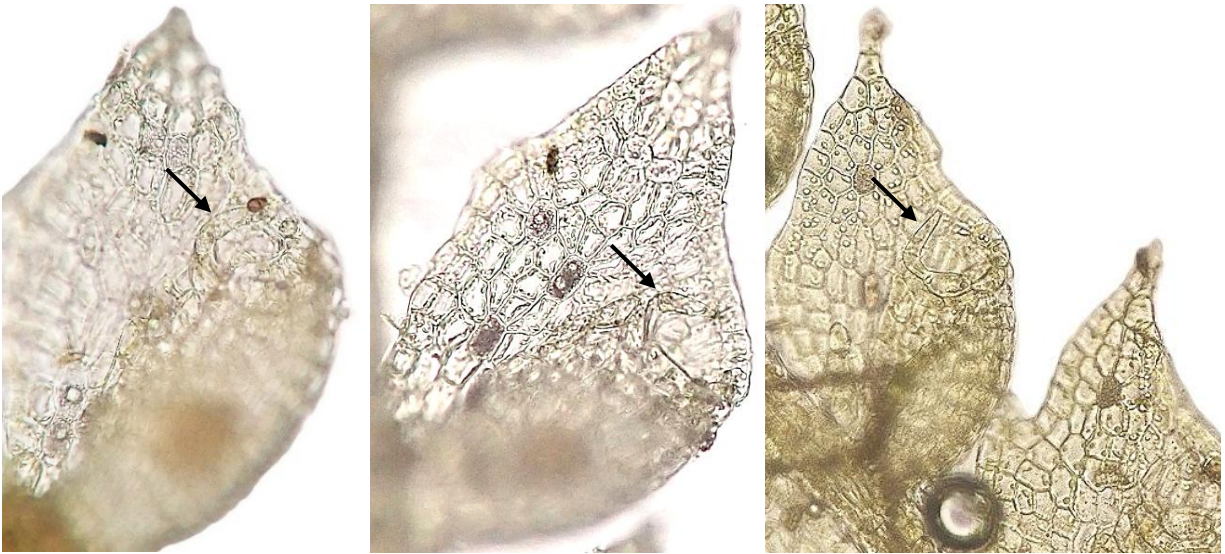
Left: Epiphyllous plants closely appressed to their substrate. Right: Plants are frequently branched and can be several mm long. Scales in mm. Volcano, Hawai‘i Island, Freire & Judziewicz 22-912a (BISH).



Drepanolejeunea anderssonii. Plant with acute leaves resembling “elves’ ears”. Scale = 1 mm. Volcano, Hawai‘i Island, Freire & Judziewicz 20-504a (BISH).



Left: Plants are often branched, Freire & Judziewicz 22-912 (BISH). Center: Plant with acute leaves, inrolled and inflated lobules, and ocelli. Right: Note bifid underleaf with divergent lobes (blue arrow), inflated lobules with curved apical tooth (red arrow), occasional blunt teeth on upper margin of lobes (black arrow), and scattered dark ocelli. Volcano, Hawai'i Island, Freire & Judziewicz 20-504 (HAVO).



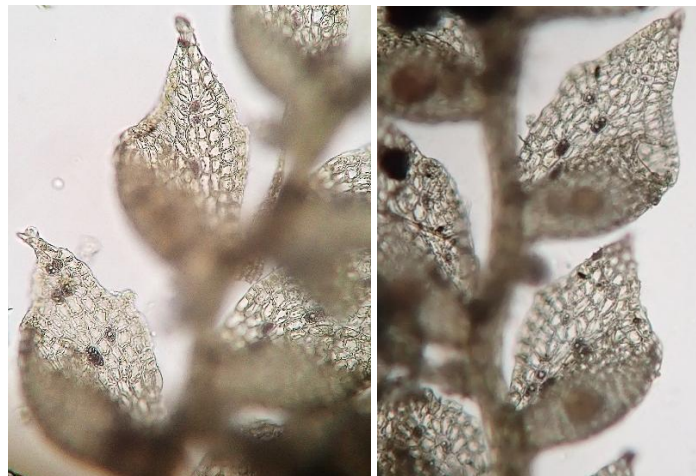
Drepanolejeunea anderssonii. Left and center: Curved lobule tooth (arrows); note scattered ocelli (center), Volcano, Hawai'i Island, Freire & Judziewicz 22-912 (BISH). Right: Some lobular teeth may be straight. Hawai'i Island, photo by Daniel Tucker, <https://www.inaturalist.org/observations/257409051>, with permission.



Branches may have some underdeveloped leaf lobules close to their origin (arrows). Freire & Judziewicz 22-912 (BISH).



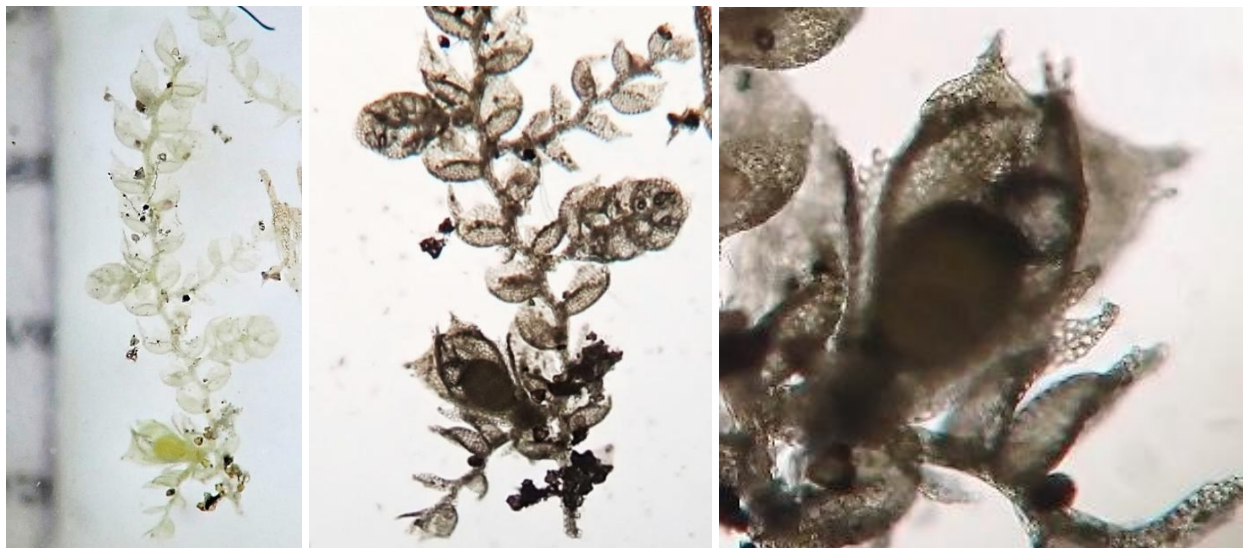
Left: Underleaves have divergent linear lobes. Center: Some underleaves with parallel lobes may be present, Freire & Judziewicz 22-912 (BISH). Right: Underleaves with parallel lobes are frequently observed on branches, Volcano, Hawai'i Island, Freire & Judziewicz 20-504 (HAVO).



Drepanolejeunea anderssonii. Ocelli are scattered on leaf lobes, Volcano, Hawai'i Island, Freire & Judziewicz 22-912 (BISH).



Left and center: Some plants may have a central row of 2-3 ocelli, Volcano, Hawai'i Island, Freire & Judziewicz 23-339 (BISH). Right: Ocelli either arranged in a central row, or scattered, may be observed on the same plant. Photo courtesy of Daniel Tucker, <https://www.inaturalist.org/observations/257409051>, Hawai'i Island.



Drepanolejeunea anderssonii. Left: Plants are monoicous. Scale in mm. Center: Plant with compressed antheridial branches and a turbinate, horned perianth. Note perianth's basal innovation. Right: Detail of horned and keeled perianth, Volcano, Hawai'i Island, Freire & Judziewicz 22-912 (BISH).

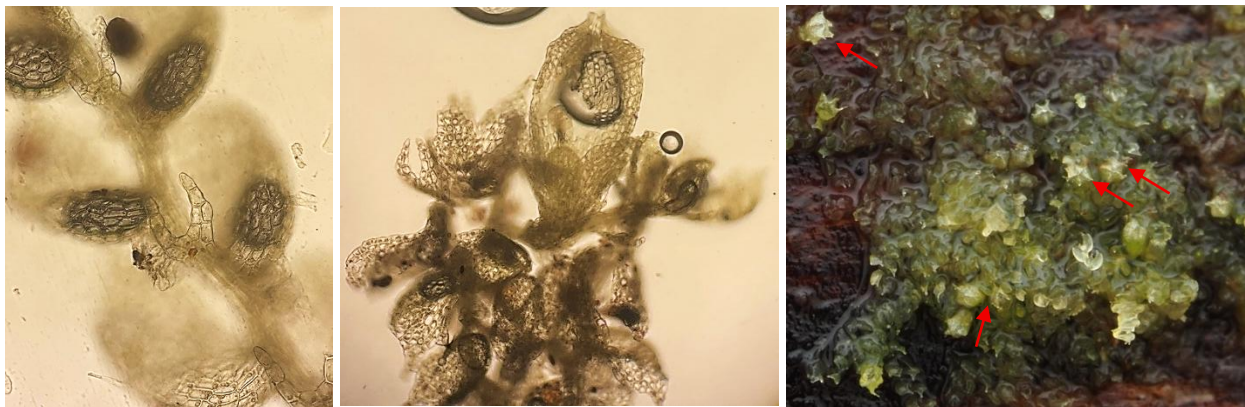
***Drepanolejeunea cf. anderssonii*.**

Some Hawaiian populations have erect rather than spreading leaves that are more concave; the leaf lobes are shorter, and small marginal teeth may be present.

Example 1: Daniel Tucker photographed and collected populations of *Drepanolejeunea* in the Saddle area and in Pu‘u Maka‘ala N.A.R., Hawai‘i Island, and noted their interesting features, (<https://www.inaturalist.org/observations/258098080>), and (<https://www.inaturalist.org/observations/255706095>). We did not study these specimens, but judging by his photos, they resemble *D. anderssonii*. We agree that the leaf lobes are smaller and more concave than in typical populations. His perianth image shown below does not have the characteristic “horns” of *D. anderssonii*; however, the *in situ* shot shows perianths that appear horned. The specimens are interesting and need detailed study.

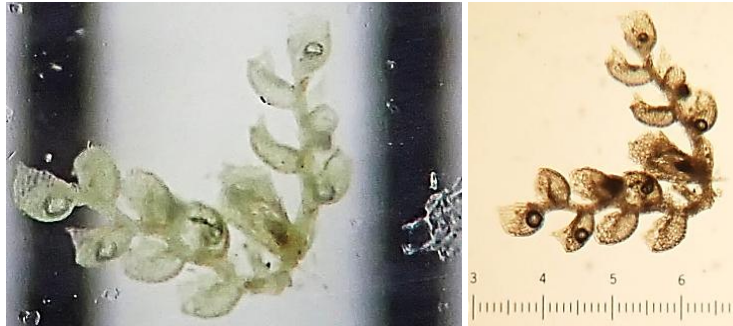


Left: Epiphytic population growing on bark. Center: Leaves are erect and concave. Right: Leaf apices are acuminate and ocelli are dark. Hawai‘i Island, Pu‘u Maka‘ala N.A.R. Photos by Daniel Tucker, with permission: <https://www.inaturalist.org/observations/255706095>.



Left: Underleaves with parallel to distant lobes as in *D. anderssonii*. Center: Perianth without horns. Right: Detail of perianths; some appear to be “horned” (arrows). Hawai‘i Island, Pu‘u Maka‘ala N.A.R. Photos by Daniel Tucker, with permission: <https://www.inaturalist.org/observations/255706095>

Example 2: This specimen from Pihea Trail, Kaua‘i (Ma et al. 14-5895, PTBG) has smaller, more concave and erect lobes, and serrulate or dentate margins.



Plants are tiny. Left: Scale = 1 mm, Right: Scale units = 26 μ m. Photos by A.V. Freire.



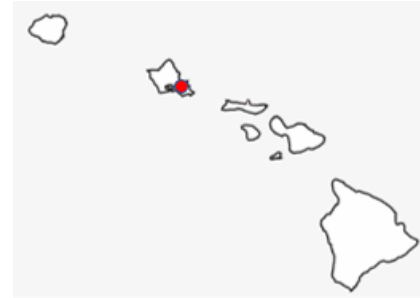
Plants have prominent leaf lobules and reduced lobes. Ocelli are dark, granular and scattered or form a poorly defined row. The perianth bracts are toothed (left). Photos by A.V. Freire.



Drepanolejeunea cf. *anderssonii*. Underleaves are small, bifid, with short and parallel linear lobes. Photos by A.V. Freire.

2. *Drepanolejeunea pentadactyla* (Mont.) Steph.

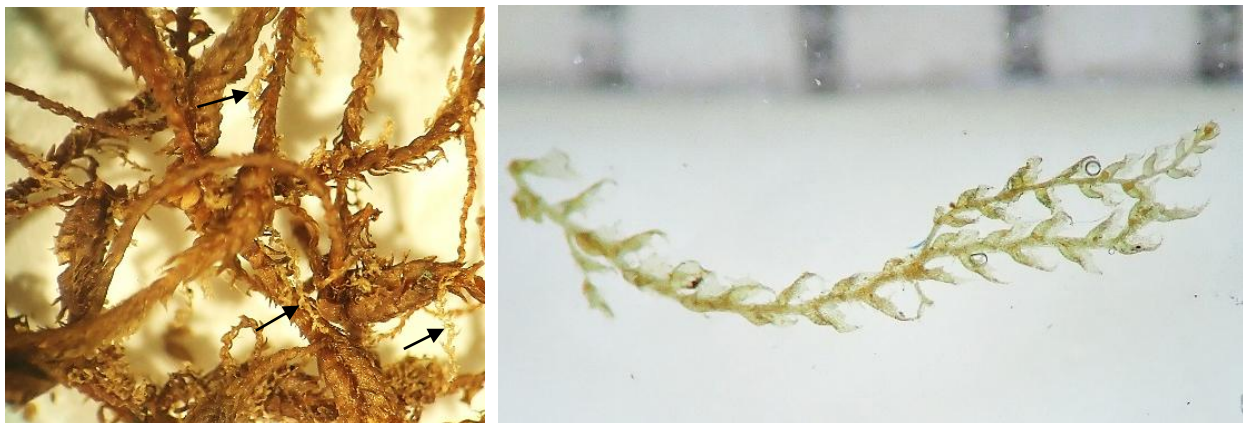
Indigenous Rare, also present in tropical Asia, Australasia, and New Caledonia. First report for Hawai‘i: Judziewicz & Freire (2023c: 163); O‘ahu (Ko‘olau Range). Elevation 2,000 ft; twining on *Herbertus gracilis*. Includes the report of *D. micholitzii* Steph. by Smith et al. (1997) from Hawai‘i, det. by P. Tixier (but with no voucher cited), this name considered a synonym of *D. pentadactyla* by Grolle (1991), Thouvenot et al. (2011), and Pócs et al. (2019).



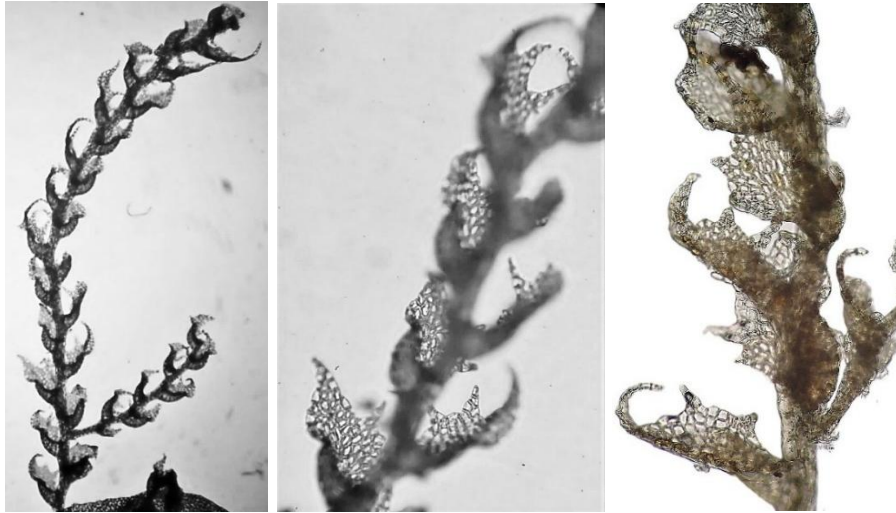
The narrow leaf lobes with a large linear-triangular and usually up-curved apical tooth; the smaller and irregular lateral teeth (mainly on the upper lobe margin); the tightly inrolled and curved lobules; and the amber-colored ocelli are distinctive for this species in Hawai‘i and separate it from the similar *D. unguolata*.

Our description below is based only on the 1933 collection made in Kīpapa Gulch, Ko‘olau Range, O‘ahu (Hosaka 951, BISH). This specimen differs from *D. pentadactyla* descriptions in the up-curved rather than plane lobe apex. This difference can be an extreme in the spectrum of this polymorphic species; the plants we studied resemble the drawings by Herzog (1934; reported as the synonym *D. micholitzii* by Pócs et al. (2019)). The characteristic four elongate, rectangular cells on the upper border of the lobule, reportedly useful to identify this species, are present. The showy amber color of the ocelli we observed is not reported in the literature.

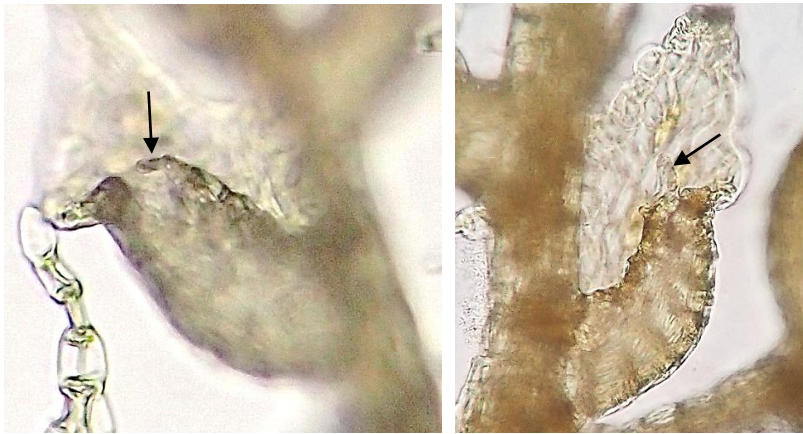
Plants are epiphytic on bryophytes and are loosely attached to their substrate; they are tiny, ca. 0.3 mm wide. Stems are flexuous, occasionally branched. Leaves are distant, concave, spreading at 45°, irregularly shaped but mostly narrowly triangular, with at least four teeth, these irregular in shape and size, with the apical tooth (usually the one closest to the leaf lobule) long and falcate (upcurved) and considerably larger than the other teeth. Lobules are inflated, tightly in-rolled, triangular-ovate, with a curved keel, about ½ the lobe length, with a long apical tooth that can be curved or straight. Leaf cells are elongate, rectangular, square to triangular, with thick walls, and lack trigones. Ocelli are amber-colored, in groups of 3-4(5), scattered or forming a weakly defined row. Underleaves slightly broader than the stem, bifid, with a lunate sinus and divergent lobes, these connivent on younger portions of stems.



Drepanolejeunea pentadactyla. Left: Tiny plants (arrows) are epiphytic on *Herbertus gracilis* Right: Leaves spread at about 45° from the stem; scale in mm. O‘ahu, Hosaka 951 (BISH), photo by A.V. Freire.



Leaves with a prominent, upcurved, falcate apical tooth. Smaller adjacent teeth of different sizes are also present. Hosaka 951 (BISH), photos by E.J. Judziewicz and A.V. Freire.



Leaf lobules are tightly inrolled and inflated. They have a curved keel and an apical tooth (arrows). Hosaka 951 (BISH). Photos by A.V. Freire.



Drepanolejeunea pentadactyla. The lobule's free margin is bordered by four elongate rectangular cells (arrows). Kīpapa Gulch, Ko'olau Range, O'ahu, Hosaka 951 (BISH). Photos by A.V. Freire.



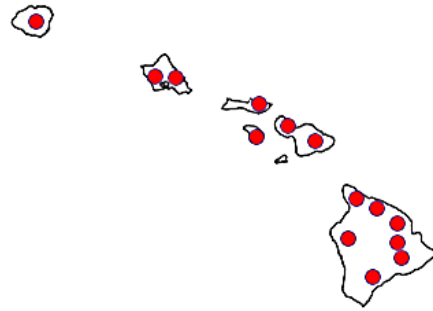
Ocelli are amber colored, conspicuous, and usually clustered in small groups. Note the thick-walled leaf cells of irregular shapes. Hosaka 951 (BISH). Photos by A.V. Freire.



Drepanolejeunea pentadactyla. First and second photos: Underleaves are small and distant. Third and fourth photos: Underleaves are small, bifid, usually with divergent lobes, but sometimes connivent (third picture). Kīpapa Gulch, Koʻolau Range, Oʻahu, Hosaka 951 (BISH). Photos by E.J. Judziewicz and A.V. Freire.

2. *Drepanolejeunea ungulata* (Steph.) Grolle. Endemic.

An abundant bark epiphyte but occasionally an epiphyll. The leaves, with clawlike ascending to spreading teeth, are distinctive. Possible closest relatives (Evans, 1900): *D. tridactyla* (Gottsche) Steph. (tropical Asia) and *D. palmifolia* (Nees) Schiffn. (tropical South America; Bishler, 1964: 99-104). In the latter species the ventral leaf margin is entire and the terminal teeth is elongate and greatly decurved. See also Grolle (1991). Found on all major islands (1,700-6,160 ft.).



Flynn 9847 (Judziewicz et al., 2025b: 138) from Kaua'i was cited as *D. pentadactyla* but is better referred to *D. ungulata* and is included in this treatment. Plants are tiny, less than ½ mm wide, light green, loosely appressed to their substrate. Stems are flexuous, moderately branched. Leaves are erect-spreading, concave, distant to contiguous, acuminate, with a large apical tooth and 2(3) large teeth mainly on the upper margin. The teeth are multicellular, 4-6 cells long, close to uniform in size, but the apical tooth is slightly larger and may curve up slightly. Occasionally, 1-2 additional teeth may be present. Ocelli are dark, granular, scattered or forming a row of 2(3) separated by 1-2 chlorophyllous cells; often they are paired close to the apex. Leaf cells are mainly rectangular, without trigones. Lobules inflated, large, over ½ the lobe length, loosely or tightly inrolled, with a curved apical tooth and bulging cells. The lobule's upper margin is bordered by 5-6 quadrate cells. Underleaves are about 1.5 times broader than the stem, with triangular to linear lobes that are divergent but sometimes connivent.



Epiphyllous population. Scale in mm. Volcano, Hawai'i Island, Freire & Judziewicz 22-912b (BISH).



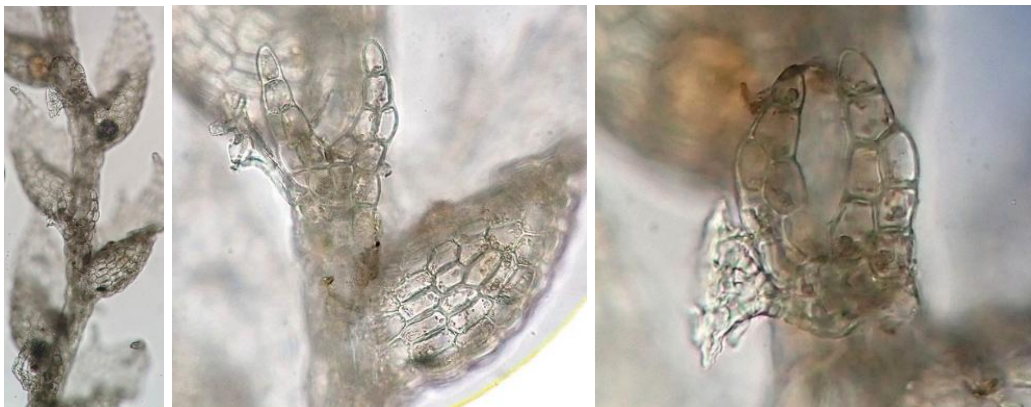
Drepanolejeunea ungulata. Here growing as an epiphyte on *Bazzania cordistipula*. Right: Scale in mm. Kaua'i (Hā'upu Range), Flynn 9847b (PTBG). Photos by A.V. Freire.



Leaves with long and coarse claw-like, uniform teeth. Ocelli are scattered or form a central row. Right: Detail of granular and dark ocelli. Left: Volcano, Hawai'i Island, Freire & Judziewicz 20-475 (HAVO). Photos 2, 3 and 4: Flynn 9847b (PTBG); photos by A.V. Freire.

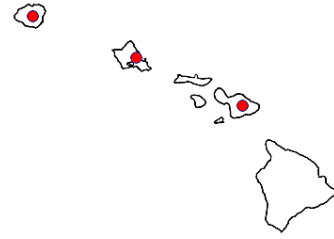


Lobules are long and inflated with a curved apical tooth (arrows). Flynn 9847b (PTBG); photos by A.V. Freire.



Drepanolejeunea unguolata. Underleaves are slightly broader than the stem. They have two lobes that can vary from divergent to parallel or connivent. Hā'upu Range, Kaua'i, Flynn 9847b (PTBG); photos by A.V. Freire.

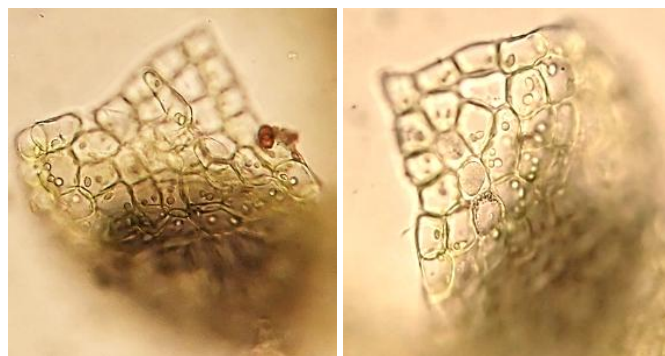
4. *Drepanolejeunea* species 1. Indigenous. Found on Kaua'i, O'ahu and Maui, in montane forests from 4,000-6,500 ft. This epiphytic, tiny species is sometimes found growing on larger liverworts including *Cuspidatula labrifolia*. It resembles the common *D. anderssonii*, but differs from it in the truncate leaves with lobules almost as large as the lobes, and in the crystalline-looking ocelli forming a lateral row.



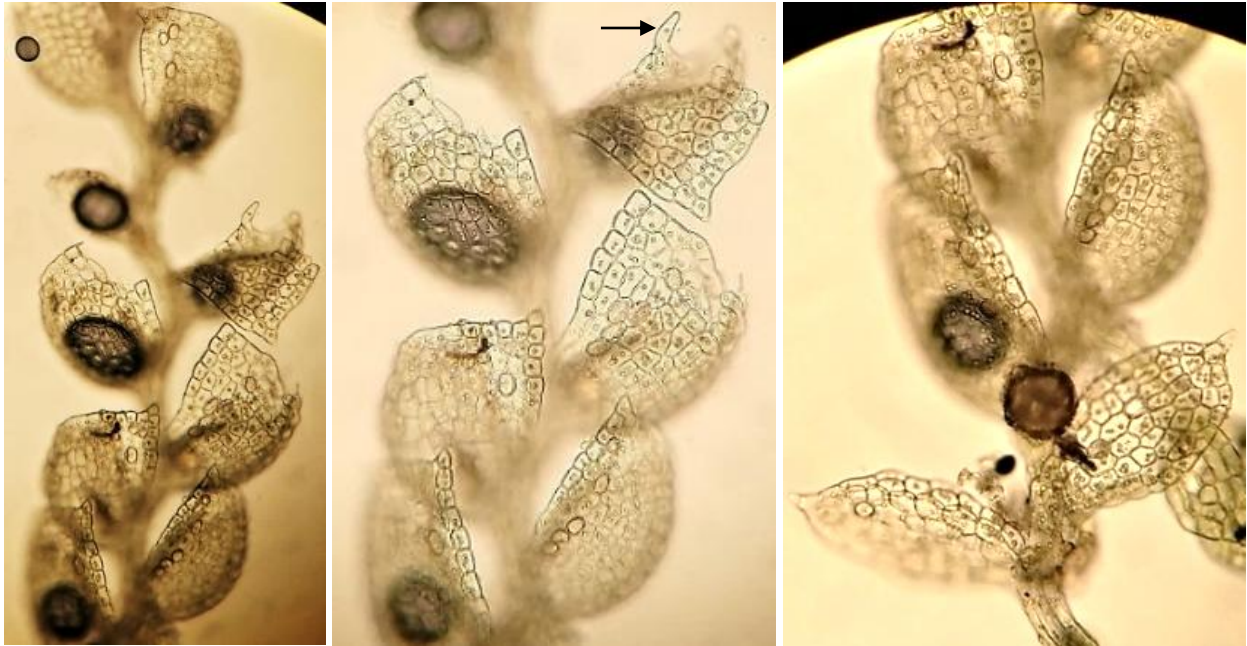
Plants are about 0.4 mm wide. Stems are fragile, with a hyalodermis-like clear area on either side (pending confirmation; a hyalodermis is not supposed to be present in *Drepanolejeunea*). Leaf lobes are truncate, with an off-center 90° angle where the flattened top joins the lateral margin; some can be apiculate. The lobules are large, almost the same size as the lobe; they have a prominent and erect tooth. The lower leaves often lack lobules; they are apiculate, concave, and elliptical. Ocelli are shiny, smooth and crystalline in appearance, arranged in a lateral row close to the lobe's free margin. Leaf cells are thin-walled, but some have small trigones. Underleaves are small and bifid, with two mainly parallel linear lobes.



Left and center: Leaves are concave and truncate with an 90° off-center angle. Center and right: Lobules are almost as large as the leaf lobe. Haleakalā, Maui, 6,500 ft., Freire, Judziewicz, Oppenheimer & Pezzillo 23-52 (BISH); photos by E.J. Judziewicz.



Drepanolejeunea species 1. Left, showing erect, fang-like lobular tooth. Right: Ocelli. Haleakalā, Maui, 6,500 ft., Freire, Judziewicz, Oppenheimer & Pezzillo 23-89 (BISH); photos by E.J. Judziewicz.



Ocelli are crystalline and smooth, forming a row close to the lobe's free margin. Left: Leaf lobes have broadly pointed to apiculate apices and no lateral teeth. Center: Lobules are large, with an erect tooth (arrow). Right: Basal leaves (branch leaves?) lack lobules. Pu'u Ka'ala, O'ahu, Thomas et al. (including Freire & Judziewicz) 507 (BISH); photos by E.J. Judziewicz.



Drepanolejeunea species 1. A clear, hyalodermis-like area can be seen at either side of the stem. Haleakalā, Maui, 6,500 ft., Freire, Judziewicz, Oppenheimer & Pezzillo 23-89 (BISH); photo by E.J. Judziewicz.

5. *Drepanolejeunea* species 2. Indigenous. Found on Hawai‘i Island, at elevations from 3,500-5,800 ft. This tiny species resembles the common *D. unguolata*, but the lower teeth on the leaf lobes are horizontally divergent to reflexed, giving the leaves a bur-like or caltrop-like aspect. We collected this species in Volcano. It was also recorded from the Saddle Area and recognized as novel by Daniel Tucker: <https://www.inaturalist.org/observations/255994555>.



See also his extensive comments on this observation from the Pu‘u Maka‘ala N.A.R., also Hawai‘i Island: <https://www.inaturalist.org/observations/255707847>.

Although this species closely resembles *D. unguolata*, and could be considered a variant of it, the perianths are clearly distinct from each other. The perianths of *D. unguolata* are described by Evans (1900) as with “...keels running out into acute or acuminate almost horizontal horns or processes...”, his drawing shows short, stout outgrowths that do not resemble the long and showy, multicellular and horizontal scales projecting from the keels photographed by Tucker for species no. 2 (see below).

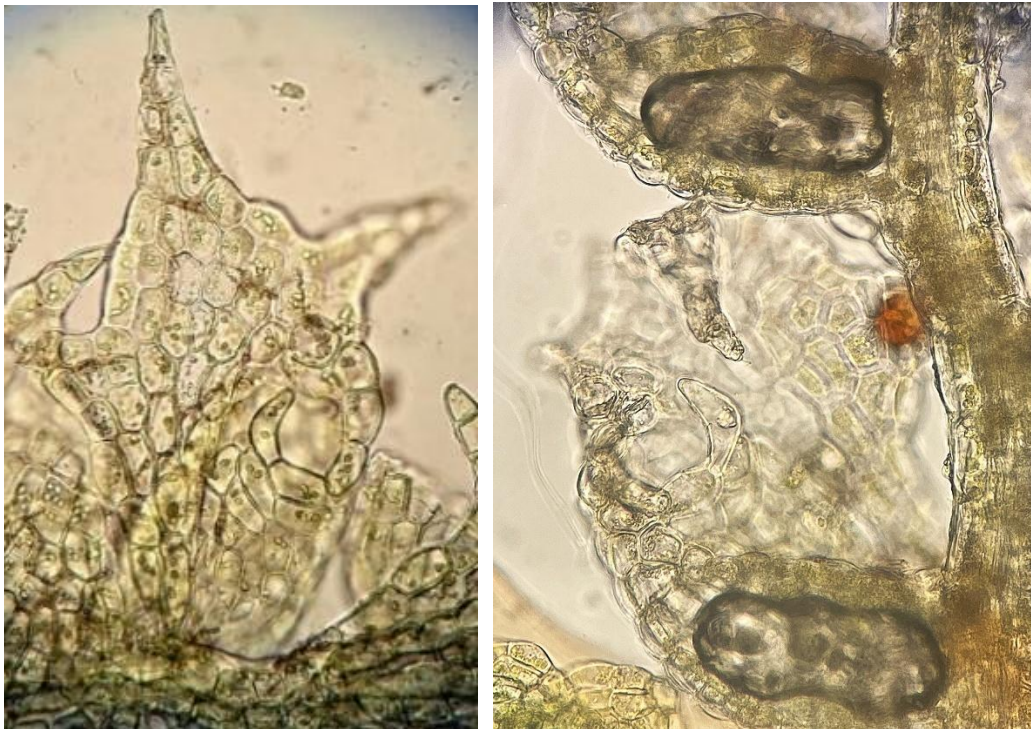
Plants are epiphytic, tiny, less than 0.5 mm wide but can be several mm long (up to 20 mm, or perhaps longer); light to yellow-green, frequently and irregularly branched; they creep loosely appressed to their substrate. Stems are flexuous, with a hyalodermis-like clear area. Leaves are contiguous to overlapping, concave, projecting from the stem at 45° angles or less. Leaf lobes are ovate, acute, with a triangular apical region, with (2)3 or more prominent marginal teeth, one at the apex, the others lateral and sharply projecting at 90° angles or reflexed. Leaf cells are thin-walled and may have small trigones. Ocelli are dark, granular, usually arranged in a row with two side-by-side close to the apex; they can also be scattered. Underleaves are small, just slightly broader than the stem, bifid, with linear lobes very to slightly divergent or parallel. The perianth is obovate, truncate, beaked, keeled(?), adorned with long, acuminate, triangular and multicellular scales that project horizontally from the keels. [The perianth and other characters included in this description are based only on images].



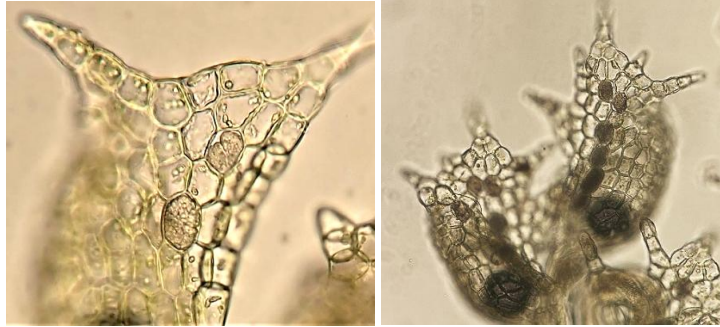
***Drepanolejeunea* species 2.** Left: Epiphyllous population. Hawai‘i Island, Saddle area; photo by Daniel Tucker with permission: <https://www.inaturalist.org/observations/255994555>. Right: Population on bark. Scale in mm. Volcano, Hawai‘i Island, Freire & Judziewicz 23-336 (BISH).



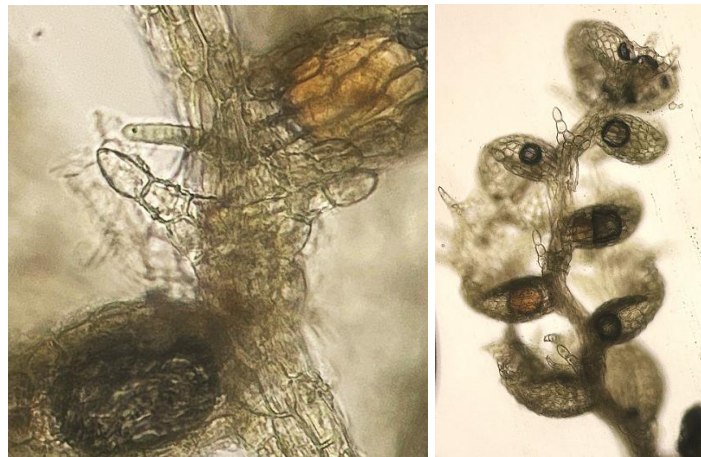
Leaves with dentate lobes. The lower teeth project at 90° or are reflexed. Left and center: Volcano, Hawai'i Island, Freire & Judziewicz 23-336 (BISH). Right: Note dark ocelli. Saddle area, Hawai'i Island, photo by Daniel Tucker, with permission: <https://www.inaturalist.org/observations/255994555>.



Drepanolejeunea species 2. Lobule tooth curved. Left: Volcano, Hawai'i Island, Freire & Judziewicz 23-336 (BISH). Right: D. Tucker photo, with permission: <https://www.inaturalist.org/observations/255707847>.



The dark and granular ocelli are usually arranged in a row but can also be scattered. Left: Volcano, Hawai'i Island, Freire & Judziewicz 23-336 (BISH). Right: Saddle area. Hawai'i Island; photo by Daniel Tucker, with permission. <https://www.inaturalist.org/observations/255707847>.



Underleaves are small, bifid, with divergent to parallel lobes. Photos by Daniel Tucker, with permission: <https://www.inaturalist.org/observations/255994555>. <https://www.inaturalist.org/observations/255707847>.



Drepanolejeunea species 2. Perianth with showy triangular scales projecting horizontally. Saddle area, Hawai'i Island; photos by Daniel Tucker, with permission: <https://www.inaturalist.org/observations/255707847>.

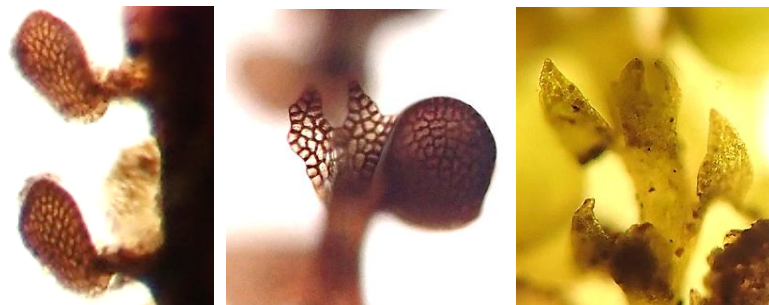
Frullania Raddi (Frullaniaceae)

At least ten species in Hawai‘i, 616 species worldwide.

Frullania is an abundant, epiphytic genus, usually occurring on tree bark. It is found in both open and closed canopy forests. The genus is distinguished by its often deep reddish-brown color, complicate-bilobed incubous leaves with prominent bifid underleaves, and especially by its usually inflated water sacs that can be cylindrical (clavate) or helmet-shaped (galeate); sessile and non-inflated (explanate) water sacs are observed in some species. With practice the species can be easily distinguished in the field with a hand lens. *Frullania apiculata*, *F. hypoleuca*, and *F. meyeniana* are among the top seven most frequently observed indigenous Hawaiian leafy liverwort species reported on iNaturalist. Evans (1900), So & Wang (2006), Miller (1953 and unpublished notes), and our observations, were the basis for this treatment.

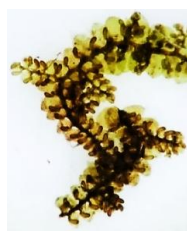
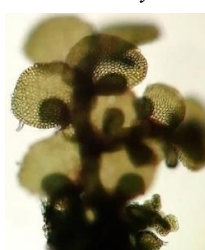


Frullania meyeniana (dark red, left) and *F. hypoleuca* (greenish, right), are pinnately branched and grow closely appressed to their substrate as is typical for the genus. Hualālai, Hawai‘i Island, Photo by Kevin Faccenda, with permission (<https://www.inaturalist.org/observations/196235030>).

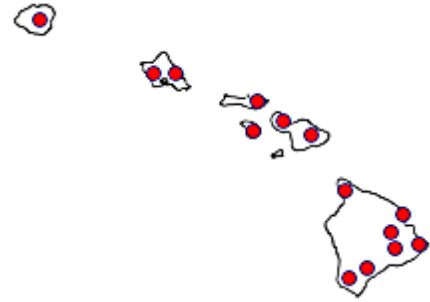


Types of leaf lobules (water sacs) found in *Frullania*: Left: Clavate (cylindrical), at least two times longer than wide. Center: Galeate, “helmet-shaped”, about as long as broad. Right: Explanate, not inflated.

1. Underleaves barely wider than stem; leaf lobules explanate; rare, Waimea Canyon, Kaua'i . ***F. species 2***
1. Underleaves at least 1.5-2 times the stem diameter; leaf lobules galeate, clavate or explanate 2
 2. Leaf lobules predominantly explanate; rare, wet, lowland, windward Hawai'i Island 3
 3. Explanate lobules dominant (at least near the plant apex), although a few galeate ones may be present ***F. species 1***
 3. Explanate lobules dominant near the plant apex, but clavate lobules may be common on older portions of the plant ***F. species 4***
 2. Leaf lobules predominantly clavate or galeate (or in *F. sandvicensis* mainly galeate, with some explanate lobules near the stem apex) 4
 4. Leaf lobules predominantly galeate 5
 5. Plants (1)1.5-2 mm wide; leaf gemmae absent; a few explanate lobules may be present ***F. sandvicensis***
 5. Plants at most 0.5 mm wide; leaf gemmae present; explanate lobules always absent 6
 6. Lobules 25-40% as wide as lobes; androecial spikes 1-1.2 mm long; rare, exotic shoreline forest, Kaua'i ***F. species 3***
 6. Lobules 50-60% as wide as the lobes; androecial spikes unknown ***F. oahuensis***
4. Leaf lobules predominantly clavate 7
 7. Lobules parallel to the stem ***F. meyeniana***
 7. Lobules predominantly divergent from the stem 8
 8. Microphyllous branches conspicuous and abundant..... 9
 9. Plants at most 1 mm wide; leaves distant to only slightly imbricate; rare ***F. hawaiiensis***
 9. Plants 1.5-3 mm wide; leaves conspicuously imbricate; common ***F. hypoleuca***
 8. Microphyllous branches absent or inconspicuous (only few per plant) 10
 10. leaf lobes conspicuously apiculate ***F. apiculata***
 10. Leaf lobes rounded or inconspicuously apiculate ***F. meyeniana***

*F. apiculata**F. hawaiiensis**F. hypoleuca**F. meyeniana**F. oahuensis**F. sandvicensis**F. species 1**F. species 2**F. species 3**F. species 4*

1. *Frullania apiculata* (Reinw., Blume & Nees) Nees. **Indigenous.** A member of subgenus *Diastaloba* Spruce (Söderström et al., 2016: 268). A common species found on all major islands (0-5,800 ft.); pantropical. This species is easily recognized by its pinnate branching, growing mostly free from its substrate, spreading horizontally, ascending or occasionally hanging down in shaggy masses; also, by its dark red color, apiculate leaves, and by its inflated and cylindrical (clavate) lobules, usually spreading from the stem.



According to Verdoorn (1930) and Miller (1953, 1983), *F. crenatiloba* Steph. is a synonym of *F. apiculata*. Although we did not study the type, Stephani's protologue for *F. crenatiloba* describes plants that fit our concept of *F. apiculata* (but see So & Wang (2006) for a different opinion; we wonder if their description and discussion of *F. crenatiloba* refers to *F. hawaiiensis*).

Frullania apiculata could be confused with the much less common genus *Jubula*. Unlike *Jubula*, *F. apiculata* has narrower and more fragile stems; the lobules are larger, closer to the stem, and connected to it by a thick keel; the lobe apiculus is always single and very short (1-3 cells long); the leaf cell walls are conspicuously trigonous; and the underleaf insertion line is not deeply arched.



Frullania apiculata. Top left: Plants project horizontally from tree trunks. Volcano, Hawai'i Island. Photo by E.J. Judziewicz. Top right: Plants may also be pendant. O'ahu. Photo by Miles K. Thomas, with permission. Bottom: Population growing on rock. Plants are loosely attached to their substrate and erect or ascending. Volcano, Hawai'i. Photo by E.J. Judziewicz.

Monoicous. Plants grow on bark or occasionally on rock; they are loosely attached to their substrate, ascending, projecting horizontally or pendant, up to 1 mm wide and 1.6-2.5 cm long, red to blackish-red. The stems have numerous pinnate branches. Leaves are imbricate, elliptical, shortly apiculate, concave, with entire margins. Lobules are inflated, clavate (cylindrical), spreading at varying angles from the stem (sometimes at almost 90° angles). They are attached to a keel of thickened leaf marginal cells that looks like a stalk. Styluses are 5 or 6 cells long. Underleaves are distant, contiguous to imbricate, round, elliptical or obovate, bifid to 1/2-2/3 their length, 2-3 times as broad as the stem, but smaller on branches. Leaf cells are isodiametric to elongate, thick-walled, with trigones and sometimes with intermediate thickenings; the basal cells are larger and clearly elongated; the marginal cells are quadrate and form a border on leaves and underleaves. Perianths are large, smooth, oblong, 3-keeled, and with long beaks; they are protected by long apiculate bracts with entire margins.



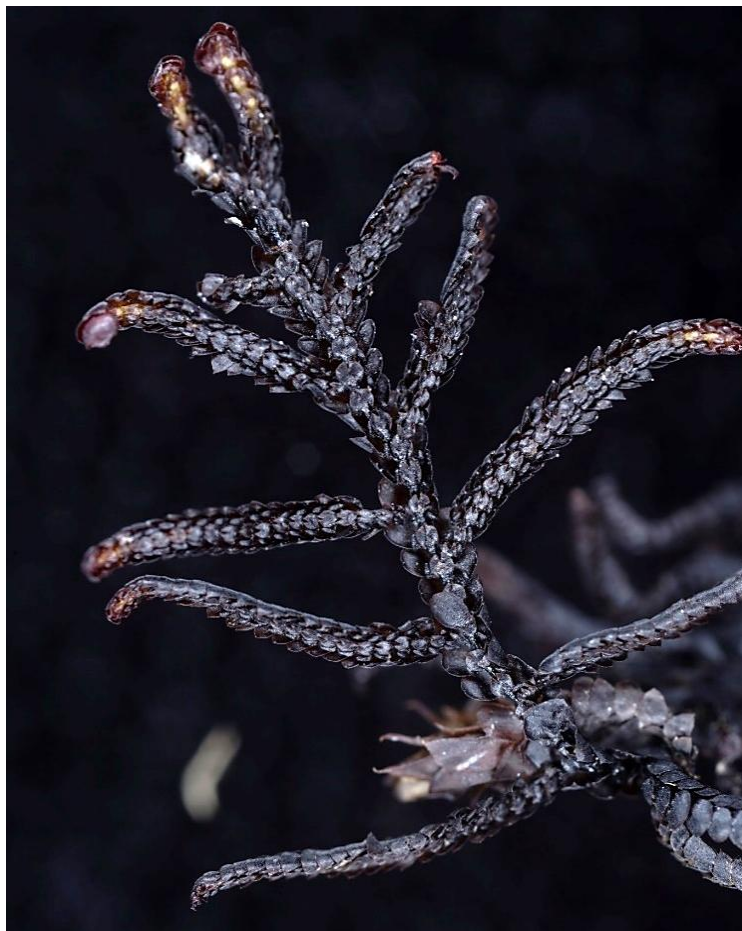
Plants are elongate, with numerous pinnate branches. Note the prominent perianths. Scales in mm. Saddle area, Hawai'i Island, Freire & Judziewicz 22-947 (BISH).



Frullania apiculata. Left: Dorsal view of plant. Note incubous, imbricate, and apiculate leaves. Volcano, Hawai'i Island. Photo by E.J. Judziewicz. Center and right: Plants in ventral view. Leaves are apiculate and concave, sometimes obscuring the apiculum; lobules are cylindrical and inflated, usually spreading. Center: Volcano, Hawai'i Island, Freire & Judziewicz 20-595 (HAVO). Right: Mauna Ulu access road, Hawai'i Volcanoes National Park, Hawai'i Island, Freire & Judziewicz 21-322 (HAVO).



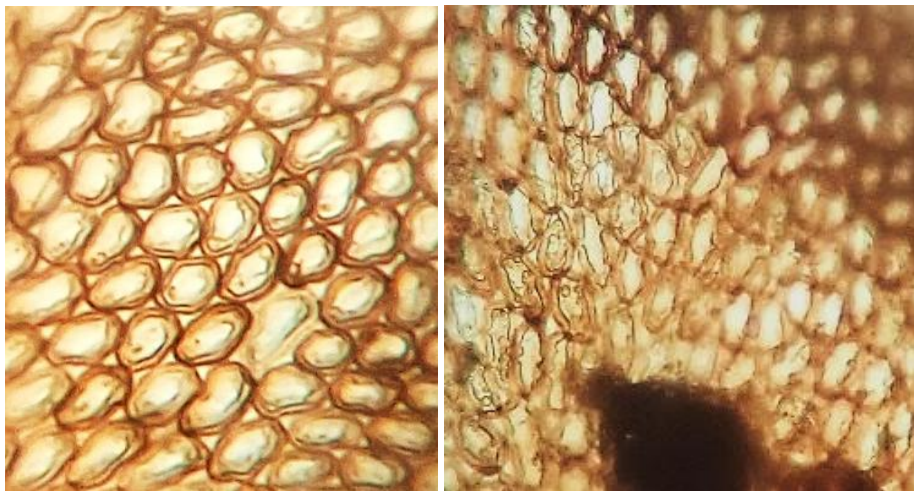
Lobules are clavate, attached to the stem by a thick keel. Note the stylus (arrow). Kūlani Prison Road, Mauna Loa, Hawai‘i Island, Miller & Lamberton 5269-A (MU). Photo by E.J. Judziewicz. Right: Leaf with lobule. Saddle area, Hawai‘i Island, Freire & Judziewicz 22-947 (BISH).



Frullania apiculata. Ventral view, showing large underleaves and perichaetial bracts. ‘Eke Bog, West Maui. Photo by Zach Pezzillo, with permission.



Left: Contiguous underleaves with apiculate lobes. Freire & Judziewicz 22-947 (BISH). Right: Imbricate underleaves, 2-3 times as broad as the stem and split to about $\frac{1}{2}$ their length. Note the border of quadrate cells. Mauna Ulu access road, Hawai'i Volcanoes National Park, Hawai'i Island, Freire & Judziewicz 21-322 (HAVO).



Frullania apiculata. Top left: Median leaf cells are elongate to isodiametric with thick walls and clear-appearing trigones. Top right: Leaf basal cells are elongate with confluent trigones. Bottom: Marginal cells are quadrate and form a border. Saddle area, Hawai'i Island, Freire & Judziewicz 22-947 (BISH).

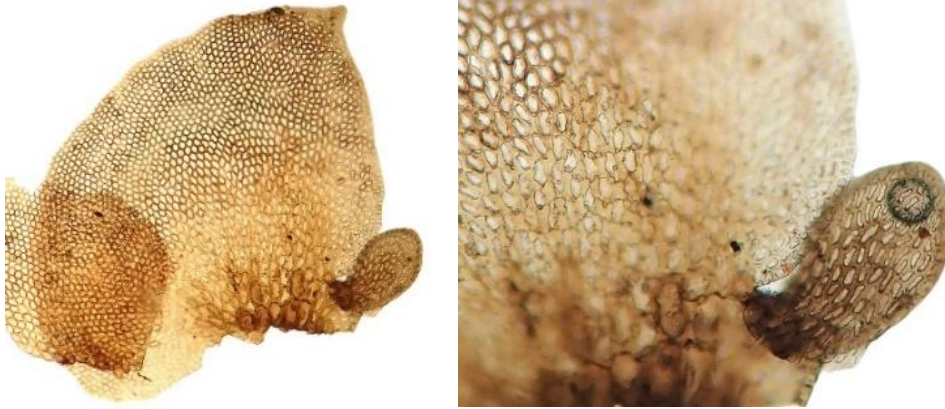


Frullania apiculata. Left: Keeled perianths at different stages of development. Volcano, Hawai‘i. Photo by E.J. Judziewicz. Center: Perianth bracts are large and apiculate. Mauna Ulu, Hawai‘i Volcanoes National Park, Hawai‘i Island, Freire & Judziewicz 21-322 (HAVO). Right: Beaked perianth with long, apiculate, entire bracts. Saddle area, Hawai‘i Island, Freire & Judziewicz 22-947. Photo by A.V. Freire.

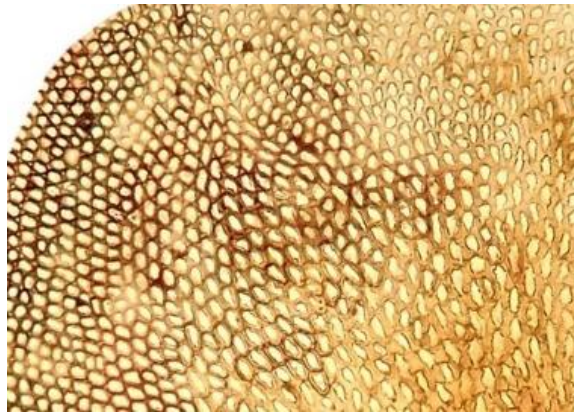
Frullania aff. *apiculata*. Some populations from Kaua‘i (below), have curved and rather elongated three-keeled perianths with a long beak (resembling a banana or plantain). The leaves have a longer apiculum and the underleaves are concave and larger.



Frullania aff. *apiculata*. Left and center: Plants are abundantly branched and large. Scales in mm. Right: Leaves are apiculate and concave when older (see lower plant portion), obscuring the apiculum; lobules are cylindrical and inflated, parallel to the stem or spreading at up to 45° angles. Līhu‘e-Kōloa Forest Reserve, Kaua‘i, Shevock 4629 (BISH). Photos by A.V. Freire.



Left: Leaf with apiculum. Right: Detail of clavate lobule. Shevock 4629 (BISH). Photos by A.V. Freire.



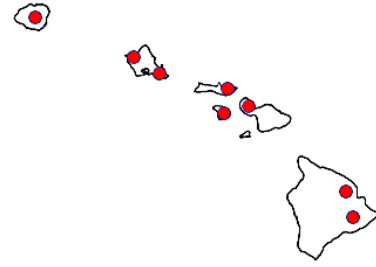
Leaf cells with thick walls and trigones. Basal cells are elongated, with thicker, confluent trigones. Marginal cells are quadrate. Shevock 4629 (BISH). Photo by A.V. Freire.



Frullania aff. *apiculata*. Left: Antheridial branches. Right: Elongate, 3-keeled (banana like) perianths. Note the long beaks and the elongate, apiculate, enveloping bracts. Līhu'e-Kōloa Forest Reserve, Kaua'i, Shevock 4629 (BISH). Photos by A.V. Freire.

2. *Frullania hawaiiensis* H.A. Miller. **Endemic.**

Found on all major islands (1,500-5,000 ft.), but uncommon. The status of this name needs revisiting. Placed in synonymy under *F. crenatiloba* by So & Wang (2006); but according to H.A. Miller (1983 and unpublished), *F. crenatiloba* should be placed in synonymy under *F. apiculata*, and *F. hawaiiensis* is a distinct species. This species is recognized by its small size, microphyllous branches, and bulging perianth cells.

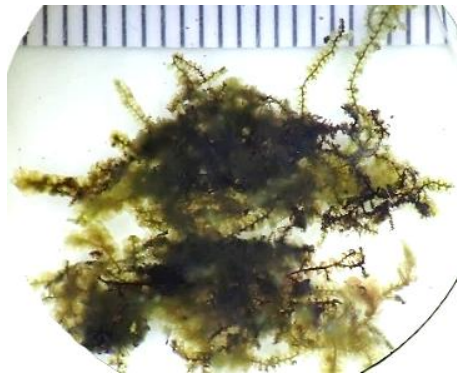


The microphyllous branches, cylindrical (clavate) lobules, foliar styluses, and the two narrowly separated ventral keels of the perianth, resemble those of *Frullania hypoleuca*, perhaps its closest relative; but plants of *F. hawaiiensis* are smaller, the leaves are only slightly imbricate to distant, and the perianth is flat-topped, with bulging cells.

Frullania hawaiiensis could be mistaken for *F. apiculata* because of its apiculate leaves, but it differs in being prostrate and creeping, in having microphyllous branches, leaves and underleaves that are not or only slightly imbricate and are smaller; moreover, the shape of the underleaves is ovate or long-elliptical rather than orbicular (on the main stem), and the perianths are obovate with a partially double ventral keel and have bulging cells.

Our concept of this species is based only on our collections from Lānaʻi, Freire & Judziewicz 22-468 (BISH) and from Hawaiʻi Island, Freire & Judziewicz 23-504 (BISH). We did not study types nor any specimens labelled as *F. hawaiiensis*.

Monoicous. Populations form loose, prostrate mats. Plants creep on bark and are loosely attached, with attachment points all along the stem. They are yellow-green, small, up to 1 mm wide, with frequently branched stout stems and abundant microphyllous branches. The leaves are slightly imbricate, contiguous to distant, elliptical; their apices are either rounded or apiculate (with a small and blunt apiculum). The leaf lobules are inflated, cylindrical, and more than two times longer than wide. The underleaves are obovate to long-elliptical, narrow, 1.5(2.5) times the stem width, bifid to about half their length. Leaf cells have rigid walls, small to large trigones, and some intermediate thickenings. Perianths are produced terminally on short lateral branches. They are obovate, flat-topped, with a short and ciliolate beak; keeled, with 2 lateral keels and a prominent ventral keel either bluntly crested or partially split above by a narrow cleft; they have bulging, thick-walled cells. Perianth bracts are in 3(4) whorls. Male branches are lateral, short and globose.



Frullania hawaiiensis. Populations are prostrate and form loose mats. Hilo Nursery Arboretum, Hawaiʻi Island, Freire & Judziewicz 23-504 (BISH).



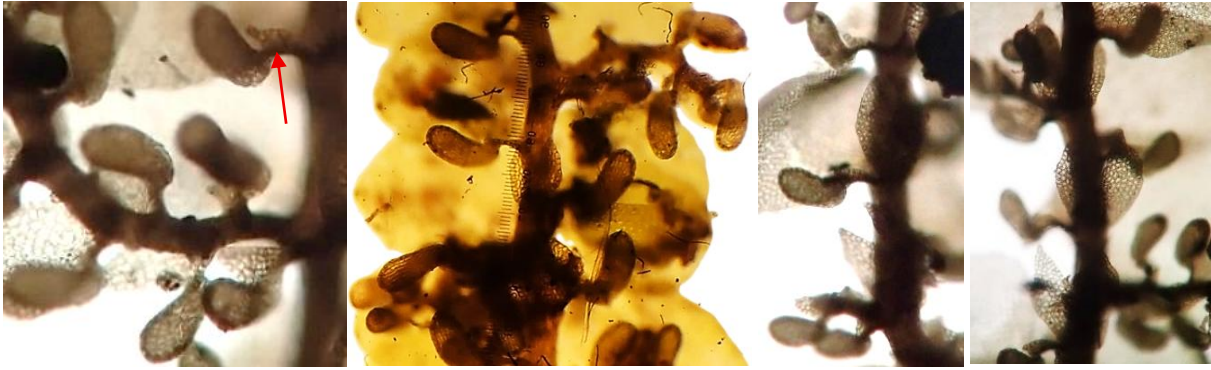
Plants are small, yellow-green, with broadly spreading lobules and abundant microphyllous branches. Scales in mm. Left: Hilo Nursery Arboretum, Hawai'i Island, Freire & Judziewicz 23-504 (BISH). Right: Lāna'i, Freire & Judziewicz 22-468 (BISH).



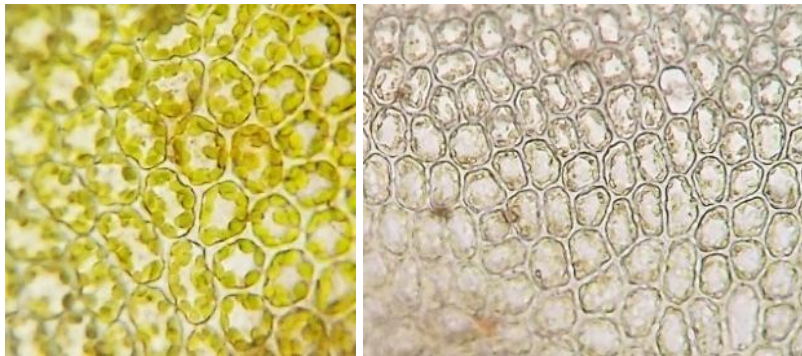
Leaves can be apiculate. Stems are stout; leaf lobules are distant from the stem and mostly broadly spreading. Lāna'i, Freire & Judziewicz 22-468 (BISH).



Frullania hawaiiensis. Leaves are slightly imbricate to contiguous or distant. They can have rounded or shortly apiculate apices. Lobules spread broadly from the stem but some may be parallel to it. Microphyllous branches are abundant. Note the short, globular male branches. 1: Lāna'i, Freire & Judziewicz 22-468 (BISH). 2-4: Hilo Nursery Arboretum, Hawai'i Island, Freire & Judziewicz 23-504 (BISH).



1: Foliar stylus (arrow). 2-4: Underleaves are distant, elongate-elliptical to obovate, 1.5-2.5 wider than the stem. 1,3,4: Hawai'i Island, Freire & Judziewicz 23-504 (BISH). 2: Lāna'i, Freire & Judziewicz 22-468 (BISH).

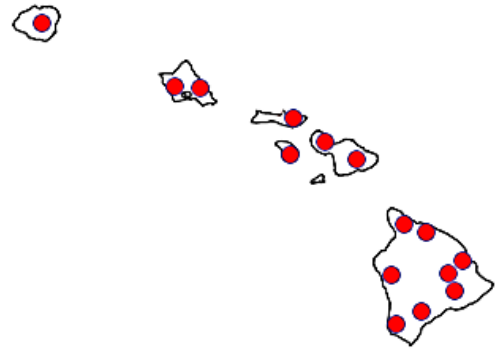


Middle leaf cells are thick-walled, with small trigones and intermediate thickenings. Left: Lāna'i, Freire & Judziewicz 22-468 (BISH). Right: Hawai'i Island, Freire & Judziewicz 23-504 (BISH).



Frullania hawaiiensis. Upper left: Monoicous; antheridial branches adjacent to plant apex (arrows), perianths produced on short lateral branches. Scale in mm. Upper center and right: Perianth has a prominent ventral keel partially separated by a narrow cleft into "two blades". Note the ciliate beak. Bottom: Bulging cells of perianth. Hilo Nursery Arboretum, Hawai'i Island, Freire & Judziewicz 23-504 (BISH).

3. *Frullania hypoleuca* Nees. Indigenous. A member of subgenus *Diastaloba* Spruce (Söderström et al., 2016: 272); Possible affinity (Evans, 1900): *F. caroliniana* (= *F. obcordata* (Lehm. & Lindenb.) Lehm. & Lindenb.), tropical America. Also found in Asia and Australia. Von Konrat & Braggins (2001: 255) give the closest affinities as *F. hypoleucula* Hatt. (New Caledonia) and *F. ptychantha* Mont. (Aotearoa/New Zealand). This is the largest species of *Frullania* in Hawai'i and is found on all major islands (0-6,500 ft.); it grows on 'ōhi'a bark, often as closely appressed, rubbery-looking, pink-purple to yellow-brown mats.

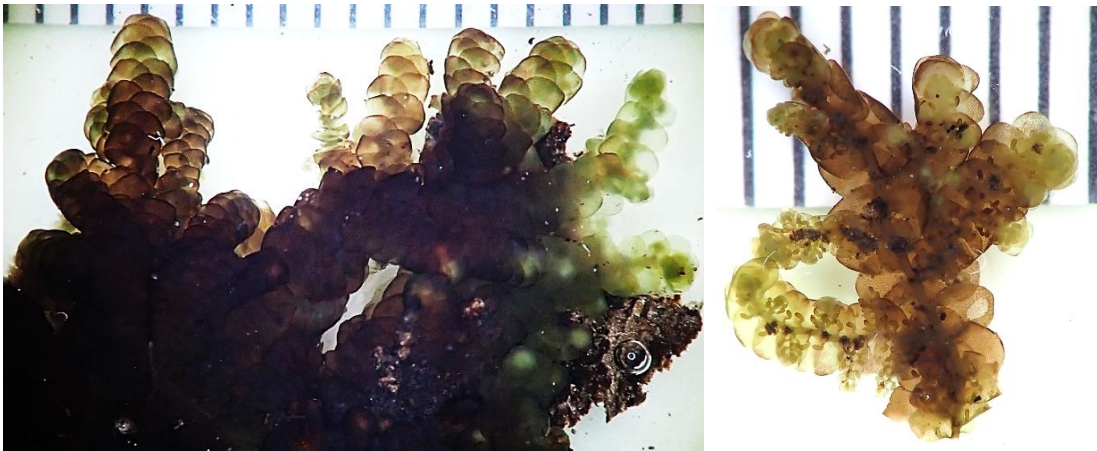


The abundance of microphyllous branches (the plants resembling millipedes) is distinctive. The large size, imbricate leaves, broader and mainly orbicular underleaves, and the obcordate, smooth perianths, separate it from *F. hawaiiensis* which can also have small microphyllous branches. The divergent lobules separate it from individuals of *F. meyeniana* that sometimes bear small (but not microphyllous) branches.



Frullania hypoleuca. Plants are large and can range from purple- or reddish-pink to yellowish- or blackish-brown, or green. They grow closely appressed to their substrate and have a rubbery appearance. Volcano, Hawai'i Island, Freire & Judziewicz 21-171 (BISH).

Populations grow appressed to bark, forming pink, purple, green, yellow, or brown mats; sometimes colors are intermixed in the same population. Plants are large, 1.5-3 mm wide; stems are pinnately branched, with abundant tiny, microphyllous branches. Leaves very imbricate, concave, round or apiculate at the apex, squarrose when wet. Lobules are clavate, diverging from the stem at 45° (or more), sometimes paired at the base of branches. Styluses are multicellular and foliose. Underleaves are large, 2-3.5 times as wide as the stem, plane or concave, distant to contiguous, orbicular to obovate, bifid to 1/3 their length, with triangular and acute lobes, with one or two small “elbows” (those on the main stem). Leaf cells are isodiametric, with thick and often pigmented walls and with small trigones. A short and narrow strand of elongated cells with larger trigones is found at the base of the leaf. Perianths are obovate, beaked, cordate above, smooth, with two lateral keels and a ventral pair of keels separated by a very narrow cleft.



Plants are large; on main stems they can be over 2 mm wide. Scales in mm. Saddle Area, Hawai‘i Island, Freire and Judziewicz 22-935 (BISH).



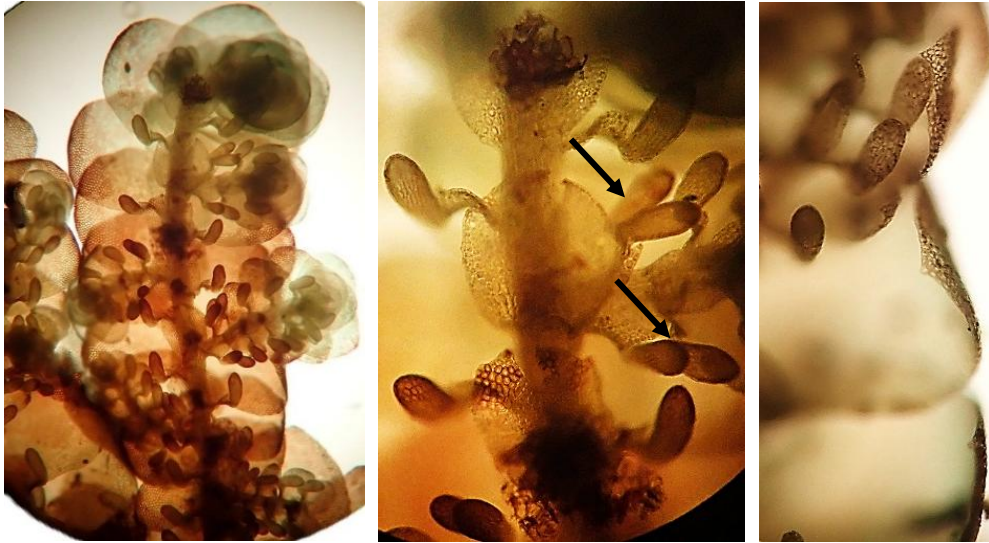
Frullania hypoleuca. Plants have a waxy look; the markedly imbricate and concave leaves give them an almost julaceous appearance. Some microphyllous branches can be seen from the dorsal side of plants (arrows). Left: Photo by Miles K. Thomas, with permission. Right: Hawai‘i Island, Freire & Judziewicz 21-171 (BISH).



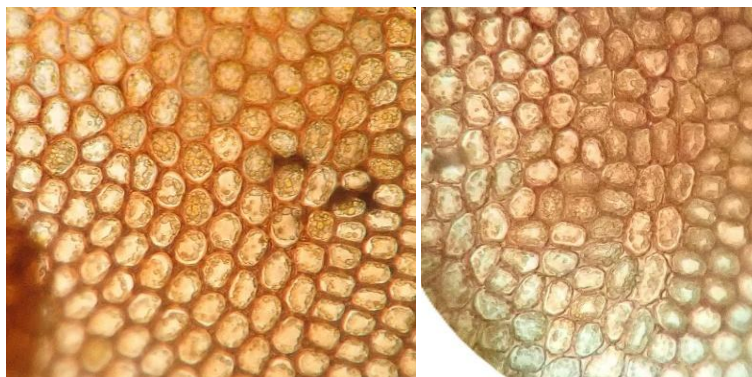
Dorsal (above) and ventral (below) views of a plant with numerous microphyllous branches of restricted growth. Note distant underleaves (below). West Maui, photos by Zach Pezzillo, with permission.



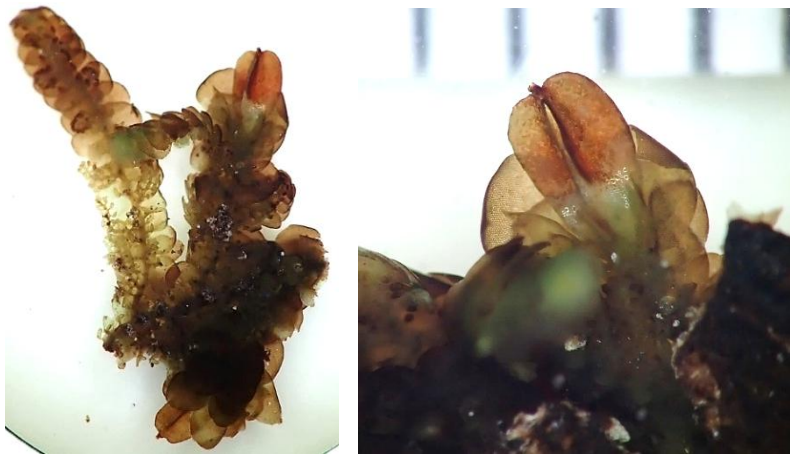
Frullania hypoleuca. Plants with numerous microphyllous branches, and wide-spreading clavate lobules. Underleaves can be contiguous (center) or distant (right). Left: Volcano, Hawai'i Island, Freire & Judziewicz 21-171 (BISH). Center and right: Saddle area, Hawai'i Island, Freire & Judziewicz 22-935 (BISH).



Lobules can be paired at the base of branches (arrows). Underleaves are orbicular, bifid and sometimes may have small elbows. Right: Leaves can be apiculate. Freire & Judziewicz 22-935 (BISH).



Left: Median leaf cells are isodiametric, thick-walled and have small trigones. Right: A strand of slightly elongated cells is present at the leaf base. Freire & Judziewicz 22-935 (BISH).



Frullania hypoleuca. Perianths are produced terminally on main branches and have a prominent ventral keel that is split in two. Saddle area, Hawai'i Island, Freire & Judziewicz 22-935 (BISH).

***Frullania* aff. *hypoleuca*:**

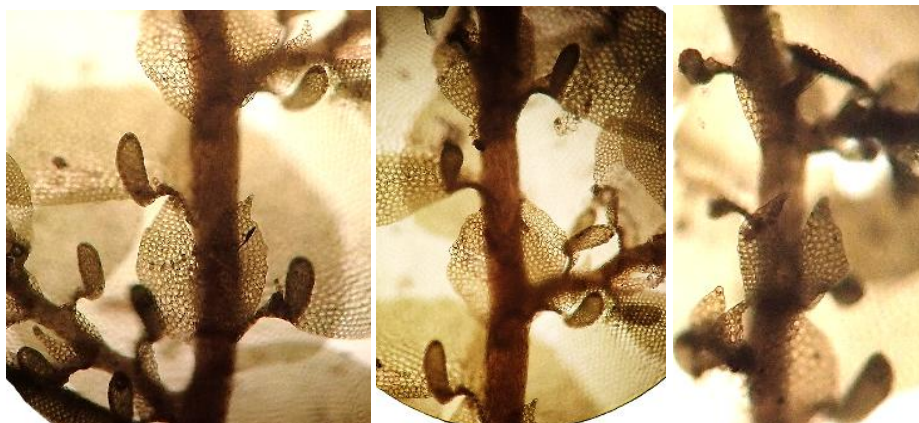
A population from Hakalau Forest National Wildlife Refuge, Mauna Kea, Hawai'i Island, has flattened, slightly imbricate, apiculate leaves with small lobules that are almost parallel to the stem. Plants have abundant microphyllous branches, some more developed than others. Leaf cell walls are thinner and non-pigmented. No perianths were observed.



Plants are about 2 mm wide, with large elliptical leaves and microphyllous branches. Freire & Judziewicz 23-401 (BISH).



Leaves are imbricate, ovate-elliptical, and apiculate. Note the microphyllous branches and small clavate lobules. Freire & Judziewicz 23-401 (BISH).



Frullania aff. *hypoleuca*. The underleaves are large, round to oblong or obovate, 2-3(3.5) times as wide as the stem; bifid, with triangular lobes, and sometimes apiculate, with a "V"-shaped sinus from 1/3 to close to 1/2 the underleaf length. Note the irregular underleaf margins, with a suggestion of an "elbow". Hakalau Forest N.W.R., Hawai'i Island, Freire & Judziewicz 23-401 (BISH).



Lobules are clavate, about three times as long as wide, parallel to the stem or slightly divergent, and have a multicellular, foliose stylus. Some lobules are paired at the base of branches. Freire & Judziewicz 23-401 (BISH).

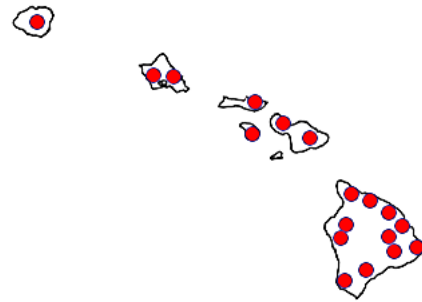


Short, globular male branch. Freire & Judziewicz 23-401 (BISH).



Frullania aff. *hypoleuca*. Leaf cells isodiametric with thin walls and small trigones, some with intermediate thickenings. Hakalau Forest National Wildlife Refuge, Hawai'i Island, Freire & Judziewicz 23-401 (BISH).

4. *Frullania meyeniana* Lindenb. Indigenous. A member of subgenus *Meteoriopsis* Spruce section *Obtusilobae* Verd. (Söderström et al., 2016: 290). Possible affinities (Evans, 1900): *F. donnellii* Austin, Florida and West Indies, and *F. kunzei* (Lehm. & Lindenb.) Mont., Americas. Also present in Asia and Australia. This is a common species in both lowland and montane forests on all major islands (0-6,400 ft.). Small, deep red in color, it grows closely appressed to bark and often has an elegant coral-like branching pattern.



It prefers mesic rather than wet forests and is particularly common and diverse in Kīpukakī and Kīpukapuaulu along the Mauna Loa Road in Hawai‘i Volcanoes National Park. It is also frequent on small ‘ōhi‘a trees at the margins of recent lava flows near the Mauna Ulu parking lot. Microphyllous branches are occasionally present. *Frullania meyeniana* prefers the bark of ‘ōhi‘a but it can grow on the stems of cultivated plants such as tī (*Cordyline fruticosa*) or avocados. It can also be epiphyllous.

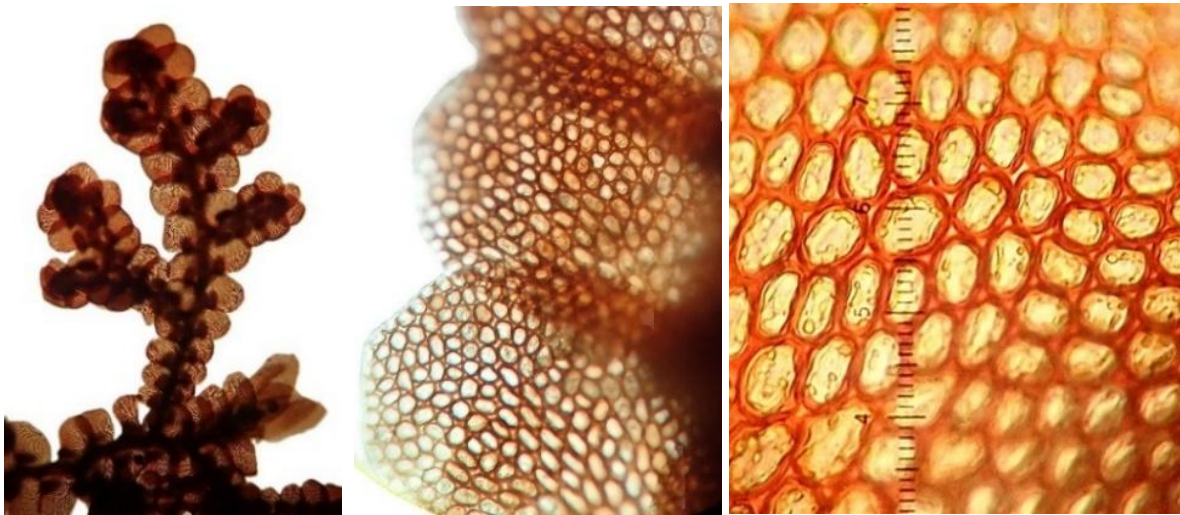


Frullania meyeniana. Plants grow closely appressed to their substrate, are red to blackish, and have a waxy appearance. They often exhibit “coralline” branching. Volcano, Hawai‘i Island, Freire & Judziewicz 20-94 (BISH).

Monoicous. Populations form dense creeping patches, closely attached to the bark of trees. Plants are red, brownish-red to almost black. They are small, less than 1 mm wide and up to 1.8 cm long. Stems are stout and very frequently pinnately branched. Some microphyllous branches may be present. Leaves are slightly imbricate to contiguous, sometimes semi-erect, elliptical, concave, entire; their apices are rounded, although some may have an obtuse point, they are never apiculate. Median leaf cells are slightly elongated, with red-tinted thick walls and with trigones. Lobules are clavate, prominent, and parallel to the stem; they can be imbricate in some branches. Underleaves are 1.5-2.5(3) times the stem diameter in width, distant to contiguous, obovate, decurrent, bifid to 1/3-1/2 their length, with acute lobes and a narrow “V”-shaped sinus. Abnormal underleaves are commonly observed. Perianths are terminal on lateral branches; they are obovate, smooth, truncate, shortly beaked, 3-sided, flat dorsally, but with a broad bulging ridge on the ventral side. Antheridia are produced on short globose branches.



Plants are less than 1 mm wide, and frequently branched. Note perianth. Scales in mm. Shevock 46193 (BISH). Photos by A.V. Freire.



Dorsal view. Leaves are rounded at the apex, occasionally with an obtuse point. Leaf cells are thick-walled and have small trigones. Shevock 46193 (BISH). Photos by A.V. Freire.



Frullania meyeniana. Ventral views. Plants are profusely branched. The leaves have a rounded apex, with large cylindrical lobules parallel to the stem. Left: Kaua'i, Shevock 46193 (BISH). Photo by A.V. Freire. Right: Volcano, Hawai'i Island, Freire & Judziewicz 20-94 (BISH).

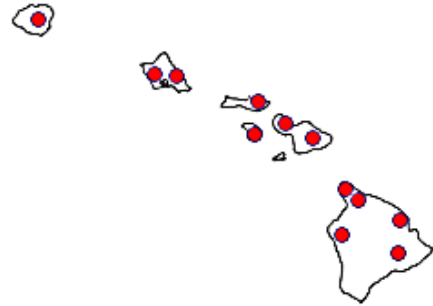


The underleaves are obovate, decurrent, contiguous to distant, split from 1/3 to 1/2 their length. Volcano, Hawai'i Island, Freire & Judziewicz 20-94 (BISH).



Frullania meyenania. Above: Perianths are obovate, truncate, and shortly beaked; they have two lateral wings or keels and a ventral keel with a lower bulge (upper right). Below: Male branches are short and globose. Kaua'i, Shevock 46193 (BISH). Photos by A.V. Freire.

5. *Frullania oahuensis* Hampe. Endemic. A member of subgenus *Frullania* (Söderström et al., 2016: 278); Possible affinity (Evans, 1900): *F. virginica* (= *F. eboracensis* Lehm.), North America. The tiniest Hawaiian species of *Frullania*. It grows on bark, in lowland to montane forests, on all major islands (0-7,500 ft.), but it is uncommon. This species has small round leaves and large globular lobules and can be found in bryophyte mixtures. The leaves are caducous and produce gemmae and rejuvenants; plant color is usually brownish-black.



Populations creep on tree bark and grow closely attached to it. Plants are tiny, 0.5 mm wide or less, brown to blackish. Stems are fragile, with irregular branching. Leaves are semi-erect, inserted at a 45° angle, entire, rounded, concave, distant, and caducous. Lobules are large and galeate, usually 50-60% the leaf lobe width, and caducous. Median leaf cells are thick-walled and sinuous, with intermediate thickenings and no trigones. Underleaves are bifid 1/4 to 1/3 their length, obovate, projecting from the stem at different angles, and sometimes have small “elbows” at the base of the lobes, or occasionally with a small tooth on one lobe. Perianths are conspicuous, obovate, truncate, with a short and broad beak, 4-keeled (with two ventral keels). Male branches were not observed by us. Unicellular gemmae and rejuvenants are produced from the margins of leaf lobes and lobules.

Plants were described as dioicous (Evans, 1900; So & Wang, 2006). So & Wang (2006) describe large androecial branches that look globose (according to their Fig. 3b). Evans (1900) describes them as globose or oblong. See *Frullania* species 3 in this treatment, which is rather similar to *F. oahuensis* but has unique male branches.



Frullania oahuensis covering trunk of hau (*Rauvolfia sandwicensis*) in *Acacia koa* forest, Koai‘a Reserve, Kohala, Hawai‘i Island. Photo by E.J. Judziewicz.



Plants are tiny and grow closely attached to their substrate. Note that the galeate lobules that sometimes approach the size of the lobes. Freire & Judziewicz 23-267 (BISH).



Plants are irregularly branched; leaf lobules are large in relation to the lobes. Note the perichaetial bracts (left). Freire & Judziewicz 21-66 (HAVO).



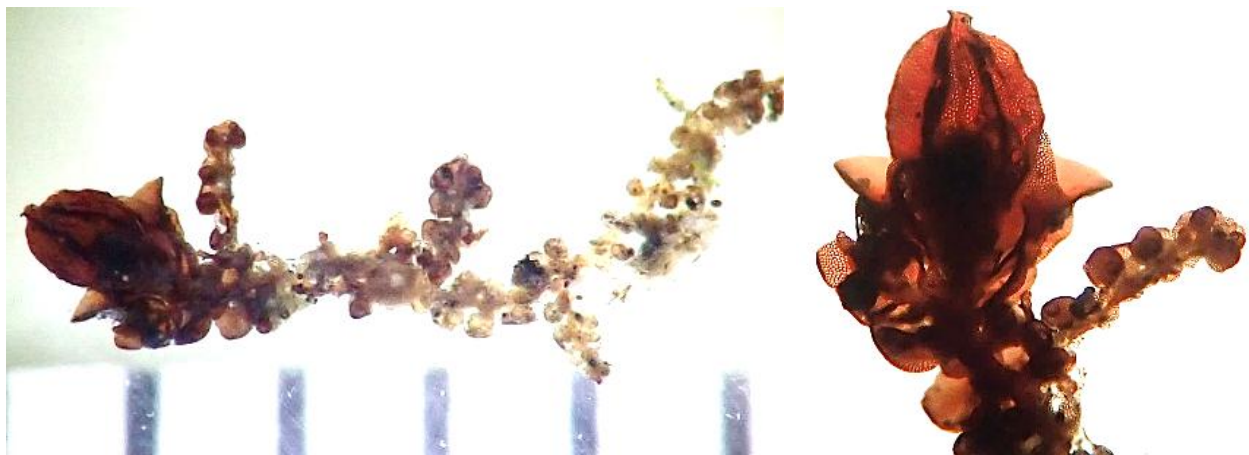
Frullania oahuensis. Leaves are elliptical, caducous, distant, concave and semi-erect. Leaf fragments remain attached to the plant after caducous leaves fall. Leaf cells are sinuous. 1-2: Hakalau Forest National Wildlife Refuge, Hawai'i Island, Freire & Judziewicz, 23-267 (BISH). 3-4: Kīpukakī, Hawai'i Volcanoes National Park, Hawai'i Island, Freire & Judziewicz 21-66 (HAVO).



1: Leaf with marginal gemmae. Kīpukakī, Hawai‘i Volcanoes National Park, Hawai‘i Island, Freire & Judziewicz 21-66 (HAVO). 2: Leaf lobe with gemmae and rejuvenant. 3: Leaf lobe with marginal, young rejuvenant. 4: Leaf lobule with marginal rejuvenant. 2-4: Freire and Judziewicz, 23-267 (BISH).



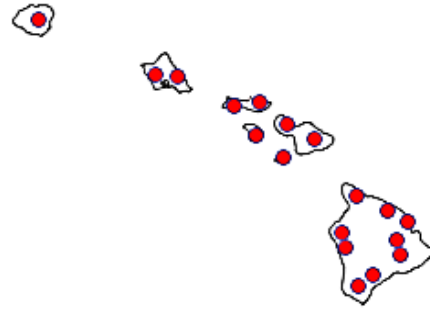
Underleaves are obovate, bifid, with “elbows” or lateral teeth (right); they project at various angles from the stem (left and center). Freire & Judziewicz, 23-267 (BISH).



Frullania oahuensis. Perianths are prominent, with four keels. Scale in mm. Hakalau Forest National Wildlife Refuge, Hawai‘i Island, Freire & Judziewicz, 23-267 (BISH).

6. *Frullania sandvicensis* Ångstr. Endemic.

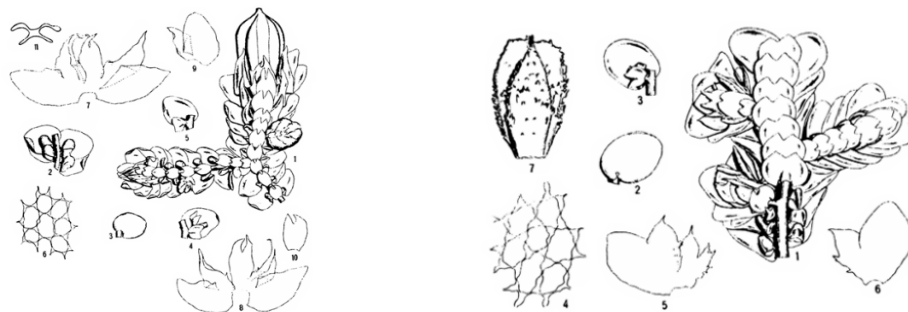
Occasionally found in wet to dry forests. A member of subgenus *Chonanthelia* Spruce, sect. *Pluricarinatae* (Yuzawa, Mues & S. Hatt.) Hentschel & von Konrat (Söderström et al., 2016: 266). Includes Staples & Imada's (2006) concept of *F. ericoides* (see Judziewicz & Freire 2023c: 161). According to Evans (1900), *F. sandvicensis* has affinities with *F. squarrosa* Dumort., a species now considered a synonym of the pantropical *F. ericoides* (Nees) Mont.



Frullania sandvicensis is recognized by its large galeate lobules; its large underleaves (6-7 times broader than the stem); leaf cells with conspicuous trigones; and coarsely ornamented (verrucose), three-keeled perianths.

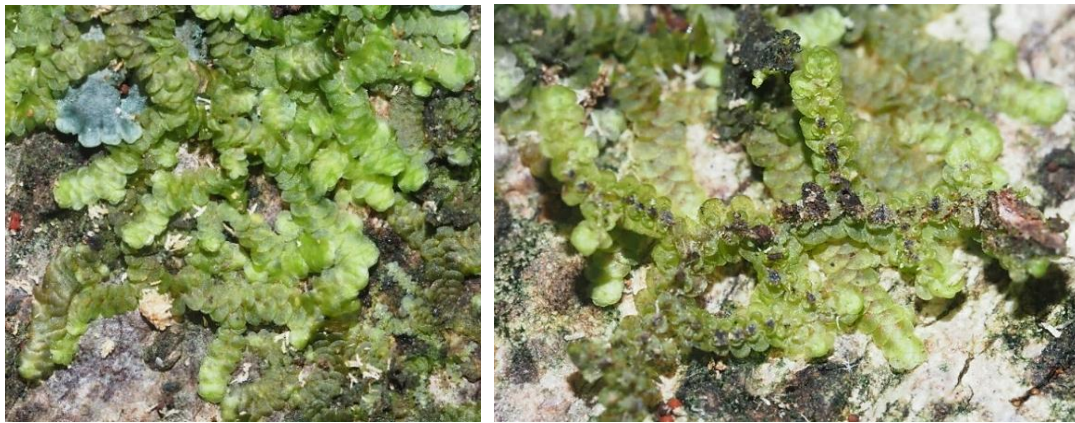
Although it often occurs in wet forests, *Frullania sandvicensis* can also be found in some of the driest habitats of any Hawaiian leafy liverwort. For example, it occurs on the dry, northwestern side of Lānaʻi (Judziewicz et al., 2023: 17), at Maunaloa in western Molokaʻi (Miller & Lamberton 3908, MU), and on Kahoʻolawe (*F. cf. sandvicensis*), where it was discovered in 2022 by Paul Higashino, and collected by Cuyler Bleecker and David Beilman (Judziewicz et al., 2025b: 136). It is also found in moister lowland to montane dry to mesic forests on all major islands (0-7,100 ft.), as well as on nearshore islets such as Mokoliʻi (Oʻahu) and Mōkapu (Molokaʻi) that are presumably subjected to salt spray.

Frullania aongstroemii, reported as a synonym of *F. sandvicensis* (see below), was not accounted for in Söderström et al. (2016). Hawaiian material of what has been called *Frullania aongstroemii* has been treated as the tropical Asian and American *F. neurota* Taylor by Staples & Imada (2006). We did not come across any Hawaiian specimens labelled as either *F. aongstroemii* or *F. neurota*. So & Wang (2006) and Brinda & Atwood (2025) place *F. aongstroemii* in synonymy with *F. sandvicensis*. However, Evans (1900) and H.A. Miller (unpublished notes at BISH) describe perianths with four smooth keels (two prominent and two reduced) in *F. aongstroemii* versus perianths with three papillose keels in *F. sandvicensis*. This seems to us a significant difference. Other differences are the obovate underleaves only up to three times the stem width in *F. aongstroemii*, versus orbicular to reniform underleaves that are 5-7 as wide as the stem in *F. sandvicensis*. Differences in lobular morphology are difficult to interpret based on the descriptions and diagrams of Evans (1900), but his drawings (1900) do appear to show clavate rather than galeate lobules in *F. aongstroemii*. The placement of *F. aongstroemii* as a synonym of *F. sandvicensis* should be revisited.



Frullania aongstroemii and *Frullania sandvicensis*, Evans (1900). Left (*F. aongstroemii*): 1. Plant with perianth and male branch. 2. Detail of lobules. 3. Non-cordate leaf lobe. 4, 5. "Bases of branches...". 6. Median leaf cells. 7. "Innermost bracts and bracteole". 8. Bracts and bracteole of second row. 9, 10. Bracts and bracteole of third row. 11. Cross section of perianth. Right (*F. sandvicensis*): 1. Ventral view. 2. Cordate leaf lobe. 3. "Base of branch..". 4. Median leaf cells with prominent trigones. 5, 6. Bracts and bracteole of innermost row". 7. Perianth.

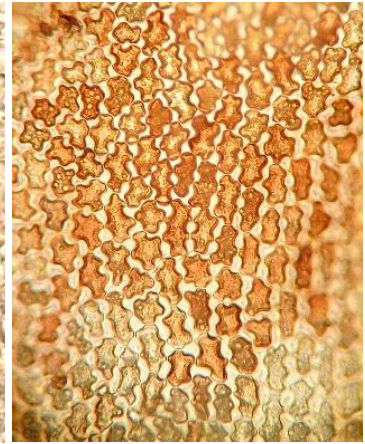
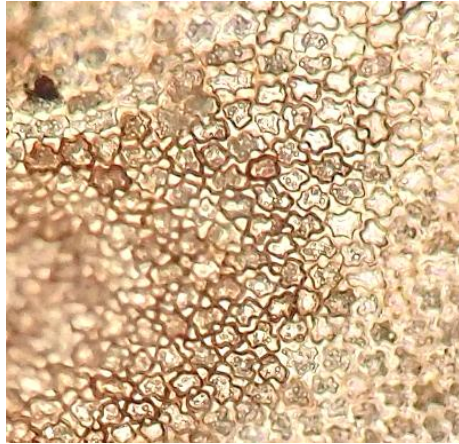
Plants grow on bark, rock or soil, and are prostrate and loosely appressed to their substrate; they are large, (1)1.5-2 mm wide, and bright green to a rich, lustrous chestnut brown. Stems are fragile and irregularly branched. Leaves are imbricate, orbicular, ovate or elliptical, entire, truncate, revolute, slightly concave, nearly squarrose, and cordate. Leaf lobules are galeate, mostly with appressed bottom halves (constricted below). Leaf cells are isodiametric to elongate, sinuous, with thick walls, and bear prominent trigones and intermediate thickenings. Underleaves are large, 5-6(7) times as wide as the stem, and nearly or completely obscure the leaf lobules; they are orbicular to reniform, shallowly bifid, with a “V”-shaped sinus to about 1/5-1/8 their length. Perianths are born on short branches, oblong-elliptical, protected by bifid bracts at their base, beaked, 3-keeled, flat on the dorsal side, with a prominent ventral and two lateral keels, with lacinate, multicellular and prominent outgrowths (as to appear coarsely verrucose). Males were not observed.



Ko‘olau Range, O‘ahu. Dorsal and ventral views; note the round underleaves in ventral view. Photos by K. Faccenda, <https://www.inaturalist.org/observations/2009848554855>, with permission.



Frullania sandvicensis. 1-2: Plants vary in size from (1)1.5-2 mm wide. Scales in mm. 2: Note perianths produced on short branches. 3-4: Leaves are imbricate, rounded and concave. Lobules are large, galeate, and compressed in their bottom half. 1: Kaua‘i, Shevock, Flynn & Ma 51106 (CAS, PTBG). Photo by E.J. Judziewicz. 2-4: Maui, Pezzillo 502 (BISH). Photos by A.V. Freire.



Left: Leaves are cordate. Center: Median leaf cells have thick sinuous walls and large trigones, some with intermediate thickenings. Right: Basal leaf cells are more elongated. Pezzillo 502 (BISH). Photos by A.V. Freire.

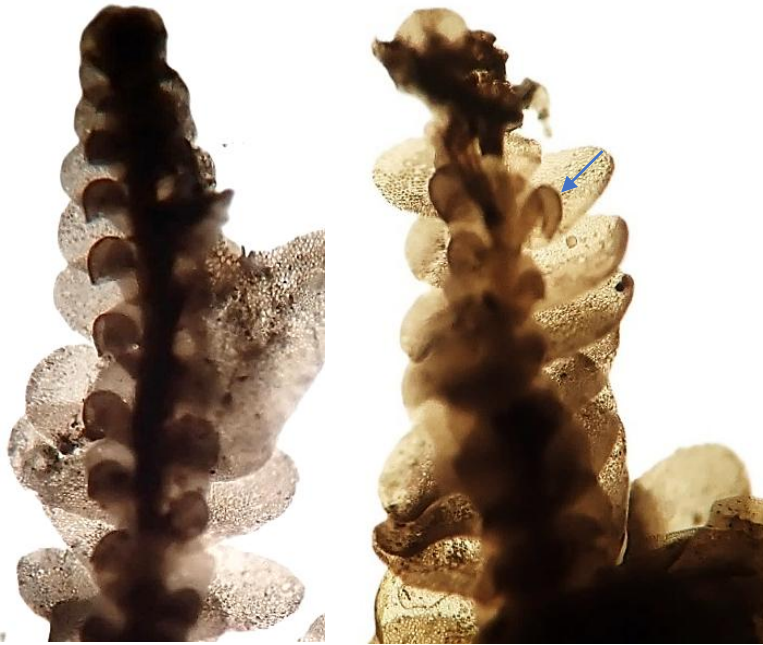


1-2: Underleaves are large, 5-6(7) times as wide as the stem, shallowly bifid, and orbicular. 3 and 4: Lobules are galeate, but constricted below. 4. Leaf lobes are cordate. 1: Kaua'i, Shevock, Flynn & Ma 51106 (CAS, PTBG). Photo by E.J. Judziewicz. 2-4: Pezzillo 502 (BISH). Photos by A.V. Freire.

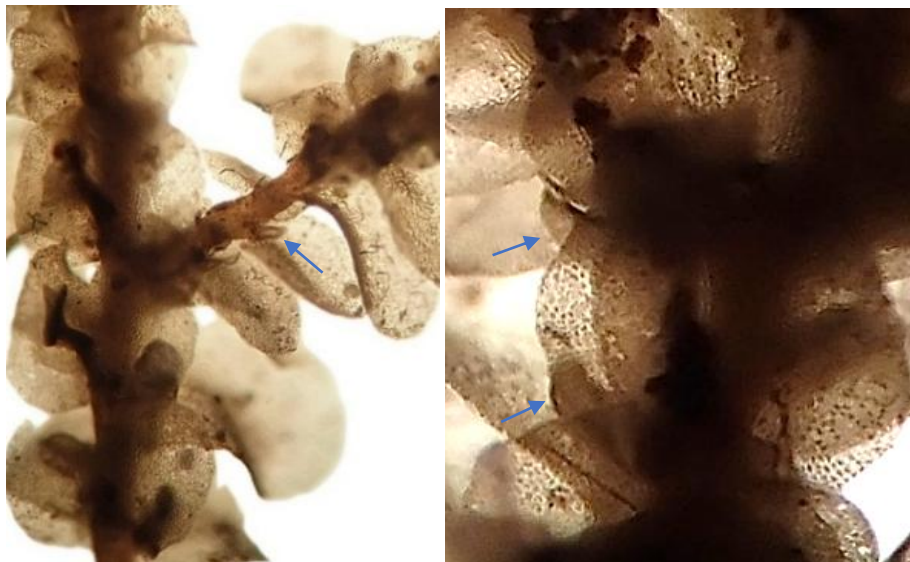


Frullania sandvicensis. Three-keeled perianth (1-2), ventral views. 1: Scale in mm. 3: Dorsal side is not keeled. 4: Detail of coarse multicellular outgrowths on perianth keels. Kīpahulu Valley, Haleakalā, Maui, Pezzillo 502 (BISH). Photos by A.V. Freire.

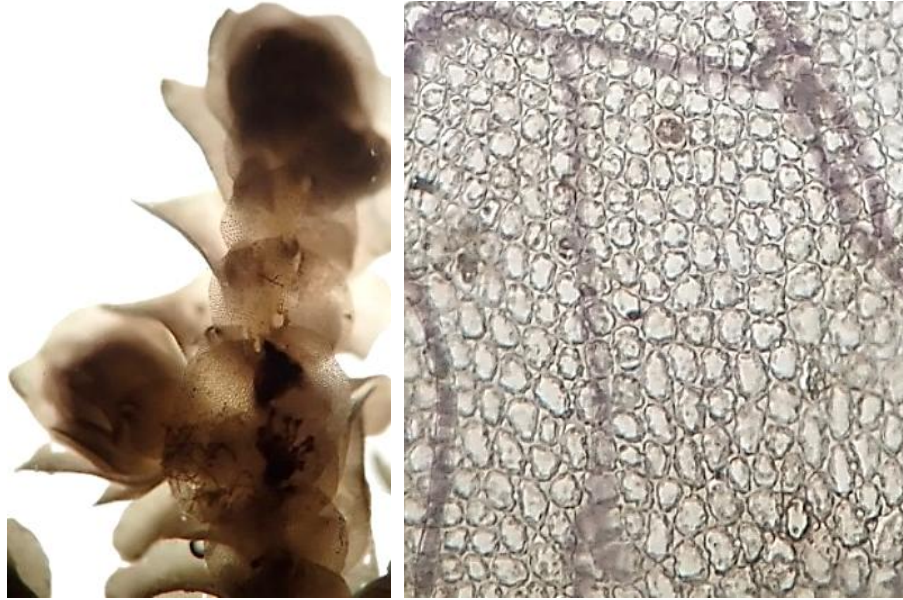
A population from Kaiwaihau District (700 ft.), Kaua'i (Shevock 51106, PTBG) has galeate lobules intermixed with some lobules that are ligulate and non-inflated. The galeate lobules are not always compressed below. The median leaf cells are not sinuous, have thinner walls and smaller trigones. No perianths were present. For now, we regard this population as *F. sandvicensis*; when a specimen with perianths becomes available, we may be able to confirm (or not) this identification.



Leaf lobules are galeate, sometimes inflated throughout (left photo), sometimes compressed below (right photo, arrow). Shevock 51106 (PTBG). Photos by A.V. Freire.



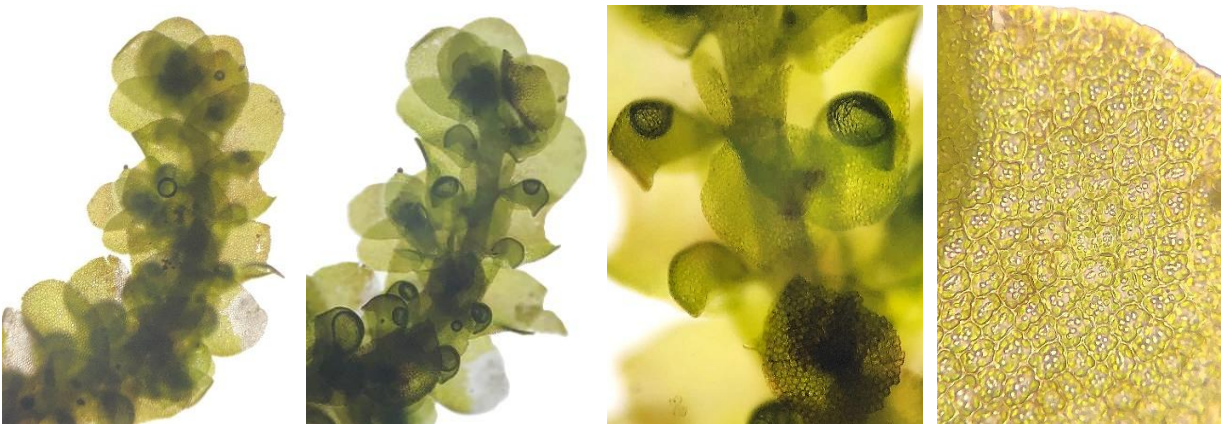
Frullania sandvicensis. Some non-inflated and ligulate lobules are intermixed (arrows) on main stem and branches. Kaiwaihau District, Kaua'i. Shevock 51106 (PTBG). Photos by A.V. Freire.



Frullania sandvicensis. Left: Underleaves are large, orbicular, and shallowly bifid. Right: Median leaf cells. Kaiwaihau District, Kaua‘i, Shevock 51106 (PTBG). Photos by A.V. Freire.

Frullania cf. sandvicensis

Photographs of a plant growing on the underside of a boulder at the summit of Kaho‘olawe, taken by W. Cuyler Bleecker (Judziewicz et al., 2025: 136), show galeate lobules that are apparently not compressed below. The underleaves are obovate rather than orbicular and are only three times as broad as the stem. The leaf cells, although sinuous, have thin walls and small trigones and intermediate thickenings. An immature perianth with a beak is observed but no mature perianths were present. We did not have access to this specimen, and the photos are of a single plant tip; plants with mature lower portions need to be studied.



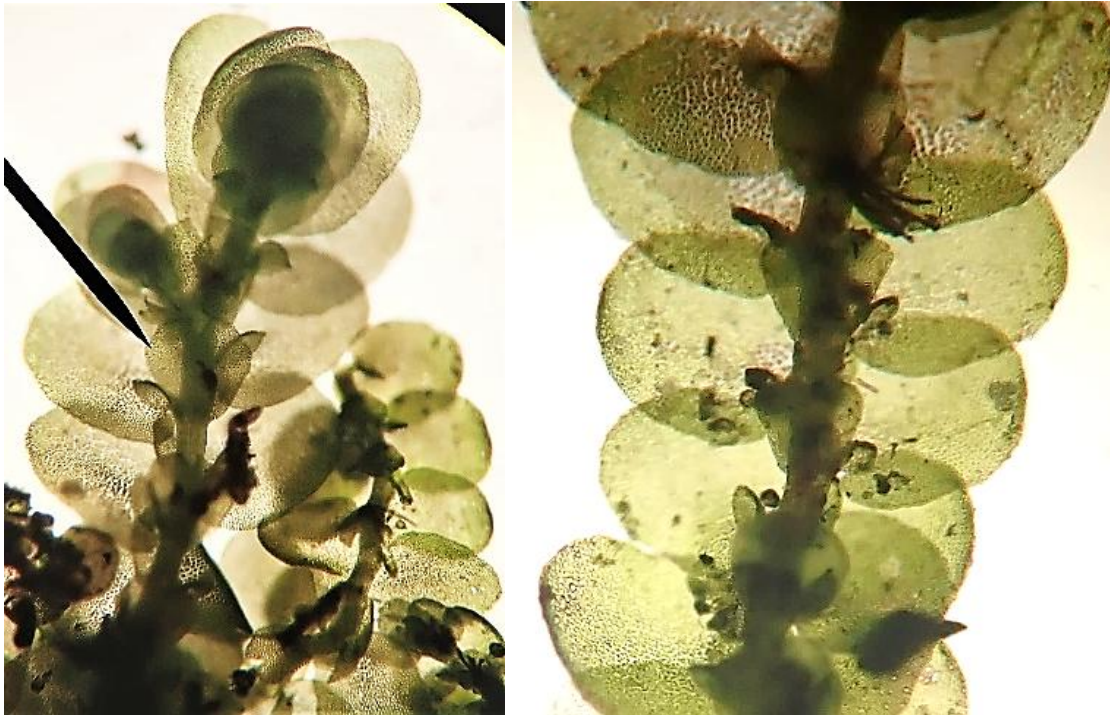
The lobules are only slightly appressed below, the underleaves are obovate, and the cell walls are thin with small trigones and intermediate thickenings. 1: Dorsal surface. 2: Ventral surface. 3: Detail of lobules and obovate underleaf. 4: Cell with sinuous, thin walls and small trigones. Summit of Kaho‘olawe, 2022, photos by W. Cuyler Bleecker, with permission.

7. *Frullania* species 1. Indigenous. On bark, in mesic forest, 4,000 ft., Kīpukapuau, Hawai‘i Volcanoes National Park, Hawai‘i Island, Freire & Judziewicz 21-743 (HAVO). This species is unique in the presence of obovate underleaves, numerous thick-walled, ocelli-like cells on the leaf lobes, and in the non-inflated, ligulate, slightly concave lobules.



Plants are olive green, 1.5-2 mm wide and prostrate. Leaves are elliptical, with rounded apices, imbricate, concave, entire, and nearly squarrose. The leaf lobules are galeate close to the plant apex, not inflated, ligulate, and slightly concave on most of the plant. The underleaves are distant to approximate, bifid, with a short “V” shaped sinus to about 1/5 of its length, vertically elongated, obovate, 2-3 times broader than the stem (but can be broader close to the plant apex), and not or only barely conceal the lobules. The leaf cells are isodiametric, irregularly shaped, thin to moderately thick-walled, with small triangular to nodular trigones, or a few with intermediate nodular thickenings. Ocellus-like cells with reddish, thick walls are abundant but irregularly scattered on the leaf lobes. Marginal cells are transversely elongated and hyaline, forming a distinct border. We did not observe sexual structures.

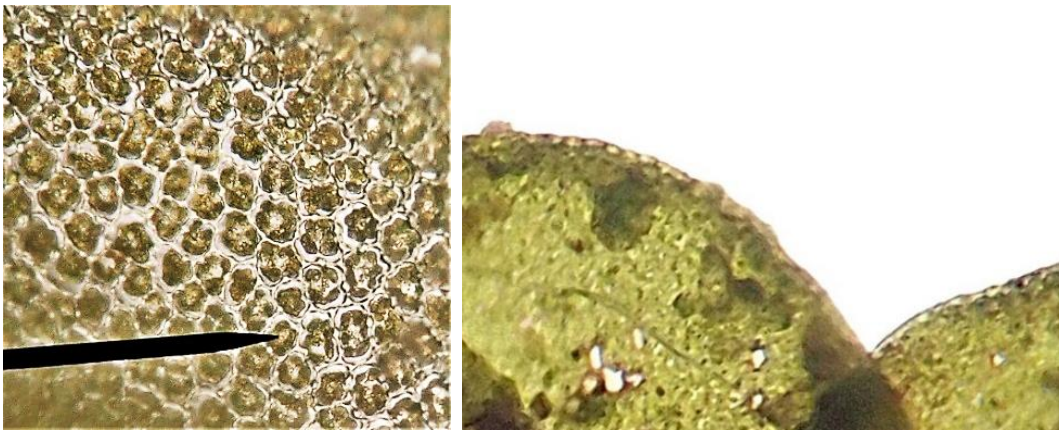
The description for this species is based only on few images taken by us from a single collection from Hawai‘i Volcanoes National Park (HAVO). The specimen needs detailed study (are perianths present?).



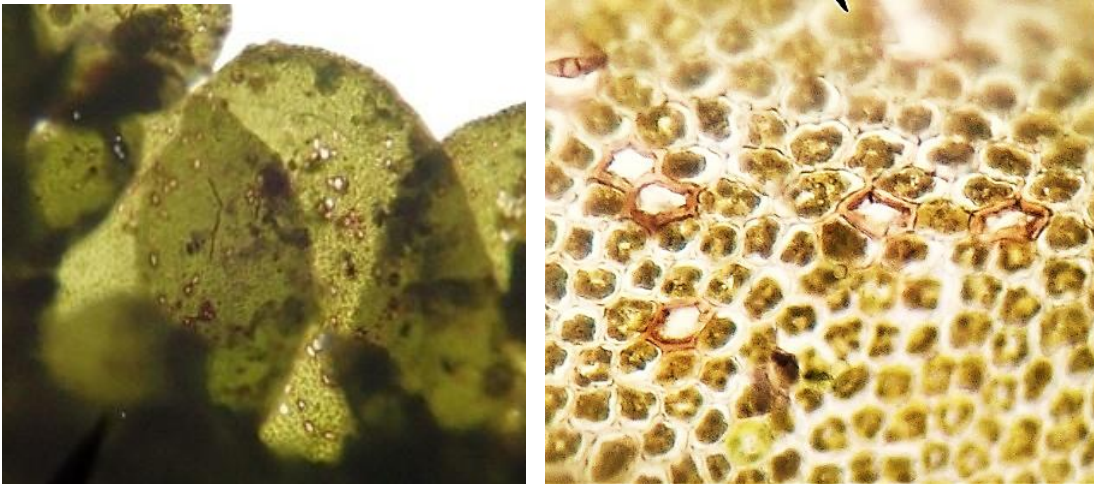
Frullania species 1. Leaves are rounded; underleaves are obovate, shallowly bifid, and most of the lobules are tongue-shaped, slightly concave, and not inflated. Freire & Judziewicz, 21-743 (HAVO).



Detail of obovate and shallowly bifid underleaf. Scale subunits = 10 μm . Freire & Judziewicz 21-743 (HAVO).



Left: cells with sinuous walls due to trigones and intermediate thickenings. Right: Border of hyaline and transversely elongated cells. Freire & Judziewicz 21-743 (HAVO).

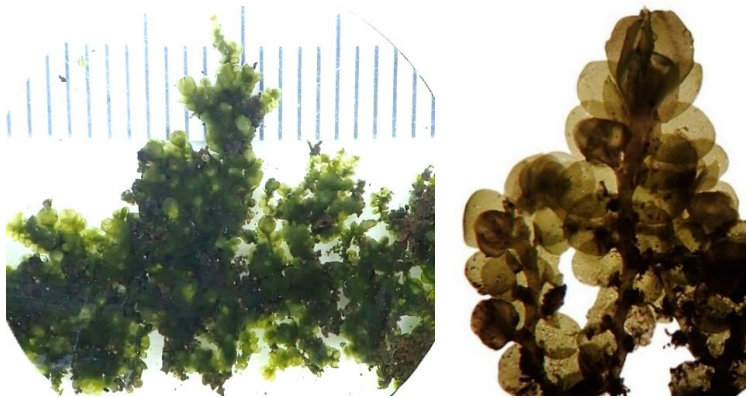


Frullania species 1. Leaves have numerous and scattered ocelli-like cells with thick, reddish walls. Kīpukapuauulu, Hawai‘i Volcanoes National Park, Hawai‘i Island, Freire & Judziewicz 21-743 (HAVO).

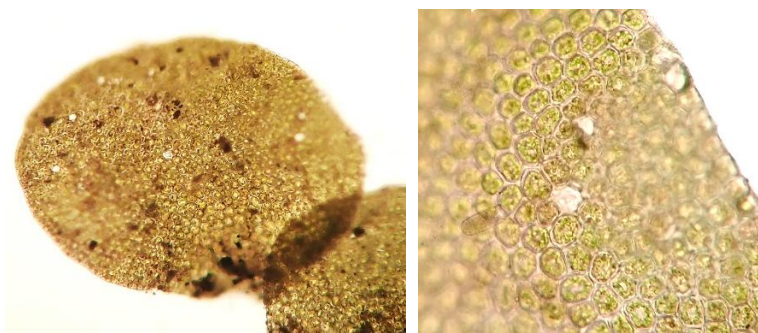
8. *Frullania* species 2. Indigenous. Known only from boulders in non-native forest at 1,670 ft. along Kawaikoi Stream, Koai'e Trail, Waimea Canyon, Kaua'i, Shevock et al. 48213 (CAS). It is distinctive in having small underleaves, explanate and triangular lobules, and perianths with four keels (two large and lateral, two smaller and ventral).



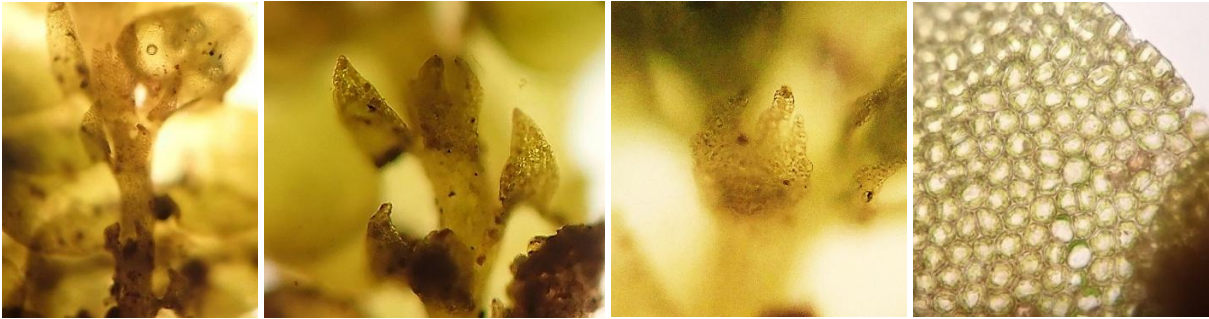
Monoicous. Plants grow prostrate and loosely attached on soil pockets on volcanic boulders. They are small, about 1.5 mm wide, dark olive-green. Stems are frequently branched. Leaves are elliptical, with rounded apices, imbricate, slightly concave, flattened, and almost squarrose. Lobules are explanate and triangular. Underleaves are small, about the same width as the stem diameter, bifid, some with a single lateral tooth so as to appear trifold (usually when associated with a branch). Leaf cells have thin walls with small, triangular trigones. Perianths are abundantly produced, about 1 mm in diameter, slightly obovate but almost globose, with a short beak, flat on the dorsal side and bulging on the ventral surface; they bear four keels, two large lateral ones and two much smaller on the bulging ventral side. Sporophyte seemingly shortly exerted; capsule with elaterophores. Male branches are short and globular, with 3-4 antheridial bracts.



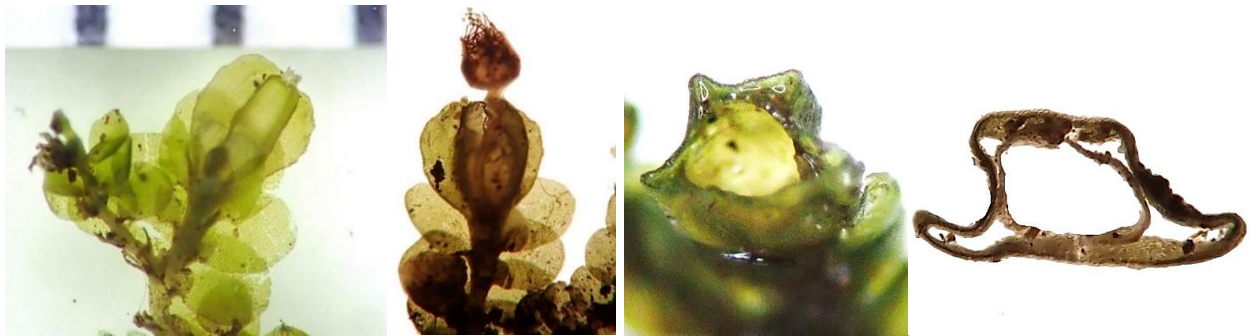
Left: Plants are small, prostrate, loosely attached, dark olive-green, with numerous perianths. Scale in mm. Right: Plant with a terminal perianth and antheridia on short lateral branches. Photos by A.V. Freire.



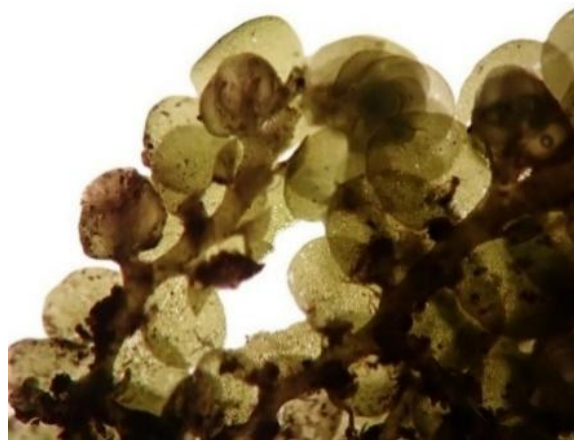
Frullania species 2. Elliptical leaf lobe with ocellus-like cells; note cellular contents in right photo. Shevock et al. 48213 (CAS). Photos by A.V. Freire.



1-2: Leaf lobules are triangular and explanate. Underleaves are small, about the same width as the stem, non-cordate, narrow, vertically rectangular to slightly obovate. 3: Some underleaves have a single lateral tooth (thus appearing 3-toothed). 4: Leaf cells are thin-walled, isodiametric, with small triangular trigones. Note border of quadrate cells. Shevock et al. 48213 (BISH). Photos by A.V. Freire.



Frullania species 2. 1: Perianths are obovate, beaked, with two prominent smooth lateral keels and two shorter ventral ones. Perichaetial bracts are asymmetrically bifid. Scale in mm. 2. Shortly emergent sporophyte. 3-4: Cross sections of perianth showing two larger lateral keels and two short, ventral ones. Shevock et al. 48213 (BISH). Photos by A.V. Freire.



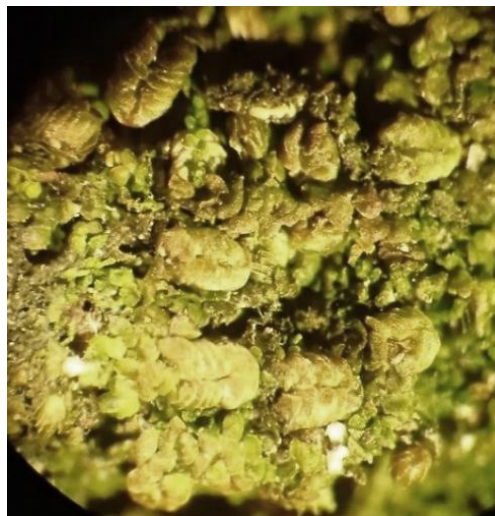
Frullania species 2. Globular antheridial branches. Waimea Canyon, Kaua'i, Shevock et al. 48213 (BISH). Photo by A.V. Freire.

9. *Frullania* species 3. Introduced? Known from a single Hawaiian record, from Kauaʻi: Kōloa District, Mahaʻlepu, just east of Gillian House, in secondary vegetation behind beach, dominated by *Casuarina* with scattered *Thespesia*, occasional *Coccoloba*, on lower trunk of *Casuarina*, elev. 6 m, 1 December 2022, Flynn 9682 (PTBG). Given the anthropogenically disturbed nature of its habitat, we wonder whether this is an exotic species. It is recognized by its small size, galeate lobules, caducous leaves with gemmae and rhizoids, and especially by its very conspicuous and compact ellipsoidal male branches.



This species resembles *Frullania oahuensis*, to which we think it is closely related. However, the very unique types of male branches (see below), the smaller lobules in relation to the lobes, the often connivent and toothed underleaves and the rhizoids at leaf margins are enough to separate this as a distinct species. Both species are dioicous; according to the photo in So & Wang (2006: Fig. 3b), in *F. oahuensis* the male branches are globose (these not observed by us) and the male plants do resemble female plants. Therefore we can exclude the possibility that our *F. species 3* represents male plants (which we did not observe) of *F. oahuensis*.

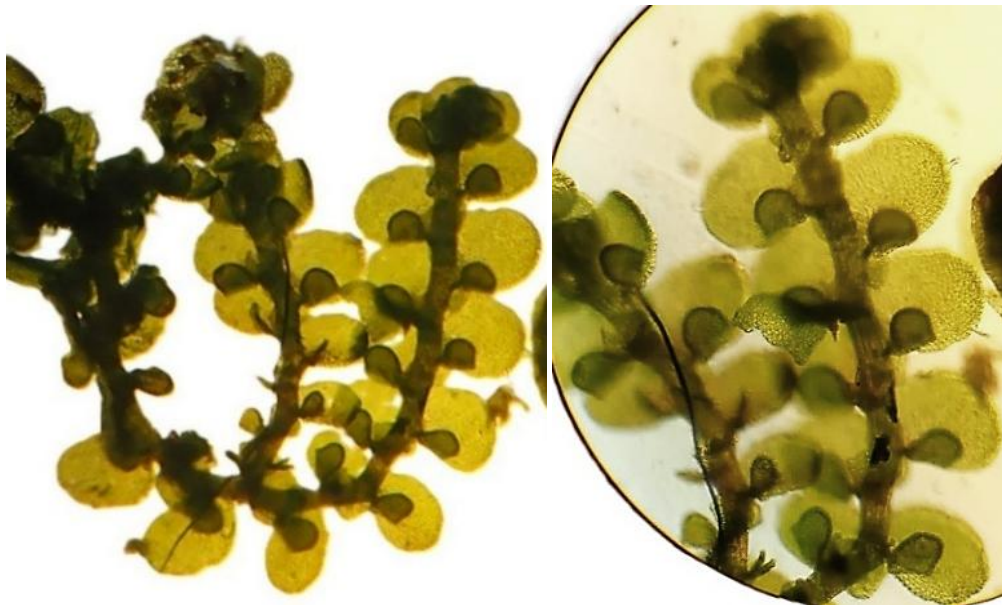
Populations form dense creeping clusters. Plants are small, about 0.5 mm wide, green to yellow or brownish green. Stems are stout and frequently branched. Leaves are elliptical, cordate, caducous, distant or contiguous to slightly imbricate, often with gemmae/buds, rhizoids, and sometimes producing rejuvenant. Lobules are galeate, sometimes with marginal rhizoids, or with gemmae. Underleaves are small, about 1.5 times the stem diameter; bifid to 1/3-1/2 their length, and have acute, triangular lobes that are connivent, parallel or divergent, with “elbows” or a tooth at each lobe base. Median leaf cells are slightly elongated, sometimes sinuous, with trigones and intermediate thickenings. Leaf marginal cells are quadrate. We observed three different types of male branches bearing antheridia: 1) Small and globular; 2) Prostrate, compact, ellipsoidal, with very imbricate and concave bracts with incurved margins, 1-1.2 mm long by 0.6-0.8 mm wide; and 3) Large (about 1.5 mm long by 0.8 mm wide), cylindrical, vertical, moss-like branches, with imbricate bracts of straight or recurved borders so as to appear “open” to release the sperm (?). Perianths were not observed.



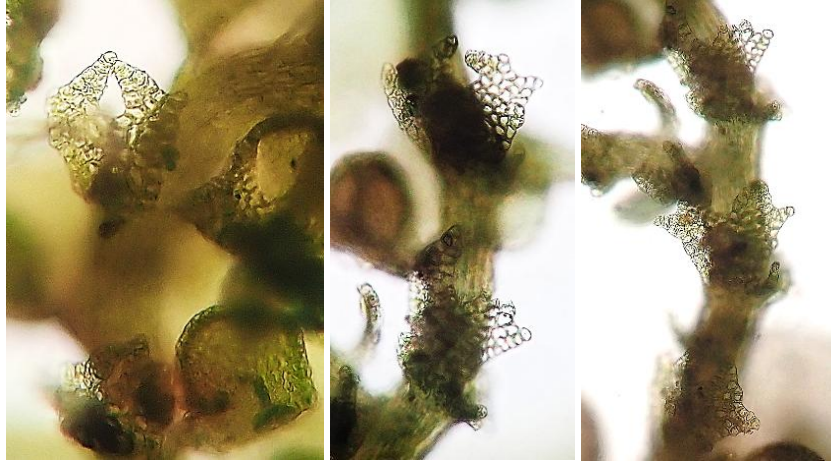
Frullania species 3. Plants with very enlarged male branches. Flynn 9682 (PTBG). Photo by E.J. Judziewicz.



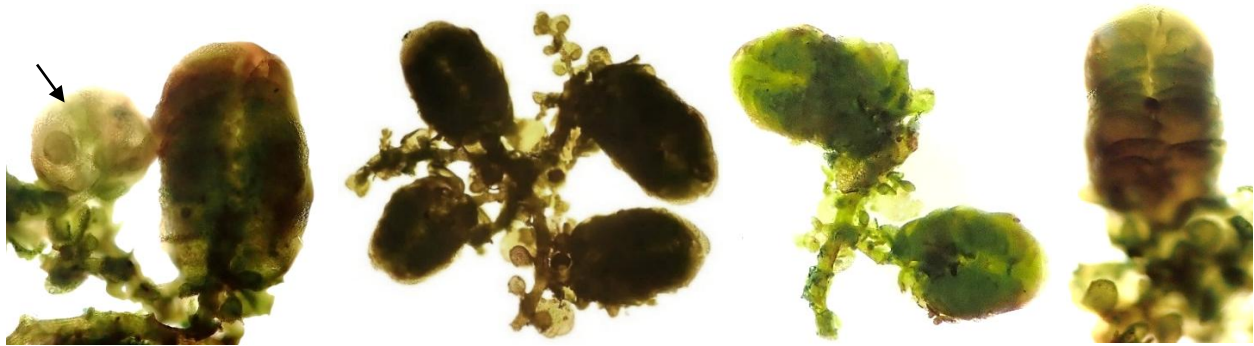
Plants are small, with very enlarged, ellipsoidal, compact male branches. Some male branches with “open” bracts are also present; these resemble a moss (right, arrows pointing at two stages of development). Note the globose male branch (red arrow). Scale in mm. Flynn 9682 (PTBG). Photo by A. V. Freire.



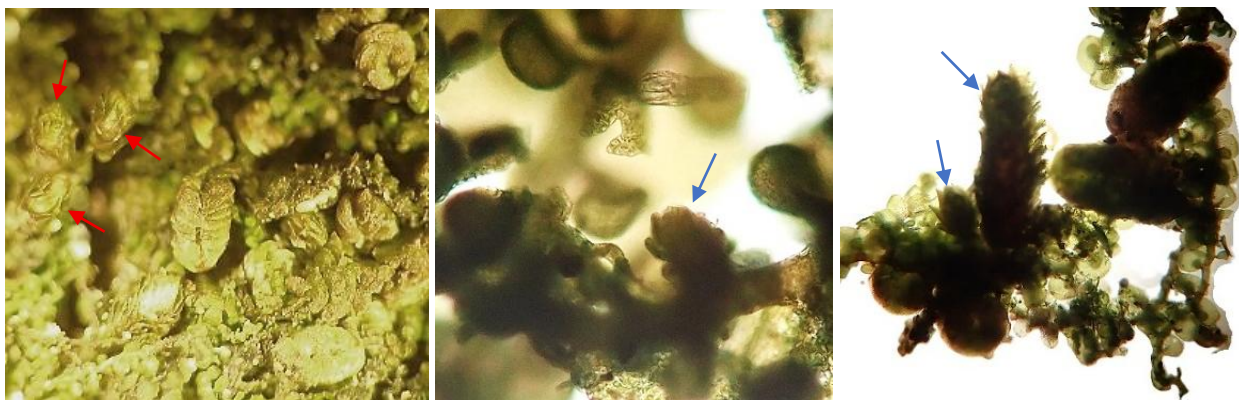
Frullania species 3. Leaves are contiguous to distant, caducous, and have galeate lobules. Note that some leaf keels persist when the lobules fall off. Kōloa District, Kaua‘i, Flynn 9682 (PTBG). Photos by E.J. Judziewicz.



Underleaves are bifid, with acute and triangular lobes, these connivent to parallel or sometimes divergent. Note the lateral “elbows” or teeth. Kaua‘i, Flynn 9682 (PTBG). Photos by A.V. Freire.



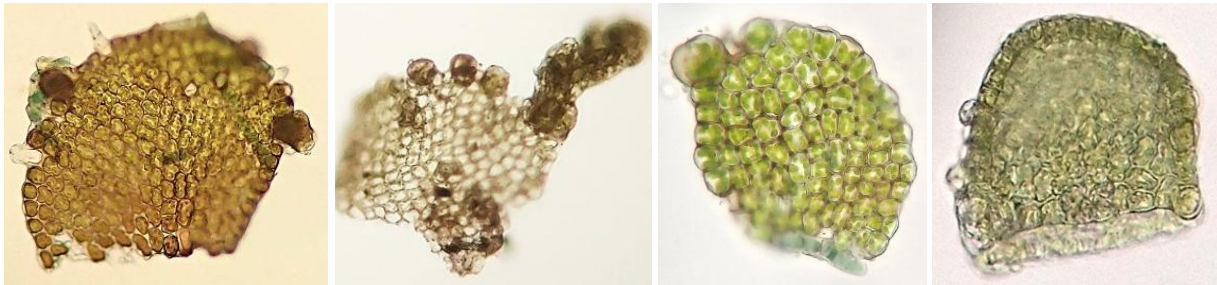
Male branches. 1: Globose male branch enclosing antheridia (arrow). Compare with the elliptical male branch next to it. 2-4: Abundant, very enlarged antheridial branches with concave, imbricate leaves. Flynn 9682 (PTBG). 2: Photo by E.J Judziewicz. 1, 3-4: Photos by A.V. Freire.



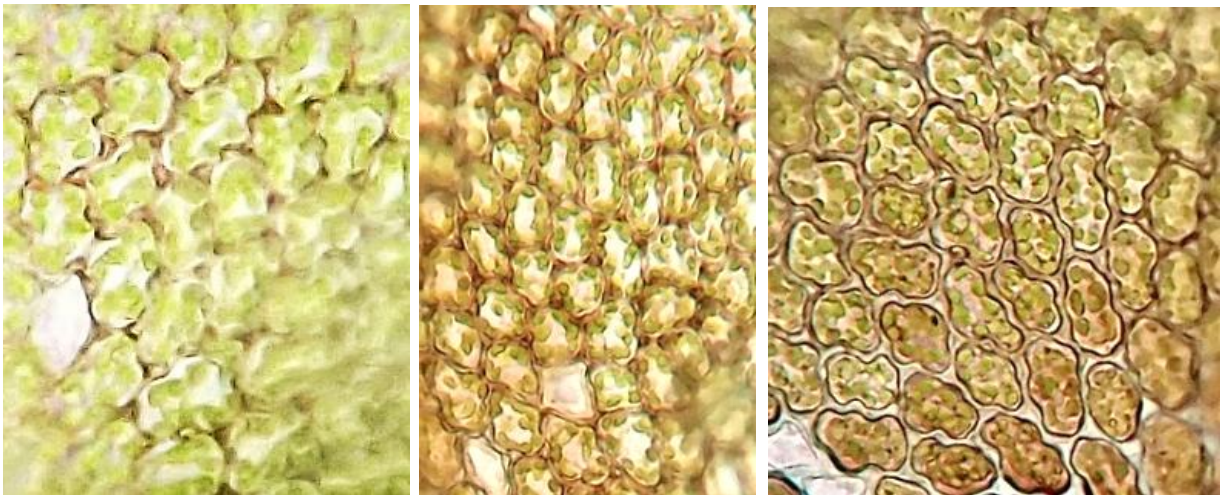
Frullania species 3. Left: Erect male branches with their bracts “open”. They resemble moss gametophytes (arrows). Of interest are the young branches (center and right) that are *not* globose, confirming this is a different type of branch. Kōloa District, Kaua‘i, Flynn 9682 (PTBG). Photos by A.V. Freire.



Rhizoids are produced at leaf margins. They can also be present on leaf lobules. Flynn 9682 (PTBG). Photos by A.V. Freire.



Leaf lobes and lobules produce gemmae/buds that may develop into young rejuvenants while attached to the leaf (first and second photos). Flynn 9682 (PTBG). Photos by A.V. Freire.



Frullania species 3. Leaf cells have prominent trigones and intermediate thickenings (left and center). Basal leaf cells are thicker-walled (right). Kōloa District, Kauaʻi, Flynn 9682 (PTBG). Left: Photo by E.J. Judziewicz. Center and right: Photos by A.V. Freire.

10. *Frullania* species 4. Introduced?

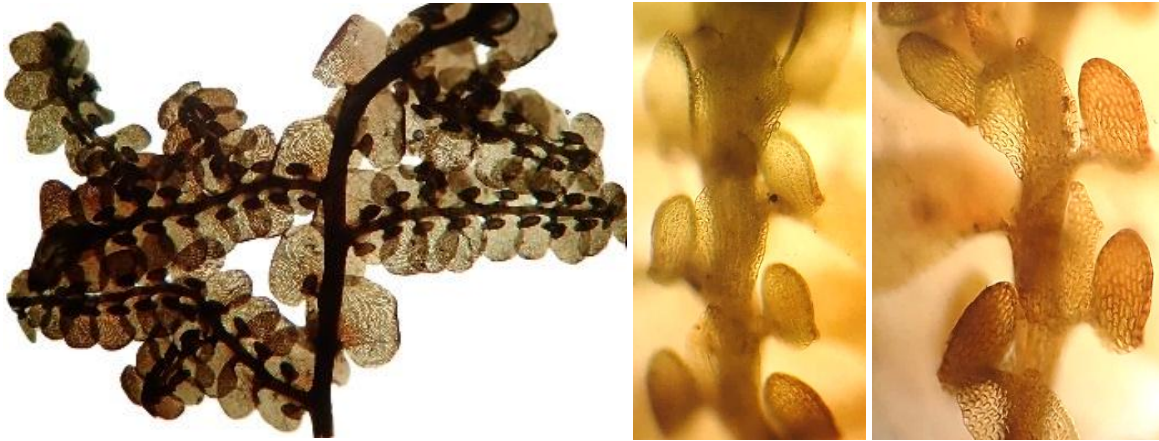
The only specimen known to us is Freire & Judziewicz 22-194 (BISH), wet shaded exotic forest, 100 ft., Onomea, Hawai'i Island. This monoicous species has a mixture of shortly cylindrical lobules that are aligned parallel to the stem (as in *F. meyeniana*), transitioning apically into elongate, non-inflated, explanate ones. At least some leaves are apiculate. The perianths are three-keeled but do not have a "bulge" on the ventral keel as in *F. meyeniana*. A few microphyllous branches are present. This specimen strongly resembles *F. meyeniana* and may be related to that species.



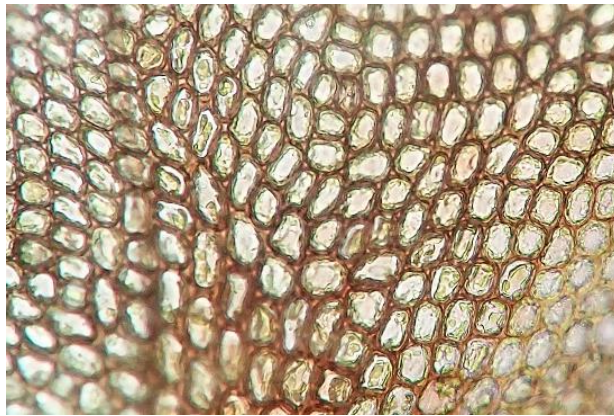
Plants are up to 1 mm wide and pinnately branched. Scale in mm. Freire & Judziewicz 22-194 (BISH).



Frullania species 4. Lobules are ligulate and explanate (not inflated) on upper branches and apical portions of the stem. Microphyllous branches are present (right). Onomea, Hawai'i Island, Freire & Judziewicz 22-194 (BISH).



Lower portions of the plant bear only clavate lobules. They are parallel to the stem as in *F. meyeniana*. Center and right: Underleaves are obovate, about twice the stem diameter in width, bifid to 1/3 their length, with parallel triangular lobes, and some have small elbows. Freire & Judziewicz 22-194 (BISH).



Median leaf cells with small trigones. Freire & Judziewicz 22-194 (BISH).



Frullania species 4. Left: Monoicous; plant with perianths and globose antheridial branches. Center and right: Perianths are three-keeled, with a short, ciliate beak. Onomea, Hawai'i Island, Freire & Judziewicz 22-194 (BISH).

Fuscocephaloziopsis Fulford (Cephaloziaceae)

Two or perhaps three species in Hawai'i. Nineteen species worldwide.

These are small, mainly creeping plants with attractive large, bulging, glistening leaf cells. The leaves are nearly longitudinally inserted (that is, nearly parallel to the main axis of the stem), decurrent, bilobed, and the lobes tend to be weakly to strongly connivent (convergent). Underleaves are absent. The stems have a hyalodermis. Spherical to ellipsoidal gemmae sometimes occur at stem apices.

Fuscocephaloziopsis is closely related to and resembles *Cephalozia* but has leaves that are longitudinally (rather than obliquely) inserted, with the lower margin of each leaf more or less decurrent along the stem. See Vána et al. (2013d) and Judziewicz & Freire (2023c: 160).

- 1. Leaves semi-erect, concave, lobed 1/5-1/3 of the way to the base; rare, Maui ***F. species 1***
- 1. Leaves prostrate, not concave, lobed 1/4-3/4 of the way to the base; widespread 2
 - 2. Plants at most 0.5 mm wide, threadlike, with very distant leaves bilobed about 1/2-3/4 of the way to the base ***F. baldwinii***
 - 2. Plants about 1 mm wide, stouter (not threadlike), with slightly imbricate to somewhat distant leaves bilobed about 1/4-1/2 of the way to the base ***F. connivens subsp. sandwicensis***



F. baldwinii

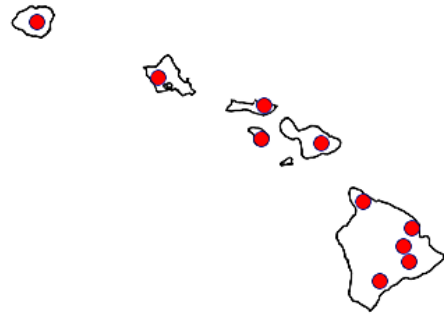


F. connivens subsp. sandwicensis

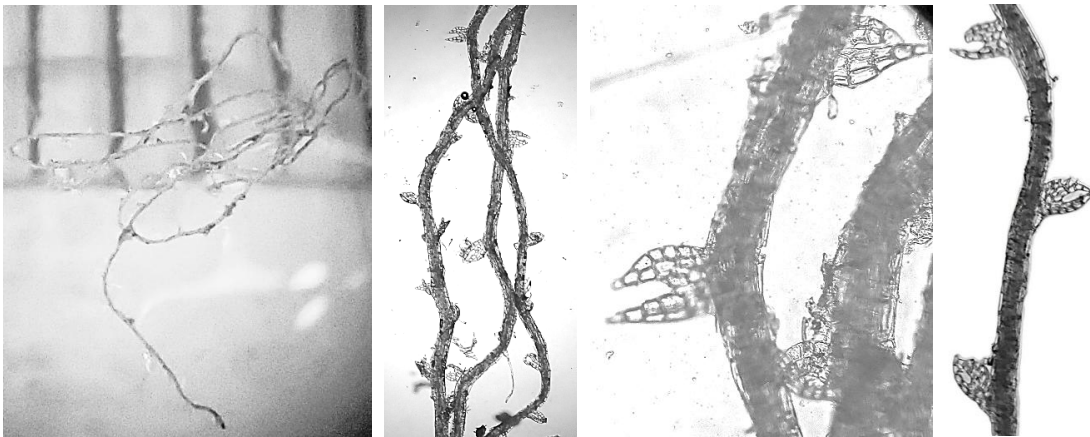


F. species 1

1. *Fuscocephaloziopsis baldwinii* (C.M. Cooke) Váňa & L. Söderstr. **Endemic.** Treated as *Cephaloziella baldwinii* by Staples & Imada (2006). Possible affinity (Cooke, 1904): *Cephalozia leucantha* (= *F. leucantha* (Spruce) Váňa & L. Söderstr.), Eurasia. This is an uncommon tiny creeping species found on all major islands in wet forests (1,600-6,100 ft.); it is often woven into mats of other liverworts, or large mosses such as *Leucobryum* species. Plants with leaves that bear a deep sinus, to at least one-half of their length. The leaf lobes are long and thin; at least some are slightly connivent.



Populations loosely threading on bark or decorticate logs, often intermixed with larger bryophytes. Plants light to whitish-green, tiny, thread-like, about 0.1 mm wide, up to 4-6 mm long. Stems are fragile, sparingly branched, with a hyalodermis. Leaves are tiny, distant, ovate, almost longitudinally to slightly obliquely inserted, some with a slightly decurrent dorsal margin; bifid, with a deep sinus to 1/2-2/3 the leaf length, the leaf lobes unequal in size, long, slightly to clearly connivent, or sometimes parallel. Underleaves are absent. Leaf cells are elongate, with thin to moderately thick walls; trigones are absent. Gemmae may be present.

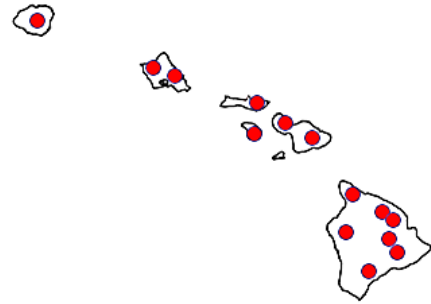


From possible holotype. Creeping over the liverwort *Lepidozia sandvicensis*, West Maui, Baldwin s.n., 1875 (BISH). Photos by E. J. Judziewicz.



Fuscocephaloziopsis baldwinii. Saddle area, Hawai'i Island. Note the gemmae (arrow) and hyalodermis. Photo by Randal Mindell, with permission: <https://www.inaturalist.org/observations/257628607>.

2. *Fuscocephaloziopsis connivens* (Dicks.) Váňa & L. Söderstr. subsp. *sandwicensis* (Mont.) Váňa & L. Söderstr. Treated as *Cephalozia sandwicensis* by Staples & Imada (2006). This taxon is **Indigenous** and is reportedly also found in French Polynesia (Bardat et al., 2021: 81). This is a common species of wet forests on all major islands (600-6,600 ft.), often woven into mats of other liverwort genera such as *Bazzania*, *Calypogeia*, *Lepidozia*, *Lophocolea*, and *Riccardia* on tree bark or in moist crevices in rocks or soil.



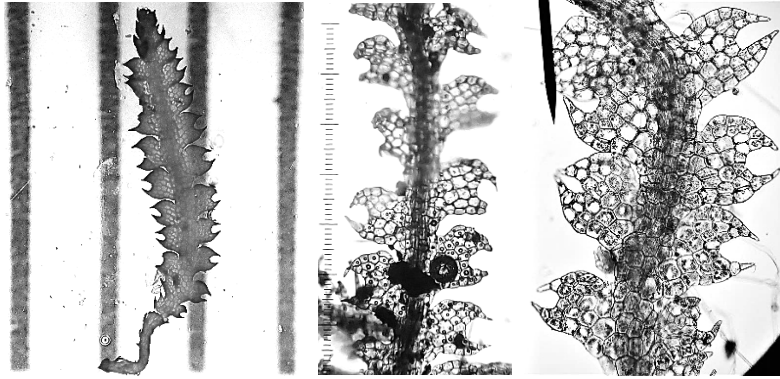
This is an easy liverwort to recognize; plants are small, emerald-green, and the tiny, distant, round leaves are bifid, with the two lobes almost “pinching” together like the “OK” sign that is made with the thumb and forefinger. The large, bulging, glistening leaf cells are evident with a hand lens. Plants have no underleaves. This is mainly a Holarctic species, with scattered locations in Africa and Oceania. When we illuminated them with UV light, the plants glowed red.

Plants are emerald- to yellow-green, prostrate, up to 0.8-0.9 mm wide (main stem). Stems are fragile, translucent, sparingly branched, with a hyalodermis. Leaves longitudinally inserted, with a decurrent dorsal margin, up to 0.3 mm long, round to ovate, distant to contiguous, sometimes slightly imbricate, rigidly projecting from the stem, flat or patent; bifid, with lunulate sinuses up to ½ the leaf length. Lobes are acute to acuminate, connivent (on main stem) to parallel (usually on branches). Leaf cells large, bulging, translucent, 78-117 µm long x 50-80 µm wide. Perianths prominent, fusiform, with long lacinate cilia.

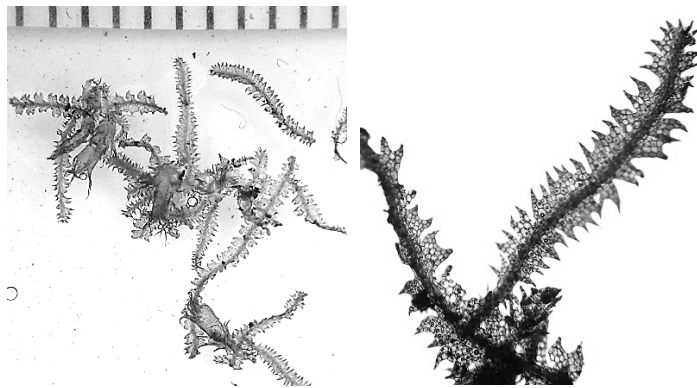
Some populations from Maui are distinctively semi-erect, have crowded leaves, and produce gemmae; see discussion at the end of this treatment.



Fuscocephaloziopsis connivens subsp. *sandwicensis*. Left: Nāhuku, Hawai‘i Volcanoes National Park, Hawai‘i, Freire & Judziewicz 21-754 (HAVO). Right: Longitudinally inserted pellucid leaves with large cells and connivent lobes. ‘Eke Bog, West Maui, photos by Zach Pezzillo, with permission: <https://www.inaturalist.org/observations/328718112>.



Examples of plants with longitudinal leaf insertion, connivent leaf lobes and leaves with large cells. Note the hyalodermis. Left: Scale in mm. Maui, Pezzillo 851 (BISH). Center: Scale subunits = 26 μ m. Freire & Judziewicz 23-463 (BISH). Right: Nāhuku, Hawai'i Volcanoes National Park, Hawai'i, Freire & Judziewicz 21-754 (HAVO). Left and center were stained with toluidine blue.



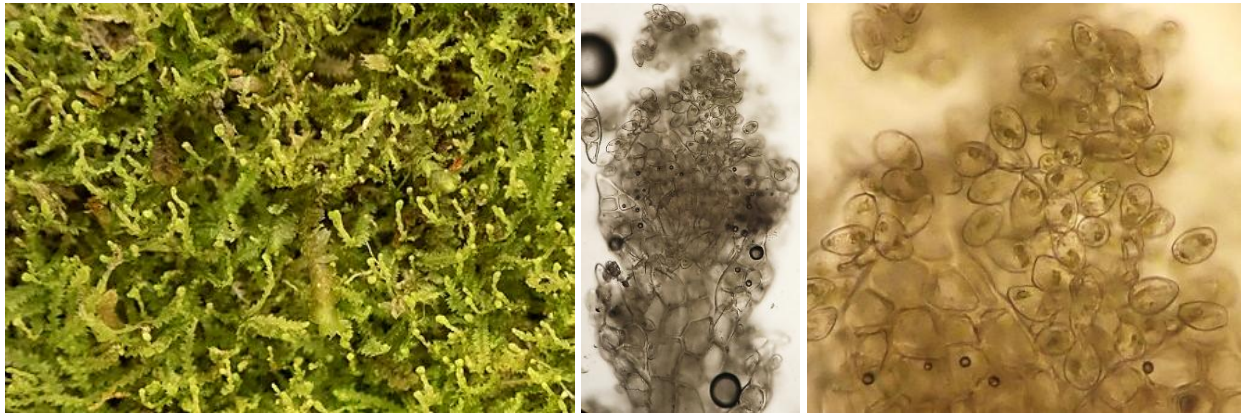
Left: Plants with perianths and branches. Scale in mm. Right: Branch with parallel leaf lobes. Both stained with toluidine blue. Freire & Judziewicz 23-463 (BISH).



Fuscocephaloziopsis connivens subspecies *sandwicensis*. Left: Population with abundant perianths. 'Eke Bog, West Maui photo by Zach Pezzillo: <https://www.inaturalist.org/observations/328718113>, Right: Fusiform perianth with lacinate cilia. Note connivent leaf lobes on main stem but parallel lobes on branches. Stained with toluidine blue. Volcano, Hawai'i Island, Freire & Judziewicz 23-463 (BISH).

Fuscocephaloziopsis cf. connivens

In the photos below, by Zach Pezzillo, we see populations from Maui with semi-erect rather than creeping plants, and leaves that are more crowded than in most Hawaiian material. Gemmiferous microphyllous stem tips are common. Gemmae are 25-33 μm long, elliptical, 1-celled, and were observed only in these Maui specimens; however, they are common in North American (Schuster, 1974: 801) and British (Paton, 1999: 115) populations of *F. connivens*. We wonder if these Maui populations could represent a broader concept of *F. connivens*, or if they could be a different species of *Fuscocephaloziopsis*.



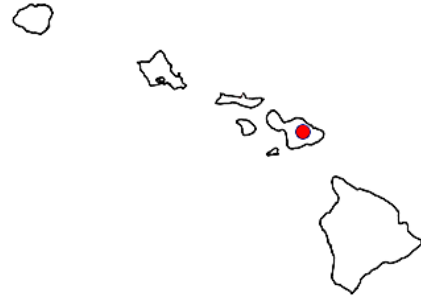
Left: Plants with abundant gemmiferous shoot tips, Maui. Photo by Zach Pezzillo, with permission: <https://www.inaturalist.org/observations/235045920>. Center and right: Gemmiferous stem tip and detail of gemmae. Kīpahulu Valley, Haleakalā, Maui, 4,700 ft., Pezzillo 851 (BISH). Photos by E.J. Judziewicz.



Note sub-erect plants with gemmiferous tips and the crowded leaves. Maui. Photo by Zach Pezzillo, with permission: <https://www.inaturalist.org/observations/235045924>.

3. *Fuscocephaloziopsis* species 1:

This taxon is known from two populations collected not far apart on Haleakalā, Maui (4,600-5,500 ft.). Plants are 0.5-0.6 mm wide. The leaves are round, sub-erect, and concave. They have a shallow sinus 1/5-1/3 of the leaf length; the leaf lobes are slightly or not at all connivent. These populations resemble *F. connivens* but the leaf stance, shallower sinuses, and less connivent lobes are distinctive. It may be a variant of *F. connivens* but it appears distinct enough to us to warrant further study.



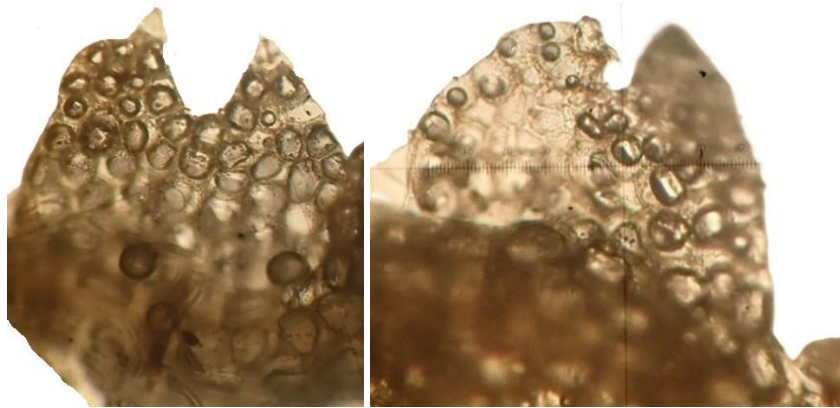
Left: Scale in mm. Center and right: Scale = 0.78 mm. Pezzillo & Henderson 986 (BISH). Plants stained with toluidine blue for contrast. Photos by A.V. Freire.



Waikamoi, Haleakalā, Maui, 4,600 ft., Pezzillo & Henderson 986 (BISH). Plants stained with toluidine blue for contrast. Photos by A.V. Freire.



Waikamoi, Haleakalā, Maui, 4,600 ft., Pezzillo & Henderson 986 (BISH). Photos by E.J. Judziewicz.



Fuscocephaloziopsis species 1. Leaves. These plants have leaves 9-11 cells wide, the cells only 25-30 μm . 'Ukulele, East Maui, ca. 5,500 ft., Forbes 1474 (BISH). Photos by E.J. Judziewicz.

***Fuscocephaloziopsis pleniceps*. Possible erroneous report?**

Long & Grolle (1990: 390) report the widespread species *F. pleniceps* (Austin) Vána & Söderstr. (as *Cephalozia pleniceps* (Austin) Lindb.) as occurring in Hawai'i, with no specimen cited. David G. Long (pers. comm., 9 Apr. 2024) states that the report is based on Vána (1988: 185). We did not examine any Hawaiian specimens resembling *F. pleniceps*, at least in the concept of Schuster (1974: 769-783).

Geocalyx Nees (Geocalycaceae)

Two species in Hawai‘i, both rare; four extant species worldwide.

Hawaiian plants are light green, with succubous, oblong-rectangular, bifid leaves that have triangular lobes and a broad, triangular sinus. Leaf cells are thin-walled, with small trigones. The distinctive elongate, bifid underleaves, with a narrow sinus and parallel, long-filiform lobes, resemble those of *Notoscyphus lutescens*, but the latter genus lacks bifid leaves. *Geocalyx* could also be mistaken for *Lophocolea*, but the latter genus has 4-lobed underleaves.

1. Gemmiferous shoots absent *G. graveolens*
 1. Gemmiferous shoots present *G. lancistipulus*

Because the two species are rare, the material available for study was limited to fragments of *G. graveolens* and a single population of *G. lancistipulus*. *Geocalyx graveolens* appears to have larger trigones, narrower and more appressed underleaves, and shorter leaves with a shorter dorsal insertion line. We did not see a clear difference in the leaf sinus depths between the two species. Much more material needs to be studied to test these differences. *Geocalyx graveolens* appears to have gemmae at the tips of the leaf lobes; these are not reported in the literature, but we do see several European photos on iNaturalist with this type of gemmae. This genus is described as having verrucose leaf cells, but these were not obvious in the plants we studied. Without clear vegetative differences, other than the presence/absence of gemmiferous shoots, molecular research is needed to check for the presence of *G. graveolens* in Hawai‘i.



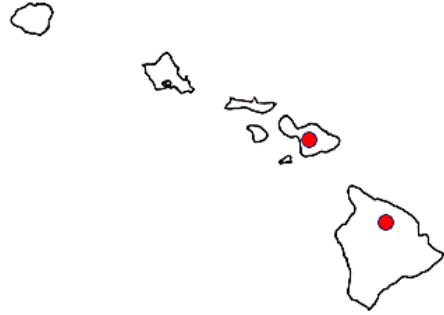
G. graveolens



G. lancistipulus

1. *Geocalyx graveolens* (Schrad.) Nees. Naturalized.

A Holarctic species. Rare, known from a collection made in 1953 in an “exposed gulch” at 6,500 ft. on the “Mauna Kea Truck Trail” (apparently on the north slope of the volcano) on Hawai‘i Island, Miller & Lamberton 5162 (MU), and two 2024 collections (589, 592) made by Zach Pezzillo from a conifer plantation on East Maui (Judziewicz et al., 2025b: 136-137), 6,500 ft. Perhaps an inadvertent introduction from the American mainland.



Populations grow on soil or rock. Plants are light green, about 1 mm wide, sparingly branched (?). Stems are stout. Leaves are succubous, oblong-rectangular, spreading, slightly imbricate to contiguous, bifid, with two broadly triangular and acute lobes separated by a broad and triangular sinus to 1/4-1/3 the leaf length. Underleaves are narrow and elongate, distant, not or only slightly broader than the stem; they are deeply bifid, with long-triangular to filiform parallel lobes, separated by a narrowly triangular sinus to at least half its length. Median leaf cells are thin-walled, with small trigones. Gemmiferous shoots are absent but clusters of gemmae at the leaf lobe tips may be present.



Left: Red scale bar = 1 mm. Mauna Kea, 6,500 ft., Hawai‘i Island, Miller & Lamberton 5162 (MU). Photos by E.J. Judziewicz.



Geocalyx graveolens. Left: Plants with bifid leaves. Center and right: Narrow, bifid underleaves with long, parallel lobes. Kula Forest Reserve, 6,500 ft, Haleakalā, Maui, Pezzillo 589 (left), 592 (center and right) (BISH). Photos by E.J. Judziewicz.

2. *Geocalyx lancistipulus* (Steph.) S. Hatt. Indigenous?

First report for Hawai‘i: Judziewicz & Freire (2023c: 161-162). Rare, an otherwise Asian species (Inoue, 1974a: 86-91; Asthana & Murti, 2009; Judziewicz & Freire 2023c: 161-162) known from one collection (Freire & Judziewicz 21-943, all photos below) from a deep, moist, shaded cleft in Nāmakaniāpaio Campground (3,950 ft.), Hawai‘i Volcanoes National Park. The long, microphyllous, gemmiferous shoot tips are distinctive.



Populations grow on soil pockets on lava rock and form dense, loose, prostrate mats. Plants are yellow-green, medium-sized, close to 2 mm wide and 5-8 mm long (possibly longer), with a turpentine odor when crushed. Stems are stout and sparingly branched, stoloniferous. The leaves are slightly imbricate to contiguous, spreading, dorsally inserted to the stem midline, prostrate, oblong, nearly rectangular; they are bifid to 1/5-1/3 their length, with triangular and symmetrical lobes separated by a broad triangular sinus. Leaf cells are thin-walled, with small trigones. Underleaves are elongate, distant, concave, spreading from the stem at acute to wide angles; they are bifid, with two long, parallel and filiform lobes, occasionally with lateral protuberances or “elbows” and a narrow sinus to at least ½ its length (but more often deeper). Rhizoids are clustered at the base of the underleaves. Antheridia are produced on short and rigid ventral branches. Archegonia are enclosed by ventral marsupia. Long, gemmiferous microphyllous shoot apices are frequent. Gemmae are elliptical.



Geocalyx lancistipulus. Population growing on soil. Plants are light green with rectangular, bifid leaves and apical microphyllous gemmiferous shoots (red arrows), and stolons (blue arrows). Hawai‘i Island, Freire & Judziewicz 21-943 (HAVO).



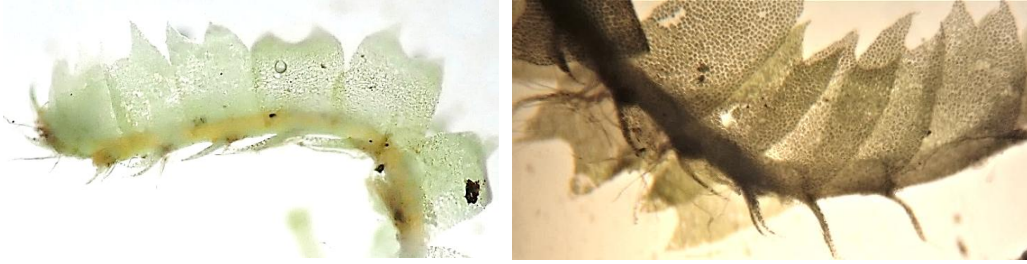
Left: Plants with gemmiferous shoot tip. Left and center: Scales in mm. Right: Scale subunits = 26 μ m.



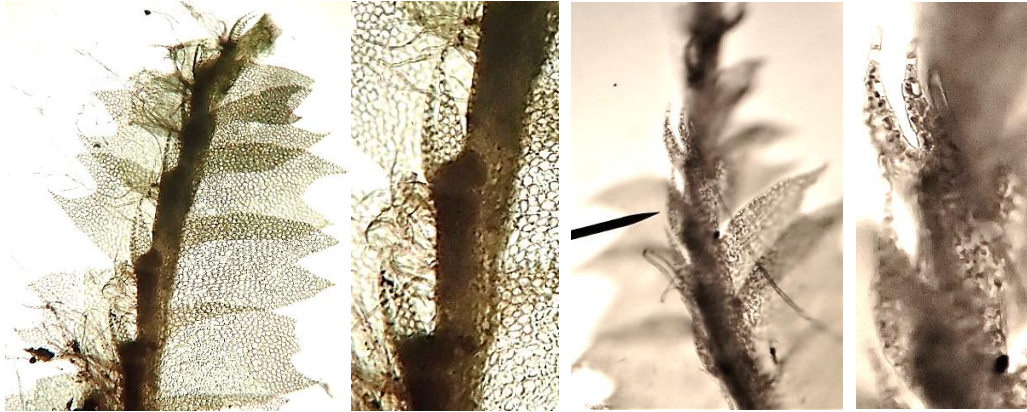
Left: Leaf insertion to stem midline (dorsal side). Center: Plant with gemmiferous shoot apex. Right: Ventral side with projecting, concave underleaves.



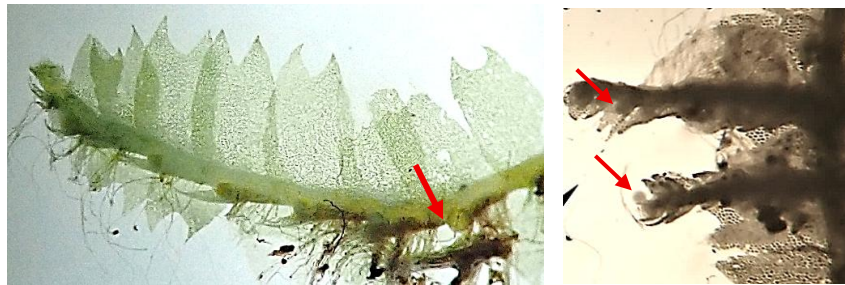
Geocalyx lancistipulus. Left: Gemmiferous apical shoot. Center: Cluster of gemmae at tip of gemmiferous shoot. Right: Round to ellipsoidal gemmae. Hawai'i Island, Freire & Judziewicz 21-943 (HAVO).



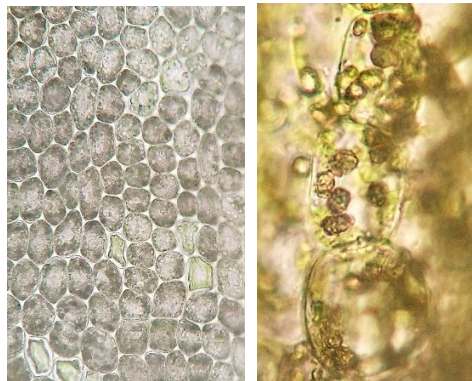
The underleaves are elongate, and slightly to widely spreading from the stem.



Underleaves are longer than wide; they are deeply bifid with a very narrow sinus and almost parallel, narrow and filiform lobes.



Left: Plant with developing marsupium (arrow). Right: Rigid, ventral antheridial branches with antheridia (arrow). We did not observe the second type of androecium reported by Asthana & Murti (2009).



Geocalyx lancistipulus. Left: Leaf cell walls are thin, with small trigones. Right: Oil bodies are dark, granular, and round to ellipsoidal. Hawai'i Island, Freire & Judziewicz 21-943 (HAVO).

***Gymnomitrium* Corda (Gymnomitriaceae)**

One species in Hawai‘i, 41 species worldwide.

Gymnomitrium is an easy genus to identify based on its dense, cushiony habit, and wormlike, very densely leafed stems, less than 0.5 mm wide. The leaves are strongly imbricate, strongly concave, and bifid; Hawaiian plants have more or less acute lobe apices. The closely related *Marsupella* is not wormlike, and its leaves are not densely imbricate and have rounded lobe apices. *Gymnomitrium* is only known from the summit of the north-south trending ridge separating Haleakalā from Kīpahulu Valley, Maui. This genus should also be sought in other alpine areas of Hawai‘i, such as the upper windward slopes of Mauna Kea and Mauna Loa on Hawai‘i Island.

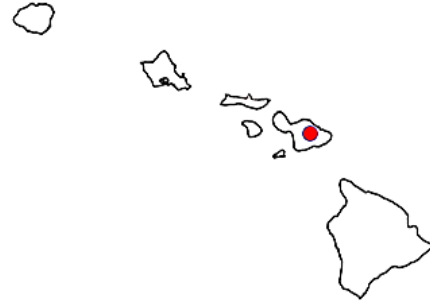
Hawaiian collections share some characters with *G. laceratum* and *G. mucrophorum*. However, because they also differ from these species, we cautiously refrain from assigning a species name at this point.

Comparison between Hawaiian specimens and literature-based descriptions of *G. mucrophorum* and *G. laceratum*.

Characters	Pezzillo 1239 (HALE)	Lewis 81-397 (F)	<i>G. mucrophorum</i> (Mamontov, FNA; Schuster, 1995)	<i>G. laceratum</i> (Mamontov, FNA)
Plant width (mm)	0.25-0.3(0.45)	0.3-0.4	Not given	0.2-0.5
Plant color	Greenish (fresh)	Grayish brown (dry)	Light green (fresh), whitish (dry)	Bright grayish-green (fresh)
Stoloniferous stems present	Yes	?	Not mentioned	Not mentioned
Rhizoids	Frequent	Absent (?)	Not given	Frequent
Depth of leaf lobing	(0.25)0.3-0.5	0.33-0.50	0.15-0.28	0.35-0.55
Central leaf cells trigones	Large, some confluent	Small to large	Coarse, more or less confluent	Small/absent
Leaf apex	Acute	Apiculate (mucronate)	One lobe is sharply acute, the other irregularly truncate or blunt or emarginate	Mostly acute
Lobe margins	Entire, some crenulate	Crenulate	Serrulate	Entire
Leaf border differentiated?	Yes, but sometimes not well defined.	Yes, but sometimes not well defined.	Apparently not (from description and drawings)	Conspicuous
Cuticle	Verruculose (at least on margins)	Verruculose	Asperulate to verruculate to vermiculate (Schuster)	Verruculose
Distribution	Maui	Maui	Alaska, Greenland	Scattered cosmopolitan

1. *Gymnomitrium* species. Indigenous.

First report of this genus for Hawai'i (Judziewicz & Freire, 2023c: 162). Rare. Known only from 3 collections (Lewis 81-388b, 81-397 and Pezzillo 1239), on the crest of the ridge separating Haleakalā from Kīpahulu Valley, on Maui. This small liverwort is recognized by its worm-like, julaceous aspect and densely imbricate bifid leaves with acute lobes. Populations form dense cushiony mats on rock or soil. W. Cuyler Bleeker (pers. comm.) also collected a specimen of this genus in 2022 near the Pezzillo site, but we have not examined the specimen.



Plants are vermiform (wormlike), green or whitish-green, sometimes with partial reddish or brown pigmentation; small, up to 7-8 mm long and less than 0.5 mm wide. Stems are robust but obscured by the leaves, occasionally branched; stem tips have densely imbricated leaves that are sometimes present at the end of slender branches with smaller leaves; stoloniform stems bear rhizoids, leaf scars, and/or distant to shortly imbricate, appressed, very reduced bifid leaves. Leaves are usually densely imbricated, transverse to slightly succubous, with adjacent leaf bases overlapping, appressed or spreading at 45°, secund (at least on densely leafy stem tips), strongly concave, oblong-ovate, with a sinus to 1/4-1/2 the leaf length, and bifid; the lobes are symmetrical, pointed and acute, with entire to crenulate margins and a single acute to mucronate apical cell. Marginal cells are isodiametric or elongated perpendicularly to the margin, thick-walled, and form a border that is single-layered above but sometimes 2-3 layered on the lower margin of the leaf. Median leaf cells are elongate and thick-walled; trigones are variable, small or large, triangular or confluent.

This species was collected in 1981 by Lewis, and more recently in 2025 by Pezzillo. Collection sites are in close proximity, about one mile apart, on the same crest of the north-south trending ridge separating Haleakalā from Kīpahulu Valley, in Maui. Lewis collected to the north, on a dirt bank above tree line, 7,900 ft., 4 Oct. 1981 (Marko Lewis 81-388b and 81-397, F, fragment at BISH [this location is at about 20°43'45"N, 156°08'25"W]). Pezzillo collected farther south, at the margin of forest and shrubland, 7,200 ft., 20.714223°N, 156.136173°W (Z. Pezzillo 1239, 21 Aug. 2025, HALE). This ridge is also the only Hawaiian location for the mainly Holarctic disjunct liverwort *Diplophyllum albicans*, and one of the few sites for *Sphenolobus minutus*. This ridge should be surveyed more intensively for other rare bryophytes.



Collection sites for the specimens studied (Lewis 81-397 and Pezzillo 1239) on Maui; they are only about one mile apart on the same north-south trending ridge.

Norton G. Miller (1942-2011) annotated both Field Museum specimens (Lewis 81-397 and 81-388b) as *Gymnomitrium laceratum*, a species with a scattered cosmopolitan distribution. However, in 2017, Yuriy Mamontov annotated them as “similar to” *G. mucrophorum* R.M. Schust., an Alaskan endemic, noting the shoots without rhizoids, leaves with crenulate margins, and verruculose cuticle. After reviewing Schuster (1974, 1995a), Mamontov et al. (2019), and the provisional Flora of North America treatment (FNA Editors, 2020; <http://www.mobot.org/plantscience/bfna/V3/Gymnomitriaceae.html>), we believe this is a different species and agree that it is similar but not identical to *G. laceratum* and/or *G. mucrophorum*.

The Lewis and Pezzillo specimens show some differences. Lewis 81-397 has crenulate leaf lobe margins and mostly a mucronate apical cell on each lobe. We did not observe rhizoids, but the material studied was limited to few fragments. We did not observe stoloniform stems. Pezzillo 1239 has mainly entire leaf margins, with acute but not mucronate apical leaf lobe cells. However, it can also have crenulate leaf lobe margins that bear a mucronate apical cell on densely leafed branch tips. Because of the close proximity of the collection sites and the overlap of leaf lobe crenulation and mucronate apical cells, we conclude they are likely expressions of the same species.

Unlike *G. laceratum*, the Hawaiian plants have at least some crenulate leaf lobe margins and mucronate lobe apical cells. Pezzillo 1239 is in closer resemblance to this species. Unlike *G. mucrophorum*, the Hawaiian plants have deeper leaf sinuses and symmetrical leaf lobe tips.

For the sake of comparison, we present separate sets of photographs of the Lewis and the Pezzillo specimens studied.

Pezzillo 1239 (HALE):



Gymnomitrium species 1. Vermiform, small plants. Scales in mm. Haleakalā, Maui, Pezzillo 1239 (HALE). Photos by E.J. Judziewicz (above) and A.V Freire (below).

Pezzillo 1239 (HALE): All photos by A.V. Freire.



Stoloniform stems have reduced leaves and produce rhizoids. Tips of stems are densely leafy. Note occasional branching.



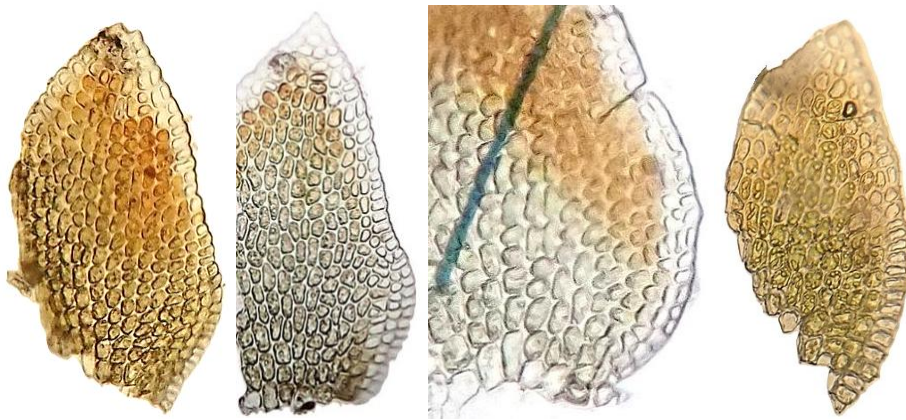
Left: Leaves are densely imbricate, sub-erect, and adjacently overlapping. Right: Two adjacent rows of strongly imbricate leaves.



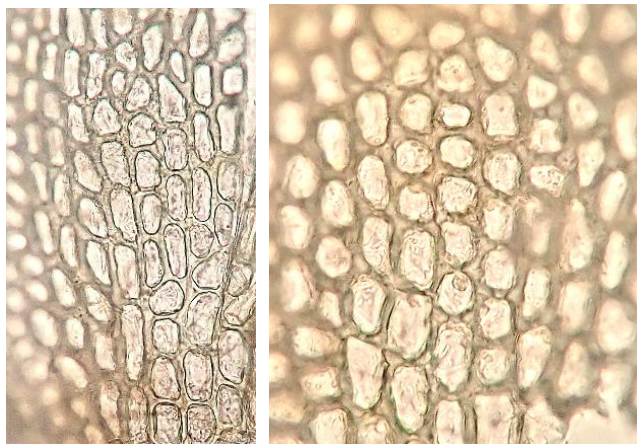
Gymnomitrium species 1. Bifid leaves with symmetrical lobes. Photos 3 and 4 are of crowded branch tips. Leaf apices acute.

Pezzillo 1239 (HALE):

Leaf apices acute to mucronate. Photos by A.V Freire.



Marginal cells form a border of thick-walled cells, sometimes in more than one layer below (center). Photos by A.V Freire and E.J. Judziewicz (right).



Gymnomitrium species 1. Median leaf cells are thick-walled, with triangular to confluent trigones. Photos by E.J. Judziewicz.

Lewis 81-397 (F):



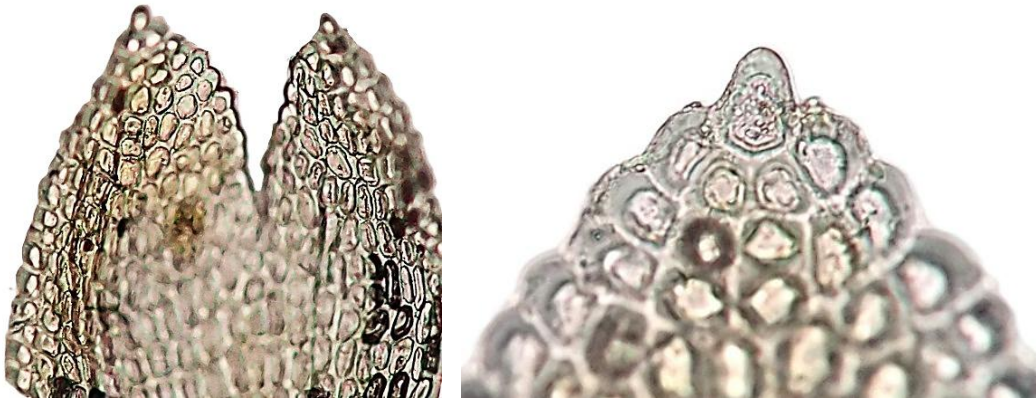
Densely tufted habit (upper left), plants are small, with wormlike aspect. Leaves are densely imbricated and concave. Scales in mm. Lewis 81-397 (F). Photos by E.J. Judziewicz (above) and A.V. Freire (below).



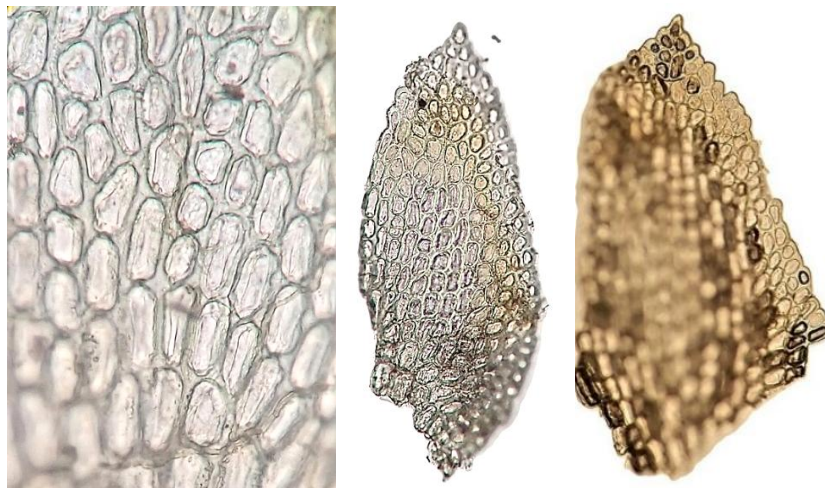
Gymnomitrium species 1. Some branches are compacted above as in *G. laceratum*. We did not observe well-developed stoloniform stems. Note the overlapping adjacent leaves. Haleakalā, Maui, Lewis 81-397 (F). Photos by A.V. Freire.

Lewis 81-397 (F):

Leaves are symmetrically bifid. Leaf margins are crenulate. Note the 2-3 rows of small marginal cells that form a border. Photos by A.V. Freire.



Leaf showing mucronate apical cells of lobes, crenulate marginal cells, and verruculose surface (right). Photos by A.V. Freire.



Gymnomitrium species 1. Left: Median leaf cells are mostly thick-walled and bear irregular trigones. Center and right: Leaf segments showing mucronate apices and border of small, thick cells that can be hyaline. Photos by A.V. Freire (left and center) and E.J. Judziewicz (right).

Herbertus Gray (Herbertaceae)

Four (or perhaps five) species in Hawai‘i, 40 species worldwide.

The following is a preliminary treatment. We thank Martin H. Hutten (Bryologist at Glacier Bay National Park) for his helpful insights into this challenging genus in Hawai‘i. Any mistakes or misconceptions are all ours.

The striking, scissors-like leaves of *Herbertus* make it one of the most conspicuous leafy liverworts, but also one that is sometimes mistaken for a moss. In montane forests the plants often grow on tree trunks in thick cushions that are frequently burnt orange or even bright red in color. *Herbertus* species are common in Hawai‘i, they spread from the trunks of ‘ōhi‘a trees, or, less commonly, from hāpu‘u stipes; they sometimes grow on soil or even rock. The leaves, which can be orange-brown, bright red, blackish-red or green, are shallowly to deeply bifid, with narrow, lanceolate to acuminate lobes, separated by a narrow to acute sinus. Stripe-like zones of larger cells (vittae) are present from the base into the leaf blade and into the leaf lobes. The underleaves are conspicuous and resemble the leaves but are slightly smaller. Sessile or stipitate slime papillae are often observed on the leaf margins. Leaf cells have large trigones and large, elliptical, granular oil bodies. We newly report that the leaves of *H. gracilis* are regularly caducous.

Despite its uniqueness at the genus level, at the species level we found *Herbertus* to be the most problematic leafy liverwort genus, with variable characters within populations and even within a given plant. Some of the (few) characters that *may* (or may not!) be useful in delineating species, at least in Hawai‘i, include: the relative length of the leaf lobes; the depth of the sinus between the lobes; the presence or absence of auricles at the lateral leaf bases; the extent of the vittate region of the leaf, and its relative branching point into the lobes. Plant color does not appear to be an important character.

We echo the following comments of Bell (2020) on *Herbertus*, and have bolded a sentence we wish to emphasize:

"The leafy liverwort genus *Herbertus* has a particularly confused taxonomic and nomenclatural history, generally attributed to a high degree of morphological plasticity in the genus... A large fraction of the systematic literature on *Herbertus* involves untangling past confusion or misconceptions. ***Herbertus* epitomizes a common problem in bryophyte taxonomy of dealing with poorly defined species limits and diversity in (morphologically) character-poor groups.** Despite being very distinctive and well-circumscribed as a genus, *Herbertus* has had a complex taxonomic history at the species level, in part due to a dearth of stable morphological characters, coupled with authors applying different criteria to delineate species for different regions. No global monograph exists for the genus, and in many cases the names applied in floristic treatments originate from disjunct floras, with locally described taxa tending to be increasingly synonymized in recent studies."

Much more work is needed to have a comprehensive understanding of this genus. Among the questions or issues to be addressed in Hawaiian *Herbertus* taxonomy are the following:

1. **Possible status of *Herbertus aduncus* in Hawai‘i.** Although we previously reported *Herbertus aduncus* (Dicks.) Gray as present and common in Hawai‘i (Judziewicz & Freire, 2024: 162; Judziewicz et al. 2025: 68), this was done based on a chain of synonyms: Miller (1963, as *H. sanguineus* (Mont.) Austin); Miller et al. (1983, as *H. sanguineus*); Staples & Imada (2006, as *H. sanguineus*); Juhlén (2006) treats *H. sanguineus* as a synonym of *H. dicranus* (Taylor) Trevis.; in turn, Sun & He (2019) present molecular evidence that *H. dicranus* is a synonym of *H. aduncus*. Given the taxonomic confusion that exists in the genus and after studying several specimens, we think that evidence is lacking to support reports of *H. aduncus* in Hawai‘i, especially given the concept of this species presented by Juhlén (2004) in which the bifurcation point of the vitta occurs in the upper portion of the leaf disk; in Hawaiian material the vitta

bifurcation occurs in the lower portion of the leaf disk. Moreover, Hawaiian material does not resemble material of *H. aduncus* from western North America (M. Hutten, pers.comm.). Much of what we had called *H. aduncus* we would now refer to the endemic species *H. helleri*.

2. *H. gracilis* and *H. herpocladoides* appear to be closely related and may even be synonymous. We found specimens with large (but indistinct) vittate areas, short leaf lobes, and intermediate sinus apertures with gradations from slit-like (as in typical *H. gracilis*) to V-shaped (as in *H. herpocladoides*) on the same plant. Some plants with V-shaped sinuses have *H. gracilis*-type underleaves.

3. *H. hawaiiensis* is extremely rare; no Hawaiian specimens have been collected since the species was described in 1965. We lack a good example for *H. hawaiiensis* and need to revisit reports from Kaua‘i and O‘ahu (Judziewicz et al., 2024: 8). The specimens we studied do not have the orbiculate, auriculate leaf disk as illustrated in the protologue (Miller, 1965).

4. *H. herpocladoides* as defined by Scott & Miller (1959) and as observed by us in the type (at MU) has rounded leaves, with shallower sinuses, and broader and rounded lobes than the specimens we collected that could belong to this species. Among these are plants with deeper sinuses we are tentatively calling *H. cf. herpocladoides*. It is possible these could belong to a species unknown to us.

Key to Hawaiian species of *Herbertus*

1. Leaf lobes separated by a slit-like (narrow with parallel sides) and shallow sinus (up to 1/3 leaf length); leaf lobes parallel to slightly connivent, conspicuously asymmetrical, one much smaller than the other; widespread..... *H. gracilis*
1. Leaf lobes separated by an acute, V-shaped, shallow to deep sinus; leaf lobes divergent, only somewhat asymmetrical, one lobe only slightly smaller than the other..... 2
2. Leaves strongly cordate forming an orbicular leaf disk; leaf lobes narrowly lanceolate; rare, East Maui *H. hawaiiensis*
2. Leaves not to only slightly cordate, with an elongate leaf disk; leaf lobes narrowly to broadly acute-lanceolate; common 3
3. Leaf lobes long and narrow, 5-8 times as long as broad at their base, long acuminate; vittae bifurcating at about ½ the height of the disk; widespread *H. helleri*
3. Leaf lobes triangular, less than ca 3 times as long as broad at the base; vittae bifurcating near the summit of the disk; Hawai‘i Island *H. herpocladoides*



H. gracilis



H. hawaiiensis?



H. helleri



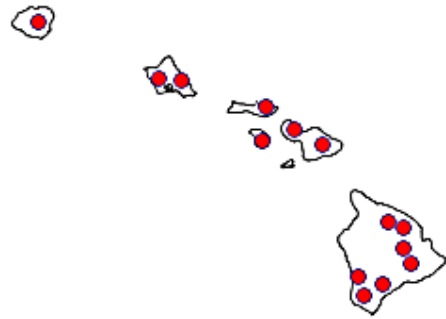
H. herpocladoides



H. cf. herpocladoides

Leaf and underleaf pairs of Hawaiian species of *Herbertus*.

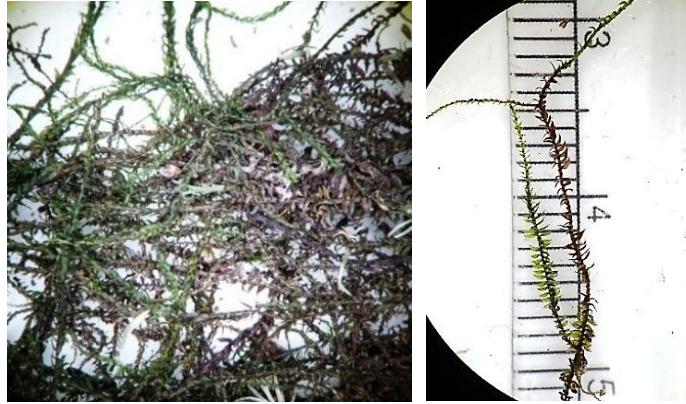
1. *Herbertus gracilis* (Mont.) Kuntze. **Indigenous.** Found on all major islands (1,400-5,800 ft.); also, on islands in southern Oceania. Common. Plants are slender, elongate, and creep on or project from rocks or the bark of trees. This species is easily recognized by its bifid leaves with a slit-like, shallow sinus that delimits a pair of asymmetric lobes. This is the only Hawaiian species of the genus with caducous leaves. *H. gracilis* may resemble *Acromastigum integrifolium*, but although the leaves of *A. integrifolium* may be minutely notched, they are never truly bifid.



Plants are slender; dark green, brown, red, or blackish; sparingly branched, but some plants with flagelliform ventral branches. The leaves are caducous, distant, appressed to the stem or broadly spreading, sometimes squarrose; asymmetrical, elliptical-ovate, sickle-shaped (falcate); shallowly bifid, with narrow lobes of different size, parallel to slightly connivent, very asymmetrical, one much smaller than the other, the large one recurved; with a narrow, parallel and shallow sinus that extends to less than 1/3 of their length. Vittae not defined. The underleaves are similar to the leaves but are slightly smaller and not sickle-shaped. The leaf cells are trigonous, with a verruculose surface. Leaf marginal cells are quadrate or shortly rectangular and form a margin. Oil bodies are large and elliptical, 2-3(4?) per cell. Antheridia develop in the axils of clustered, pouched bracts, at the apex of or in the middle of branches.



Herbertus gracilis. Example of red to orange population forming a dense mat. Mauna Loa Estates, Volcano, Hawai'i Island, Freire & Judziewicz 21-341 (BISH).



Example of a dark green population. They resemble a moss, even when studied with a handlens. They are slender and sparingly branched. Freire & Judziewicz 22-882 (HAVO).



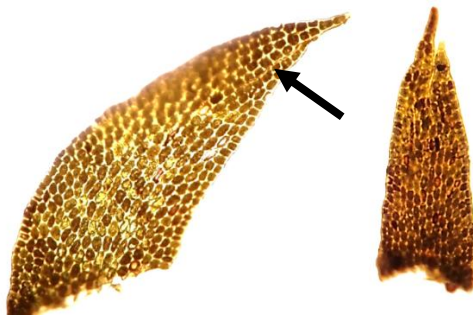
Ventral-intercalary flagelliform branches are present. The leaves and underleaves are caducous. Freire & Judziewicz 22-882 (HAVO).



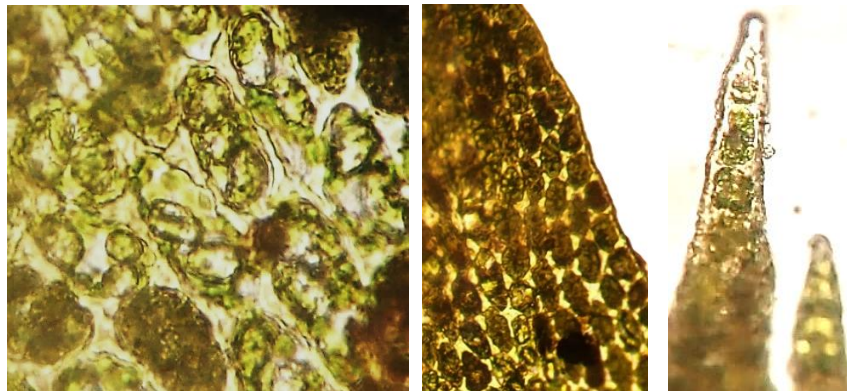
Herbertus gracilis. Leaves and underleaves are squarrose or nearly so when moist. The narrow slit-like sinus can be difficult to see with a handlens. The underleaves are smaller than the leaves and not falcate. Center and right: Androecia develop at the apex of or in the middle of branches. Note the caducous leaves. ‘Akihi ravine, Kahuku Unit, Hawai‘i Volcanoes National Park, Freire & Judziewicz 22-882 (HAVO).



The leaves bear a fanciful resemblance to the profile of a leaping dolphin – the sinus is the mouth, and the asymmetrical lobes the upper and lower jaws. Note the large, elliptical oil bodies. Photos by Miles K. Thomas, with permission.

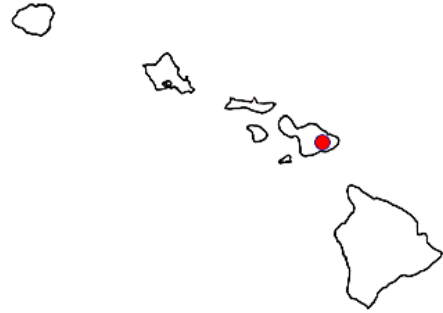


Leaf and underleaf (not to scale): Left: Sinus can be slit like, and hard to notice (arrow). Right: Underleaves are not falcate, they are ovate-elongate, and they also have asymmetrical lobes. Freire & Judziewicz 22-882 (HAVO).



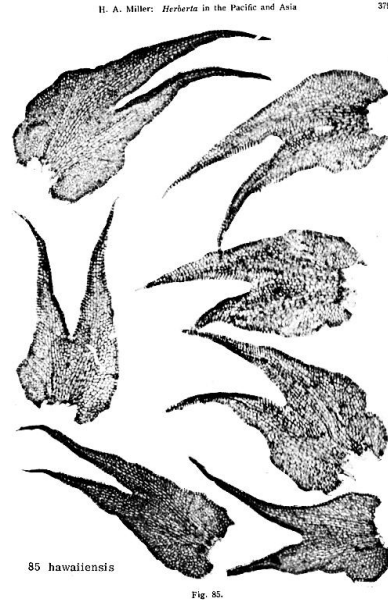
Herbertus gracilis. Left: Leaf cells with large trigones and large oil bodies. Center: Quadrate to rectangular cells. Right: Lobe apex showing verruculose leaf surface and single-celled tip of 3-4 quadrate to slightly elongate cells. ‘Akihi ravine, Kahuku Unit, Hawai‘i Volcanoes National Park, Freire & Judziewicz 22-882 (HAVO).

2. *Herbertus hawaiiensis* H.A. Mill. **Indigenous. Rare.** Maui (Ko‘olau Gap, about 7,500 ft., Haleakalā, the type) and perhaps also Kaua‘i and Hawai‘i Island, also in British Columbia, Canada (Stotler & Crandall-Stotler, 2018: 626) and possibly Alaska (M. Hutten pers. comm.). Miller et al. (1983: 346) report it only from East Maui and Haida Gwaii, British Columbia, Canada. It is interesting that we have not encountered any Hawaiian specimens of *Herbertus* closely resembling those of Miller’s illustrations of the type. Open circles represent unconfirmed reports.



Plants are characterized by a conspicuously auriculate and almost orbicular leaf disk; long, triangular, and acuminate leaf lobes; the quadrate apical cells of the leaf lobes; and leaves that are reportedly “crisp and reflexed when dry, revolute when moist” (Miller, 1965: 317). According to Miller’s illustration, the bifurcation point of the vitta occurs about 2/3 of the way from the base to the apex of the leaf disk and extends into the lobes.

According to molecular data presented by Bell (2020; based on a specimen he collected in Canada), *H. hawaiiensis* may be most closely related to the widespread Holarctic species *H. sakuraii* (Warnst.) S. Hatt.; it is also related to *H. delavayi* (Steph.) Steph., a mainly Asian species also known from Alaska and British Columbia, Canada.



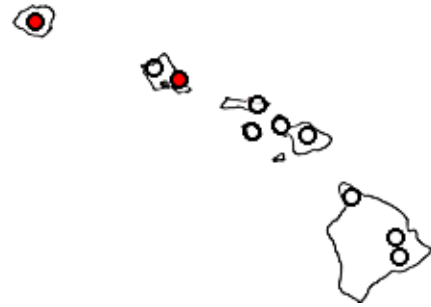
Herbertus hawaiiensis. Illustrations by Miller (1965). In the right figure, we presume that the two bottom drawings are underleaves.

The following three photographs are of a specimen collected in the Tongass National Forest, Alaska by Martin H. Hutten 17,529 (UWSP), who identified it as *H. hawaiiensis*. The leaves are as in Miller's illustration, with large auricles that form a rounded leaf disk. The leaf lobes are lanceolate, about 3-4 times longer than broad at their base, and the bifurcation point of the vitta occurs about 2/3 of the way from the base to the apex of the leaf disk. We agree that it resembles *H. hawaiiensis*. We hypothesize that this species arrived in Hawai'i from boreal regions of Canada and Alaska, perhaps carried by migratory birds. Because of its rarity in Hawai'i, we think this species may be present in difficult-to-access gulches. Targeted botanical exploration is needed.



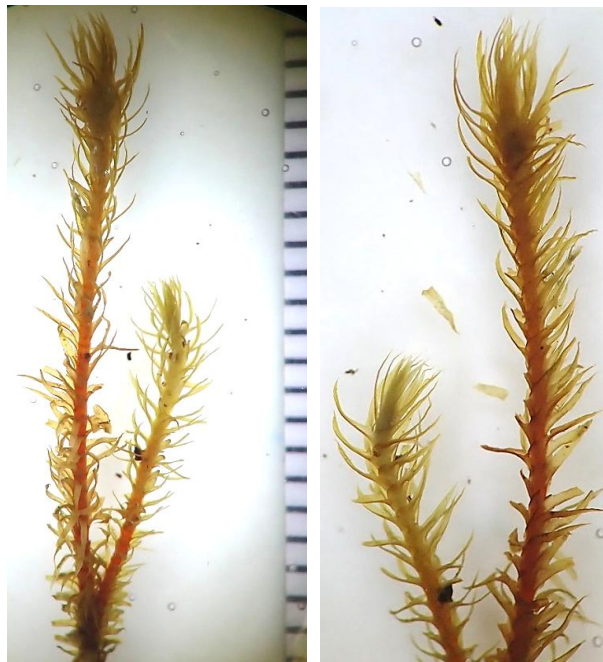
Herbertus hawaiiensis. Above: Scale in mm. Below: Leaves with auricles. Tongass National Forest, Alaska, Hutten 17,529 (UWSP). Photos by E.J. Judziewicz.

3. *Herbertus helleri* (Steph.) W.E. Nicholson. Endemic. Confirmed (by microscopic examination of leaves) from Kaua‘i and O‘ahu. The type (Heller 2261, holotype G, isotypes MIN, NY) is from on and near the summit of Kōnāhuanui in the Ko‘olau Range on O‘ahu. Miller et al. (1983: 346) report it only from O‘ahu. However, based on macroscopic examination of specimens and photos, this is probably the common “narrow-lobed” species found on all major islands from 3,000-7,000 ft. that we had previously identified as *H. aduncus*. The red dots indicate confirmed localities, while the open dots indicate probable localities.



Miller (1965: 310, figs. 37-40) notes that the leaf lobes are “narrowly lanceolate”; measuring his drawings, the length to width ratio of the leaf lobes varies from 5-5.7 times as long as wide at the base. The specimens we studied, from Kaua‘i, have leaf lobes even narrower, varying from 6-7(8) times as long as wide.

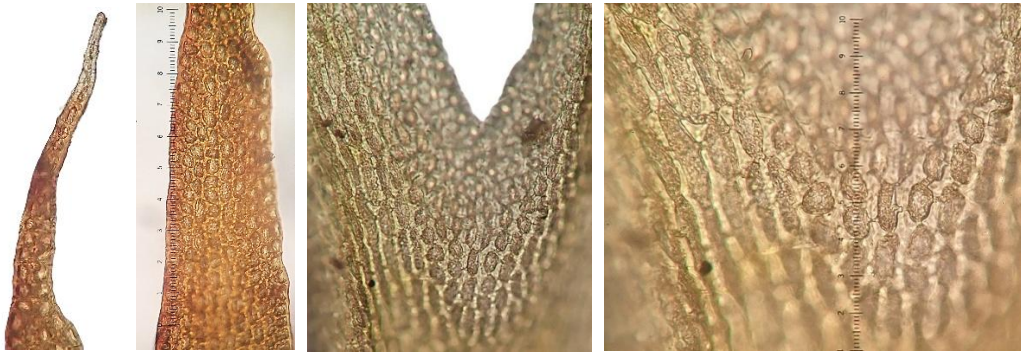
Plants stout, 2-5 mm broad and several centimeters long, projecting from their substrate, forming dense mats, intermixed with other bryophytes. Stems strong, reddish, about 0.5 mm in diameter, sparingly branched. Leaves distant to slightly imbricate, secund, the base of adjacent leaves overlapping, obscuring the stem on dorsal view, leaf disk slightly auriculate, leaf lobes separated by a broad and deep V-shaped sinus to $\frac{3}{4}$ the leaf length or deeper; lobes long and narrow, 6-8 times longer than broad, acuminate, strongly divergent, with long uniseriate tips. Leaf margins sometimes with a few teeth or outgrowths. Vitta bifurcation is deep, to about $\frac{1}{2}$ of the leaf disk but usually deeper. Leaf cells have conspicuous trigones. Underleaves with parallel or divergent lobes, vittate, sometimes with outgrowths, with small auricles. We wonder whether this species could be synonymous with the cosmopolitan *H. dicranus*; we are unfamiliar with that species.



Herbertus helleri. Left: Scale in mm. Alaka‘i Swamp Trail, Kaua‘i, Shevock 48164 (PTBG). Photos by A.V. Freire.



Leaves with long, narrow lobes, a deep sinus and deeply bifurcating vitta. Note the small auricles. Shevock 48164 (PTBG). Photos by A.V. Freire.



1. Leaf lobes are acuminate with long uniseriate tips of elongated cells. 2. Lobe cells. Scale units = 5.1 μm . 3. Median leaf cells and vitta. 4. Scale units = 2.5 μm . Shevock 48164 (PTBG). Photos by A.V. Freire.



Herbertus helleri. Underleaves usually have parallel lobes but can also be divergent. 1. Scale units = 26 μm . Note the marginal tooth and the underleaf disk marginal outgrowths; also note the small auricles. Alaka'i Swamp Trail, Kaua'i, Shevock 48164 (PTBG). Photos by A.V. Freire.

The following set of photos are from the Blue Hole, North Fork of the Wailua River, Kauaʻi, Flynn 8278 (BISH). This specimen was determined by Kathrin Feldberg (Ludwig-Maximilians-Universität, München, 2016) as *H. hawaiiensis*, however, note the smaller auricles, long-lanceolate leaf lobes, and the bifurcation point of the vitta occurring about 1/3-1/2 of the way from the base to the apex of the leaf disk. We believe this is *H. helleri*. All photos by A.V. Freire.



Robust plants. Scales in mm.



Leaves are slightly auriculate. Scale in mm.



Herbertus helleri. Underleaves. Scale in mm. Blue Hole, Kauaʻi, Flynn 8278 (BISH).



Herbertus helleri. Leaf cells and tips of leaf lobes. Blue Hole, Kaua'i, Flynn 8278 (BISH). Photos by A.V. Freire.

The next set of photos is from Stainback Highway, Pu'u Maka'ala Natural Area Reserve, Hawai'i Island, Freire & Judziewicz 21-838 (BISH), and the last two are from the same area of Pu'u Maka'ala N.A.R., and were made by Daniel Tucker. The leaves are moderately auriculate, forming an only weakly orbicular disk, and the bifurcation point of the vitta occurs about 1/3-1/2 of the way from the base to the apex of the leaf disk; note the long and narrow lobes. These characters suggest *H. helleri* rather than *H. hawaiiensis*.



Plants are robust, with stout stems, sparingly branched and with secund, falcate leaves. Scales in mm. Freire & Judziewicz 21-838 (BISH). Photos by A.V. Freire.



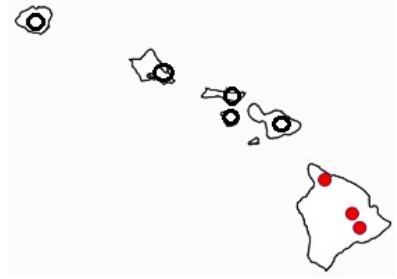
Herbertus helleri. Photos 1, 2 and 3: The leaves are auriculate. Note the the bifurcation point of the vitta occurring about 1/3-1/2 of the way from the base to the apex of the leaf disk, the vittae projecting well into the lobes. 4, 5, 6: The underleaves are smaller and are not clearly auriculate (here not at the same scale as the leaves). Stainback Highway, Pu'u Maka'ala Natural Area Reserve, Hawai'i Island, Freire & Judziewicz 21-838 (BISH). Photos by A.V. Freire.



Herbertus helleri. Stainback Highway, Pu'u Maka'ala N.A.R., Hawai'i Island. Photos by Daniel Tucker, with permission: <https://www.inaturalist.org/observations/255702916>.

4. *Herbertus herpocladoides* E.B. Scott & H.A. Mill. Indigenous.

Found only on Hawai'i Island (3,000-5,000 ft.), and apparently elsewhere in Oceania (Vanuatu; Miller et al., 1983: 346). Resembling *H. gracilis*, but the leaves are not or only slightly falcately shaped and the sinuses are not slit-like; instead, the sinuses are "V" shaped and to about ½ the leaf length or shallower. We think *H. herpocladoides* and *H. gracilis* are closely related. We have not yet confirmed reports from Kaua'i, Moloka'i, and Maui by Miller et al. (1983: 346), and we need to re-examine retract our report from Lāna'i (Judziewicz et al., 2023: 17). Open circles represent unconfirmed reports.



The plants are red to green, with secondary branches and abundant ventral flagelliform branches. The leaves are contiguous to overlapping, spreading, bifid up to about ½ of their length, with a "V"-shaped sinus, and they have broad, triangular, acute, symmetrical to slightly asymmetrical lobes. These are about twice as long as they are broad at their base. Vittae occupies a good portion of the leaf and underleaf and are well defined. Cells have prominent trigones.

We examined the type at MU (photos below). The specimen is as illustrated in the protologue by Scott & Miller (1959), with a shallow sinus and broad, well-defined vittae, and with triangular and broad leaf lobes. Specimens from Hawai'i Island, Freire & Judziewicz 21-246 (HAVO), and photographs from Kūlani Road, Hawai'i Island, Randal Mindell: <https://www.inaturalist.org/observations/255687264>, and from Mānoa Falls Trail, O'ahu, Shevock 14665 (BISH) are the closest to Scott & Miller's concept for this species. We also studied specimens from Hawai'i Island and Honolulu that resemble *H. herpocladoides* but they do not have vittae as well defined and the leaf sinuses are deeper, sometimes beyond ½ the leaf length. We refer to these as cf. *H. herpocladoides*.

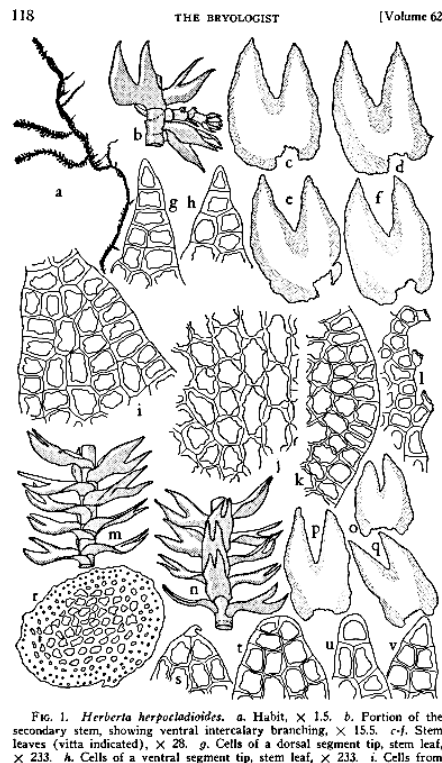


FIG. 1. *Herbertus herpocladoides*. a. Habit, $\times 1.5$. b. Portion of the secondary stem, showing ventral intercalary branching, $\times 15.5$. c-f. Stem leaves (vitta indicated), $\times 28$. g. Cells of a dorsal segment tip, stem leaf, $\times 233$. h. Cells of a ventral segment tip, stem leaf, $\times 233$. i. Cells from a dorsal segment, stem leaf, $\times 233$. j. Cells from a ventral segment, stem leaf, $\times 233$. k. Cells from a dorsal segment, stem leaf, $\times 233$. l. Cells from a ventral segment, stem leaf, $\times 233$. m. Cells from a dorsal segment, stem leaf, $\times 233$. n. Cells from a ventral segment, stem leaf, $\times 233$. o. Cells from a dorsal segment, stem leaf, $\times 233$. p. Cells from a ventral segment, stem leaf, $\times 233$. q. Cells from a dorsal segment, stem leaf, $\times 233$. r. Cells from a ventral segment, stem leaf, $\times 233$. s. Cells from a dorsal segment, stem leaf, $\times 233$. t. Cells from a ventral segment, stem leaf, $\times 233$. u. Cells from a dorsal segment, stem leaf, $\times 233$. v. Cells from a ventral segment, stem leaf, $\times 233$.

Herbertus herpocladoides. Scott & Miller (The Bryologist 62: 116–117. 1959).



Herbertus herpocladioides. Scale above in mm. Bottom: Leaf (left) and underleaf (right). Note the broad, well-defined vittae. Kohala Mountains, Hawai'i Island, 4,000 ft., 19 June 1953, Miller & Lamberton 4878 (MU, isotype). Photos by A.V. Freire.



The plants are loosely attached or closely appressed to their substrate, rusty brown to orange, and have small leaves. Escape Road, Hawai'i Volcanoes National Park, Freire & Judziewicz 21-246 (HAVO). Photos by E.J. Judziewicz.



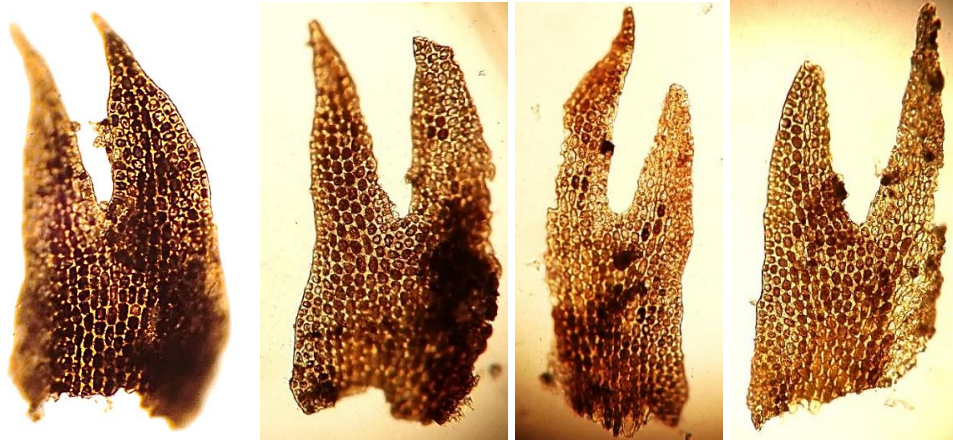
Herbertus herpocladoides. Plant with irregular branching and antheridial clusters. Note the presence of flagelliform branches. Scale in mm. NPS Research Village, Hawai'i Volcanoes National Park, Hawai'i Island, Freire & Judziewicz 21-253 (HAVO).



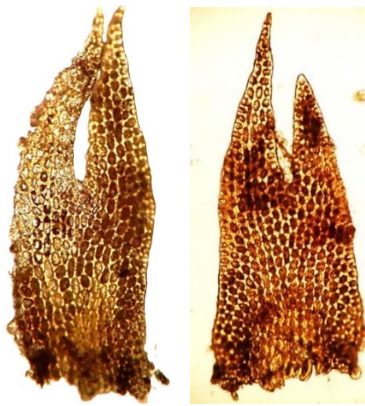
Leaves spreading from the stem. Note antheridial clusters subtended by inflated bracts (arrows). Freire & Judziewicz 21-253 (HAVO).



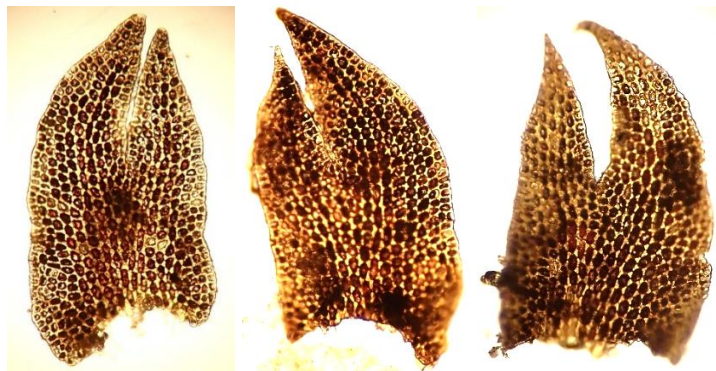
Herbertus herpocladoides. Plants are long and slender; leaves and underleaves spread from stem at about 45° angles. The underleaves are ovate with acute, parallel, unequal lobes separated by a narrow sinus, much like *H. gracilis*. Research Village, Hawai'i Volcanoes National Park, Freire & Judziewicz 21-253 (HAVO).



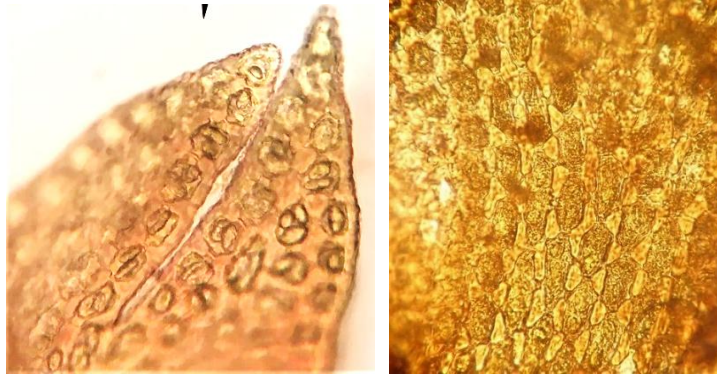
Leaves are elongate and rectangular with broad lobes and "V"- to "U"-shaped sinuses. Lobes can be asymmetrical. Freire & Judziewicz 21-253 (HAVO).



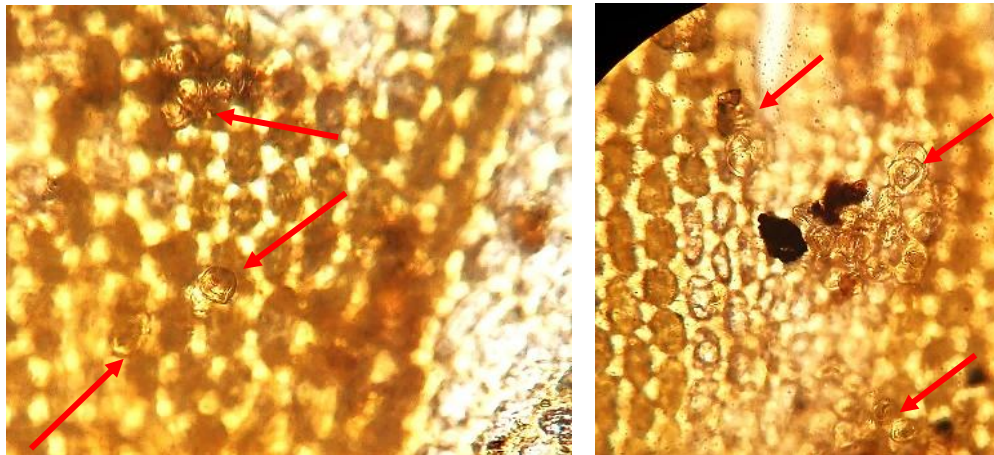
The underleaves of the main stem are elongate and rectangular. Freire & Judziewicz 21-253 (HAVO).



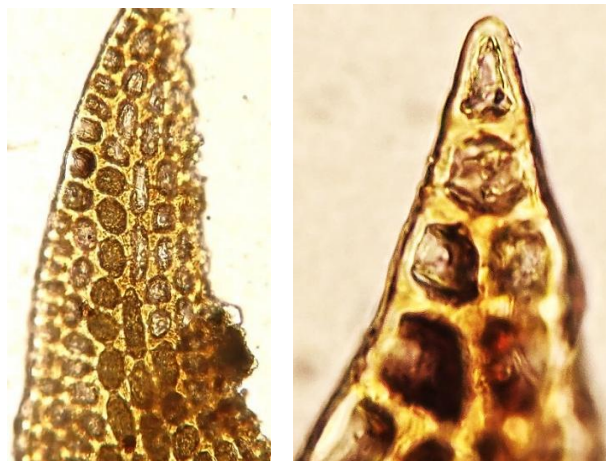
Herbertus herpocladoides. The underleaves of branches are ovate, with narrow sinuses and unequal lobes that can be parallel to slightly connivent. Research Village, Hawai'i Volcanoes National Park, Hawai'i Island, Freire & Judziewicz 21-253 (HAVO).



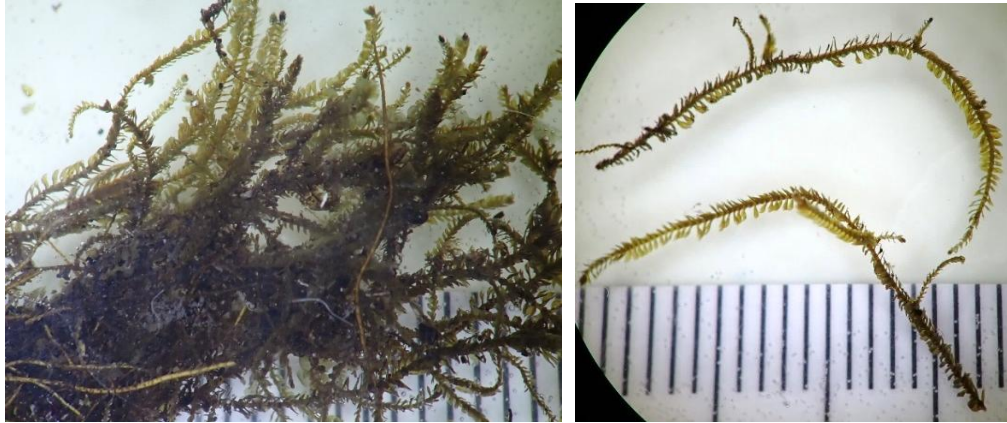
Left: Detail of underleaf lobes with slit-like sinus (as in *H. gracilis*) and large trigones; large, elliptical, and granular oil bodies; and verrucose leaf surface. Right: Leaf cells with large trigones. Freire & Judziewicz 21-253 (HAVO).



Slime papillae are observed on the leaf surface. Freire & Judziewicz 21-253 (HAVO).



Herbertus herpocladoides. Left: Vittae ascend the lobes but end before reaching the apex. Right: Lobe apex with isodiametric cells. Research Village, Hawai'i Volcanoes National Park, Hawai'i Island, Freire & Judziewicz 21-253 (HAVO).



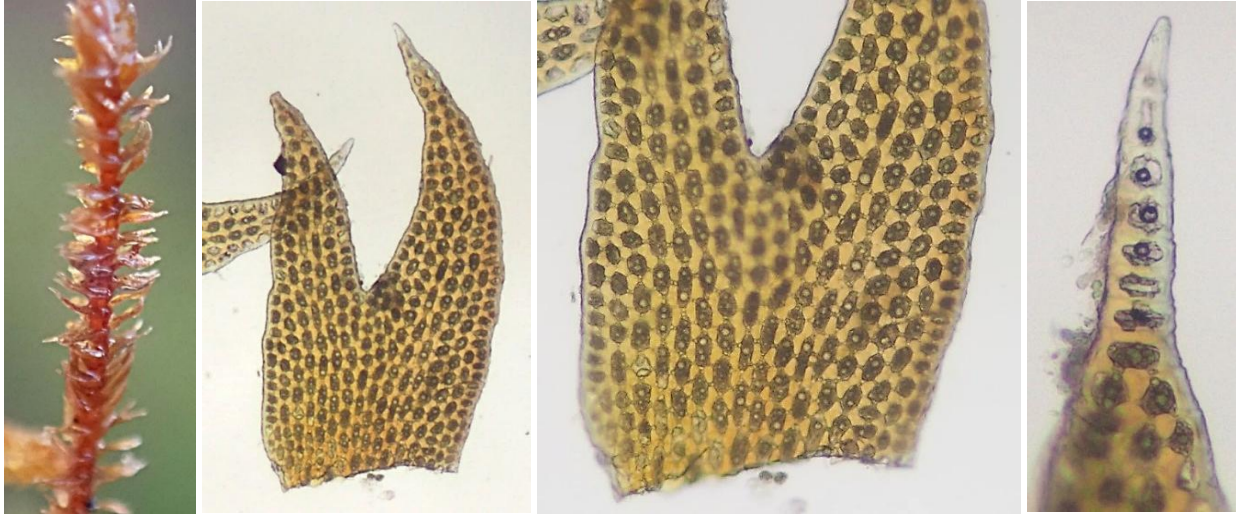
Example of olive green population. Scales in mm. Shevock 14665 (BISH).



Ventral flagelliform branches, squarrose leaves and underleaves, both shallowly bifid. 3: Scale units = 26 μm . Right: leaf cells with trigones. Shevock 14665 (BISH).



H. herpocladoides. Note similarities to *H. gracilis* (photos 2-5). 1, 2, 3. Leaves. 4, 5. Underleaves. Mānoa Falls Trail, O'ahu, Shevock 14665 (BISH).



Note poorly developed vittae and uniseriate apical cells on one of the leaf lobes. Kūlani Road, Hawai‘i Island, 4,300 ft., Dec. 2024, Randal Mindell photographs:
<https://www.inaturalist.org/observations/255687264>, with permission.



Herbertus herpocladoides. Plants reddish-brown, projecting horizontally from tree trunk. Mauna Loa Estates, Volcano, Hawai‘i Island, Freire & Judziewicz 21-236 (BISH).



Left: Plants are blackish-brown when dry. Right: Plants are reddish when moist, with spreading leaves. Note microphyllous branches. Scale in mm. Freire & Judziewicz 21-236 (BISH).



Leaves are imbricate, falcate, and deeply bifid with a broad “V”-shaped sinus, split to $\frac{1}{2}$ or over, lanceolate and divergent lobes, and vittae extending to lobes but ending below their apices. Freire & Judziewicz 21-236 (BISH).



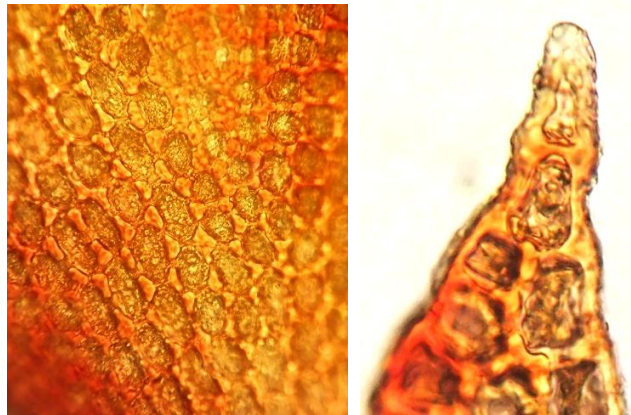
Herbertus herpocladoides. Left: Underleaves are large and squarrose when moist. Right: Underleaf with asymmetrical lobes, similar to the leaves but slightly smaller, with a narrower sinus and lobes not as divergent. Mauna Loa Estates, Volcano, Hawai‘i Island, Freire & Judziewicz 21-236 (BISH).



Left: Plants with flagelliform ventral branches. Right: Detail of ventral branch. Freire & Judziewicz 21-236 (BISH).



Flagelliform branches with elliptical leaves and underleaves, both with narrow sinuses and parallel to slightly connivent lobes (superficially similar to *H. gracilis*). Freire & Judziewicz 21-236 (BISH).



Herbertus herpocladoides. Left: Leaf cells with prominent trigones. Lobe apex with two uniseriate, elongate cells and verruculose surface. Mauna Loa Estates, Volcano, Hawai'i Island, Freire & Judziewicz 21-236 (BISH).

Herbertus cf. herpocladoides. Plants projecting horizontally from tree trunks, soil, or rock. Variable in size and color, from green to brown to deep red, usually falcate-secund. Leaves and underleaves of main stem and branches are contiguous to imbricate, bifid, with an acute “V”-shaped sinus, split over half their length; they have elongate, acute to acuminate and divergent lobes. Vittae not always easy to observe; the leaf cells have prominent trigones. These plants closely resemble our concept of *H. herpocladoides* but the sinus is deeper and the vittae are not clearly defined.



Ventral view of stem. Brown plant with bifid nearly squarrose leaves when wet. Note row of underleaves; these are also squarrose. Leaf with deep sinus. Freire & Judziewicz 20-608 (BISH).



Leaf and underleaf at the same scale. Hale Alema, Volcano, Hawai'i Island, Freire & Judziewicz 20-608 (BISH).



1. Plants are olive-green, and ascend a tree trunk, scale in mm. 2: Dry plant with falcate-secund leaves. 3: Slender, elongate plant. Scale in mm. 4: Plant with flagelliform ventral branch. Freire & Judziewicz 22-892 (BISH).



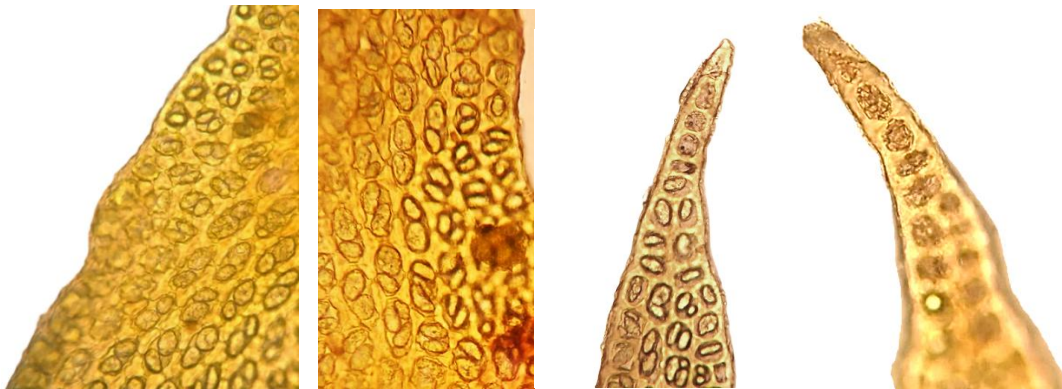
Herbertus cf. *herpocladoides*. Leaves and underleaves are squarrose. The leaves are deeply divided and with divergent lobes. Flagelliform ventral-intercalary branches are present. Hale Alema, Volcano, Hawai'i Island, Freire & Judziewicz 22-892 (BISH).



The leaves are deeply divided to 2/3 their length, with acute lobes. Freire & Judziewicz 22-892 (BISH).



The underleaves are long-ovate with a deep narrow sinus and parallel lobes. Freire & Judziewicz 22-892 (BISH).



Herbertus cf. *herpocladoides*. Leaf cells with large trigones and cells with large, elliptical, granular oil bodies. Leaf apices with quadrate cells. Hale Alema, Volcano, Hawai'i Island, Freire & Judziewicz 22-892 (BISH).

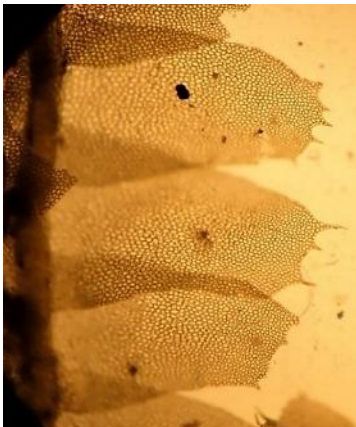
Heteroscyphus Schiffn. (Lophocoleaceae)

One or two species in Hawai'i, 109 species worldwide.

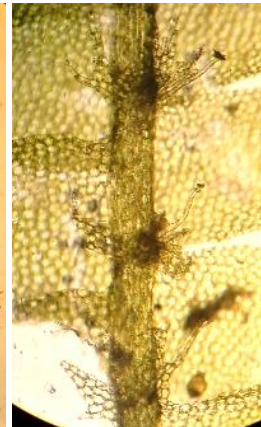
This genus is recognized in Hawai'i by the large size of the plants, the spreading, alternate, oblong leaves with truncate apices that bear from 1-5 teeth of variable shapes and sizes within a plant, by its bisbifid underleaves, and by its thin-walled leaf cells without trigones (or with tiny ones).

Heteroscyphus in Hawai'i could be confused with *Lophocolea*, *Cryptolophocolea* and *Chiloscyphus*. Unlike *Chiloscyphus*, the leaves are alternate rather than opposite. Unlike *Lophocolea*, they have a variable number of teeth only at the leaf apex; the leaves of *Lophocolea* are either entire or bifid, or, when with many teeth, these are dispersed along the entire leaf margin rather than only at the apex. Unlike *Cryptolophocolea*, the leaf cell walls of *Heteroscyphus* only have tiny trigones, rather than prominent ones. We did not observe sexual organs, but from published descriptions (Gradstein et al., 2001) gynoecia are produced on short ventral branches, and the perianths are smooth and not keeled. Some Hawaiian species of *Chiloscyphus* may belong to *Heteroscyphus* instead; see discussions in Vol. 1 under *Chiloscyphus*.

1. Leaves truncate-triangular, broadest at the base, sometimes rectangular; leaf teeth rudimentary or long and slender (needle like), 3-5 per leaf apex; underleaves only slightly wider than the stem ***H. argutus***
1. Leaves short-rectangular, not broadest at base; leaf teeth (1)4-7, variably sized and coarsely triangular; underleaves 2-3 times wider than the stem ***H. aff. argutus***



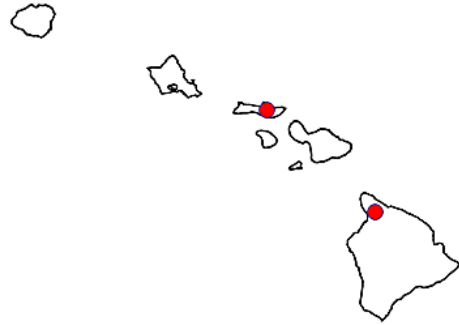
H. argutus



H. aff. argutus

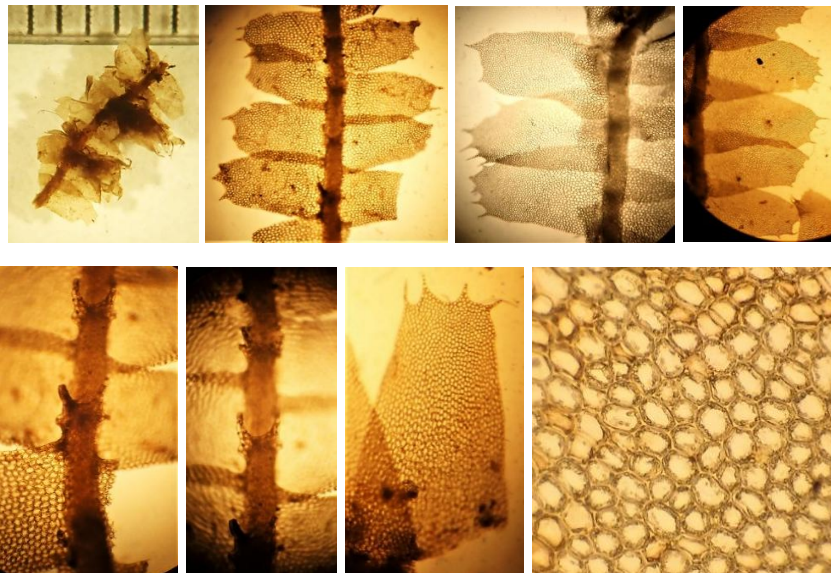
Heteroscyphus argutus (Reinw., Blume & Nees) Schiffn.

Indigenous. A mainly Asian species of montane forests, rare in Hawai'i. Miller (1963: 508, as *Chiloscyphus argutus*, based on Fagerlind & Skottsberg 6919, Stockholm Herbarium), from Kohala, Hawai'i Island. We have not seen this specimen. Miller's unpublished drawing of this collection (housed at BISH) appears congruent with descriptions of this species. There is also reportedly a specimen from Moloka'i (Miller & Lamberton 3791, from rim of upper Waikolu Valley) at MU, but we did not relocate it during our visit. This species is a member of Section *Neoheteroscyphus* J.J. Engel (Engel & Glenny, 2019a: 517).



This following morphological description is based on our interpretation of Miller's unpublished drawings (BISH). Plants are long and infrequently branched. Leaves are alternate, imbricate, spreading, ovate-triangular, with a broad base or sometimes rectangular, with truncate apices that bear 2-4 small teeth, variable in number within individual plants. The underleaves are small, connate to one or both adjacent leaves, about 1.5 times broader than the stem, bisbifid, with the apical lobes divergent, more prominent, separated by a broad and rounded sinus; lateral teeth (lobes) are smaller than the apical ones. Leaf cells are thin-walled and without trigones, while marginal cells are thick-walled.

Below are photos of A.C. Smith 6349 (BISH) from Fiji, used here to exemplify *Heteroscyphus argutus*. We find Miller's drawings congruent with this specimen, with a few differences. The Fijian plants have longer leaves, with longer and ciliate teeth, and leaf cells with small trigones. We did not observe thickened marginal cells, but a closer examination is needed.



Heteroscyphus argutus. Fiji, A.C. Smith 6349 (BISH), determined by Margaret Fulford. Photos by E.J. Judziewicz.

***Heteroscyphus* aff. *argutus*. Naturalized? Indigenous?**

Known only from a cultivated but long neglected *Camellia* plant in Volcano, Hawai‘i Island, in 2023. We had previously identified this specimen as *H. argutus* (Judziewicz, Freire & Thomas 2024: 13). However, because of the rectangular rather than triangular leaves, the coarser apical teeth, and the larger underleaves (but see Thouvenot’s (2023) concept, with larger underleaves), we now cautiously separate it as *H. aff. argutus*. Paul Bell-Butler (pers. comm., 12 June 2025) also suggests that this collection may not be *H. argutus*.



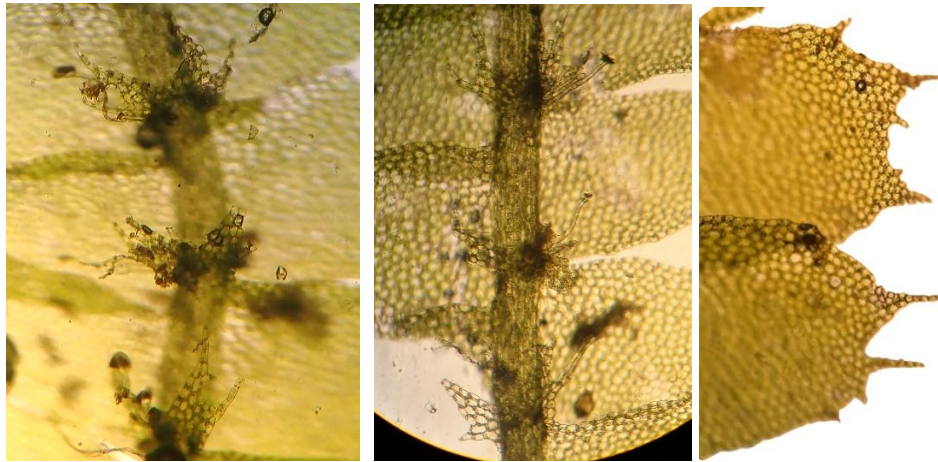
The leaves resemble those of *Chiloscyphus greenwelliae*, but are alternate rather than opposite, and the number of teeth is mostly greater than two. In our opinion, based on Stephani’s drawings, it resembles *Heteroscyphus varians* (Steph.) J.J. Engel (Southeastern Australia and Tasmania), differing in its longer leaves and more uniformly bisbifid underleaves.



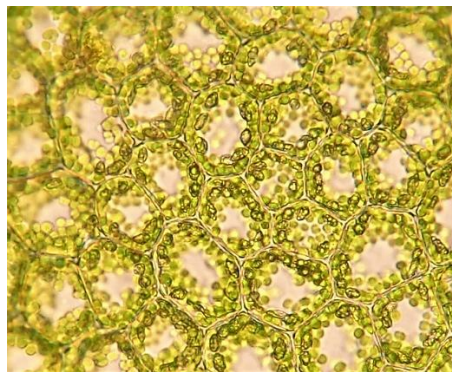
Heteroscyphus aff. *argutus*. An epiphyte growing on the bark of cultivated *Camellia* plants in *Metrosideros polymorpha* forest, 3,445 ft., 19°25'29"N, 155°12'27"W. Plants are large (scale in mm). Hale Alema, Volcano, Hawai‘i Island, Freire & Judziewicz 23-1 (BISH).



Plants are large (scale in mm). Leaves are alternate, spreading, with coarse, variable apical teeth. Freire & Judziewicz 23-1 (BISH).



Ventral view showing quadrifid underleaves about three times as wide as the stem. Detail of leaf apices with coarse and variable teeth. Freire & Judziewicz 23-1 (BISH).



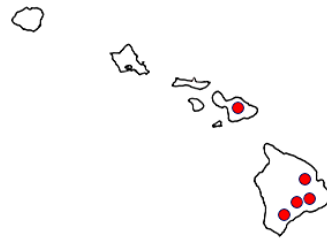
Heteroscyphus aff. *argutus*. Note thin-walled cells with tiny or no trigones. Volcano, Hawai'i Island, Freire & Judziewicz 23-1 (BISH).

Isopaches H. Buch (Anastrophyllaceae)

One species in Hawai‘i, five species worldwide.

Isopaches bicrenatus (Hoffm.) H. Buch.

Indigenous. First report for Hawai‘i: Judziewicz & Freire (2023c: 169-170). This is the first record of this Holarctic genus (and species) between the Americas and Aotearoa/New Zealand (Engel & Glenny, 2008: 665); there are also scattered records from South America (Gradstein, 2021).



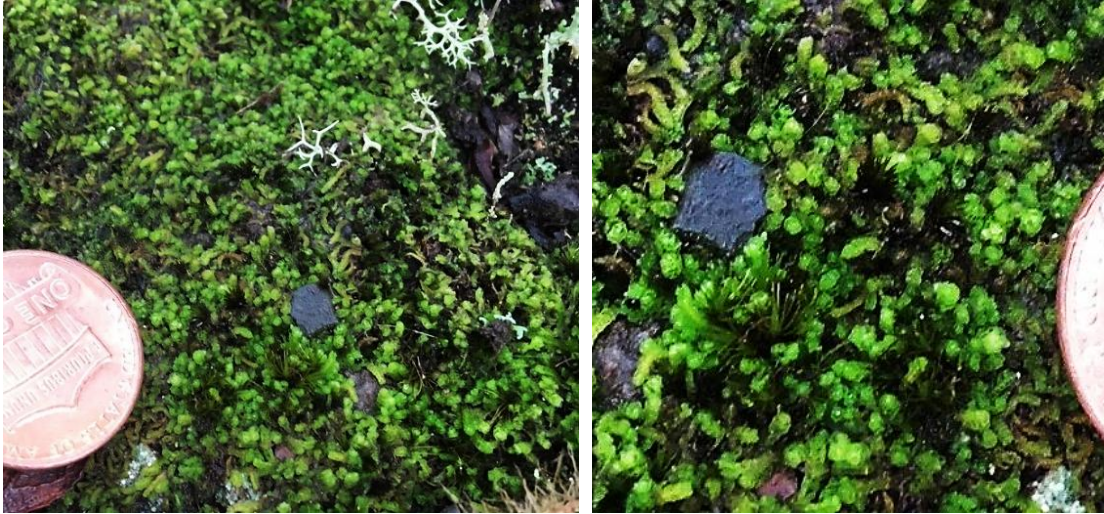
William Hoe first collected this species in Hawai‘i in 1966 on the trail beyond the end of the Mauna Loa Road (Hoe 1036.0, MU) on Hawai‘i Island, but it was unidentified until we examined it at MU in 2024.

This is one of the most drought-tolerant liverwort in Hawai‘i Volcanoes National Park (2,500-7,900 ft.), growing throughout the Ka‘ū desert in suitable habitats: Partly shaded, seasonally moist ash soil pockets among lava rocks. It is locally common in the Footprints area, Tree Molds area, and in Kīpuka Keanabihopa on the Hilina Pali Road; it also occurs in the Kahuku Unit. *Isopaches bicrenatus* was also found recently by us on both Haleakalā, Maui and on Mauna Kea, Hawai‘i Island. On Maui, Zach Pezzillo has also found it on numerous sites on both the windward and leeward sides of Haleakalā (4,700-7,900 ft.). It should be sought on other islands on sunny clay embankments at elevations of over 2,500 ft. Other high elevation, heliophytic liverworts that may grow in *Isopaches* habitats include *Cephaloziella heteroica*, *Fossombronina pusilla*, and *Targionia hypophylla*. The plants have a distinctive and penetrating odor of cedar oil when even a few are crushed; we suggest the common name “Kīlauea cedarwort”.

Plants are bright green, sometimes slightly reddish or brown at tips, especially with age. Stems ca. 0.15 mm wide, lacking microcellous layer on ventral side; outermost layer of cells with slightly thicker walls. Flagelliform branches are common. Leaves are small, imbricate, concave, succubous, 0.6-0.8 mm long, 0.7-0.9 mm wide, bifid to about 1/4 to 1/3 deep, lobes acute. Leaf insertion transverse to slightly oblique. Leaf cells 25-40 µm in diameter, quadrate, with small papillae, thick-walled, with small trigones occasionally present; oil bodies gray, abundant, ellipsoid to spherical and finely granular. Possibly with cyanobacteria in some cells. Hyaline rhizoids are abundant on the ventral side of the stem. Underleaves absent. Gemmae are sometimes observed at tips of plants, they are brown, angular, quadrate to star-shaped. Perianths long, cylindrical, with a constricted and furrowed mouth. Setae long emergent. Spores small, red, with papillate ornamentation. Elaters large, red, with two spiral thickenings.



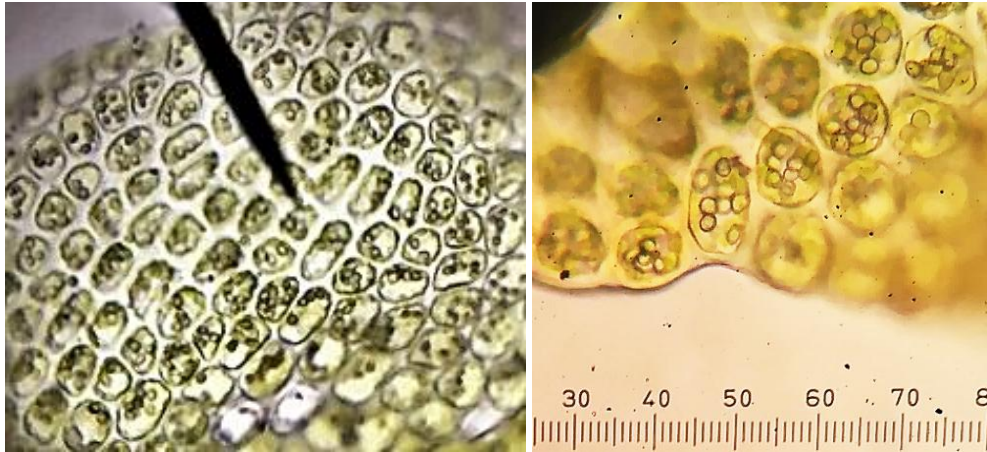
Left: E.J. Judziewicz pointing to *Isopaches* habitat. Right: A.V. Freire in moist ash embankment habitat, where *Isopaches* grows with *Cephaloziella heteroica*. Footprints Trail, Ka‘ū Desert (3,000 ft.), Hawai‘i Volcanoes National Park, Hawai‘i Island, 22 Oct. 2020.



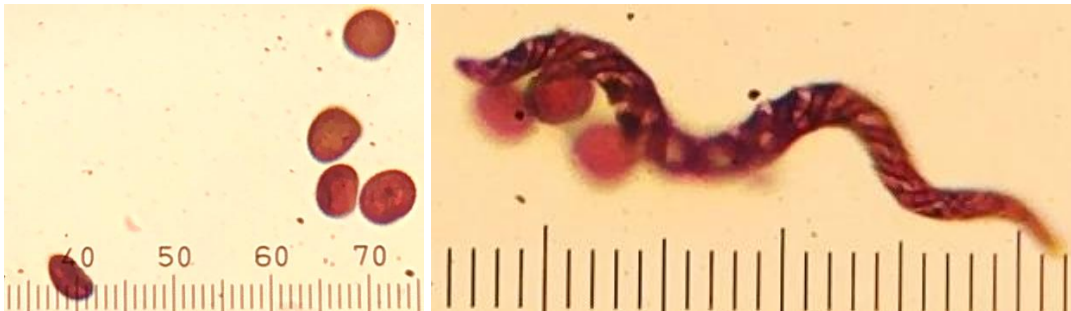
Note the bright light green color of the plants, their small size, and their “worm-like” appearance. Ka‘ū Desert, Hawai‘i Island, Freire & Judziewicz 20-15 (HAVO).



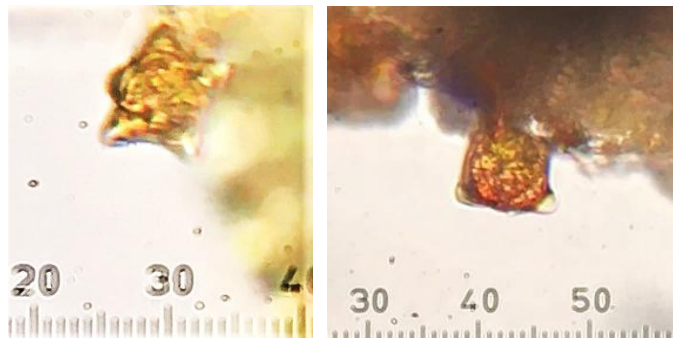
Isopaches bicrenatus. Above: Imbricate, erect and bifid leaves. Photo to the right is a plant longitudinal section, note the concave and erect leaves, abundant rhizoids, and lack of underleaves. Ka‘ū Desert, Hawai‘i Island, Freire & Judziewicz 20-15 (HAVO). Below: Long and narrow, furrowed perianth with constricted, hyaline mouth. Ka‘ū Desert, Hawai‘i Island, Freire & Judziewicz 21-392 (HAVO).



Left: Rectangular to isodiametric cells with thick walls and occasional trigones. Freire & Judziewicz 21-392 (HAVO). Right: Oil bodies are spherical to elongate, finely granular and gray. Scale units = $2.5\mu\text{m}$. Ka'ū Desert, Hawai'i Island, Freire & Judziewicz 20-15 (HAVO).



Left: Spores are small, papillose and red. Scale units = $2.45\mu\text{m}$. Right: Elaters long and stout with two spiral thickenings. Scale units = $4.9\mu\text{m}$. Freire & Judziewicz 21-392 (HAVO).



Isopaches bicrenatus: Red or brown gemmae on leaf margins, ornamented with angular points. 1 unit = $2.45\mu\text{m}$. Ka'ū Desert, Hawai'i Island, Freire & Judziewicz 21-392 (HAVO).



Golden-orange *Isopaches bicrenatus* (below) and ruby-red *Odontoschisma denudatum* subsp. *denudatum* (above), Kahuku Unit, Hawai‘i Volcanoes National Park, Hawai‘i Island, Freire & Judziewicz 22-684 (HAVO).

Isopaches cf. *bicrenatus*



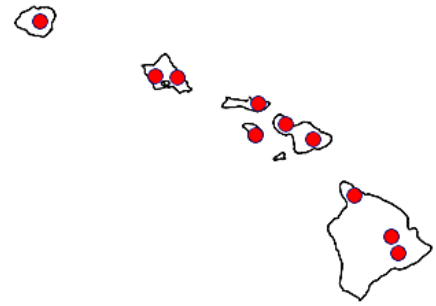
Isopaches cf. *bicrenatus*. Robust population. Note the bifid leaves and abundant gemmae and stout perianths. There is also a much smaller unidentified leafy liverwort intermixed. Near the ‘Āinapō Trail, Kapāpala Forest Reserve, ca. 19°23’22”N, 155°39’45”W, 7,900 ft., 18 Feb. 2024, Hawai‘i Island, photos by Zach Pezzillo: <https://www.inaturalist.org/observations/199970015>, with permission.



Isopaches bicrenatus is also found on Maui, where we observed it and Zach Pezzillo photographed it on the Halemau‘u Trail at 7,900 ft. in open shrubland in Haleakalā National Park, on 24 Feb. 2023; Zach also collected it at Kahikinui on the lee side of Haleakalā, Pezzillo 659 (BISH), with permission: <https://www.inaturalist.org/observations/202131325>.

Jubula Dumort. (Jubulaceae)

Two species in Hawai‘i, six species worldwide. The map shows all occurrences of the genus in Hawai‘i.



Growing in wet montane forests; usually trailing on soil or on tree bases, also reported as epiphyllous by Dey et al. (2011). Hawaiian material is terrestrial, on tree bases, or epiphyllous on ferns such as *Asplenium*, *Vandenboschia*, and *Microsorium spectrum* (Forbes 2265 (BISH), O‘ahu). The genus is found on all major islands, but is rare; we agree with Miller (1953) that the genus is “either rare or generally overlooked” in Hawai‘i: iNaturalist lists no occurrences for the genus in Hawai‘i versus 468 occurrences for the related, superficially similar genus *Frullania*.

Plants are drab green to brown; they closely resemble the much commoner *Frullania apiculata*, but with more robust stems, longer leaf apiculums, the water sacs (lobules) attached away from the stem; refer to that species for a more complete comparison. Stems are firm and frequently branched. The leaves are incubous, spreading, apiculate to acuminate, sometimes with marginal teeth. Lobules are clavate, galeate or explanate, attached to the leaf lower margin, away from the stem and without a conspicuous keel. Underleaves are bifid, about twice the stem width, with acute to acuminate lobe apices and a narrow to wide sinus to or beyond ½ of their length, with an arched insertion. Leaf cells are thin-walled, sometimes with minute trigones. Plants are monoicous. Perianths are 3-keeled. Antheridia are produced on short lateral branches.

Jubula collections from Hawai‘i need more attention. So far, all specimens are reported as *J. javanica*, but we believe that *J. pennsylvanica* is also present (Judziewicz & Freire, 2023c: 162-163). The key below is based on Guerke (1978) and Dey et al. (2011); we also consulted Sukkharak (2013); however, inconsistencies are found in the latter two papers regarding *J. javanica*.

1. Leaves narrowly ovate, their apices long-acuminate; leaf margin with (0-)1-3 teeth; female bracts and bracteoles with irregularly toothed or spinose margins; perianths with serrate keels *J. javanica*
1. Leaves broadly ovate, their apices shortly-apiculate; leaf margin entire, without teeth; female bracts and bracteoles with entire margins; perianths with smooth keels *J. cf. pennsylvanica*



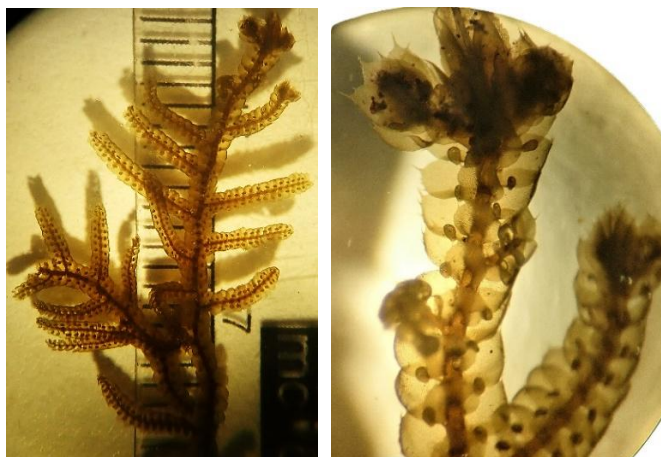
J. javanica



J. cf. pennsylvanica

1. *Jubula javanica* Steph. Indigenous. Treated as *Jubula hutchinsiae* subsp. *javanica* in Staples & Imada (2006); see Lee & Gradstein (2021: 89). A mainly Asian species. Possibly found on all major islands (2,500-4,000 ft.), but specimens need study to corroborate their identity. We only saw this species twice in our Hawaiian fieldwork, and yet the Hawaiian Bog Survey of 1938 collected this species seven times at one locality (Miller 1963; Mile 23 on the Hilo to Kīlauea Road).

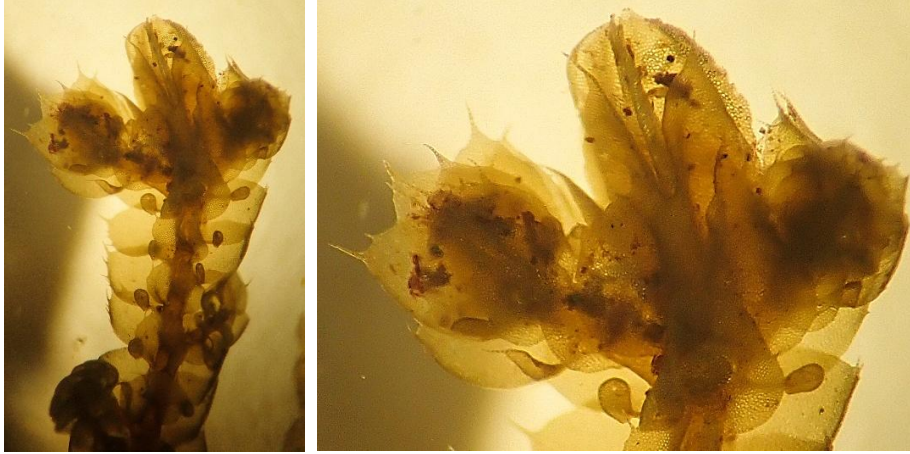
This species is recognized by its ovate, spreading leaves with long-acuminate apices, often with one to three marginal ciliate teeth. The ventral side has *Frullania*-like cylindrical to galeate water sacs that are attached to the lower leaf margin, away from the stem. Underleaves are contiguous to slightly distant, with an arched insertion, three times as broad as the stem, round, with entire margins or with ciliate marginal teeth, bifid, with convergent and ciliate lobes; the sinus is “U” shaped and narrow, to about $\frac{1}{2}$ its length. Female bracts and bracteoles are toothed or serrate. Perianths have three serrate keels. Antheridial branches are short and latero-ventral, and they curve down like a catkin. Leaf gemmae have been reported for non-Hawaiian material by Katagiri et al. (2010).



Plants are frequently branched and monoicous. Scale in mm. Haleakalā, Maui, Severson 051 (BISH). Photos by A.V. Freire.



Jubula javanica. Leaves are acuminate, some with ciliate teeth. Underleaves are round, with acuminate and convergent lobes, some with ciliate teeth. Lobules are galeate to clavate. Haleakalā, Maui, Severson 051 (BISH). Photos by A.V. Freire.



Left: Plant with female and male branches. Right: Detail of perianth with three serrate keels and toothed bracts. Haleakalā, Maui, Severson 051 (BISH). Photos by A.V. Freire.



Catkinlike male branches with concave antheridial scales. Haleakalā, Maui, Severson 051 (BISH). Photos by A.V. Freire.



Jubula javanica. 'Ōla'a Tract, Hawai'i Volcanoes National Park (only collection of this species in the Park), Svihla 2026 (BISH). Photos by A.V. Freire & E.J. Judziewicz.

2. *Jubula pennsylvanica* (Steph.) A. Evans. Indigenous.

First report for Hawai‘i (Judziewicz & Freire, 2023c: 163); North America, the West Indies, and India (Dey et al., 2011). Known from Maui and Hawai‘i Island (1,700-6,200 ft.). This species is recognized by the broad apiculate leaves with entire margins, by the presence of clavate and explanate lobules on the same plant and by the ovate and bifid underleaves. We encountered this species only twice in our fieldwork: Saddle area, 5,100 ft., Freire & Judziewicz 21-784 (BISH), and Judziewicz 17020 (BISH), at 1,700 ft., Kīkala Stream, Kaiwīki Road, near Hilo.

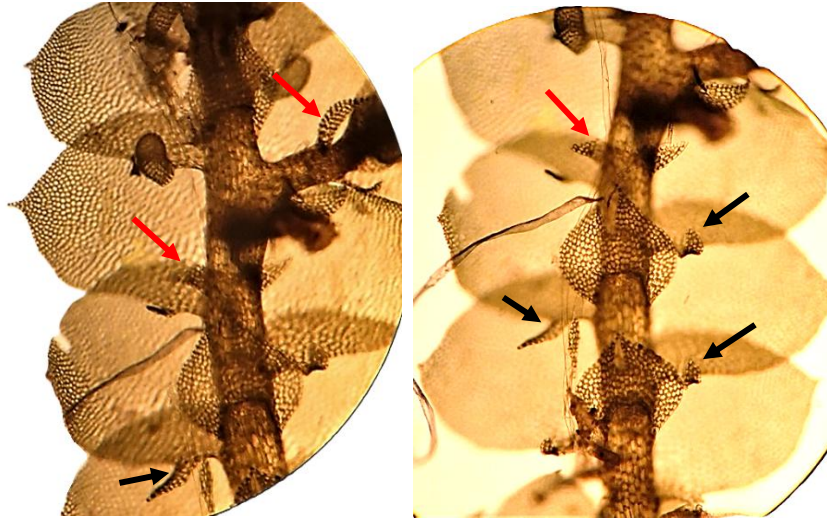


Leaves imbricate and widely spreading, broadly ovate, only slightly longer than broad; apiculate, margins entire, the upper margin strongly arched, the lower one more or less straight; leaf lobules dimorphic, both inflated (clavate) and explanate on the same plant. The underleaves are ovate, twice as broad as the stem, distant to contiguous, with an arched insertion, bilobed to $\frac{1}{2}$ their length or deeper, with a narrow to wide “U” shaped sinus; lobes parallel to convergent, with acute to acuminate apices. Males on short lateral branches. Gynoecium terminal with 1-2 innovations; bracts and bracteoles are entire. Perianth is 3-keeled, with smooth keels.

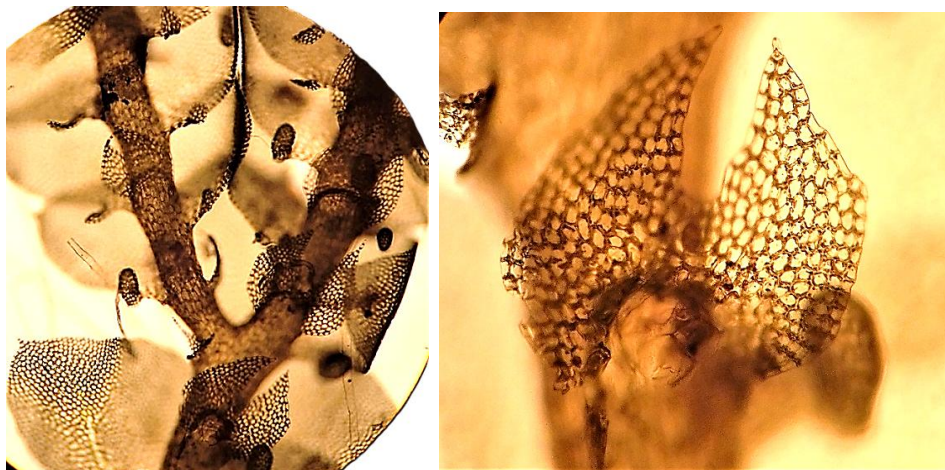
Our description fits the concept by Dey et al. (2011), with the difference that the Hawaiian plants have clavate (cylindrical) rather than galeate lobules.



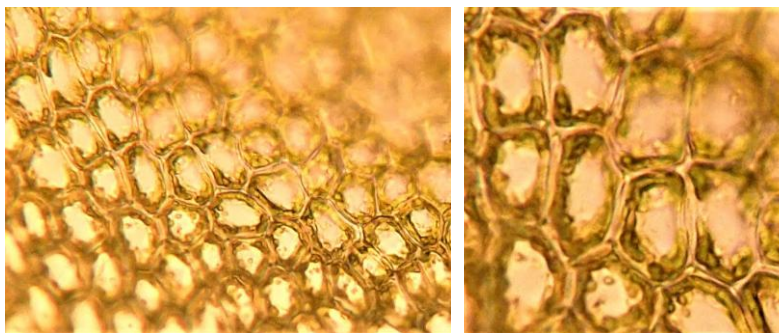
Plants with robust stems, irregularly branched with branches of the *Frullania* type. The leaves are imbricate and spreading, with an arched upper margin and a flat lower one. Hawai‘i Island, Freire & Judziewicz 21-784 (BISH).



Leaves apiculate, underleaves distant, ovate, with a narrow sinus and acute-acuminate lobes; underleaves below branch are reduced (red arrows). Inflated lobules intermixed with some explanate-lanceolate ones (black arrows). Freire & Judziewicz 21-784 (BISH).



Underleaves have an arched insertion, narrow or wide sinuses, and are divided to or more than $\frac{1}{2}$ their length. Note mix of inflated and explanate lobules (black arrows) and some modified underleaves associated with branches (red arrow). Freire & Judziewicz 21-784 (BISH).



Jubula pennsylvanica. Leaf cells are thin-walled and without trigones. Hawai'i Island, Freire & Judziewicz 21-784 (BISH).



Plants are monoicous. Terminal, 3-keeled perianth, with smooth keels, sub-apical innovations. Note the short antheridial branches (arrow). Severson 048e (BISH).



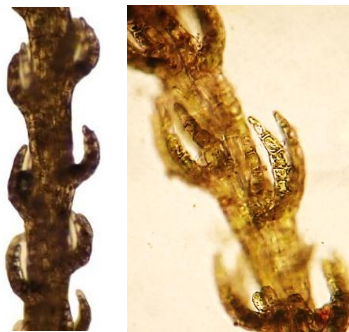
Jubula pennsylvanica. Antheridial branch with concave bracts. Haleakalā, Maui, Severson 048e (BISH). Photo by A.V. Freire.

Kurzia G. Martens (Lepidoziaceae)

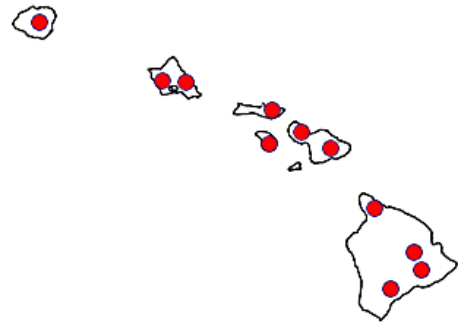
Four species for Hawai‘i, 47 species worldwide.

All Hawaiian species are incertae sedis within the genus (Söderström et al., 2016: 166). Plants tiny, creeping on bark, decaying wood, soil, or rocks, often mixed with other liverworts. Frequently branched, often with flagelliform branches (but caution, the morphology of leaves and underleaves differs between main stems, branches, and flagelliform branches). Leaves transversely inserted, deeply lobate, with 3-4 linear lobes; leaf disks small, one to two cells high. Underleaves to about half the size of the leaves, deeply segmented into 2-3 linear symmetric or asymmetric lobes. Cells verruculose, with firm walls lacking trigones. Miller (1963, 1967) recognized three species and we tentatively add a fourth; species boundaries appear fluid in Hawai‘i, and it’s possible that one or several of these species may prove to be synonyms; in which case the oldest name *K. hawaica* would apply.

1. Leaves squarrose or nearly so, with straight or slightly curved lobes ***K. species 1***
1. Leaves not squarrose, with concave or flexuous lobes **2**
 2. Leaf lobes flexuous, not clearly concave, filiform with at least some very elongated cells that are 3 or more times longer than wide; rare, Kaua‘i and Maui ***K. tayloriana***
 2. Leaf lobes firm rather than flexuous, concave, with cells less than 3 times longer than wide; common or rare **3**
 3. Leaves spreading; lobes narrowly linear, mainly uniseriate, biseriate only near their base, the cells elongated, up to twice as long as wide; common and widespread ***K. hawaica***
 3. Leaves appressed or slightly spreading; lobes triangular, mostly biseriate, uniseriate near the apex, the cells mainly quadrate; rare, Maui and perhaps Kaua‘i and Hawai‘i Island ***K. mauiensis***

*K. hawaica**K. mauiensis**K. tayloriana**K. species 1*

1. *Kurzia hawaica* (C.M. Cooke) Grolle. **Endemic.** Possible affinity (Cooke, 1904): *Lepidozia setacea* (= *K. pauciflora* (Dicks.) Grolle), Eurasia, North America. This is the commonest species and is found on all major islands (1,000-5,800 ft., or possibly 7,800 ft. on Hawai'i Island based on Miller & Lamberton 5257, MU, not examined). Plants resemble miniature clubmosses, or old-fashioned "pipe-cleaners". They are usually found intertwined with other bryophytes on bark, logs, humus, soil, or rocks. When we illuminate them with UV light, the plants glow red.



Plants are tiny, pale to bright green, with concave, distant to imbricate leaves that spread from the stem; the leaf disk is two cells high and divided into 3(4) erect, linear lobes (4)5-6 cells long. The cells are thin-walled, mainly rectangular (up to twice as long as broad), biseriate at the lobe base, or sometimes to about half the length of the lobe, and uniseriate above. Underleaves are mainly bifid but sometimes trifid, usually with asymmetric, concave lobes that are mainly uniseriate, except at the very base which may have a few paired cells. Dioicous. Perianths produced on short branches, fusiform, whitish, with a compressed, ciliate mouth. Antheridia are also produced on short branches.



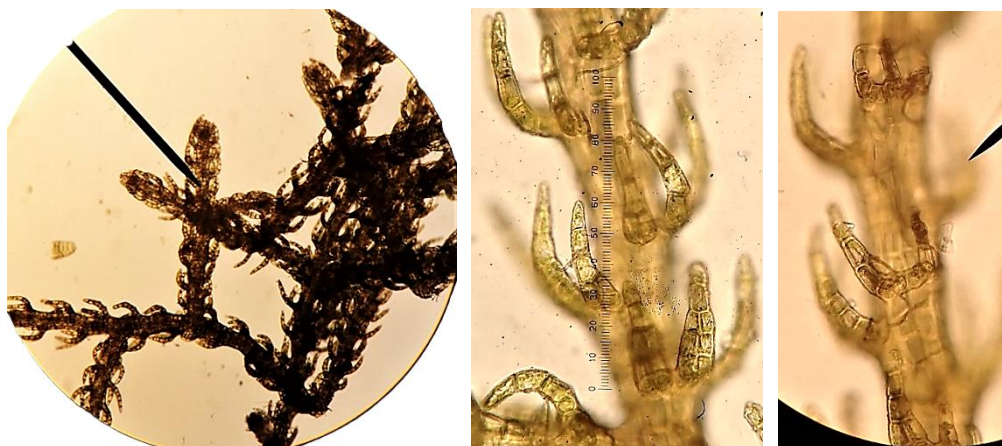
Kurzia hawaica. Isosyntype. Above: Dense population, plant aspect and leaf orientation. Below: Detail of leaf lobes (first and second photos) and underleaves (third and fourth photos). Nu'uanu, O'ahu, 11 June 1898, Cooke s.n. (MU). Photos by A.V. Freire.



Plants are small and stiff looking, with densely imbricate leaves. They resemble tiny clubmosses or pipe-cleaners. Note male branches with light-colored bracts. Freire & Judziewicz 21-754 (HAVO).

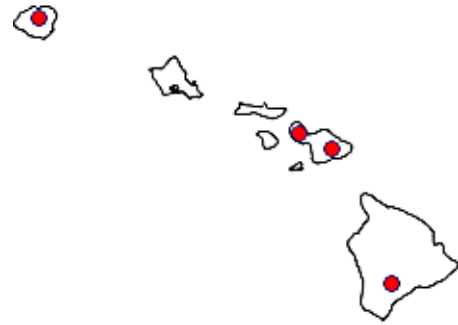


Left: Plants with male branches; note antheridia in bract axils (arrows). Right: Plants with white, fusiform perianths. Nāhuku, Hawai'i Volcanoes National Park, Freire & Judziewicz 21-754 (HAVO).



Kurzia hawaica. Left: Leaves transversely inserted with erect, concave lobes. Center: 3-lobed leaves with linear, concave lobes; lobes two cells broad below and uniseriate above. Cells are slightly elongate and thin-walled. Scale units = 5 μ m. Right: Trifid to bifid and concave-spreading underleaves, with asymmetric lobes. Hawai'i Volcanoes National Park, Freire & Judziewicz 21-493 (HAVO).

2. *Kurzia mauiensis* (H.A. Mill.) H.A. Mill. **Indigenous.** Rare, Maui (the type from Pu'u Kukui, West Maui), and perhaps Kaua'i (Faccenda 3323, BISH and others; see Judziewicz, Faccenda & Freire, 2025: 75) and Hawai'i Island (Kahuku Unit, Hawai'i Volcanoes National Park; Freire & Judziewicz 22-737c, HAVO); from 3,200-6,200 ft. Piippo (1985: 175-178) gives further occurrences from Indonesia (Western New Guinea), Papua New Guinea, and the Solomon Islands, and the figure and description in her paper closely resembles the Hawaiian type material. Miller (1963, 1967) describes and illustrates this species.



Similar to *Kurzia hawaica*, but the leaves are more appressed to the stem and concave, giving the plants a julaceous aspect. The leaf lobes are broader and shorter than in *K. hawaica*. *Kurzia mauiensis* is reportedly recognized by its numerous flagelliform branches (Miller, 1963) but these (although not abundant), are also reported for *K. hawaica* (Cooke, 1904; Miller, 1967). We saw reduced branches and attenuate stem tips but no evident flagelliform branches.

Plants are tiny, frequently branched. Leaves round in outline, short, distant to contiguous, moderately concave, appressed and erect; with 3-4 leaf lobes, these two cells broad for most (or at least half) of their length, the lobe tips rounded. The leaf cells are quadrate or slightly elongated and are thick-walled. The trifold underleaves are similar to the leaves but smaller.

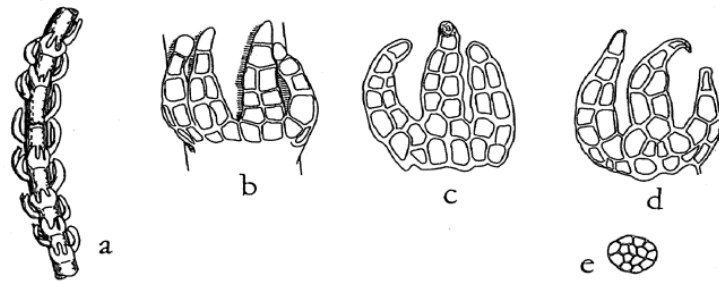
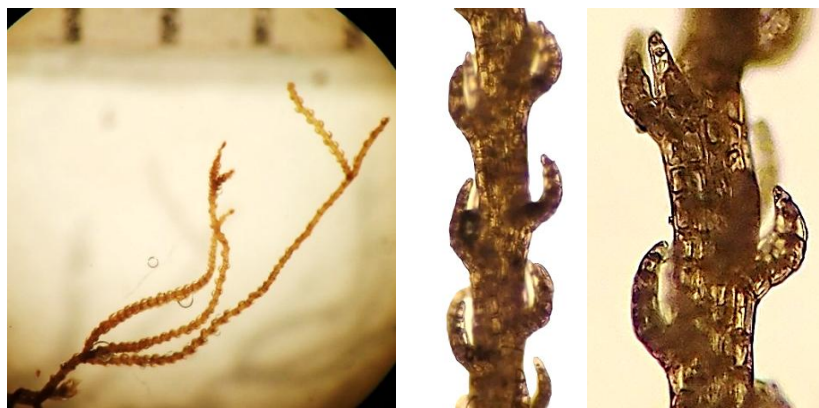


Fig. 2. *Microlepidozia mauiensis* Miller n.sp. a ventral aspect, $\times 55$. b, c leaves, $\times 240$. d underleaf, $\times 240$. e stem, cross-section, $\times 123$. (Drawn from the type.)

From Miller (Arkiv för Botanik 5(2): 489–531. 1963).

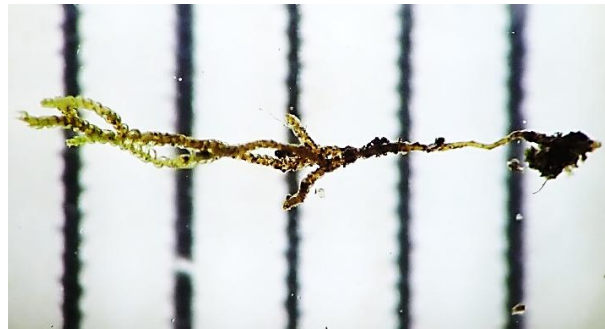


Kurzia mauiensis. Holotype of *Microlepidozia mauiensis*, Pu'u Kukui, West Maui, Cranwell & Skottsberg 5028 (MU). Scale in mm. Photos by A.V. Freire.

We collected *K. mauensis* at 6,000 ft. in the Kahuku Unit, Hawai'i Volcanoes National Park (Freire & Judziewicz 22-737, HAVO). These plants are julaceous, with mainly ascending concave leaves and frequent branching. Leaves and underleaves have lobes with 2-celled tiers for most of their length. Plants are smaller than *K. hawaica*. The leaves are not as appressed to the stem nor as small as described for *K. mauensis*.



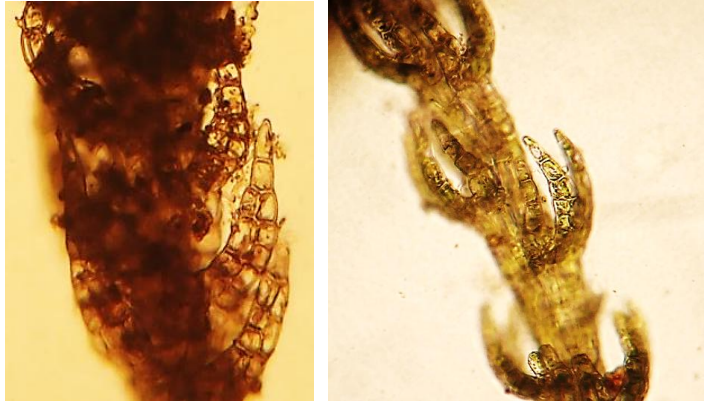
The plants appear julaceous due to their concave, erect, appressed leaves. Freire & Judziewicz 22-737 (HAVO).



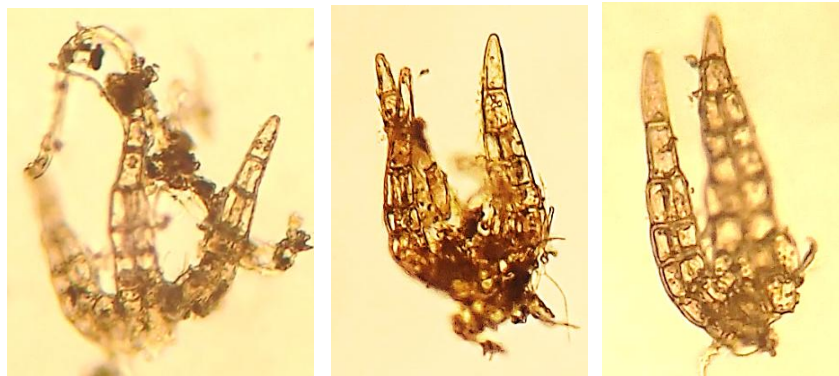
Plants grow forming thick mats on soil and are very small. Freire & Judziewicz 22-737 (HAVO). Scales in mm.



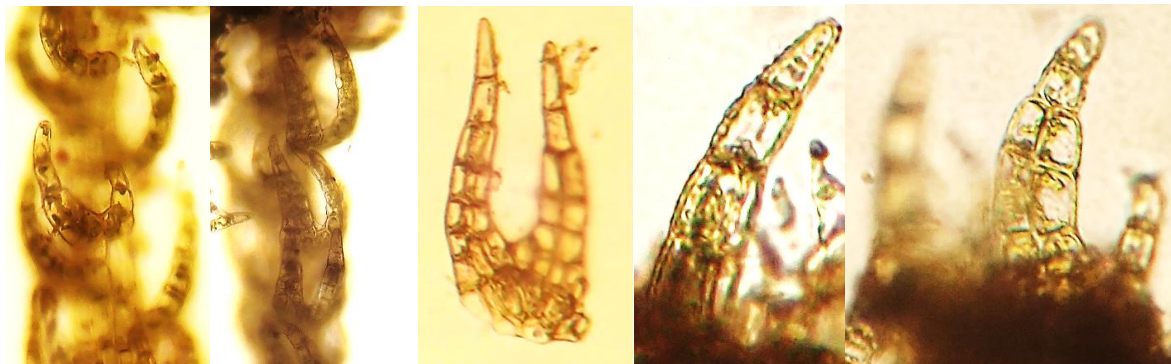
Kurzia mauensis. Left: Plants are frequently branched with attenuate stem apices. Right: Note the erect, concave leaves; some are slightly spreading. Kahuku Unit, Hawai'i Volcanoes National Park, Hawai'i Island, Freire & Judziewicz 22-737 (HAVO).



Leaves are concave, erect, ascending (left), or slightly spreading (right), trifid or quadrifid, two cells broad for at least half of their length, but usually beyond. Freire & Judziewicz 22-737 (HAVO).



Examples of leaves, right photo showing just two of the three lobes. Note the paired cells for 2/3 to most of the length of the lobes. Also note the firm-walled, quadrate to short-rectangular cells. Freire & Judziewicz 22-737 (HAVO).



Kurzia muiensis. 1. Underleaves with asymmetric lobes on branch. 2,3. Robust and bifid underleaves. 4,5. Note verruculose cells on leaf and underleaf lobes, also seen in the other Hawaiian species of *Kurzia*. Kahuku Unit, Hawai'i Volcanoes National Park, Hawai'i Island, Freire & Judziewicz 22-737 (HAVO).

3. *Kurzia tayloriana* (H.A. Mill.) H.A. Mill. **Endemic.** Rare, Kaua'i (Wai'alae Valley) and Maui (3,000-4,300 ft.). This species is reported to grow on trees in boggy areas. According to Miller's descriptions and figures (1963), the plants are delicate and profusely branched. They resemble *K. hawaica* but are more robust. The stem cortical cells are thick-walled. Leaves are imbricate and quadrifid, flexuous, with lobes 4-6 cells long and narrowly linear. The underleaves are trifid and asymmetrical. Both leaves and underleaves have elongated and firm-walled cells. The cells of the lobes are 3-5 times longer than broad. We did not observe *K. tayloriana* in the field and wonder whether it may be a variant of *K. hawaica*.

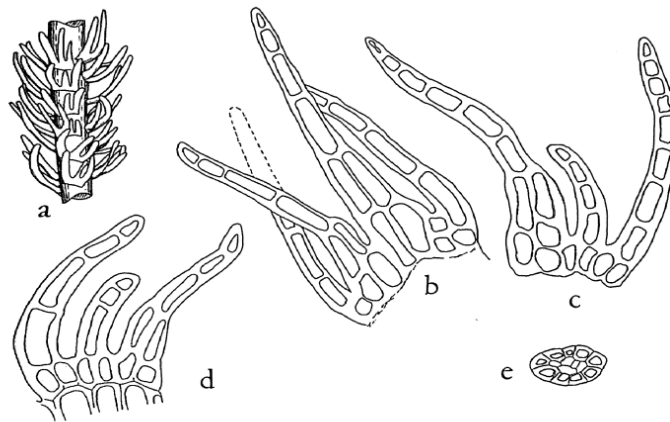
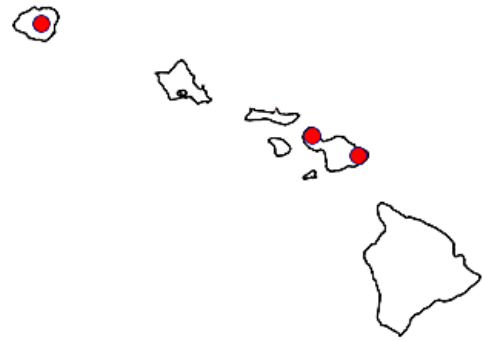


Fig. 3. *Microlepidozia tayloriana* Miller n.sp. a ventral aspect, $\times 55$. b leaf, $\times 240$. c, d underleaves, $\times 240$. e stem, cross-section, $\times 123$. (Drawn from the type.)

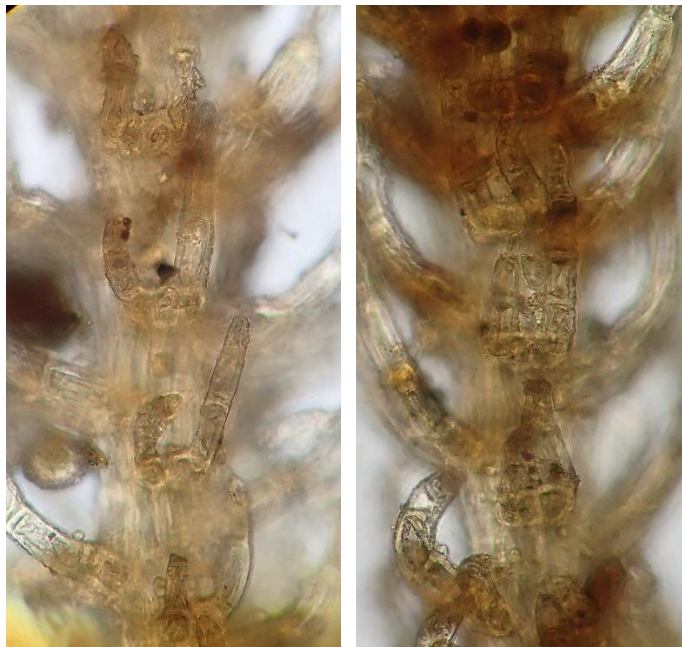
From Miller (Arkiv för Botanik 5(2): 489–531. 1963).



Kurzia tayloriana. Isotype of *Microlepidozia tayloriana*, Wai'alae, Kaua'i, Selling 5235b (MU). Plants are robust and frequently branched. Scale in mm. Photos by A.V. Freire.



Selling 5235b (MU). Leaf lobes are flexuous, not clearly concave, with some cells three or more times longer than wide. Photos by A.V. Freire.



Kurzia tayloriana. Isotype of *Microlepidozia tayloriana*, Wai‘alae, Kaua‘i, Selling 5235b (MU). Underleaves are mainly bilobed. Photos by A.V. Freire.

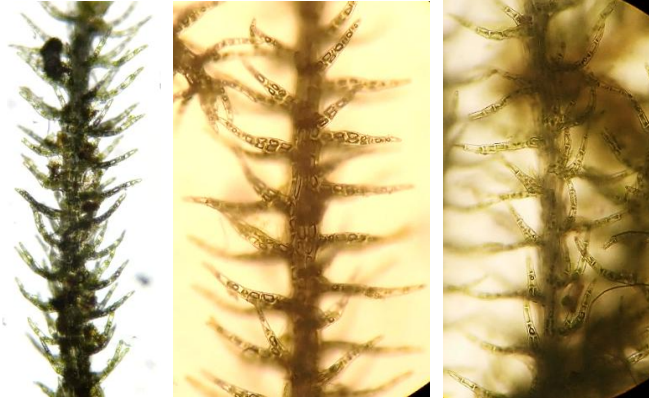
4. *Kurzia* species 1. A possible new species was collected on ridges about 3 miles apart in Kaua'i by Wood 18103 (BISH, PTBG), 4,280 ft., on Nāmōlokama summit, and by Faccenda 4129c (BISH), 4,100 ft., on Lā'au Ridge. Specimens have squarrose leaves, with lobes not or only slightly concave. These characters separate it from its Hawaiian congeners. The leaves have 3 (rather than 4) elongate linear lobes, each 4-6 cells long and biseriate in the two basal lobe tiers, while uniseriate above. Some of the lobe cells are quite elongate, three or more times longer than broad. The underleaves are smaller than the leaves, mainly bifid, but sometimes trifid, with asymmetric lobes, but they may be symmetrical on smaller branches. The slender plants appear soft, fragile, and flexuous.



Faccenda 4129c (BISH), 4,100 ft., Lā'au Ridge, Kaua'i, 2025. Left: Photo by Kevin Faccenda, with permission: <https://www.inaturalist.org/observations/292067853>. Right: Scale in mm. Photo by E.J. Judziewicz.



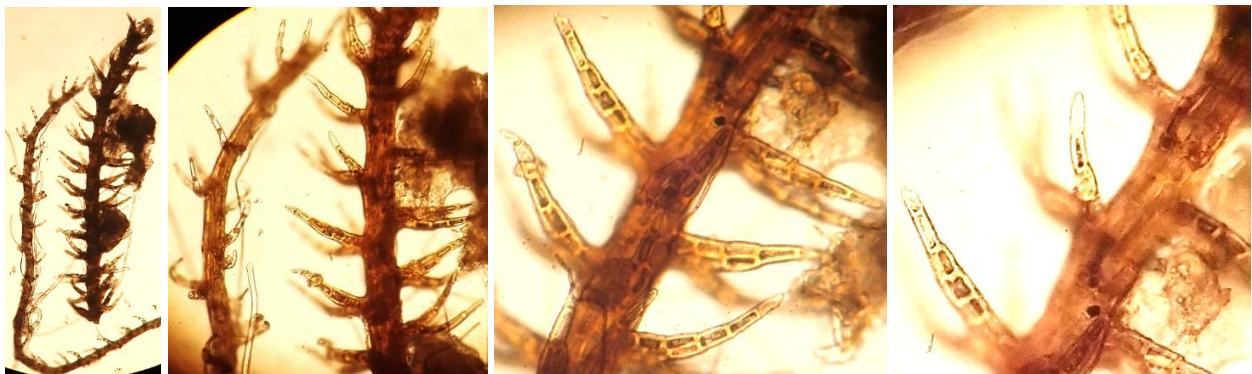
Kurzia species 1. Plants are small, and the leaves are squarrose or nearly so. Scales in mm. Faccenda 4129c (BISH), 4,100 ft., Lā'au Ridge, Kaua'i, 2025. Left: Photo by E.J. Judziewicz. Center and right: Photos by Kevin Faccenda, with permission: <https://www.inaturalist.org/observations/292067853>.



Leaves are squarrose or nearly so. Faccenda 4129c (BISH), 4,100 ft., Lā‘au Ridge, Kaua‘i, 2025. 1: Photo by Kevin Faccenda, with permission. <https://www.inaturalist.org/observations/292067853>. 2, 3: Photos by E.J. Judziewicz.



Plants are tiny, fragile looking, branched, and have flagelliform branches. Right: leaves are trifold and squarrose. Wood 18103 (PTBG). Photos by A.V. Freire. Scales in mm.



1,2: Squarrose leaves; to the left of it, note microphyllous branch with rhizoids (1). 2,3: Detail of linear leaf lobes with mainly elongated cells. Note lobe bases with two rows of cells. 3,4: Bifid and trifold underleaves with asymmetric lobes. Wood 18103 (PTBG). Photos by A.V. Freire.



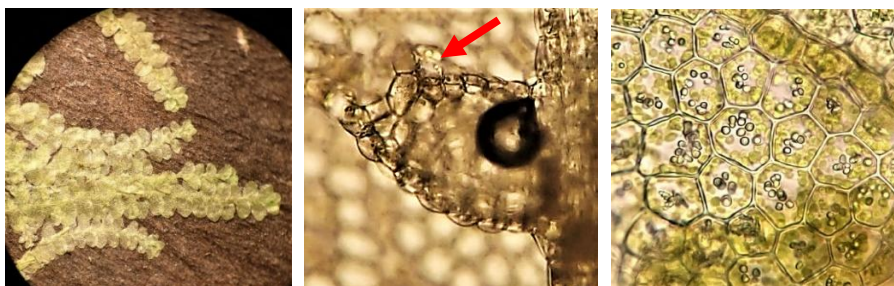
Kurzia species 1. Microphyllous branches with slightly concave leaf and underleaf lobes. The underleaves tend to have more symmetrical and divergent lobes. Nāmolo-kama, Kaua‘i, Wood 18103 (PTBG). Photos by A.V. Freire.

Lejeunea Lib. (Lejeuneaceae)

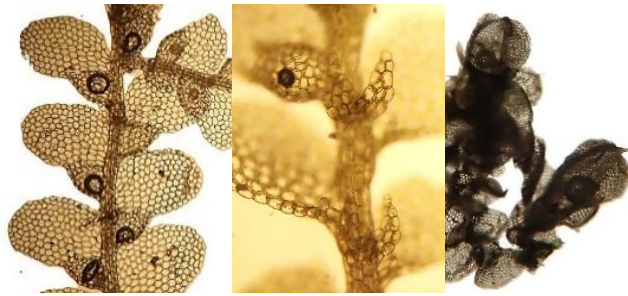
At least six species in Hawai'i; 412 species worldwide, one the largest genera of liverworts worldwide. We anticipate more species when recent collections are analyzed in more detail. The genus is characterized by small incubous plants with complicate-bilobed leaves and bifid underleaves. The genera *Lejeunea* and *Cheilolejeunea* are very similar: *Lejeunea* has many small oil bodies per cell (versus few and large in *Cheilolejeunea*); a proximal rather than a distal slime papilla on the lobules; generally smaller lobules; and a generally greenish (versus often slightly brownish) color when dry.

This is a problematic genus in Hawai'i. Both indigenous (*L. adpressa* versus *L. pacifica*) and exotic species can be difficult to delimit, and elucidating the variation in these taxa is beyond the scope of this notebook. Lee et al. (2026a) note that: "...We identified complexes that may include several independent entities, such as the sub-cosmopolitan *L. flava* [exotic in Hawai'i] and the pantropical *L. adpressa* [indigenous to Hawai'i] and several polyphyletic groups like the Neotropical *L. laetevirens* [exotic in Hawai'i]. To revise the taxonomy of these problematic species, expanding the sampling is crucial for a comprehensive examination of genetic and morphological variation. Additionally, morphometric investigations, supported by molecular data, could unveil complex patterns of morphological variation..." Lee et al. (2026b) indicate that *L. adpressa*, *L. cocoes*, *L. flava*, and *L. laetevirens* all pertain to subgenus *Crossotolejeunea* Spruce.

1. Plants 0.2-0.4 mm wide; naturalized 2
 2. Leaves caducous, truncate, with minute lobules less than 30% the size of the lobes; rare, Hawai'i Island *L. cocoes*
 2. Leaves persistent, pointed, with large lobules 30-40% the size of the lobes; O'ahu and Hawai'i Island *L. laetevirens*
1. Plants 0.5-2 mm wide; indigenous or naturalized 3
 3. Plants 1.8-2 mm wide; underleaf lobes conspicuously connivent, (4)5-10 cells wide at their base; rare, Hawai'i Island *L. species 1*
 3. Plants 0.5-1.5 mm wide; underleaf lobes parallel or divergent, not conspicuously connivent (or only slightly so in *L. pacifica*), usually less than 5 cells broad at the base 4
 4. Underleaves 4-5 times broader than the stem with lobes 9-10 cells wide at the base *L. flava*
 4. Underleaves 1.5-3 times broader than the stem with lobes (3)4-5 cells wide at the base 5
 5. Underleaves lobed to about their middle, the sinus acute or narrowly lunulate; lobes (2-)3-5 cells wide at base; perianths flat at their apex, not retuse, plants 0.5-0.9 mm wide *L. adpressa*
 5. Underleaves lobed to beyond their middle, the sinus broadly lunulate; lobes 2-3(-4) cells wide at base; perianths apically retuse, plants about 1 mm wide *L. pacifica*



Left: Typical habit of *Lejeunea*: Closely appressed and creeping on bark. Center: The slime papillae (arrow) of the lobules are proximal to the lobule tooth. Volcano, Hawai'i Island, *Lejeunea adpressa*, Freire & Judziewicz 23-456 (BISH). Right: Numerous small oil bodies per cell. *Lejeunea cocoes*. Hilo Arboretum Nursery, Hawai'i Island, Freire & Judziewicz 23-500 (BISH).



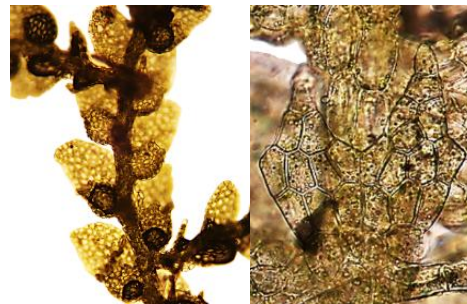
Lejeunea adpressa



Lejeunea cocoes



Lejeunea flava



Lejeunea laetevirens



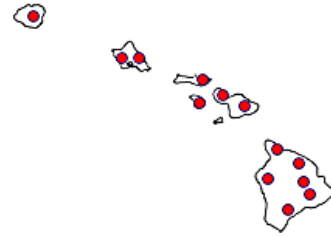
Lejeunea pacifica



Lejeunea species 1

1. *Lejeunea adpressa* Nees/*L. anisophylla* Mont. Indigenous.

Present on all major islands from 0-6,100 feet; common. Cosmopolitan; treated as *L. anisophylla* in Staples & Imada (2006). *L. anisophylla* has been synonymized under *L. adpressa*, see S.R. Gradstein (2021: 514) and Judziewicz & Freire (2023c: 161), but Lee et al. (2026b) consider them separate species, although morphologically indistinguishable.



The *L. adpressa*/*L. anisophylla* complex is not a natural group, but members of this complex do pertain to sect. *Minutilobae* R. M. Schust. (Lee et al. 2026b). We do not attempt to account for all variation in this complex here.

Populations form loose to dense mats, growing closely appressed to bark, hāpu‘u stipes, leaves or rocks; plants are small, (0.5)0.6-1 mm wide, whitish-green, slender and sparingly branched. Leaves are ovate-oblong, broadly spreading from slender stems, with rounded to truncate apices (sometimes slightly acute). Lobules are generally large, about 1/3 the leaf length, inrolled, with a prominent apical tooth, but poorly differentiated lobules are sometimes present. Leaves often have a constriction or are slightly curved where the lobe’s postical (lower) margin meets the lobule. The underleaves split to about ½ their length, with lobes (2)3-5 cells wide at their base; sinuses are acute or narrowly lunulate. Some underleaves with broader and deeper sinuses are sometimes intermixed. The leaf cells usually have small trigones and some intermediate thickenings. Perianths are obovate, keeled, and flat-topped.

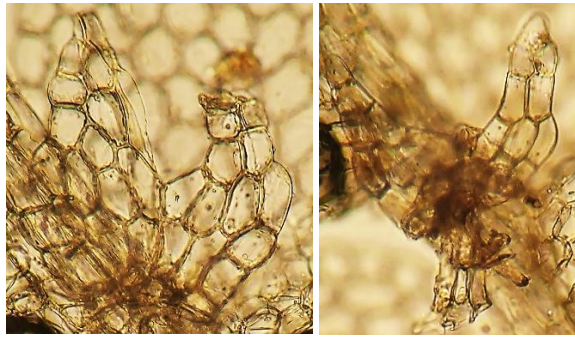
We sometimes found it difficult to clarify the boundaries between sterile plants of *L. adpressa* and *L. pacifica*; intermediate forms were often observed. Miller (unpublished notes) and Evans (1900) used the presence of trigones in *L. adpressa* and their absence in *L. pacifica* as a good character to tell them apart, but we have observed individuals of both species with small trigones. Perianth morphology is a good way to separate the two species (flat-topped in *L. adpressa* while retuse in *L. pacifica*), but specimens of both species are often sterile. Below are some examples of the variation we observed in *L. adpressa* in Hawai‘i.



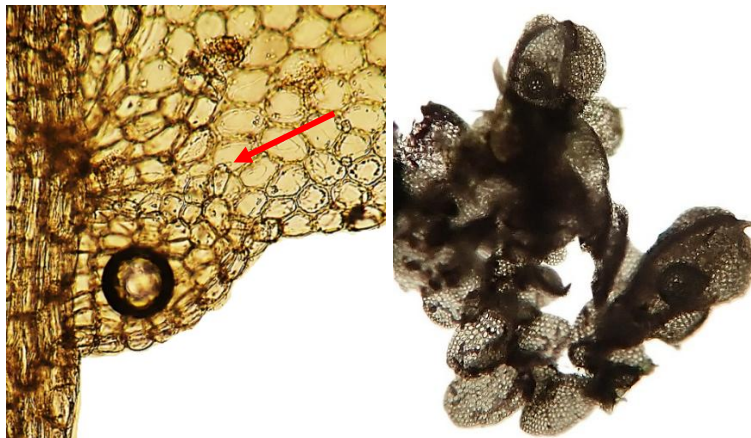
Lejeunea adpressa. Left: Population loosely arranged on hāpu‘u stipe. Right: Plants are whitish-green, about 0.8 mm wide. Scale in mm. Nāhuku, Hawai‘i Volcanoes National Park, Hawai‘i Island, Freire & Judziewicz 20-314 (HAVO).



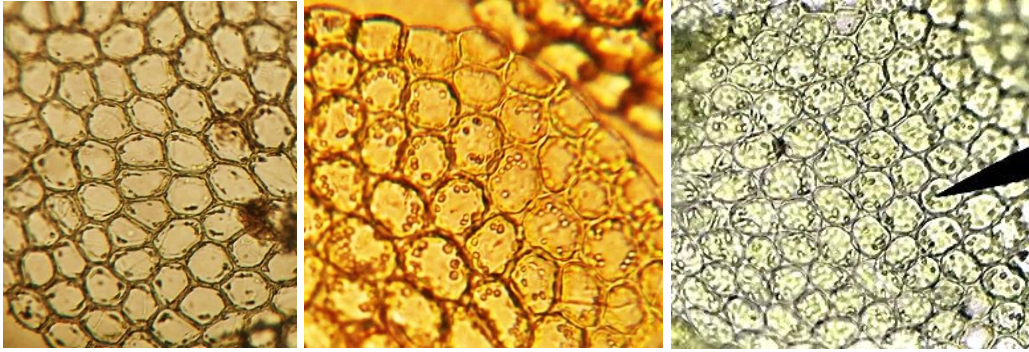
Plants are slender, with leaves broadly spreading, flat, oblong, rounded to truncate, and sometimes slightly pointed at the apex. Note the leaf lower margin with a slight constriction where the lobe meets the lobule. Lobules are prominent and inrolled. Freire & Judziewicz 20-314 (HAVO).



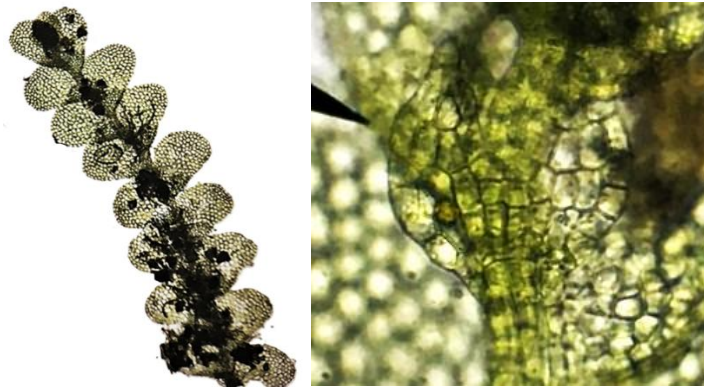
Typical underleaf, split to about the middle by an acute sinus. Lobes are four cells wide at their base. Within the same plant, some underleaves have a broader sinus and are divided beyond their middle (much like those of *L. pacifica*), and the lobes are three cells broad at their base. Nāhuku, Hawai'i Volcanoes National Park, Hawai'i Island, Freire & Judziewicz 20-314 (HAVO).



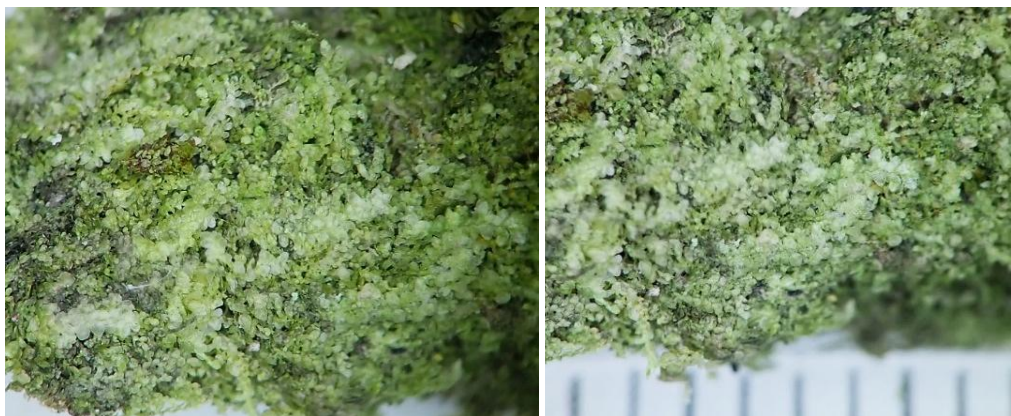
Lejeunea adpressa. Left: Inrolled lobule with prominent apical tooth (arrow). Nāhuku, Hawai'i Volcanoes National Park, Hawai'i Island, Freire & Judziewicz 20-314 (HAVO). Right: Flat-topped, obovate and keeled perianths. Upper Kāhuku Unit, Hawai'i Volcanoes National Park, Freire & Judziewicz 22-773 (HAVO).



Left: Cells with tiny trigones. Nāhuku, Hawai'i Volcanoes National Park, Hawai'i Island, Freire & Judziewicz 20-314 (HAVO). Center: Leaf cells with small oil bodies, small trigones and intermediate thickenings. Freire & Judziewicz 22-992 (BISH). Right: Leaf cells with trigones and several small, elongate oil bodies. Freire & Judziewicz 20-498a (BISH).



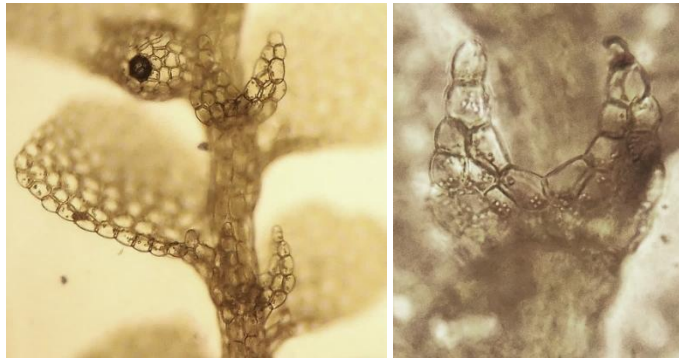
Example of morphological variation in *Lejeunea adpressa*. Left: Plants with obovate leaves that are straight rather than constricted on the leaf lower margin. Note the rounded apices. Midleaf cells have trigones (see above). Right: Underleaf showing typical *L. adpressa* morphology. Pu'u Maka'ala N.A.R., Hawai'i Island, Freire & Judziewicz 20-498a (BISH).



Left: Some populations can be light green and can form dense mats, here growing on bark. Right: Plants can be tiny, about 0.5 mm wide. Scale in mm. Volcano, Hawai'i Island, Freire & Judziewicz 22-992 (BISH).



Examples of morphological variation in *Lejeunea adpressa*. This set of pictures shows a population with smaller plants and slightly different leaves. Left: Small plants, slightly less than 0.5 mm wide. Scale in mm. Center: Plants with distant and slightly pointed apical leaves with underdeveloped lobules intermixed. Leaves are not flat, but tilted at least 45°. Right: Underleaves are typically small and distant but some have a broad lunulate sinus beyond the middle (arrow). Freire & Judziewicz 22-992 (BISH).



Left: Underleaves small and distant, split to about their middle, with an acute or narrowly lunulate sinus. Lobes 3-4 cells broad at their base. Also note the inrolled lobule on top, and a poorly developed one at bottom. Right: Detail of underleaf with lunulate sinus. Freire & Judziewicz 22-992 (BISH).



Lejeunea adpressa. Flat-topped, keeled perianth. Volcano, Hawai'i Island, Freire & Judziewicz 22-992 (BISH).

2. *Lejeunea coco* Mitt. Naturalized. A tropical Asian species ranging east to Fiji and French Polynesia. First report from Hawai'i: Judziewicz et al. (2025b: 138-139). Freire & Judziewicz 23-500 (BISH), collected on bark of cultivated *Brownea macrophylla* (Fabaceae) and several other tree species in the Hilo Nursery Arboretum, 25 Aug. 2023. Growing in dense mats with occasional plants of the much larger *Lejeunea flava*.



Plants tiny, 0.2-0.5 mm wide, green, rarely branched, forming dense, loosely attached mats on tree bark. Leaves caducous, distant to contiguous, slightly spreading, obovate, roundish above, tapering to a narrow base below, slightly decurrent. Lobules reduced to two cells, tipped by a slime papilla. Underleaves bifid, markedly squarrose, with a broad sinus and acute lobes. Oil bodies are small, spherical, smooth and numerous. Leaf and underleaf cells bulging, thin-walled, lacking trigones. Gemmae are produced on leaf margins. Only sterile plants were observed.

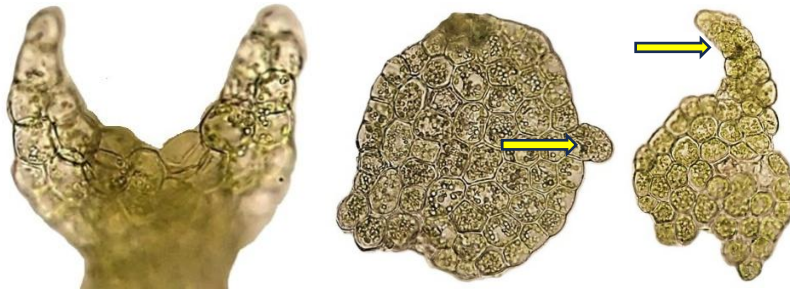
See Lee (2013), Lee et al. (2022), and Zhu & Grolle (2003) for information of the Asian related species *L. exilis* (Reinw., Blume & Nees) Grolle and *L. malaysiana* G.E. Lee & Pócs. More recently, it has been shown that *Lejeunea coco* is polyphyletic (Lee et al., 2026a), but members of this complex do pertain to sect. *Minutilobae* R. M. Schust. (Lee et al. 2026b).



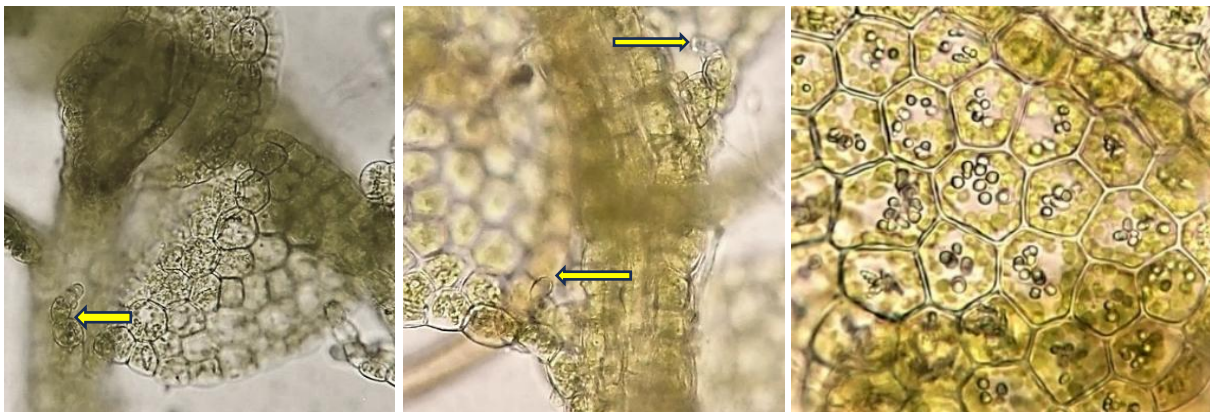
Lejeunea coco. As bark epiphyte on exotic tree *Brownea macrophylla*. Associates include *Lejeunea flava* and the ferns *Crepidomanes parvulum* and *Lepisorus thunbergianus*. Scales in mm. Hilo Arboretum Nursery, Hawai'i Island, Freire & Judziewicz 23-500 (BISH).



1. Plants are tiny (scale in mm). 2. Leaves are contiguous and spread at about 45°. Note squarrose underleaves. 3,4. Two views of tapering leaf bases (arrow). Freire & Judziewicz 23-500 (BISH).

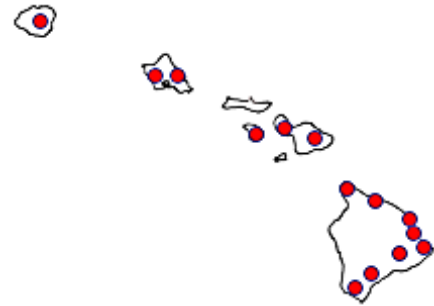


Left: Bifid underleaf with broad sinus. Center: Gemma or rejuvenant developing on lobe margin. Right. Caducous leaf fragments with rejuvenants. Freire & Judziewicz 23-500 (BISH).



Lejeunea cocoens. Left: 3-celled lobule at very base of lobe. Center: Arrows point to slime papillae at the tip of lobules. Right: Thin-walled leaf cells with 8-12 small oil bodies per cell. Hilo Arboretum Nursery, Hawai'i Island, Freire & Judziewicz 23-500 (BISH).

3. *Lejeunea flava* (Sw.) Nees. **Naturalized.** First report from Hawai‘i: Judziewicz, Freire & Bogner (2023: 20). On all major islands (0-4,400 ft.) except Moloka‘i (where it also likely occurs by now). Apparently first collected in Hawai‘i in 1977, based on a Miami University specimen from Foster Botanical Garden in Honolulu, on Kaua‘i in 1993, and becoming widely distributed by about 2000. *Lejeunea flava* is an unresolved species complex (Lee et al., 2026a), but members of this complex do pertain to sect. *Flavae* R. M. Schust. (Lee et al. 2026b).

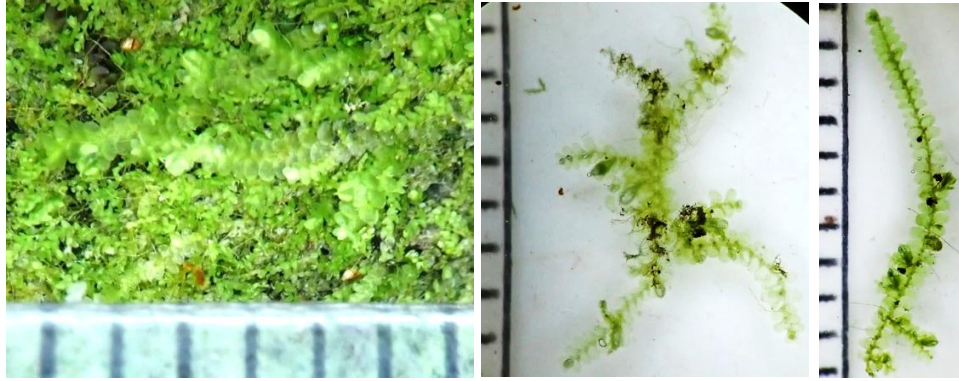


There is considerable unresolved diversity within this complex in Hawai‘i, for example in the southern Ko‘olau Range on O‘ahu, that we do not attempt to account for here. *Lejeunea flava* (in the wide sense) is now the dominant liverwort in wet, lowland areas and is the most frequently photographed Hawaiian leafy liverwort on iNaturalist, with 286 observations as on 4 May 2026. First confirmed for Hawai‘i by Jochen Heinrichs (1969-2018) in 2016, based on 1993 Kaua‘i collections.

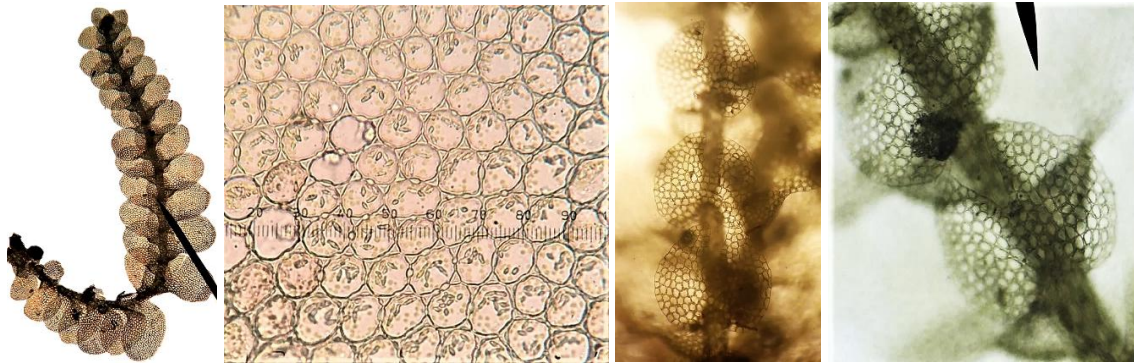
Plants 0.7-1.5 mm wide, with few branches. Leaves spreading, flat, with a strong constriction where the lobe joins the apex of the lobule, as in *Cheilolejeunea* (see introduction to *Lejeunea* for differences). Leaf lobes usually with rounded apices but may be acute (pointed) in the proximity of perianths. Distinct in its large underleaves, over 3 times broader than the stem, with a “V shaped” sinus and acute, broad lobes. Trigones and some intermediate thickenings are present on leaf and underleaf cell walls. Plants are monoicous and often fertile, with perianths and antheridia produced on separate branches on the same plant (autoicous); the perianths are flat-topped, beaked, and keeled. Antheridia are clustered on short lateral branches. When we illuminate *L. flava* with UV light, the plants glow red.



Left: Plants are milky green and form loose mats that skirt the base of trees. Onomea, Hawai‘i Island, Freire & Judziewicz 20-217 (BISH). Right: Plants with rounded leaves (red arrow); they are much larger than *L. laetevirens*, here its associate (black arrows). Onomea, Hawai‘i Island, Freire & Judziewicz 22-985a (BISH).



Plants are about 0.8 mm wide and often fertile. Scales in mm. Freire & Judziewicz 22-985a (BISH).



Lejeunea flava. 1. Leaves are oblong, with rounded apices, spreading at almost 90°. Lobules are inrolled. 2. Leaf cells are isodiametric, with numerous small, elongate oil bodies; the walls have conspicuous trigones and intermediate thickenings. Scale units = 2.5 μ m. Mauna Ulu access road, Hawai'i Island, Freire & Judziewicz 21-323 (HAVO). 3. Underleaves are large and round, 3-5 times broader than the stem, with a V-shaped sinus and broad lobes. Freire & Judziewicz 22-985a (BISH). 4. Detail of underleaves with trigones. Hilo, Hawai'i Island, Freire & Judziewicz 20-217 (BISH).



Lejeunea flava. Plants with flat-topped, beaked, and keeled perianths; note the broadly pointed leaves close to them. Perianths are produced singly, on short lateral branches (left side of stem). Antheridia on short lateral branch above (right). Onomea, Hawai'i Island, Freire & Judziewicz 22-985a (BISH).

4. *Lejeunea laetevirens* Nees & Mont. Naturalized. First report for Hawai'i: Judziewicz & Freire (2023c: 164). An American species found recently on O'ahu and Hawai'i Island; on bark (0-1,800 ft.). **O'ahu:** First found in Ho'omaluhia Botanical Garden in Nov. 2021 by Judziewicz 21-989 (BISH), apparently spreading rapidly and now known from 32 iNaturalist observations (most by Kevin Faccenda) from throughout the southern Ko'olau Range, mostly below 500 ft. but up to over 1,800 ft. on Kekoalele Ridge, Faccenda: <https://www.inaturalist.org/observations/328996757>.



Initially at Onomea, Hawai'i Island on 20 Nov. 2019 (sparse populations; Freire & Judziewicz 154, 155, BISH) but greatly spreading at this site by Dec. 2023; later at Maku'u Market, Pāhoa, Jan. 2024, Hawai'i Island (Judziewicz & Faccenda 17,278a (BISH) (<https://www.inaturalist.org/observations/196256057>).

Lejeunea laetevirens is polyphyletic (Lee et al., 2026a), but members of this species complex pertain to sect. *Nanolejeunea* (R. M. Schust.) G.E. Lee & Gradst. (Lee et al. 2026b).

A minute bark epiphyte or epiphyll, in urban areas and botanical gardens; often associated with the commoner exotic *L. flava*. First noted in 2019 and 2021 from our collections, and apparently spreading, especially in the Honolulu area. Populations form densely packed, frequently branched mats of tiny yellow-green plants, 0.3-0.4 mm wide (but reportedly up to 0.8 mm wide in non-Hawaiian material). The leaves are acute and erect-spreading (diverging from the stem at 45°). The lobules are large, inrolled, and are roughly 1/2 the length of the lobe. The bifid underleaves are small, lobed halfway; the lobes are acute and have minute lateral projections ("elbows"). Stems are thin and fragile, probably fragmenting for asexual reproduction as reported by Gradstein (2021). Leaf cells have small trigones.



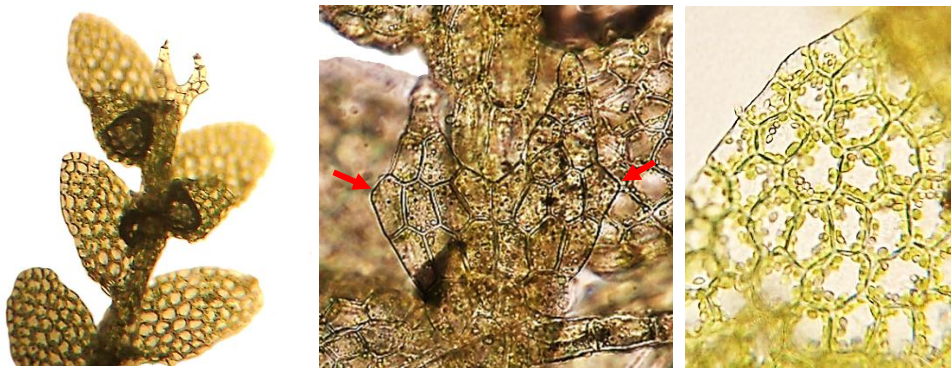
Lejeunea laetevirens. Covering bark of exotic tree, Onomea, Hawai'i Island, Dec. 2023. It had become locally abundant at this site over a period of four years; we did not observe such luxuriant growths such as shown here in Nov. 2019. Judziewicz 17,054 (BISH).



Left: Population forms a dense mat on a leaf. Right: Plants frequently branched and tiny, about 0.3 mm across. Scales in mm. Freire & Judziewicz 22-988 (BISH).

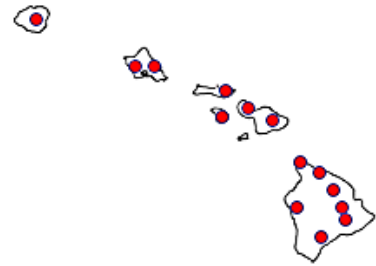


Leaves are tiny, acute, diverging at approximately 45° from the stem. Left: Lobules large and inrolled. Freire & Judziewicz 22-988 (BISH).



Lejeunea laetevirens. Left: Leaf lobules are large and inrolled but alternate with poorly developed ones. Center: Underleaves are small, bifid, about as broad as long, with one or two lateral “elbows” (arrows). Right: Leaf cells are thin-walled, with no trigones. Oil bodies are small and numerous per cell. Onomea, Hawai‘i Island. Center and right: Freire & Judziewicz 21-516 (BISH). Left: Freire & Judziewicz 22-988 (BISH).

5. *Lejeunea pacifica* Mont. Indigenous. Found on all major islands (0-5,800 ft.); common; mainly Asian. See notes under *L. adpressa*; based on its similarity with that species, we suggest that *L. pacifica* may also be a member of sect. *Minutilobae* R. M. Schust. as defined by Lee et al. (2026b). The small underleaves with a broad and deep sinus and two acute lobes and the retuse perianth are distinctive for this species.

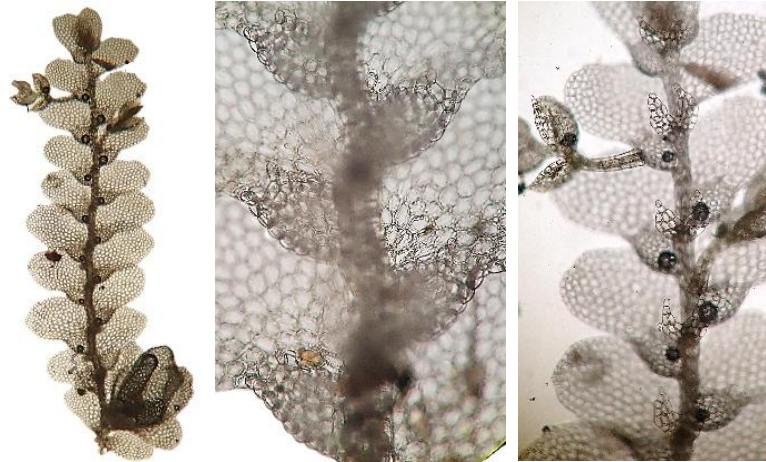


The light green plants grow closely appressed to bark, rocks, or leaves. They are frequently branched and about 1 mm wide. Leaves are oblong-obovate with a rounded apex; they are imbricate and spread at nearly 90° from the stem; often with marginal rhizoids*. Leaf lobules are triangular and inrolled; some poorly developed lobules are intermixed. The lobule's keel forms a nearly straight line with the lower (postical) leaf margin. The most distinctive character is the deeply lobed nature of the underleaves; these are split to well beyond ½ their length, mostly with a broad lunulate sinus, and lobes only 1-2(3) cells wide at their base. The leaf cell walls are thin, with no trigones (or with only tiny ones). Perianths are cuneiform, broad and retuse at the apex, and gradually narrowing towards the base (as reported by Evans, 1900).

*Leaf marginal rhizoids have been observed in other species of *Lejeunea*, for example in two Malesian taxa, *L. dimorpha* Kodama and *L. patriciae* Schäf.-Verw. (Lee, 2013: 392, 413-415, 459-462). However, these species differ in having much more robust underleaves with broad triangular lobes, among other differences.



Populations form flat, closely appressed mats. Plants are about 1 mm broad. Volcano, Hawai'i Island, Freire & Judziewicz 23-456 (BISH). Scale in mm.



Left: Plants are frequently branched. Note the retuse perianth. Left and center: Leaves have rounded apices and nearly straight lower margins. Lobules are inflated and less than 30% the lobe area. Right: Underleaves are distant and deeply lobed. Freire & Judziewicz 23-456 (BISH).



Underleaves are distant, with a deep sinus, beyond $\frac{1}{2}$ its length, and with narrow lobes. Lateral protuberances or "elbows" may be present at each lobe's base. Left and center: Freire & Judziewicz 23-456 (BISH). Right: Volcano, Hawai'i, Freire & Judziewicz 20-1039 (HAVO).



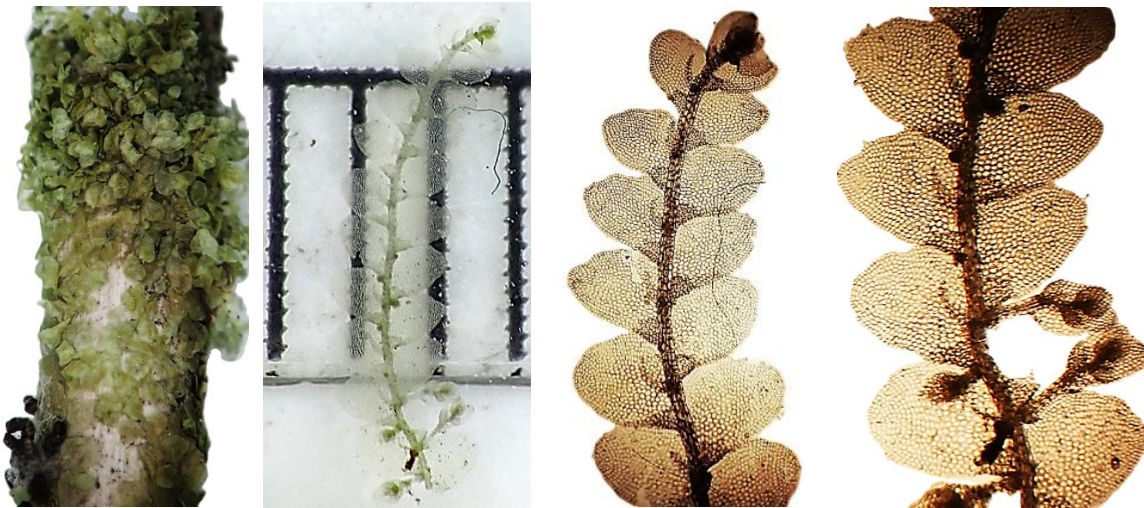
Lejeunea pacifica. Left: Cell walls are thin and may or may not have tiny trigones. Right: Leaf margins produce rhizoids. Volcano, Hawai'i Island, Freire & Judziewicz 23-456 (BISH).



Lejeunea pacifica. Perianths are cuneate, with a broad, retuse apex. Volcano, Hawai'i Island, Freire & Judziewicz 23-456 (BISH).

Lejeunea cf. pacifica

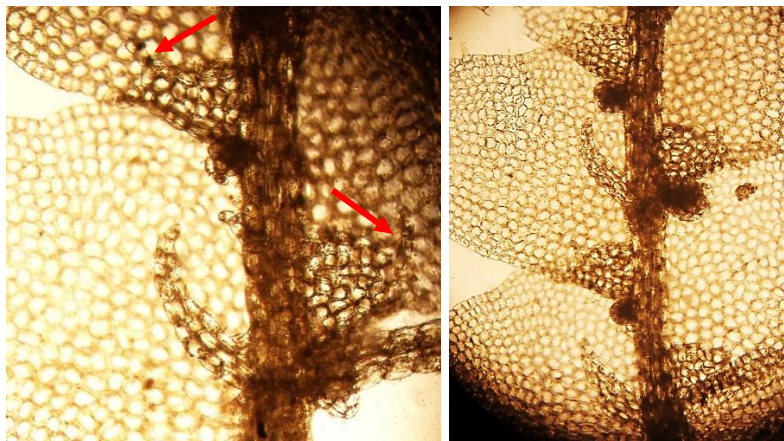
The following specimen was collected on a twig at the entrance to Kīpukapuau (3,900 ft.), Hawai'i Volcanoes National Park. The most salient characters are the large and deeply divided underleaves with narrow, elongate, slightly connivent lobes, and the plants grow more loosely attached to their substrate. Plants are slightly larger (1.3 mm wide), and some leaves have pointed rather than round apices and can spread at smaller angles from the stem. Perianth only slightly retuse, not clearly cuneate (based on photo of a single perianth, specimen needs more study).



1. Population growing on twig. Whitish-green plants can sometimes be loosely attached to their substrate. Perianths are present. 2. Plants can be over 1 mm wide. Scale in mm. 3. Leaves are flat, ovate, and round to slightly acute at the apex. Lobules are inrolled and about 1/5 as long as the leaf lobe. 4. Lateral branches are sometimes observed. Note the large and deeply lobed underleaves. Kīpukapuau (3,900 ft.), Hawai'i Volcanoes National Park, Hawai'i Island, Freire & Judziewicz 21-487 (HAVO).



The leaves produce marginal rhizoids, some of which may be branched. Freire & Judziewicz 21-487 (HAVO).



Underleaves very deeply lobed, well beyond their middle; the lobes are slightly connivent and 2-4 cells broad at their base. Also note the inrolled lobules with multicellular apical tooth (arrows). Freire & Judziewicz 21-487 (HAVO).



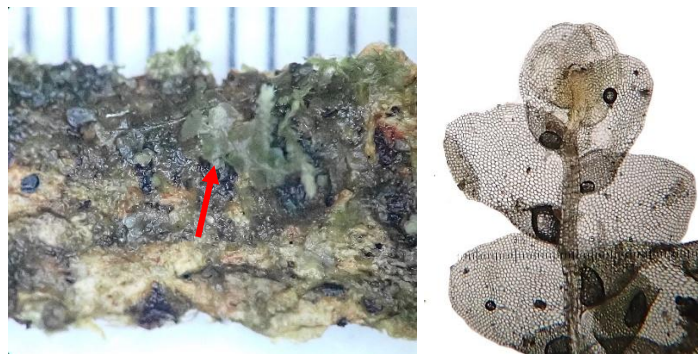
Lejeunea cf. *pacifica*. Left: Keeled perianth with slightly retuse apex. Note pointed leaves that spread at about 45° from the stem. Right: Median leaf cells have thin walls and no or very tiny and inconspicuous trigones. Kīpukapuau, Hawai‘i Volcanoes National Park, Freire & Judziewicz 21-487 (HAVO).

6. *Lejeunea* species 1. Rare. Found only in Volcano, Hawai'i Island (3,400 ft.), on the slopes of Kīlauea. This is the largest Hawaiian species of *Lejeunea*. This species is recognized by the round, large underleaves, with clearly connivent lobes that are broad at their base and separated by a broad and lunulate sinus. They resemble a "Rocking C".

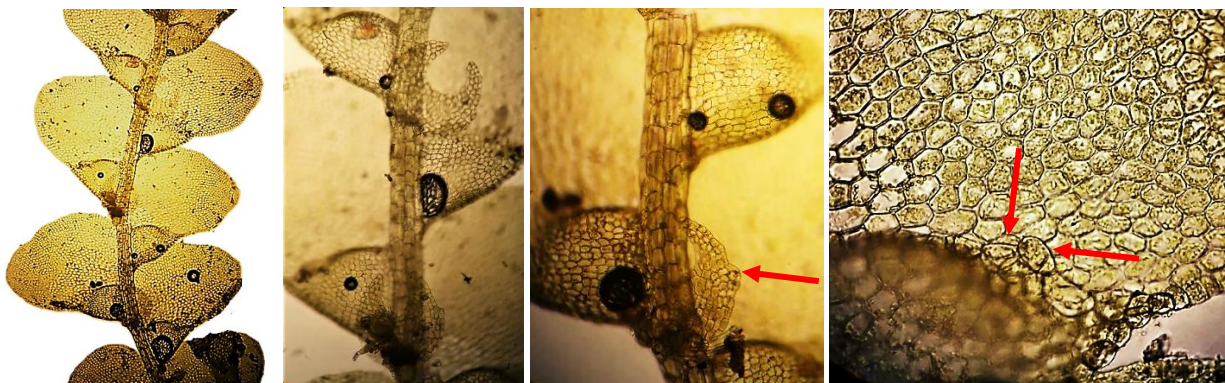


Plants grow loosely attached to bark; they are large, 1.8-2 mm wide, and rarely branched. Stems are fragile. Leaves are flat, broadly ovate, and imbricate; with round to slightly pointed apices. The robust, inflated lobules are triangular-ovate, and large, 1/4-1/3 as long as the leaf lobe. Underleaves are large, about 3 times as broad as the stem; they are connivent, with a broad, lunate (round) sinus to 1/3-1/2 deep, and with curved lobes (4)5-10 cells broad at their base and with a hint of lateral "elbows". Leaf cells are thin-walled, without trigones or with tiny ones. Cells with many small oil bodies.

Photos below from Hale Alema, Volcano, Hawai'i Island, Freire & Judziewicz 22-544 (BISH), from canopy branches of an 'ōhi'a (*Metrosideros polymorpha*) tree and from Freire & Judziewicz 22-818 (BISH).



Plants grow loosely attached to their substrate and are large. Scale in mm. Right: Scale units = 26 μ m. Volcano, Hawai'i Island, Freire & Judziewicz 22-544 (BISH).



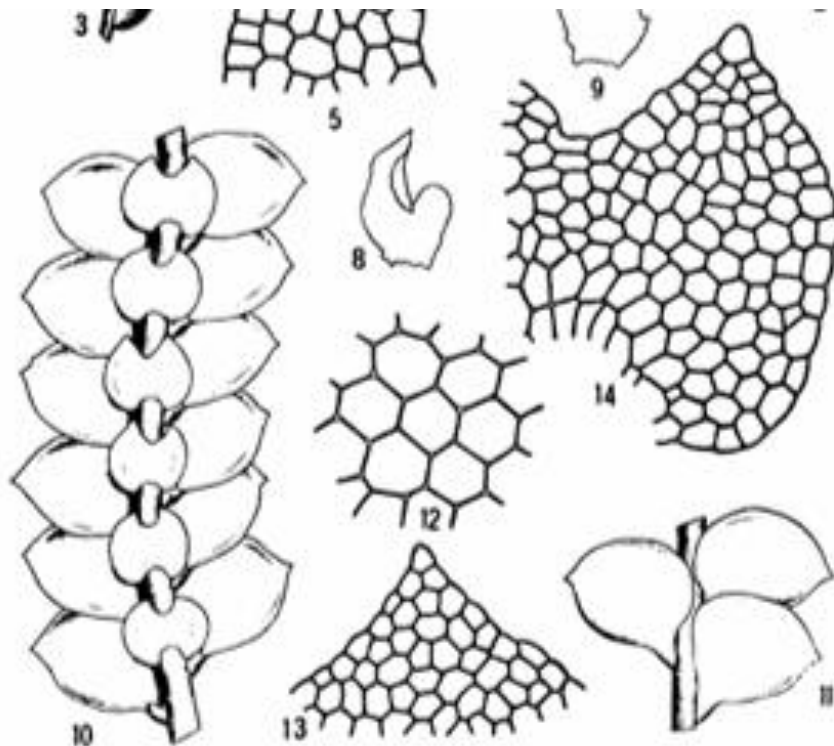
Lejeunea species 1. Plants with fan-shaped leaves and large inflated lobules. 2. Large underleaves with broad, connivent lobes separated by a broad sinus. 3. Underleaves have a hint of an "elbow" (arrow) below the lobes. 4. Arrow points to proximal slime papillae (left arrow) proximal to the lobule tooth (right arrow). Note the absence of trigones (or only very tiny ones), and the numerous small oil bodies. Volcano, Hawai'i Island, Freire & Judziewicz 22-544 (BISH).

Lepidolejeunea R.M. Schust. (Lejeuneaceae)

One species in Hawai‘i, 16 species worldwide.

Lepidolejeunea involuta (Gottsche) Grolle. **Indigenous.** A member of subgenus *Kingiolejeunea* (H. Robs.) R.M. Schust. (Söderström et al., 2016: 391). Rare, known in Hawai‘i only from a 1793 collection by Archibald Menzies from an undetermined locality (Piippo, 1986: 45; Heinrichs et al. 2015: 223), probably from a lowland location. Evans (1900) comments that “A few Hepaticae from the Hawaiian Islands were collected by Menzies in 1793. They consist of small specimens and of fragments picked from other plants and are for the most part in the herbarium of Sir William J. Hooker, now preserved in the collections of the Royal Gardens at Kew...” The late Jochen Heinrichs suspected that the Hawaiian material, described as *Lejeunea owaihiensis* Gottsche, may represent a separate species because it “... represents a robust morphotype with leaves that gradually taper into an acute apex rather than having the apiculate apex of Neotropical *L. involuta*...” (2015: 225). If his interpretation is correct, the new combination *Lepidolejeunea owaihiensis* (proposed in manuscript by Miller) will be necessary.

The figure below was drawn from the Menzies specimen (Evans, 1900). It does not show the most distinctive feature of this tropical American species, namely that ocelli are scattered throughout both the lobes and lobules (but perhaps the drawing was made from dried material in which the ocelli had faded). We did not find any specimens to study in the field or at BISH, HAVO, MU, or PTBG.



Lepidozia (Dumort.) Dumort. (Lepidoziaceae)

At least four species in Hawai'i, 135 species worldwide.

Species of *Lepidozia* grow in wet forests and are epiphytic or terrestrial. Plants are of various sizes, profusely pinnately branched, with a tendency to produce flagelliform stem tips. The leaves are incubous to transversely inserted, quadrate to rectangular, usually with 3-4 triangular lobes, or rarely ciliate; underleaves are rectangular to quadrate, as broad as the stem or smaller, mainly with 3-4 triangular lobes. Leaf cells are quadrate, thick-walled, and lack evident trigones.

1. Leaves inconspicuous, narrower than the stem width, appressed, stems coarse and prominent; plants with the appearance of a fruticose lichen ***L. sandvicensis***
1. Leaves conspicuous, wider than the stem width, not appressed, stems not coarse and prominent; plants with no resemblance to a fruticose lichen 2
2. Leaves with ciliate teeth; rare, and a questionable record from Hawai'i ***L. holorrhiza***
2. Leaves with triangular teeth 3
3. Leaves with 3-4 equally-sized triangular teeth ***L. australis***
3. Leaves with 3(4) unequally-sized teeth ***L. selligiana***



L. australis



L. holorrhiza

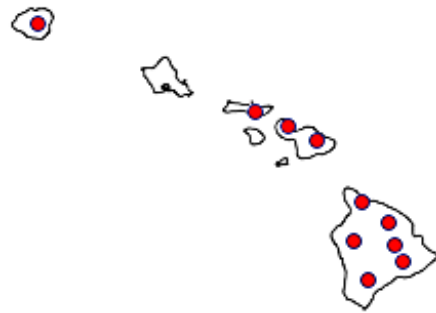


L. sandvicensis



L. selligiana

1. *Lepidozia australis* (Lehm. & Lindenb.) Mitt. **Endemic.** Kaua'i, Moloka'i (Judziewicz et al., 2025b: 140), Maui, and Hawai'i (3,500-6,500 ft.); it is notably absent from O'ahu. Possible affinity (Cooke, 1904): *L. reptans* (L.) Dumort., temperate and tropical Eurasia, North America. This species thrives in shaded wet forests, where it commonly grows intermixed with other bryophytes on decaying wood, soil, or base of trees. Plants are light green, conspicuously pinnately branched, often with flagelliform branches and/or flagelliform branch apices.



Plants are loosely attached, projecting from their substrate, 3-4 cm long or longer; the main stems have leaves about 1 mm wide. Stems are stout and profusely pinnately branched. Leaves are imbricate to distant, incubous and spreading, rectangular, longer than the stem is wide, usually slightly constricted at their base, flat to slightly concave and much longer than the stem width. Leaves and underleaves are coarsely segmented at their apices into 3-4 equal triangular teeth. Sinuses between lobes are acute-triangular, about 1/3 the length of the leaves and 1/2 the length of the underleaves or slightly less. Underleaves are rectangular, broader than long, distant, about as broad as the stem, slightly concave and projecting from the stem. Leaf cells are large, quadrate to rectangular, thick-walled with some trigones; oil bodies are granular and elongated, several per cell. When we illuminate the plants with UV light, they glow red.



Left: Plants grow intermixed with other bryophytes. They are easily recognized because of their conspicuously pinnate branching. Volcano, Hawai'i Island, Freire & Judziewicz 21-258 (HAVO). Right: Typical pinnate branching. Plants project from their substrate and have a cedar-like aspect; the leaves are large and flat. Volcano, Hawai'i Island, Freire & Judziewicz 22-162 (BISH).



Lepidozia australis. Left: Plants are 3-4 cm long. Note the flagelliform tips of branches. Freire & Judziewicz 22-562 (HAVO). Right: Plants are flattened; stem leaves large, about 0.5 mm long; branches taper towards the apex. Pu'u Maka'ala N.A.R., Hawai'i Island, Freire & Judziewicz 22-614 (HAVO). Both scales in mm.



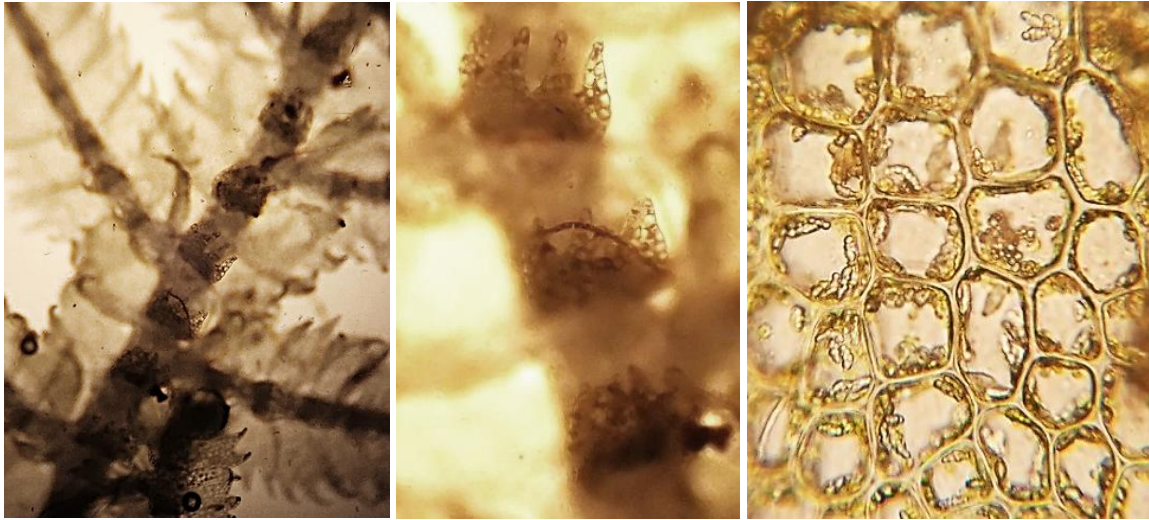
Lepidozia australis. Top row: Dorsal views. Bottom row: Ventral views. East Maui, photos by Zach Pezzillo (<https://www.inaturalist.org/observations/200155839>), with permission.



Ventral views. Pinnately branched plants with conspicuous flagelliform branch apices. Freire & Judziewicz 22-562 (HAVO).



Lepidozia australis. Leaves imbricate to distant, spreading, rectangular, slightly constricted at their base, with 3-4 equal triangular lobes. Volcano, Hawai'i Island, Freire & Judziewicz 22-562 (HAVO).



Left and center: Underleaves. Right: Median leaf cells. Note the oil bodies, Volcano, Hawai'i Island, Freire & Judziewicz 22-562 (HAVO).

We found gemmae on the leaf surfaces of a specimen from the Alaka'i Plateau, Kaua'i, Faccenda 3868a (BISH, PTBG). Gemmae are 1-3-celled and 18-25 μm in diameter. This is the first Hawaiian report of gemmae in *Lepidozia*. Gemmae are rare or absent in this genus; they are not mentioned as occurring in the ca. 20 tropical American species (Gradstein, 2001: 183), the 23 Aotearoa/New Zealand species (Engel & Glenny, 2008: 196), the British species (Paton, 2014: 65), Papua New Guinea species (Piippo, 1984) or the North American species. Schuster (1969, Vol. II: 17) reports that in North America: "... asexual reproduction in the genus is unknown or occurring rarely by 1-2-celled gemmae. Neither Müller nor I have seen gemmae. Degenkolbe (1938: 87) reports them, without detail, for *L. reptans*. I question the correctness of his report...".



Lepidozia australis. Gemmae pointed by arrows. Alaka'i Plateau, Kaua'i, Faccenda 3868a (BISH, PTBG).

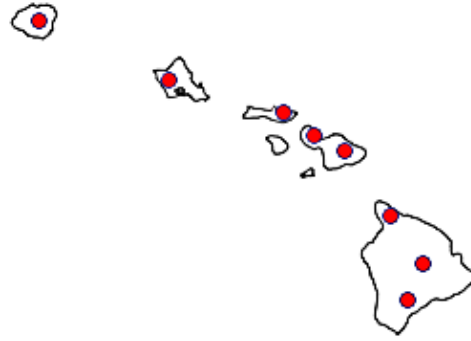
2. *Lepidozia holorrhiza* (Reinw., Blume & Nees) Nees. **Dubious report for Hawai‘i.** Miller (1983) includes this tropical Asian species, based on a Baldwin specimen “probably from Maui” (no other information) at MU (Judziewicz et al., 2025b: 140). We did not find this species in the field or at HAVO, BISH, or PTBG. No records of *L. holorrhiza* for Hawai‘i are found in iNaturalist.

Based on our study of the Baldwin specimen (below), plants superficially resemble *Sphagnum* moss; they are julaceous, about 3 cm long and 0.5 mm wide. The most distinct characters are the profuse branching with flagelliform branch tips; and the imbricate and appressed leaves that are very concave and bear multiple, long cilia rather than triangular lobes. Leaf cells are thickly walled.



Lepidozia holorrhiza. Plants are julaceous, worm-like, narrow and long. Leaves are densely imbricate, concave and incubous. Note cilia on leaf margins – a character absent from other Hawaiian species of *Lepidozia*. Collection by Baldwin, from Hawai‘i (MU herbarium). Photos by A.V. Freire.

3. *Lepidozia sandvicensis* Lindenb. ex Gottsche, Lindenb. & Nees. **Indigenous.** Possible affinity (Cooke, 1904): *L. commutata* (= *L. patens* Lindenb.), tropical America. Found on all major islands except Lānaʻi (2,900-6,200 ft.); on Hawaiʻi Island found in Kohala (above Alakahi Stream, Degener 19861, BISH), the Saddle area (Stemmermann 2553, BISH), and Kaiholena (Wood 12894, BISH). Plants resemble a fruticose lichen, especially when dry. It is typically terrestrial and can be found on the base of tree trunks.



The type is from Hawaiʻi, but it is also found from Alaska to British Colombia, perhaps suggesting dispersal to Hawaiʻi by migratory birds. However, Martin Hutten, bryologist from Glacier Bay National Park, indicates that Hawaiian plants look quite different from Alaskan populations (10 May 2023 pers. comm.).

Cooke (1904) suggested *Lepidozia patens* Lindenb. (as *L. commutata* Steph.) as a related species; this is a tropical American species characterized as having “Stems to 15 cm long, with very long branches” and “long pendent, thread-like stems with very small, distant leaves that are spreading away from the stem...” (Gradstein, 2021); unlike *L. sandvicensis*, which forms compact turfs or cushions on the ground or on tree trunks, and has leaves that are erect and mostly appressed.

We suggest that *Lepidozia sandvicensis* is a member of *Lepidozia* sect. *Microphyllae* (Lindenb.) Grolle and may be close to *L. microphylla* (Hook.) Lindenb., found in Aotearoa/New Zealand (Engel & Glenny, 2008: 204-206), Tasmania, and the Solomon Islands (<https://www.gbif.org/species/7580248>), as per the description and illustration (Engel & Glenny, 2008: plate 5E-F, page 125). The main difference between the two species is in the symmetry of the leaves: *L. sandvicensis* has mostly symmetrical leaves whereas these are clearly asymmetrical in *L. microphylla* (Engel & Schuster, 2001).

Lepidozia sandvicensis, *L. hasskarliana* (a tropical Asian species occurring east to Fiji), and *L. trichodes* (Reinw., Blume & Nees) Nees (tropical Asia and Australasia) are related and were all described in the same paper (Gottsche et al., 1844: 201-203), which also cited *L. microphylla*. It is beyond the scope of these notes to elucidate the relationships of these four taxa, and we maintain *L. sandvicensis* as a good species. A duplicate (at TAL) of Oppenheimer & Espaniola 11516 (PTBG) from Olokui N.A.R. (el. 4,200 ft.), Molokaʻi, which we identified as *L. sandvicensis*, was previously identified in 2017 by M.A.M. Renner (<https://www.gbif.org/occurrence/2463924757>) as *L. hasskarliana* (Lindenb.) Steph.

Engel & Glenny (2008) note that “A distinctive field character of [*L. microphylla*] is the presence of tiny, glistening water droplets in the branch axils...” We have seen these droplets in *L. sandvicensis* in the field, and nearly all the 30 Hawaiian field observations posted on iNaturalist show them. These droplets can be useful to spot *L. sandvicensis* in Hawaiʻi but are likely to occur in other members of sect. *Microphyllae*.

Populations form dense round clusters and resemble fruticose lichens. Plants are loosely attached and can be yellowish to bright green, with prominent coarse and slightly flattened stems that branch profusely with primary and secondary branches to form rounded clusters. A hyalodermis is present (as in other members of sect. *Microphyllae*). Leaves and underleaves are highly reduced and inconspicuous, distant, appressed to the stems, scalelike, with (2)3-4 triangular-filiform lobes. Leaves are slightly larger than the underleaves.



Dense clump, with “collar” of the moss *Acroporium fuscoflavum*. Pu‘u Ka‘ala, O‘ahu, 13 Aug. 2025; photo by Miles K. Thomas, with permission: <https://www.flickr.com/photos/mileskt/54723987109/in/photolist-2nmc8b6-2nmibFC-2nmgYiF-2rnLJP8>



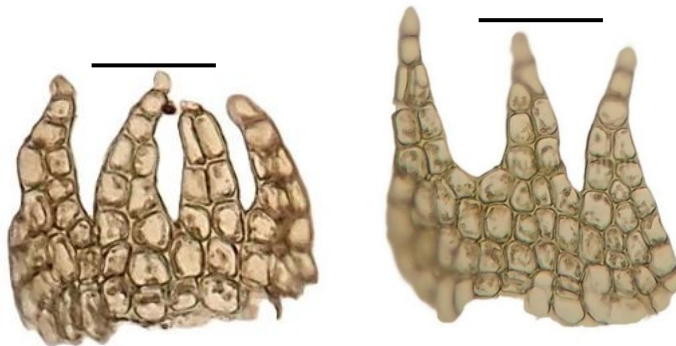
Lepidozia sandvicensis. Left: Profusely branched, whitish-green plants. Populations form crowded, rounded clusters. Alaka‘i Wilderness Preserve, Kaua‘i, Wood 17903 (PTBG), photo courtesy of National Tropical Botanical Garden/Ken Wood. Right: Example of population with yellow-green plants. Note the water droplets on branch axils. Pu‘u Ka‘ala, O‘ahu, Thomas 375 (BISH). Photo by Miles K. Thomas, with permission.



Left: Dry specimen with the aspect of a fruticose lichen. Right: Dried plant showing the coarse main stem with branches that narrow towards their tips. Haleakalā, Maui, Severson 056 (BISH). Photos by A. V. Freire.



Left: Detail of branch with tiny scalelike leaves and underleaves. Pu‘u Ka‘ala, O‘ahu, Thomas 375 (BISH). Photo by Miles K. Thomas, with permission. Right: Section of stem with underleaves (facing viewer) and leaves (in profile on sides of stem). Moloka‘i, Thomas s.n. (BISH). Photo by A.V. Freire.



Lepidozia sandvicensis. Underleaf and leaf. Moloka‘i, Thomas s.n. (BISH). Scales = 100 μ m. Photos by A.V. Freire.

4. *Lepidozia selligiana* H.A. Mill. **Endemic.**

Rare; wet forests on Kaua'i and perhaps Maui (4,000-6,000 ft.). According to Miller (1963), these plants resemble *L. australis* but are "smaller and more delicate". We studied an isotype from Kaua'i, Selling 5235a (MU) and present a collection by Wood 18168 (PTBG) from Lā'au Ridge, Kaua'i as an example. Also see recent collections by Kevin Faccenda (BISH, PTBG) that may pertain to this species: Faccenda 3864, 3868, and 3921 respectively:

<https://www.inaturalist.org/observations/254878345>;

<https://www.inaturalist.org/observations/254805324>;

<https://www.inaturalist.org/observations/254800666>.



We found populations with intermediate characters between *L. australis* and *L. selligiana* from Maui and probably Hawai'i Island (see at the end of this treatment). These are more robust, darker green, and with more crowded leaves that are not always asymmetrical. Molecular research would help elucidate the relationship between the two species.

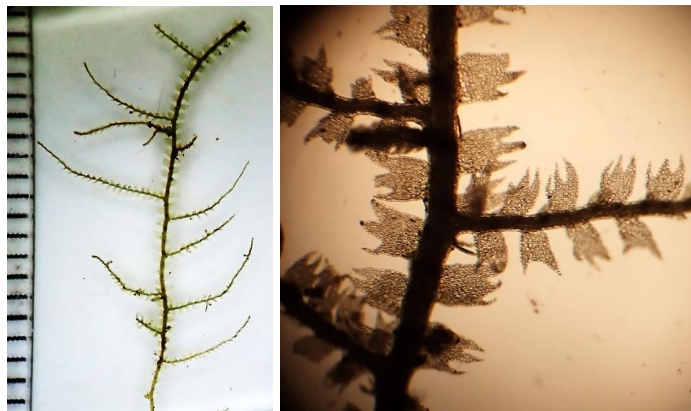
Populations form loose mats. Plants are pale green to whitish-yellow, fragile looking, 0.6-0.9 mm wide and about 2 cm long. They have numerous branches with attenuate apices. Leaves are distant to contiguous or only slightly imbricate, squarrose, alternate, rectangular, and slightly falcate, with curved upper margins and slightly decurrent lower margins. They are lobate, split to 1/2-1/3 their length; mainly trifid, occasionally quadrifid or bifid, with triangular sinuses. Leaf lobes are long, of irregular shape and size, the lower tooth smaller, shaggy looking, laciniate (resembling the wings of a bird in flight). Underleaves are small, equal to or only slightly broader than the stem; quadrate to rectangular, split to about 1/2 their length, with (3)4 linear lobes. Cells of irregular size and walls irregularly thickened, with some trigones.



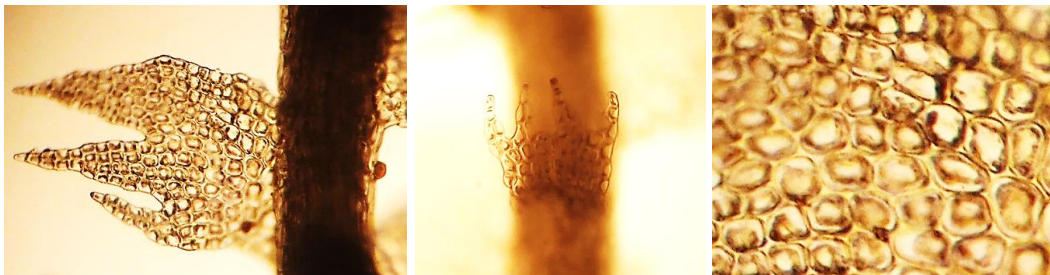
Lepidozia selligiana. Isotype from Kaua'i, Selling 5235a (MU). Top left scale in mm, top center scale units = 25 µm. Photos by A.V. Freire.



Example of the slender, delicate, lighter colored populations of *Lepidozia selligiana*. Plants are pale, forming dense, loose mats; they are fragile looking, with small leaves that spread at right angles from the stem. Wood 18168 (PTBG), photo by A.V. Freire.



Plants less than 1 mm wide, with tiny, distant leaves and numerous flagelliform shoot apices. Leaves squarrose, distant, mainly trifid, with teeth irregular in shape and size. Plants frequently branched. Wood 18168 (PTBG). Photos by A.V. Freire.

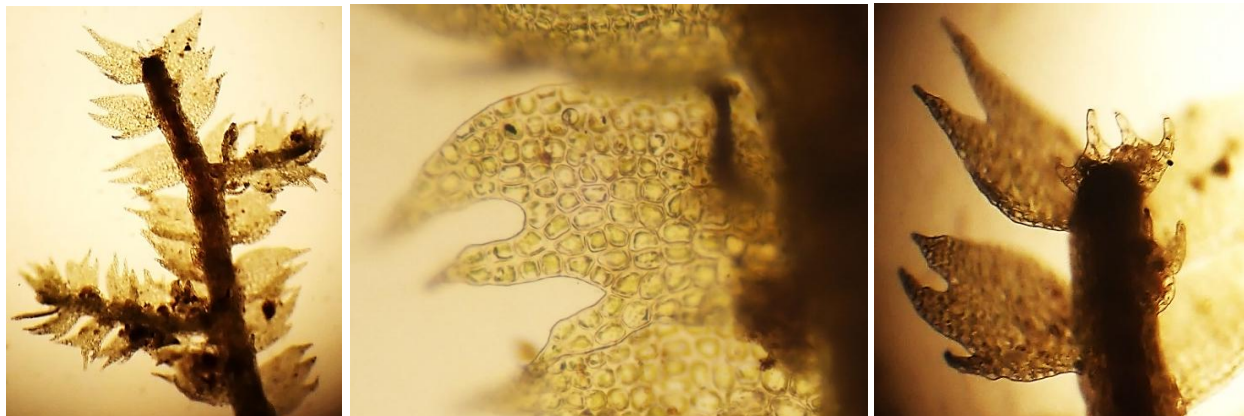


Lepidozia selligiana. Left: Note the three teeth with irregular shape and size, and their acute sinuses. The stem appears to have a hyalodermis. Center: Underleaves are small, quadrate, quadrifid, split to $\frac{1}{2}$ their length, with linear lobes and "U"-shaped sinuses. Right: Leaf cells of irregular shape and size, cell walls irregularly thickened, with small trigones. Lā'au Ridge, Kaua'i, Wood 18168 (PTBG). Photos by A.V. Freire.

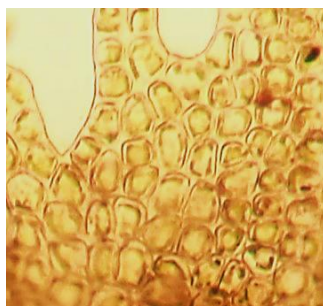
On Haleakalā, Maui and Mauna Loa, Hawai'i Island, we collected more robust, greener populations with contiguous to imbricate larger leaves, some of which are not asymmetrical. Because of the presence of some asymmetrical, falcate leaves and the smaller plant size, we tentatively identified them as *L. selligiana*. However, we do wonder whether they could be morphological variants of *L. australis*.



Left: Field picture from Haleakalā, Maui, exemplifying the more robust, brightly green-colored *L. selligiana*. Center: The plants are frequently branched with flagelliform shoot apices. Scale in mm. Right: Leaves distant to contiguous to slightly imbricate. Freire & Judziewicz 23-145 (BISH).



Lepidozia selligiana. Leaves often have recurved upper margins and are trifold, with long, “shaggy” teeth of different sizes. Right: Underleaf with four lobes. Freire & Judziewicz 23-145 (BISH).



Lepidozia selligiana. Median leaf cells with small triangular trigones. Haleakalā, Maui. Freire & Judziewicz 23-145 (BISH).

Leptolejeunea (Spruce) Steph. (Lejeuneaceae)

Possibly one species in Hawai‘i, 53 species worldwide.

Leptolejeunea is a small, schizostipous member of the Lejeuneaceae with underleaf disks with a bordered of distinctively large cells; the leaf lobes have ocelli. It is a tiny and easy to overlook plant that always grows on living leaves.

There was reportedly a 1997 collection from O‘ahu (Ko‘olau Range, Tantalus Trail, elev. 300 m, as an epiphyll on the exotic fern *Blechnum*), made by and determined by distinguished bryologist John E. Braggins (1944-2025) of the University of Auckland (AK) (<https://www.gbif.org/occurrence/2883313546>, this record now removed from gbif.org); we did not examine it, and curator D. Ranatunga (12 Nov. 2023 communication to B. Kennedy, BISH) advises that the specimen was a unicate that was lost in transit during a loan. Five species have been reported from French Polynesia (Bardat et al., 2021), so the presence of *Leptolejeunea* in Hawai‘i, if confirmed, would not be surprising.



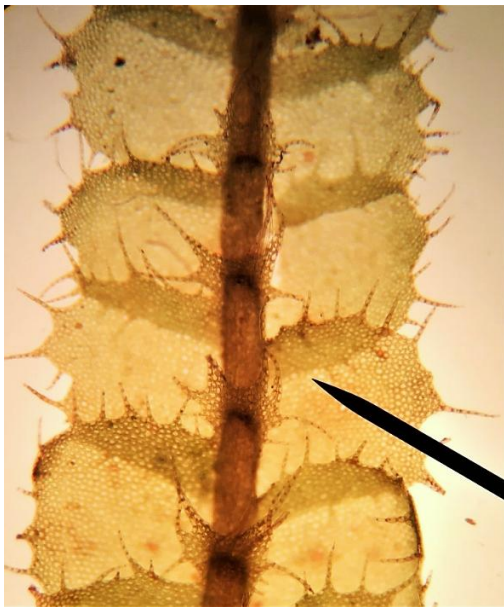
Leptolejeunea elliptica. This is one of the commonest and most widespread species in the genus. Note the presence of leaf lobe ocelli (lower left) and the distinctive underleaves (right) with disks bordered by larger cells. Photos of Aotearoa/New Zealand material by Larry Jensen, University of Auckland, with permission.

***Leptoscyphus* Mitt. (Lophocoleaceae)**

Three species in Hawai‘i, 50 species worldwide.

Plants are large, with succubous and spreading leaves, large underleaves, and cells with prominent trigones. Most populations have numerous ciliate teeth on their leaves, but some higher elevation populations (on Kaua‘i, Maui and Kohala, Hawai‘i Island) have fewer teeth, or can even be edentate (our species 1). Miller (1963: 503, as *Lophocolea baldwinii*) notes: “This is a polymorphic species... I have repeatedly found the full spectrum of variation on a single plant.”

- 1. Leaves with (0-)1-2(-4) ciliate teeth; rare, Kaua‘i, Maui, and Hawai‘i Island ***L. species 1***
- 1. Leaves with (4-)8-12 ciliate teeth **2**
 - 2. Cells prorulose; leaves strongly imbricate, coarsely dentate; rare, Hawai‘i Island ***L. cf. baldwinii***
 - 2. Cells smooth; leaves moderately imbricate, not coarsely dentate; common and widespread ***L. baldwinii***



Leptoscyphus baldwinii



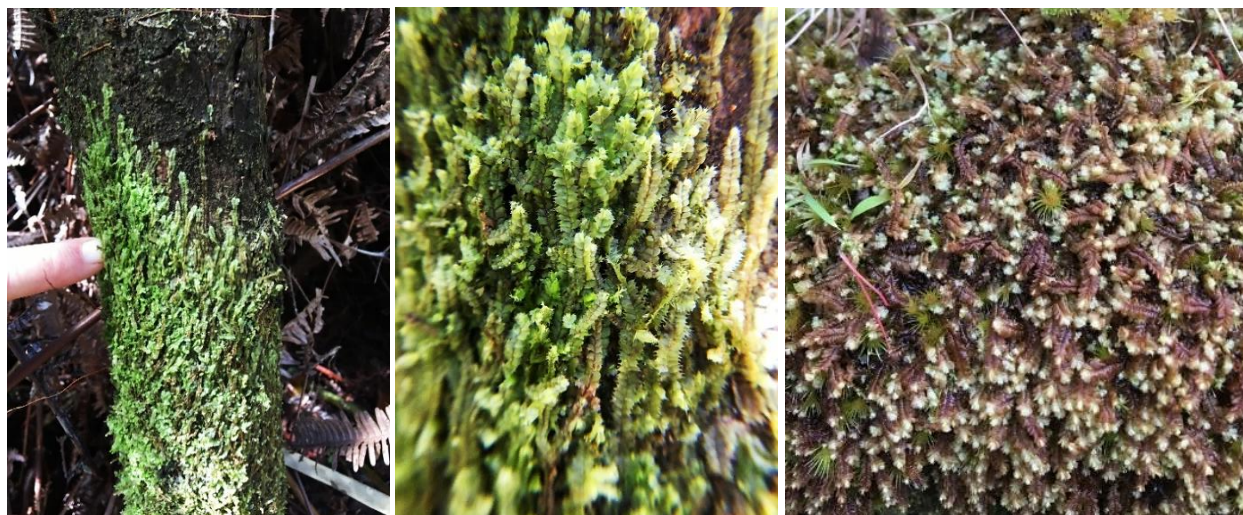
Leptoscyphus cf. baldwinii



Leptoscyphus species 1

A common species found on all major islands (2,000-6,160 ft.); on bark, rotted wood, and moist shaded soil in wet forests. Elegant *L. baldwinii* is unmistakable. The leaves are round to squarish and resemble ticks on a string because the leaf margins are fringed with 8-12 long spreading cilia. With age or upon drying, the plants, especially the stem, become orange or reddish to purplish-brown. The leaf cells have large trigones.

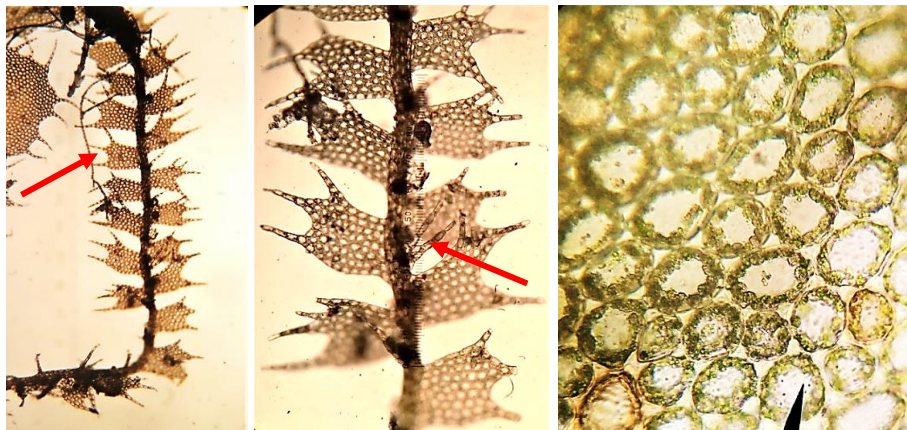
Populations form dense creeping mats, loosely to closely attached to bark, rotted wood or soil. Plants are flattened, large, several cm long by 2 mm wide. Leaves are spreading, prostrate, flattened to slightly convex, slightly overlapping and succubous, rectangular to rounded, with margins fringed by long cilia. Stems are stout, dark, and occasionally branched. The underleaves are bifid with 4-6 long cilia, with a disk about twice as broad as the stem. Leaf cells are thin-walled and bear prominent trigones, oil bodies are elliptical, coarsely granular, and numerous per cell. The perianths are large and bucket-like with a broad and ciliate mouth. Some plants produce flagelliform branches with leaves and underleaves of different morphology; if studied separately, they could be mistaken for a different liverwort. Leaves of these branches are rectangular with few cilia at their apex and underleaves reduced to two cilia.



Leptoscyphus baldwinii. Left and center: Population on tree trunk. Note ascending plants that can be either closely or loosely attached. Nāhuku, Hawai'i Volcanoes National Park, Hawai'i Island, Freire & Judziewicz 21-170 (HAVO). Right: Plants often turn orange to purplish-brown with age. Nāhuku, Hawai'i Volcanoes National Park, Hawai'i Island.



Plants are elongate, with rounded succubous leaves and frequent branching. Leaf margins have long cilia resembling eyelashes. The large underleaves are broader than the stem; they are bilobed, with a broad sinus and 2-3 ciliate teeth on the sides of each lobe. Freire & Judziewicz 21-170 (HAVO).



Left: Flagelliform branch (arrow). Center: Note the small rectangular leaves with large apical ciliate teeth, and bilobed underleaves (arrow). Right: Median leaf cells with prominent trigones. Note the numerous granular oil bodies. Nāhuku, Hawai'i Volcanoes National Park, Hawai'i Island, Freire & Judziewicz 21-170 (HAVO).



Leptoscyphus baldwinii. Note the large, bucket-shaped perianths. Hawai'i Volcanoes National Park, Hawai'i Island, Freire & Judziewicz 23-360 (BISH) (left and center) and 23-375 (BISH) (right). Scales in mm.

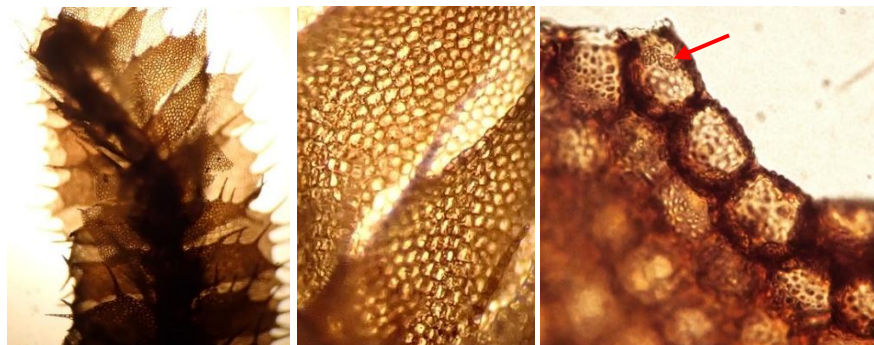
Leptoscyphus cf. baldwinii. A collection we made at a high elevation forest (growing with such rare species as *Blepharostoma trichophyllum*, *Lophozia silvicola*, and *Tritomaria exsecta*) in the Kahuku Unit of Hawai'i Volcanoes National Park has ciliate leaves and underleaves but is different from the typical *L. baldwinii* in its leaf cells being conspicuously prorulose. Plants are mostly heavily pigmented, brownish-black. The leaves are strongly imbricate and coarsely dentate where they bear cilia. As in *L. baldwinii*, the cells have conspicuous trigones, and the perianths are bucket-shaped.



A darkly pigmented population. Note perianths in the upper left. Kahuku Unit, Hawai'i Volcanoes National Park. Photo by Brooke Fleischman, with permission.

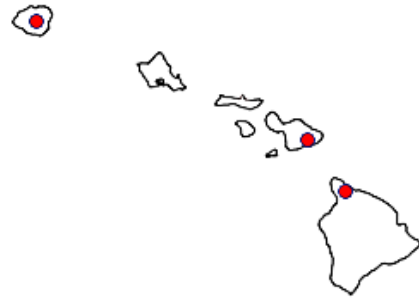


Plant with dark brown pigmentation and leaves with several long cilia. Freire & Judziewicz 22-743 (HAVO).



Leptoscyphus cf. baldwinii. Left: Long cilia on coarsely dentate leaf margins. Center: Cells with prominent trigones. Right: Leaf cells are abundantly prorulose. Oil bodies are large, elliptical and granular (arrow). Kahuku Unit, Hawai'i Volcanoes National Park, Freire & Judziewicz 22-743 (HAVO).

2. *Leptoscyphus* species 1. **Kauaʻi:** Kawaikini (5,200 ft.), Wood 18547, 18563 (PTBG), Waiʻaleʻale (5,200 ft.), Faccenda 3521.5 (BISH). **Maui:** Kīpahulu Valley (4,700 ft.), Pezzillo 871c (BISH). **Hawaiʻi Island:** Kohala Mountain (5,100 ft.), Freire & Judziewicz 23-555.5k, 585a (BISH). These populations resemble *L. baldwinii* but have only 0-4 cilia on their leaf margins and tend to have more rectangular leaves. Perianth shape is not “bucket” like but more elongate than in *L. baldwinii*.



We present several photos of various specimens to exemplify the range of variation within this species.



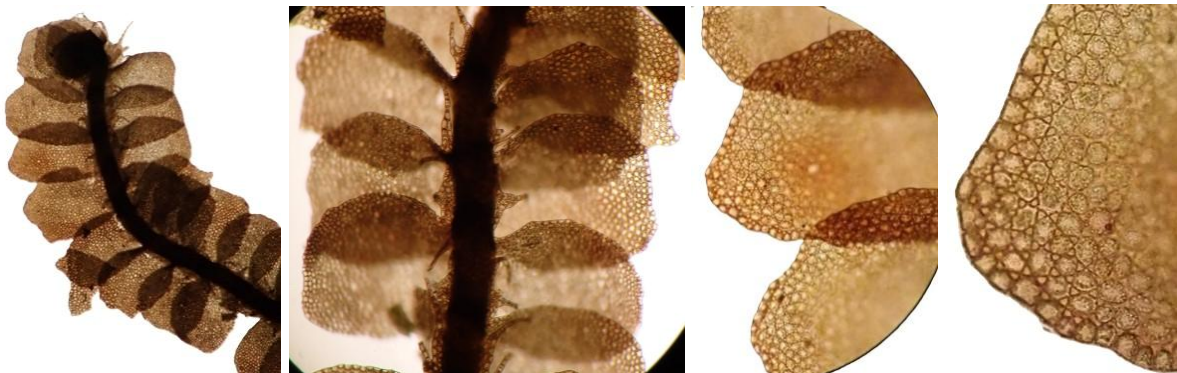
Plants are brown, large, flattened, with elongated rectangular leaves and 0-4 cilia. Underleaves are bifid with long cilia. Kauaʻi, Wood 18563 (PTBG). Scale in mm. Photos by A.V. Freire and E.J. Judziewicz.



Leptoscyphus species 1. Leaves are more rounded, occasional leaf teeth are present. Note detail of underleaf. Waiʻaleʻale (5,200 ft.), Kauaʻi, Faccenda 3521.5 (BISH). Photo 1: Scale in mm. Photos by A.V. Freire & E.J. Judziewicz.



Nodulose leaf trigones, and broad, ciliate perianth (but not bucket-like as in *L. baldwinii*). Wai‘ale‘ale (5,200 ft.), Kaua‘i, Faccenda 3521.5 (BISH). Scale in mm. Photos by A.V. Freire & E.J. Judziewicz.



This specimen has an occasional leaf tooth, or an irregular leaf margin. Kohala Mountain (5,100 ft.), Hawai‘i Island, Freire & Judziewicz 23-555.5k (BISH).

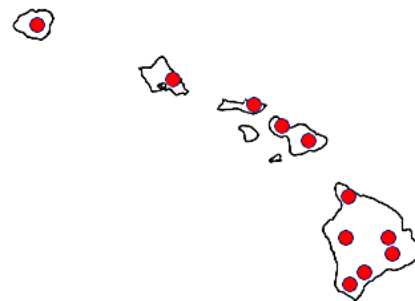


Leptoscyphus species 1. Note the variably rounded, entire, shallowly lobed, or unispiculate leaves with prominent nodulose trigones. Male shoot (photo 2). Kohala Mountain (5,100 ft.), Hawai‘i Island, Freire & Judziewicz 23-585a (BISH).

Liochlaena Nees (Jungermanniaceae)

One species in Hawai‘i, three species worldwide.

Liochlaena subulata (A. Evans) Schljakov. **Indigenous.** A temperate and subtropical Eurasian species (also found in North America; Stotler & Crandall-Stotler, 2018: 636), found on all major islands except Lāna‘i (3,000-6,600 ft.). The type specimen, from Hawai‘i, was collected by Baldwin (on Maui?). This uncommon leafy liverwort grows in shaded mesic forests and wet semi-shaded cracks and earth embankments. Leaf cells have conspicuous trigones. Plants are aromatic, with a turpentine-like scent.



Liochlaena subulata differs from species of *Solenostoma* in its production of 1-2-celled ellipsoidal gemmae at the apices of microphyllous shoot tips, and pale (never purplish) rhizoids. It differs from *Odontoschisma denudatum* (another succubous liverwort that produces gemmiferous shoots) in its decurrent leaves.

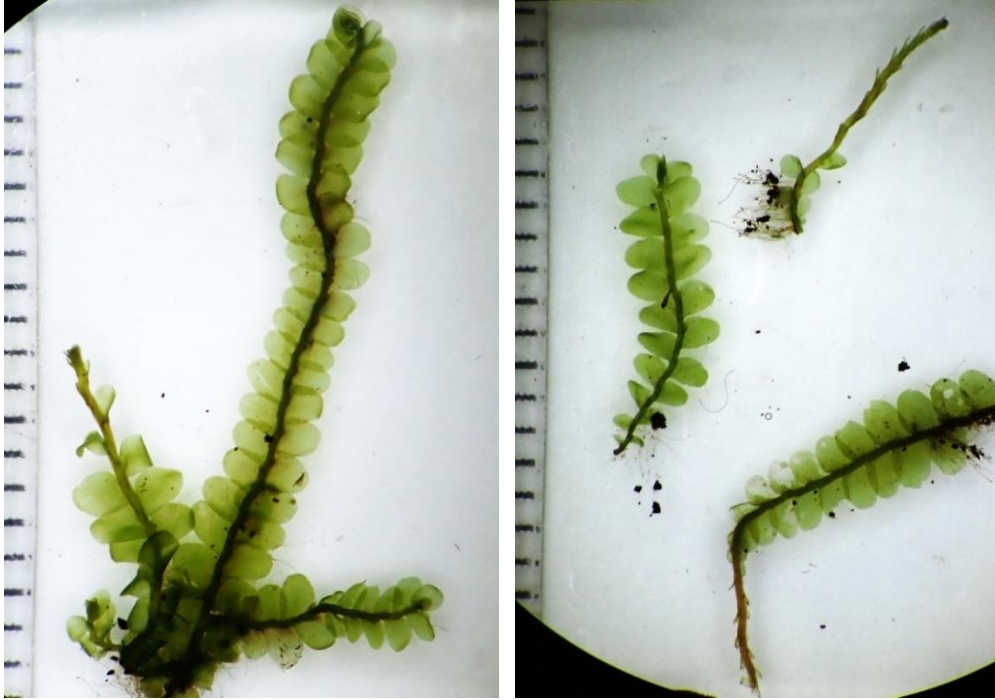
Populations form dense, ascending mats that grow loosely attached to rock or soil. Plants are green, occasionally branched, about 2 cm long by 2-3 mm wide, frequently with a long and erect microphyllous tip that bears a terminal cluster of (1?) or 2 celled ellipsoidal gemmae. Leaves are ligulate, mostly rounded but a few emarginate at the apex, contiguous to imbricate, spreading, decurrent, inserted to the stem midline and obscuring it. Underleaves are absent. Leaf cells have prominent trigones.



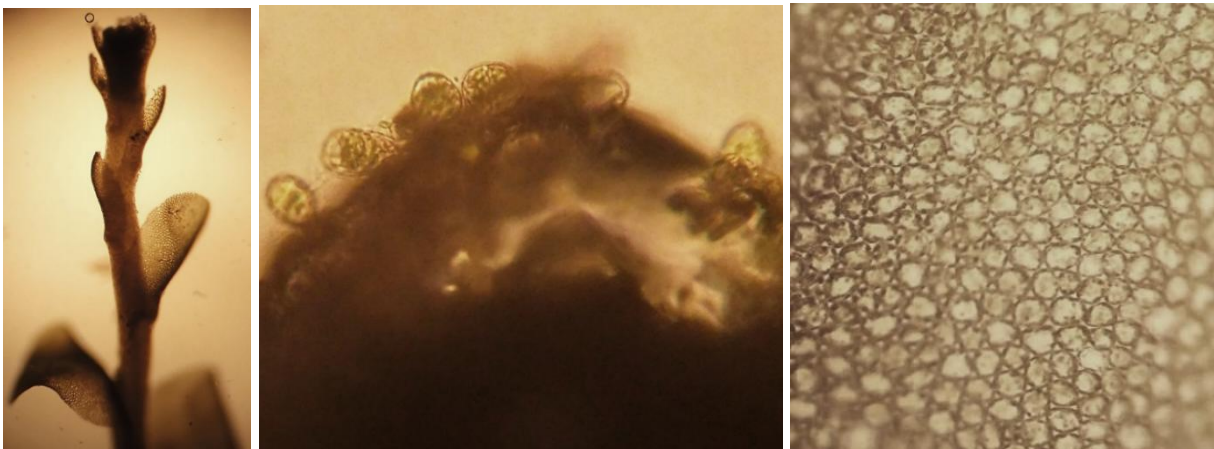
Liochlaena subulata. Population loosely attached to rock, with rounded, basally decurrent leaves. Note clusters of gemmae at tips of erect microphyllous plant apices. Mixed with *Lepidozia australis* (lower right) and *Leptoscyphus baldwinii* (lower left). Pu‘u Maka‘ala N.A.R., Hawai‘i Island, Freire & Judziewicz 22-613a (BISH).



Liochlaena subulata. Note the pale, emergent, microphyllous shoot apices (below); these bear gemmae. Honua‘ula Reserve, Hualālai, Hawai‘i Island. Photos by Graham Steinruck, with permission: <https://www.inaturalist.org/observations/260779984>.



Plants are medium-sized, with some branching and flagelliform shoot tips that often bear gemmae at their apices. Scales in mm. Freire & Judziewicz 22-613a (BISH).



Liochlaena subulata. Left: Microphyllous shoot apex with apical gemmae. Center: detail of ellipsoidal gemmae. Right: Leaf cells with conspicuous trigones. Pu'u Maka'ala N.A.R., Hawai'i Island, Freire & Judziewicz 22-613a (BISH).

Lophocolea (Dumort.) Dumort. (Lophocoleaceae)

Eight species in Hawai'i, 129 species worldwide.

Lophocolea closely resembles *Chiloscyphus*. They share a succubous leaf insertion and bifid underleaves with at least one lateral tooth on each lobe. Species of *Lophocolea* differ from *Chiloscyphus* in their 3-angled rather than smooth perianths that are produced on long shoots rather than on short lateral branches. Plants are generally of smaller size, and with alternate rather than opposite to subopposite leaves. Leaf trigones are usually small or absent. *Cryptolophocolea* is another similar genus with 3-keeled perianths (as in *Lophocolea*) but it has opposite leaves with conspicuous leaf trigones. *Heteroscyphus* is also similar but with perianths lacking keels and gametangia on short ventral branches. See Söderström et al. (2016).

We've transferred *Lophocolea baldwinii* to *Leptoscyphus* (Judziewicz & Freire 2023c: 167), and *Lophocolea pusilla* might possibly also be more properly assigned to that genus. *Lophocolea bicuspidata* and *L. hawaica* may form a species complex and appear to be related to the nearly cosmopolitan *L. bidentata* L. (Miller, 1956); perhaps they are conspecific. *Lophocolea autoica* appears to be closely related to the cosmopolitan *L. heterophylla* (Schrader) Dumort. (Miller, 1956). *Lophocolea muricata*, *L. spinosa*, and *L. species 1* all appear to belong to subgenus *Microlophocolea* (Spruce) Vogelpoel.

1. Plants with leaves up to 0.6 mm long 2
 2. Leaves covered with minute spines on all surfaces; Hawai'i Island *L. muricata*
 2. Leaves not covered with minute spines 3
 3. Leaf lobes with minutely toothed margins and shallowly bidentate apex *L. spinosa*
 3. Leaf lobes with entire margins (or occasionally with a small lateral tooth on one of the lobes) and shallowly to deeply bidentate apex *L. species 1*
1. Plants with leaves over 0.7 mm long 4
 4. Leaves entire, rounded; leaf cells with prominent trigones *L. pusilla*
 4. Leaves bifid; leaf cells with trigones absent or small 5
 5. Leaves variable on same plant: entire, slightly retuse, or with 1-2 small teeth *L. autoica*
 5. Leaves consistently bidentate 6
 6. Leaf teeth short, triangular, up to 5 cells long; leaves triangular, less than twice as long as wide at the base; underleaves small, 1.5-2 times broader than the stem *L. kilauensis*
 6. Leaf teeth long, ciliate, well over 5 cells long; leaves ovate to rectangular, more than twice as long as wide at their base; underleaves 3-5 times broader than the stem 7
 7. Plants light green; microphyllous branches not present; leaves ovate and ventrally concave *L. bicuspidata*
 7. Plants straw-yellow to yellow-green; microphyllous branches present and abundant; leaves rectangular to narrowly ovate and flat *L. hawaica*



L. autoica



L. bicuspidata
(photo by K. Faccenda)



L. hawaica



L. kilauensis



L. muricata
(photo by L. Jensen)



L. pusilla



L. spinosa



L. species 1

1. *Lophocolea autoica* Steph. Endemic.

Chiloscyphus autoicus in Staples & Imada (2006). Erroneously reported by Miller (1983) from New Caledonia (see Thouvenot, 2023: 55). It resembles the nearly cosmopolitan *L. heterophylla* (Schrad.) Dumort. (Miller, 1956). See Judziewicz & Freire (2023c: 167). Found on all major islands (1,800-6,500 ft.), often in mesic rather than wet forests. On Hawai‘i Island, this is a locally common species on rotten wood or rock, or in deep shade in both Kīpukakī and Kīpukapuau, along the Mauna Loa Road in Hawai‘i Volcanoes National Park.



This is a rather plastic species with great variability in leaf and underleaf morphology. Plants creep on rock, soil or bark, they are 1.5-2 mm wide and 1-1.5 cm. long, often branched, olive to yellow-green, or sometimes dark green. They mostly grow appressed to their substrate. This species is unusual in Hawai‘i in that the leaves are often variable in shape on the same plant. Some or all can be entire, slightly retuse, or with one or two low teeth. Stem leaves are imbricate, prostrate to suberect or sometimes erect; they can be concave, decurved, or ligulate. Leaf cells are thin-walled, with small trigones. Oil bodies are large, elliptical, and granular. Underleaves are 2.5-3 times broader than the stem (occasionally larger); bifid, with a broad sinus and divergent lobes with small lateral projections. Perianths are oblong, truncate, and spinose-dentate at the mouth. Higher elevation populations on Hawai‘i Island sometimes produce rejuvenant plants from the leaf margins (Freire & Judziewicz 20-962, 5,700 ft., Kīpuka Kulalio, Mauna Loa Road, Hawai‘i Island).



Lophocolea autoica. Populations grow on rocks (left), tree trunks or logs (right), or occasionally on soil. Plants grow appressed to their substrate. Kīpukakī, Hawai‘i Volcanoes National Park, where this species is common, Freire & Judziewicz 23-45 (HAVO).



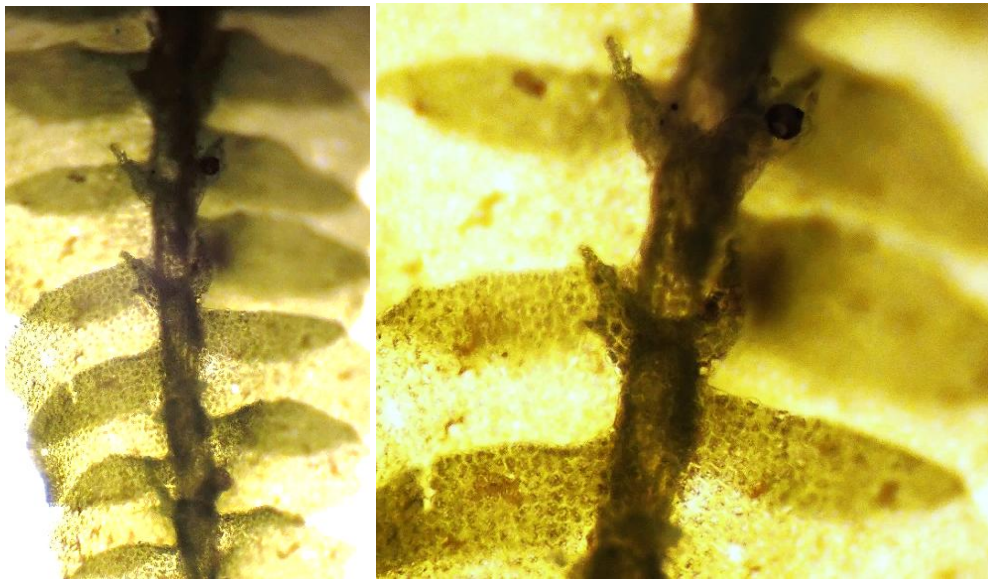
Population on decorticate log. Kīpukakī, Hawai‘i Volcanoes National Park. Photo by E.J. Judziewicz.



Lophocolea autoica. Plants are medium-sized; the leaves are ligulate, prostrate, and light olive-green. Scale in mm. Kīpukakī, Hawai‘i Volcanoes National Park, Freire & Judziewicz 23-45 (HAVO).



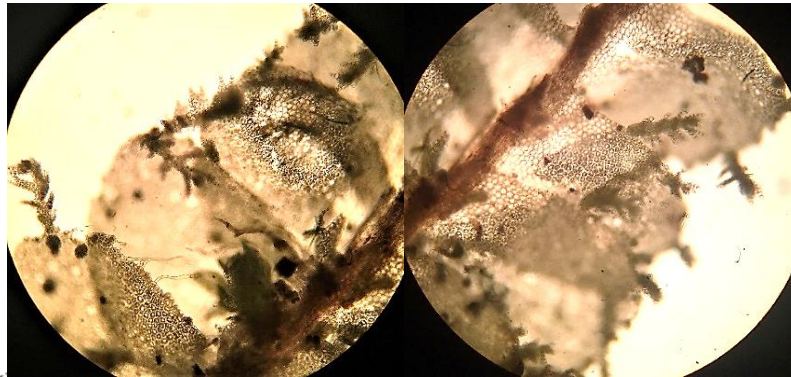
Left: Plant with prostrate and spreading leaves, with variable leaf apices (rounded to retuse). Note larger leaves closer to the apex, and apical perianth. Right: Profile of plant with erect leaves. Underleaves spreading from the stem at 45° (arrow). Freire & Judziewicz 23-45 (HAVO).



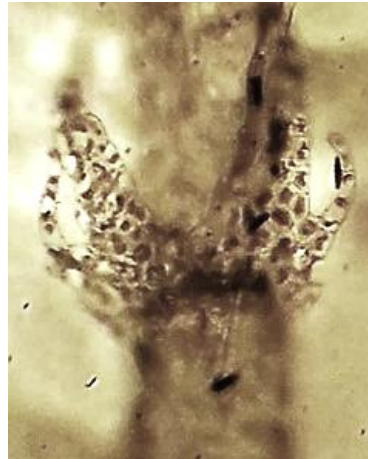
Lophocolea autoica. Underleaves are small, clearly fused to one of the adjacent leaves, “lightly” or not at all fused to the other leaf. They are deeply divided by a broad, lunate sinus. Lobes are divergent, with a lateral tooth at their base (sometimes only on one side). Kīpukakī, Hawai‘i Volcanoes National Park, Freire & Judziewicz 23-45 (HAVO).



Perianths are terminal and lacinate. Right: Isodiametric cells with small trigones. Oil bodies are numerous, granular and elliptical. Kīpukakī, Hawai'i Volcanoes National Park, Freire & Judziewicz 23-45 (HAVO).



Plants with numerous rejuvenants produced on leaf margins. Kīpuka Kulalio, 5,700 ft., Mauna Loa Road, Hawai'i Volcanoes National Park, Freire & Judziewicz 20-962 (HAVO).



Lophocolea autoica. Left: Plant showing leaf apex variation, Kīpukakī, Hawai'i Island, Freire & Judziewicz 20-860 (HAVO). Center and right: Plants have very shallowly lobed leaves and underleaves with well-developed, ciliate, lateral teeth. Plants from shaded rocks in the Amy Greenwell Botanical Garden (1,400 ft.), Ka'awaloa (Captain Cook), Hawai'i Island, Freire & Judziewicz 21-907 (BISH).

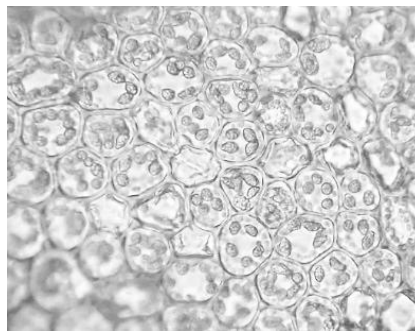
Next, we present images of plants growing on rock at Kīpukakī, Hawai‘i Volcanoes National Park, Freire & Judziewicz 22-807 (HAVO). The population is interesting because of its larger underleaves with variable morphology within the same plants or among plants.



Left: Plants with ligulate leaves. Note variable leaf apices, from entire, to slightly retuse, to truncate with a small tooth. Note variation in underleaf shape within same population. Right: Deeply quadrifid underleaves bearing small teeth.



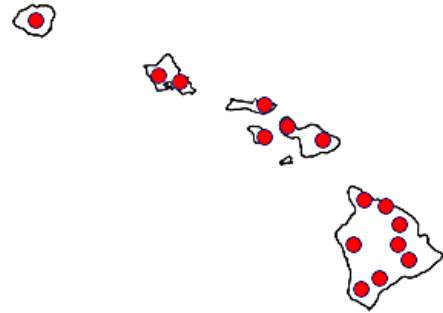
Plants from the same population as shown above. Left: Plant with rounded leaves and large underleaves. Right: Unusually large, bifid underleaves, without lateral lobes.



Lophocolea autoica: Median leaf cells have small trigones and granular, elliptical oil bodies.

2. *Lophocolea bicuspidata* Steph. Endemic.

Chiloscyphus bicuspidatus in Staples & Imada (2006). See Judziewicz & Freire (2023c: 167) and Judziewicz et al. (2025b: 141). Locally common, in wet forests (2,100-6,100 ft.) on all major islands. Plants grow loosely attached to bark, decorticate logs or soil. They resemble *L. hawaica*, but *L. bicuspidata* plants are dioicous (according to Stephani), darker green, lack microphyllous branches, and have broader, more crowded leaves and underleaves.



Plants are large, 1.5-2.5 cm long and up to 3(-4) mm broad; they are sparingly branched, creeping, loosely attached to their substrate, and green in color. Leaves look “inflated” because they are ventrally concave, they are ovate, imbricate, prostrate, spreading; bifid to about ¼ their length, with a lunate sinus; leaf lobes taper from a broad bases to short- or long-setaceous tips. Cells have moderately to pronouncedly thickened walls; trigones lacking or tiny. Underleaves are 3-6 times broader than the stem (setaceous lobes included), deeply lobed, bifid, with a broad sinus; they have long-setaceous and divergent lobes, and a setaceous, shorter lateral tooth at the base of each of the two lobes, sometimes with additional small teeth on margins; we observed variability in underleaf morphology.

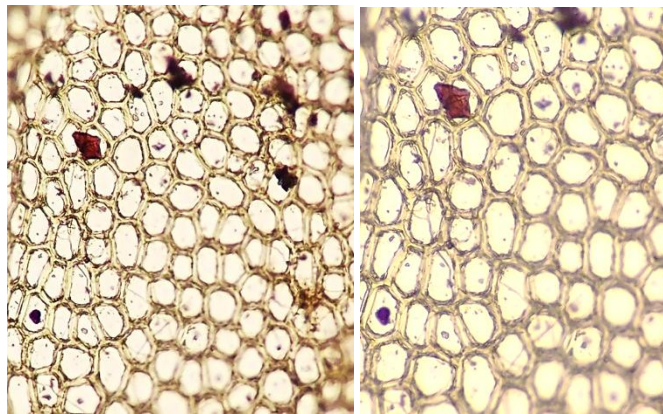


Lophocolea bicuspidata. Lāna‘i, Zach Pezzillo photo, with permission.
<https://www.inaturalist.org/observations/235045949>.

Photos below are from an isotype of *Lophocolea bicuspidata* (at MU), elevation 4,000 feet, [Hawai'i Island?], date 1911, Newell 170 (MU). Photos by A.V. Freire.



Plants are large (a), with ovate elongate leaves (b,c,d). Leaves bear a broad lunate sinus and two long setaceous lobes (b,c,d). Underleaves are large and often imbricate (e,f). Underleaves are deeply lobate and with a lateral tooth at the base of each lobe, some with an extra tooth (e,f); they are asymmetrically connate to both lateral leaves (e).



Lophocolea bicuspidata. Leaf cells with thick walls and no trigones.

Examples of *Lophocolea bicuspidata*.



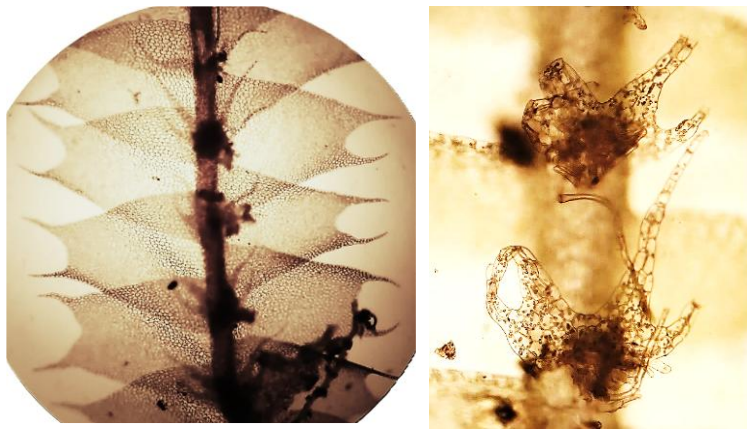
Population creeping, loosely appressed to a decorticate log. Pu'u Maka'ala N.A.R., Hawai'i Island, Freire & Judziewicz 22-599 (BISH).



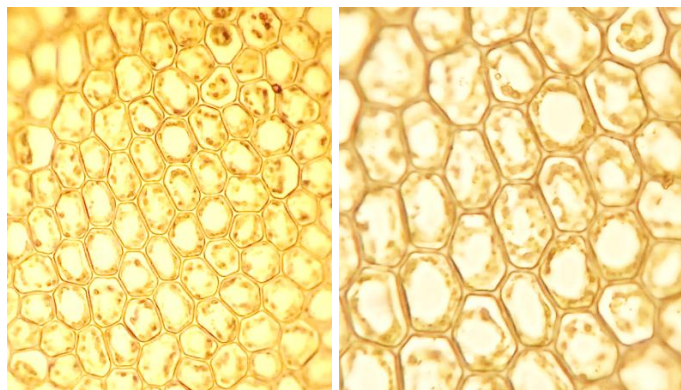
Lophocolea bicuspidata. Left: Plant creeping on bark, associated with *Riccardia*. Center: Plants are large, with imbricate ovate leaves. Scale in mm. Kahuku Unit, Hawai'i Volcanoes National Park, Freire & Judziewicz 22-760 (HAVO). Right: Ventrally concave leaves. Note underleaves 3-4 times as wide as stem. Pu'u Ka'ala, O'ahu. Photo by K. Faccenda: <https://www.inaturalist.org/observations/161483230>, with permission.



Left: Ovate leaves with curved margins. Right: Leaf apices with broadly lunate sinus and lobes tapering from broad bases to setaceous tips. Freire & Judziewicz 22-599 (BISH).



Left: Plant with large underleaves bearing long-setaceous, divergent lobes, and large setaceous lateral teeth on either side. They are 5-6 times broader than the stem (including the lobes). Freire & Judziewicz 22-760 (HAVO). Right: Smaller underleaves only 3 times broader than the stem. Pu'u Maka'ala N.A.R., Hawai'i Island, Freire & Judziewicz 22-599 (BISH).

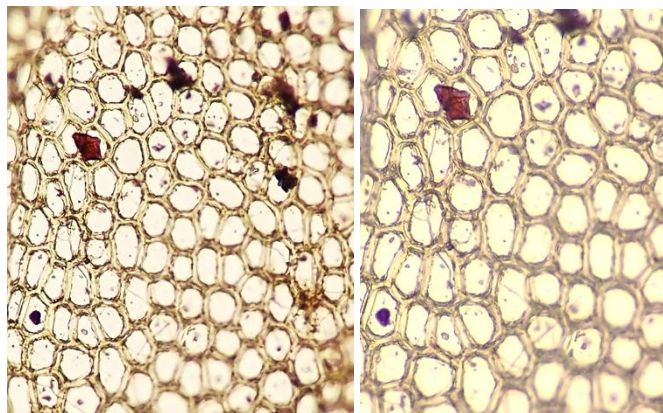


Lophocolea bicuspidata. Median leaf cells with slightly thickened walls, some with tiny trigones. Kahuku Unit, Hawai'i Volcanoes National Park, Freire & Judziewicz 22-760 (HAVO).

Photos below are from an isotype at MU: *Lophocolea bicuspidata*, elevation 4,000 feet, [Hawai'i Island?], date 1911, Newell 170 (MU). Photos by A.V. Freire.



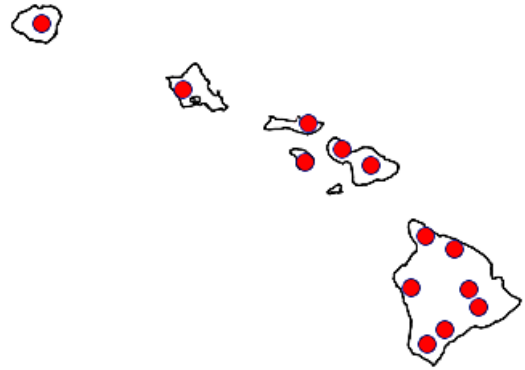
Plants are large (a), with ovate elongate leaves (b,c,d). Leaves bear a broad lunate sinus and two long setaceous lobes (b,c,d). Underleaves are large and often imbricate (e,f). Underleaves are deeply lobate and with a lateral tooth at the base of each lobe (e,f); they are asymmetrically connate to both lateral leaves (e).



Lophocolea bicuspidata. Leaf cells with thick walls and no trigones.

3. *Lophocolea hawaica* Steph. Endemic.

Chiloscyphus hawaicus in Staples & Imada (2006). See Judziewicz & Freire (2023c: 167). A common species found on all major islands (1,600-7,000 ft.). Long-creeping on rotted wood, rock, or bark; although it prefers wet forests, it can also grow in drier areas such as moist cracks on the margins of the Ka'ū Desert on Hawai'i Island. We have also seen it growing near the waterline in several artificial ponds in Volcano. It can be recognized by its straw-yellow or light green color, and by its narrow-rectangular leaves that are deeply bifid, with a broad U-shaped sinus and setaceous lobes.



Populations form dense mats. Plants are whitish yellow to light green, closely to loosely attached to their substrate; they are up to 2-2.5 cm long and up to 2-2.2 mm wide; they are frequently branched and often fertile; often with microphyllous branches bearing small bifid leaves and underleaves of different morphology from those of the main stem. Leaves are contiguous to slightly overlapping, spreading, narrow-rectangular, deeply bifid to about 1/3-1/4 their length, with a broad U-shaped sinus and setaceous lobes. The leaf cells have very small and inconspicuous trigones, or trigones are lacking. Oil bodies are elliptical and granular. Underleaves are about three times the stem width; they are deeply bifid, with long, setaceous apical lobes and a long lateral tooth on each side. Perianths are long tubular and narrow, with 3 prominent lacinate keels. Capsules are long and cylindrical and dehisce in 4 valves. Spores are tiny, about 12 µm in diameter and are not conspicuously ornamented; elaters are robust, tapering and 2-spiraled.



Lophocolea hawaica. Left: Pale-colored plants can form dense mats on bark of trees, soil, or rocks. Right: Sporophytes with long setae. Volcano, Hawai'i, Freire & Judziewicz 21-151d (HAVO).



Populations are often fertile. Note the rectangular, bifid leaves, the microphyllous branches (arrow), and conspicuous perianths. Scale in mm. Hale Alema, Volcano, Hawai'i Island, Freire & Judziewicz 23-340 (BISH).



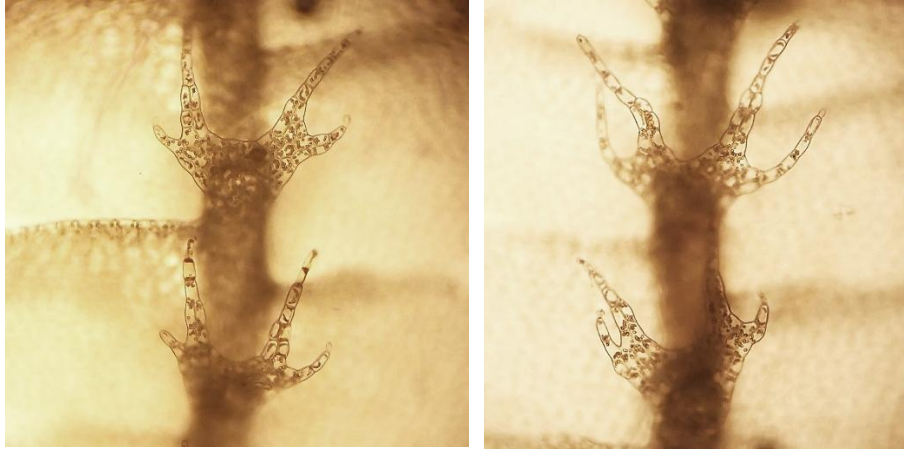
Lophocolea hawaica. Left: Plants are elongate, yellow to yellow-green, and have two long setaceous teeth per leaf. Volcano, Hawai'i, Freire & Judziewicz 21-260 (HAVO). Right: Plants can be several centimeters long and slightly over 2 mm wide. Volcano, Hawai'i Island, Freire & Judziewicz 23-335 (HAVO).



Left: Leaves with a deep “U”-shaped sinus. Right: Leaves contiguous to slightly imbricate, rectangular. Freire & Judziewicz 23-335 (HAVO).



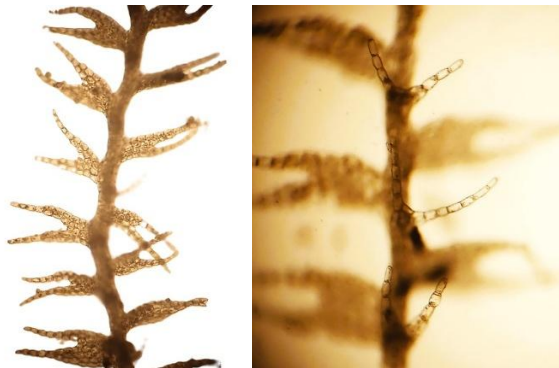
Lophocolea hawaica. Left: Plants frequently branched. Volcano, Hawai‘i. Freire & Judziewicz 23-335 (HAVO). Right: Cells with no trigones or with tiny ones. Note the segmented, elongated oil bodies. Hale Alema, Volcano, Hawai‘i Island, Freire & Judziewicz 23-340 (BISH).



Underleaves are deeply bifid with long, setaceous lobes and lateral teeth. Freire & Judziewicz 23-340 (BISH).



Left: Microphyllous branches are abundant (arrow). Right: Tiny microphyllous branch, 0.6-0.8 mm wide. Freire & Judziewicz 23-340 (BISH).



Lophocolea hawaica. Left: Microphyllous branches have a different leaf morphology; the sinus is deeper, over $\frac{1}{2}$ the leaf length and V-shaped. Right: Underleaves are deeply bifid, without lateral teeth. Hale Alema, Volcano, Hawai'i Island, Freire & Judziewicz 23-340 (BISH).



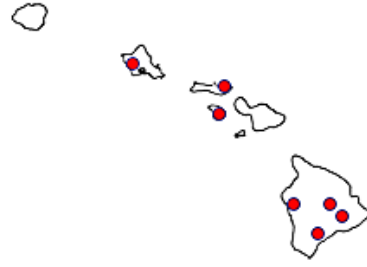
Lophocolea hawaica. Perianths are keeled and lacinate. Right: Keels branch to form a “V” or the branches join again, delimiting a large areola (arrow). Freire & Judziewicz 23-340 (BISH).



Lophocolea hawaica. Perianth with lacinate mouth and three keels, those usually lacinate. Center: Capsule dehisces in four valves. Right: Spores are small (12 μm in diameter) and are apparently unornamented. Elaters are robust, tapering, and double-spiraled. Hale Alema, Volcano, Hawai‘i Island, Freire & Judziewicz 23-340 (BISH).

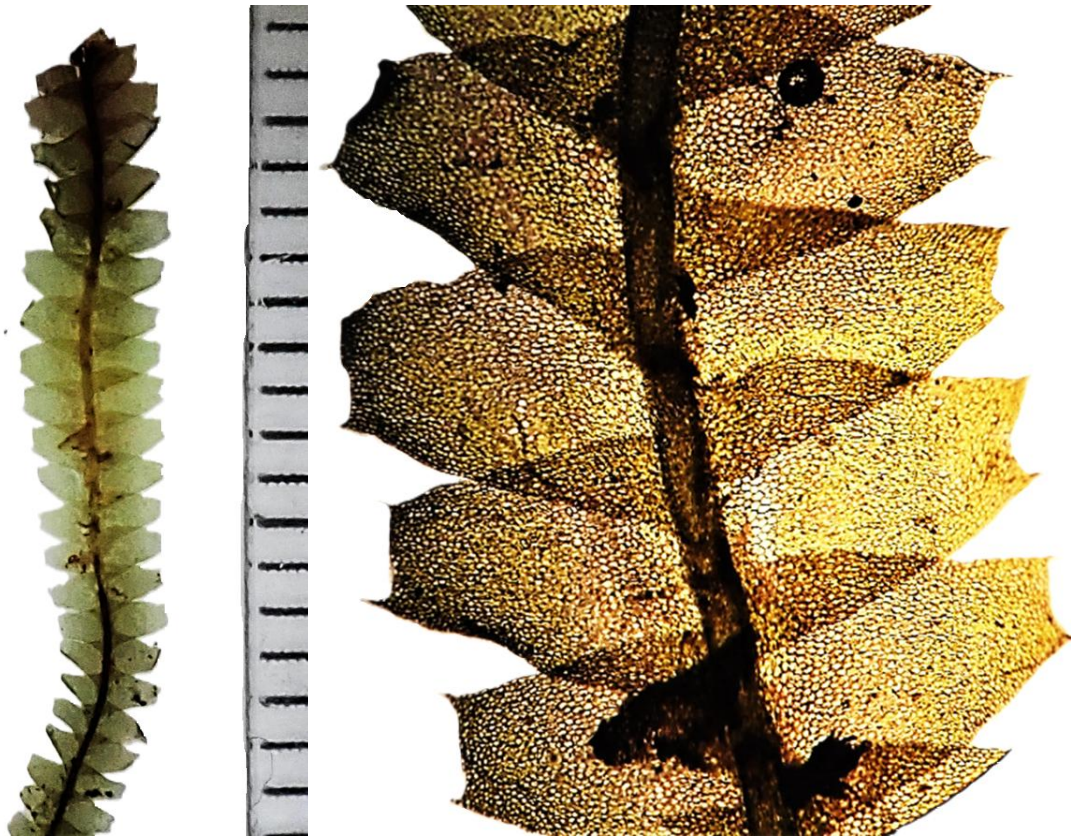
4. *Lophocolea kilauensis* Steph. Endemic.

Chiloscyphus kilauensis in Staples & Imada (2006). See Judziewicz & Freire (2023c: 167). Uncommon, on O‘ahu, Moloka‘i, Lāna‘i and Hawai‘i (3,000-6,200 ft.). The large size of the plants, the broadly triangular leaves with truncate apices bearing two small triangular teeth, and the small underleaves, are characteristic of this uncommon wet forest species.

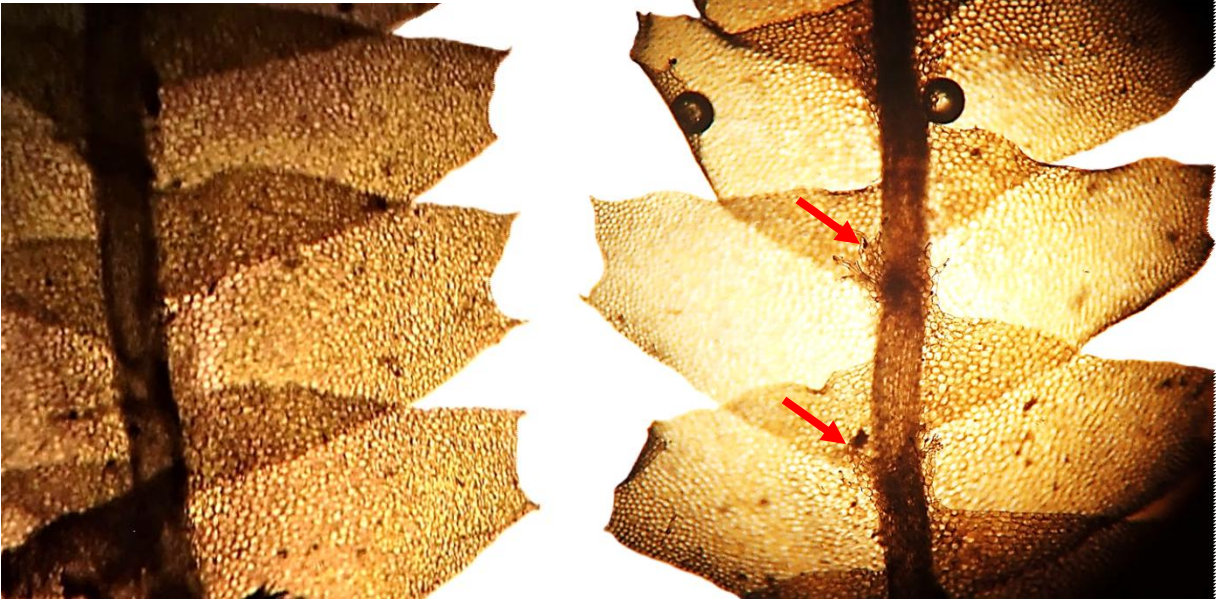


Plants are large, 5 cm long or longer and up to 3 mm wide; they tend to be reddish-brown. The leaves are alternate, mainly bifid with two tiny teeth on opposite sides of a truncate apex; leaf apices can be variable in shape. The leaf cells have thin walls with tiny trigones. The underleaves are small, less than two times the stem width; bifid, with 0-3(4) broad, short-triangular lobes, and short (one to several cells long) lateral teeth (sometimes more of them on one side of the underleaf than the other). Underleaves are fused to one of the adjacent leaves. The Geneva type was collected in 1909 at “Volcan de Kilauea” by U. Faurie:

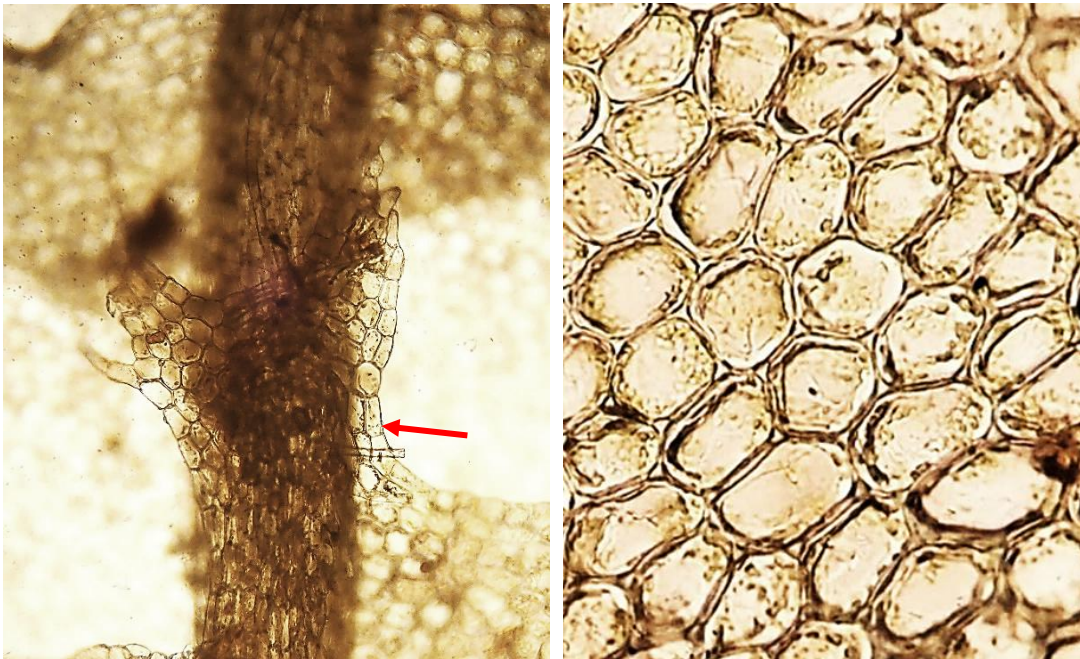
<https://www.ville-ge.ch/musinfo/bd/cjb/chg/adetail.php?id=116446&base=img&lang=en>.



Left: Plants are elongate and robust, up to 3 mm wide. Scale in mm. Right: Plants have broadly triangular leaves with truncate apices. Nāhuku, Hawai‘i Volcanoes National Park, Hawai‘i Island, Freire & Judziewicz 21-400 (HAVO).



Left: Leaves are bifid, with very small teeth and truncate apices. Right: Underleaves are small, less than twice as broad as the stem. Freire & Judziewicz 21-400 (HAVO).



Lophocolea kilauensis. Left: Underleaf about 1-1.5 times the width of the stem, fused to one of the adjacent leaves (red arrow). Note three teeth on right side. Right: Cells with small, triangular trigones. Nāhuku, Hawai'i Volcanoes National Park, Hawai'i Island, Freire & Judziewicz 21-400 (HAVO).

5. *Lophocolea muricata* (Lehm.) Nees. **Indigenous.** Rare. Known in Hawai'i from just several collections made "in forest" at Mile 23 (el. 2,500-3,000 ft.) on the Hilo-Volcano Road, Hawai'i Island, in 1938 (Miller, 1963: 502; Skottsberg 5030, Stockholm Herbarium, not examined by us and requiring study). There are no Hawaiian specimens at BISH, MU, or PTBG, and we have not examined any Hawaiian material. We have searched diligently but unsuccessfully for this species. It may occur as a tiny epiphyte on fern fronds or stipes.

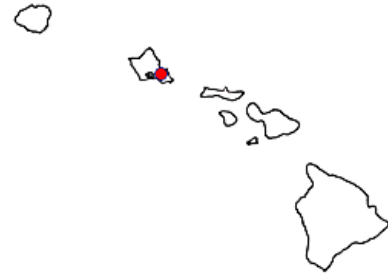


The Skottsberg specimen is a mixed collection, with *Calypogeia tosana*, *Cryptolophocolea ciliolata*, *Jubula javanica*, *Plagiochila gaudichaudii*, and *Riccardia pectinata*. This is mainly a species of tropical mountains and temperate areas of the Southern Hemisphere, with some records from warm temperate eastern Asia and North America (southern Appalachians; Engel 2010: 198). A member of subgenus *Microlophocolea*; treated as *Chiloscyphus muricatus* by Engel (2010) and Staples & Imada (2006); see Judziewicz & Freire (2023c: 168). The plants are small and covered by short, spinelike teeth on the leaves and perianths.



Lophocolea muricata. Photos of Aotearoa/New Zealand material by Larry Jensen, University of Auckland, with permission.

6. *Lophocolea pusilla* Steph. Rare, if present in Hawai‘i. Cited as a dubious record by Staples and Imada (2006). Although reported by us in Judziewicz & Freire (2023c: 168), we have not confirmed its presence in Hawai‘i with complete certainty. This species is recognized by its rounded leaves, small bifid underleaves, and by the presence of large leaf trigones. We did not encounter this species in the field, nor did we examine any specimens labelled as *L. pusilla* with this set of characters.

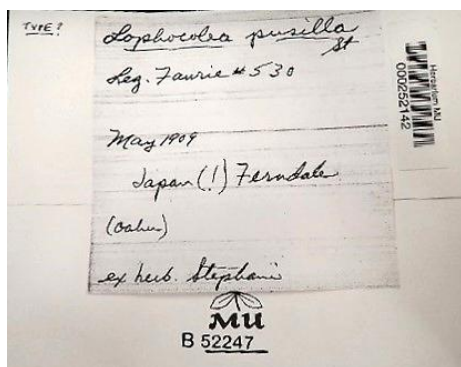


The presence of trigones in this species argues for its possible placement in a different genus, perhaps *Leptoscyphus*. However, the underleaves have broad and blunt rather than long and ciliate lobes.

We recently studied a possible isotype, ex herb. Stephani (MU). As cited in the protologue, the collector is Faurie but the location is unclear. Two different places are written on the label: “Japan (!)” and “Ferndale” (see specimen label below). According to Miller’s annotation on the Geneva type, Ferndale was an estate in the Nu‘uanu Valley, near Honolulu.

Plants are small, about 1 mm wide, with rounded, entire, leaves and cells with large trigones. Underleaves are small, up to twice as broad as the stem, bifid with broad and triangular lobes, each with a lateral tooth. They are loosely appressed to the stem or project at angles up to 45°. No reproductive structures were observed. Vegetative characters concur with the original description, except for the underleaf size: Stephani writes that they are only as wide as the stem; however, his drawings show them to be twice the stem width, as in the plants studied by us.

We studied a Hawai‘i Island specimen from Haleloulou, in the saddle between Mauna Loa and Mauna Kea (ca. 3,000-4,000 ft.), Forbes 672b (BISH), identified by H.A. Miller in 1960 as *L. pusilla*. The plants do not have large trigones (small ones are present), nor round leaves. It seems possible that this specimen is *L. autoica* rather than *L. pusilla*. We also studied Hoe 1335.1 (BISH), from Hawai‘i Volcanoes National Park: Kīlauea, along Old Kalapana Trail at 2,900 feet; identified as *Chiloscyphus lambertonii* by Hoe. The round leaves, the shape, position and size of the underleaves, as well as the presence of trigones fit the description of *Lophocolea pusilla*. However, a more detailed study of the specimen is needed. We do not have a good photograph of the trigones to confirm their size and shape (although they seem large). We do not have information on the size of the plants. If perianths are found, they would certainly help clarify the generic placement of this individual.



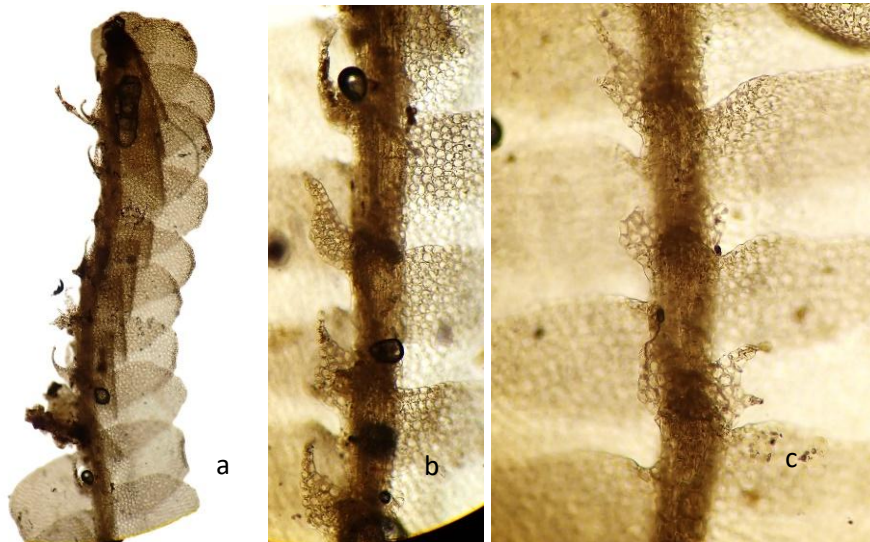
Possible isotype of *Lophocolea pusilla*. The collector is Faurie as stated in the protologue by Stephani. We are bothered by the unclear collecting location. Both Japan and Ferndale, O‘ahu are written on the label. The exclamation symbol after Japan might indicate that this location is regarded as implausible. Faurie 530 ex herb. Stephani (MU). Right: Crop of Geneva herbarium photo of holotype.



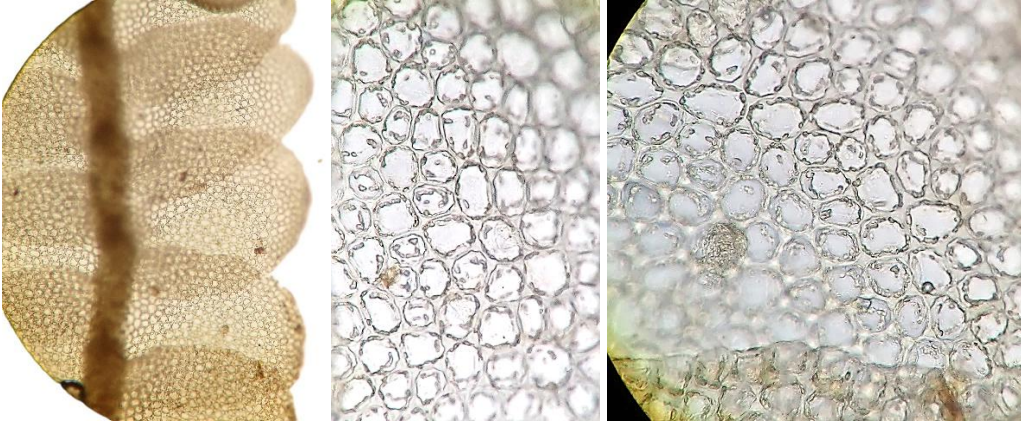
Plants are small, slightly more than 1 mm wide. Scale in mm. Faurie 530 ex herb. Stephani (MU). Photos by A.V. Freire.



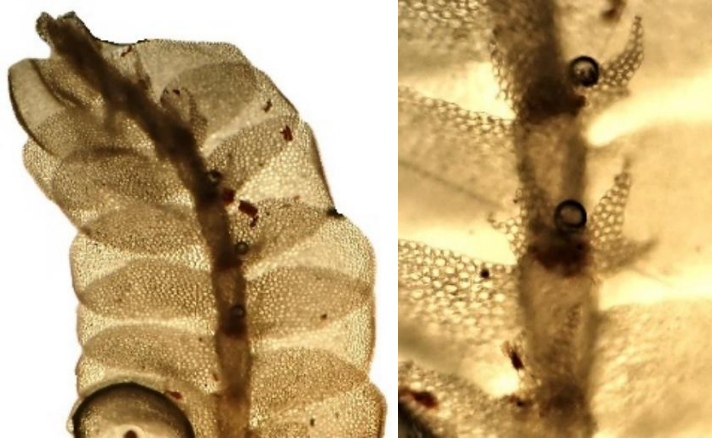
Round leaves that are never lobed or with teeth (Left, center), but can occasionally be slightly retuse to truncate (right). Faurie 530 ex herb. Stephani (MU). Photos by A.V. Freire.



Lophocolea pusilla (?). Left: Underleaves are loosely appressed to the stem or projecting from it to up to 45°. Center and right: Underleaves are small, 1.5-2 times the stem width (c, d). Faurie 530 ex herb. Stephani (MU). Photos by A.V. Freire.



Leaf cells have pronounced trigones. Cell walls are not colored. Cells are isodiametric to moderately elongated. Faurie 530 ex herb. Stephani (MU). Photos by A.V. Freire.

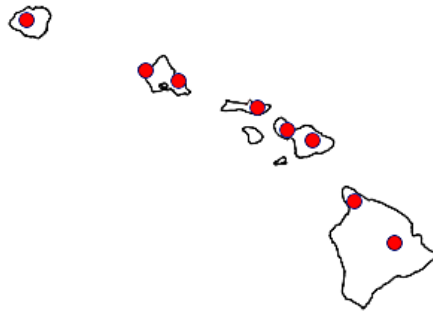


Plant with round leaves and underleaves about twice as broad as the stem, and projecting from it at about 45°. Kīlauea, Hawai‘i Island, Hoe 1335.1 (BISH). Photos by A.V. Freire.



Lophocolea pusilla (?). Leaf cells seem to have large trigones. Cells are isodiametric with some slightly elongated (as in *L. pusilla*). Hawai‘i Volcanoes National Park: Kīlauea, Hawai‘i Island, Hoe 1335.1 (BISH). Photos by E.J. Judziewicz.

7. *Lophocolea spinosa* Gottsche. Endemic. This is an inconspicuous, small species found in bryophyte mixtures on Kaua‘i (but see below), O‘ahu, Maui, Moloka‘i, and Hawai‘i (2,900-7,200 ft.). Like *L. muricata*, it is probably a member of subgenus *Microlophocolea*. *Chiloscyphus spinosus* in Staples & Imada (2006). See Judziewicz & Freire (2023c: 168). Plants are exquisitely delicate and often twining on other liverworts such as *Bazzania* and *Herbertus* and resemble tiny “snowflakes on a string”.

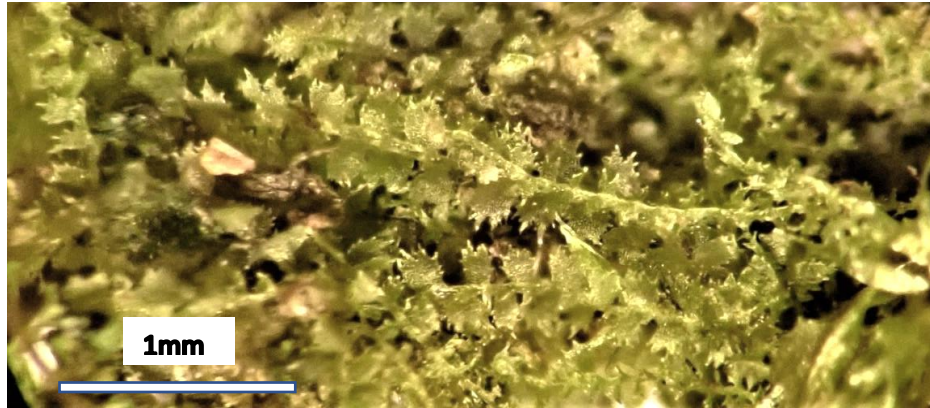


Populations are usually sparse, usually intertwined on other bryophytes or growing appressed on bark. Plants are tiny, about 3 mm long and less than 0.5 mm wide; they are light- to yellowish-green, with fragile stems, loosely attached, and trailing. Leaves are bifid, with triangular lobes separated by a triangular or lunate sinus to 1/3-1/4 the leaf length; they are distant and spreading, with conspicuously toothed margins, the teeth 1-3 cells long. The leaf cells are somewhat inflated, with thickened walls and small trigones. The leaf margins and surfaces produce gemmae. Underleaves are 2-3 times wider than the stem, bifid, with long setaceous lobes and with 1-3 marginal teeth. Perianths are large, cylindrical, with parallel sides, spinose on their surface, truncate, with a lobate and toothed mouth. Antheridia are produced on prominent branches with at least 6 pairs of concave and toothed bracts.

Miller's (1963: 502) reports from Kaua‘i, based on Hawaiian Bog Survey specimens (5204, 5361, S, not examined) from the Alaka‘i region, needs to be confirmed.



Lophocolea spinosa. Left: Plants *in situ*. Saddle area, Hawai‘i Island, Freire & Judziewicz 21-1047 (BISH). Center: As an epiphyte twining on the liverwort *Herbertus* aff. *helleri*, Saddle area, Hawai‘i Island, Freire & Judziewicz 21-792 (BISH). Right: Leafy stem with bifid, dentate leaves. Note gemmae. Haleakalā, Maui, Freire, Judziewicz, Oppenheimer & Pezzillo 23-64 (BISH).



Plants are tiny, often less than 0.5 mm wide. Freire, Judziewicz, Oppenheimer & Pezzillo 23-64 (BISH).



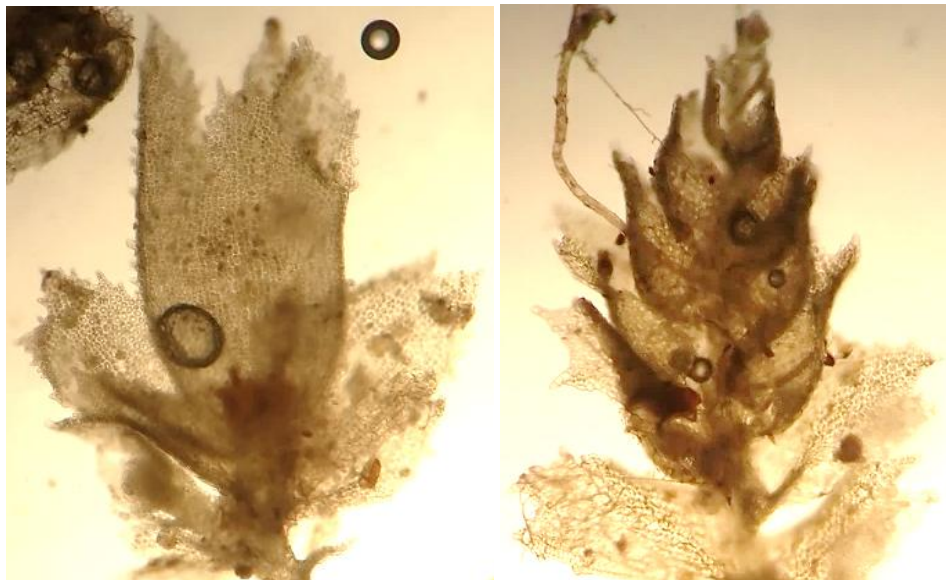
Left: Plants are tiny (scale in mm). Note perianth below and androecium above. Center: Leaves are bilobed and have spine-like teeth. Saddle area, Hawai'i Island, Freire & Judziewicz 21-1047 (BISH). Right: Leaves are irregularly dentate, Freire & Judziewicz 21-792 (BISH).



Lophocolea spinosa. Bifid underleaves with long lobes and short lateral teeth. Center and right from Saddle area, Hawai'i Island, Freire & Judziewicz 21-792 (BISH). Cell walls are thickened, with small trigones. Oil bodies are elliptical. Haleakalā, Maui, Freire, Judziewicz, Oppenheimer & Pezzillo 23-64 (BISH).

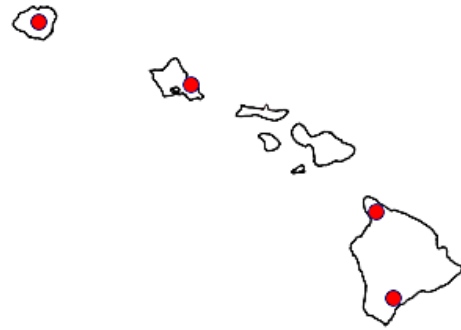


Lophocolea spinosa. Mile 12, Saddle Road, Hawai‘i Island. Note large, inflated perianths. Photo by Daniel Tucker (<https://www.inaturalist.org/observations/255994110>), with permission.



Lophocolea spinosa. Note spinose perianth (left) and large androecium (right). Saddle area, Hawai‘i Island, Freire & Judziewicz 21-1047 (BISH).

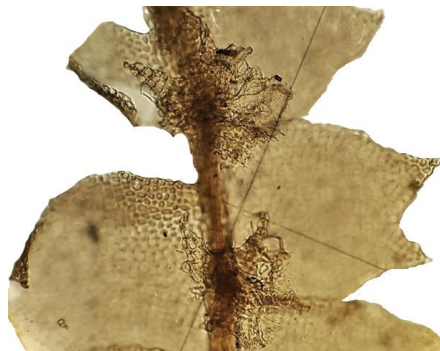
8. *Lophocolea* species 1. Perhaps related to *L. spinosa*; known (in the wide sense) from Kaua‘i, O‘ahu, and Hawai‘i Island (235-5,300 ft.). Perhaps related to *L. fragrans* (Moris & De Not.) Moris & De Not. ex Gottsche, Lindenb. & Nees, a species found in Europe and various tropical islands worldwide. A tiny species with nearly round leaves tipped with a small lunate sinus and broad, triangular, short lobes and occasional small teeth. Underleaves are bifid, with a broad sinus and parallel to slightly divergent, triangular to setaceous lobes that may bear a bulging cell close to their base, so as to resemble a small elbow and usually with a lateral tooth at the base. Leaf cells are thick-walled, trigones are absent or small.



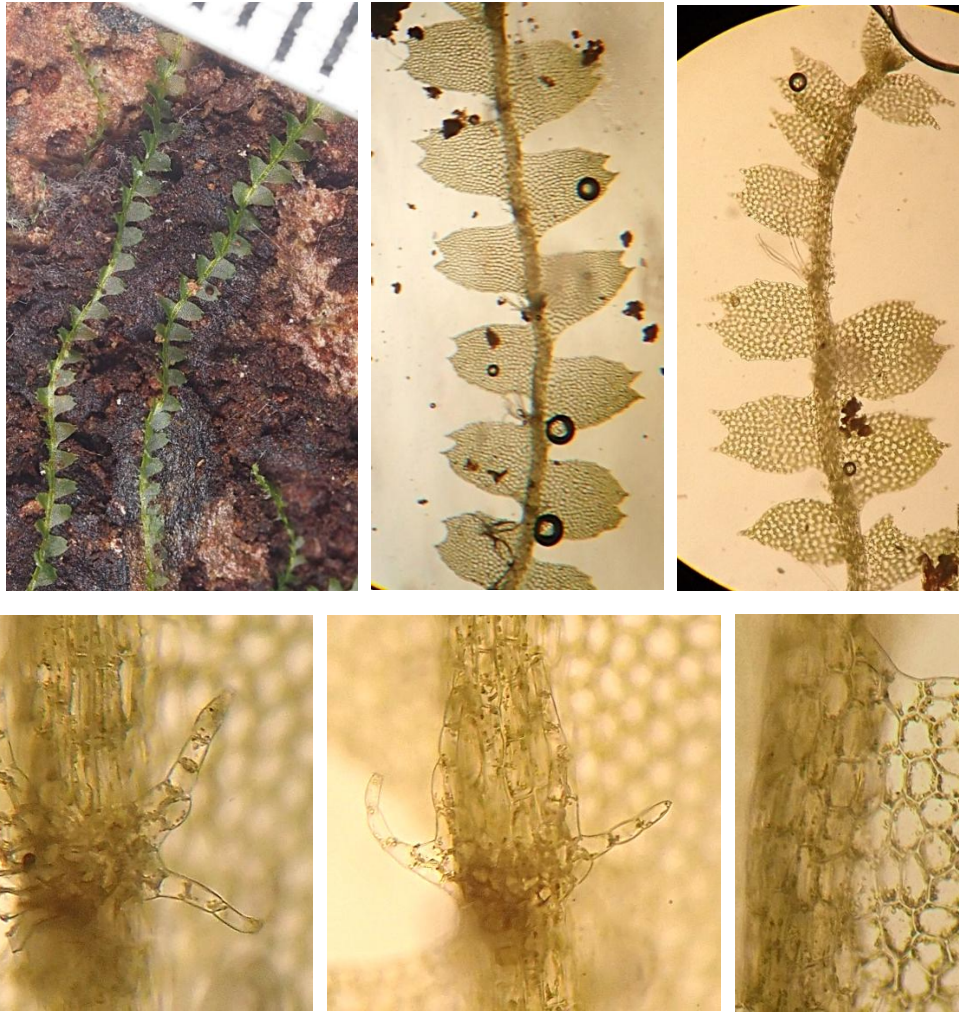
Kaua‘i: Ke‘āku (Cooke 61, BISH), the west side of the Waimea drainage basin (Forbes 1682-K, BISH), and more recently (2014) from the Halemanu-Kōke‘e Trail, 3,600 ft., Kaua‘i, Flynn & Boucher 7752 (PTBG). O‘ahu: Ko‘olau Range, Waiāhole Forest Reserve, wet exotic forest, on bark of *Terminalia myriocarpa*, Faccenda & Arthur 4195 (BISH). Hawai‘i Island: Wai‘akaloa Gulch, Ka‘ū, 1,950 ft., Judziewicz 17,091 (BISH); trail to ‘Eke summit, Kohala, 5,000-5,300 ft., Freire & Judziewicz 23-556 (BISH).



Left: Plants are small (scale in mm.). Right: Leaves are rounded, with a shallow lunate sinus and triangular lobes. Cooke 18 (BISH). Photos by E.J. Judziewicz.



Lophocolea species 1. Underleaves are about 3 times broader than the stem, with a broad sinus and divergent lobes, sometimes with small lateral “elbows”. Kaua‘i, Cooke 18 (BISH). Photo by E.J. Judziewicz.



Lophocolea species 1. In wet exotic forest, on bark of *Terminalia myriocarpa*. Note bulging cells at base of the right lobe (lower left and center). Leaf cells have tiny trigones (lower right). O'ahu: Ko'olau Range, Waiāhole Forest Reserve, 6 Nov. 2025, Faccenda & Arthur 4195 (BISH), Upper left photo by K. Faccenda: <https://www.inaturalist.org/observations/325785145>. Other photos by E.J. Judziewicz.



Lophocolea species 1. Top left: plants with flagelliform branches. Top center and right: leaves with two lobes and small occasional marginal teeth. Bottom left and right: underleaves with two lobes and 2-3 lateral teeth and basal protruding cells. On bark of *Metrosideros polymorpha*, intertwined among other liverworts (*Frullania hypoleuca* and *Lejeunea pacifica*). Kohala Mountain, Hawai'i Island, Freire & Judziewicz 23-556 (BISH).

Lopholejeunea (Spruce) Steph. (Lejeuneaceae)

Two species in Hawai‘i, 47 species worldwide.

Both Hawaiian species are members of subgenus *Eulophae* Verd. (Söderström et al., 2016), with the apex of the lobule only one cell broad at the most apical point of attachment to the lobe. The plants are either strikingly shiny and ebony black or, less commonly, dull olive-green; creeping or pendant on bark or rocks. The leaves are spreading and rounded at their apex, with lobules small or up to $\frac{1}{2}$ the leaf length, inflated below or flattened throughout. The underleaves are large, orbicular, and entire. The cell walls usually have dark pigmentation and trigones. The stems have a hyalodermis.

1. Leaf lobules triangular, $\frac{1}{4}$ - $\frac{1}{5}$ the length of the lobe; plants loosely hanging from their substrate, opaque and olive green when fresh; perianth keels not conspicuously winged, keels smooth or with few irregular small teeth; rare, Hawai‘i Island ***L. eulopha***
1. Leaf lobules horizontally elongated, about $\frac{1}{2}$ the length of the lobe; plants appressed to their substrate, not hanging, shiny and blackish when fresh; perianth keels winged, keels conspicuously toothed to lacinate; widespread ***L. nigricans***



Lopholejeunea eulopha



Lopholejeunea nigricans

1. *Lopholejeunea eulopha* (Taylor) Schiffn. Indigenous; first report for Hawai‘i. A pantropical species; Freire & Judziewicz 22-57, Manukā N.A.R. (2,000 ft.), Hawai‘i Island (Judziewicz & Freire, 2023c: 167). **Rare.** Found on lava rock in moist, shaded grottos or on bark of trees. This species is recognized in Hawai‘i by its long, pendant, olive green plants; and by its flattened leaves with small, triangular lobules. We thank S.R. Gradstein for his assistance in identifying our photos of this plant.



Plants in Hawai‘i are at least 3 cm long, and around 2 mm wide, monoicous (autoicous), olive green, darker green when older, long and pendant, loosely attached. They often project horizontally and/or curve up at their tips. Fragmentation occurs on older leaves, presumably for asexual propagation. The clustered rhizoids are dark brown to dark violet. Leaves are imbricate, ligulate to oblong-ovate, slightly falcate, horizontally spreading at 90° angles, with round and often incurved apices. Leaf lobules are triangular, small, 1/5 to 1/4 of the leaf length, flat or inflated. No teeth were observed. Underleaves are round, 4(5) times as broad as the stem, often inflated and with an arched insertion. Trigones are absent or present but small. Oil bodies are numerous, large and elongated. Plants are monoicous (autoicous), with both androecia and gynoecia produced in separate short lateral branches. Perianths are produced on short intercalary branches, sometimes more than one per branch; they are broader at their apex (obovate), have four keels, and lack pronounced wings; the keels are smooth or with a few irregular short teeth. Gynoecial bracts have few small, irregular teeth. Antheridia are produced on modified intercalary branches with reduced leaves and underleaves.

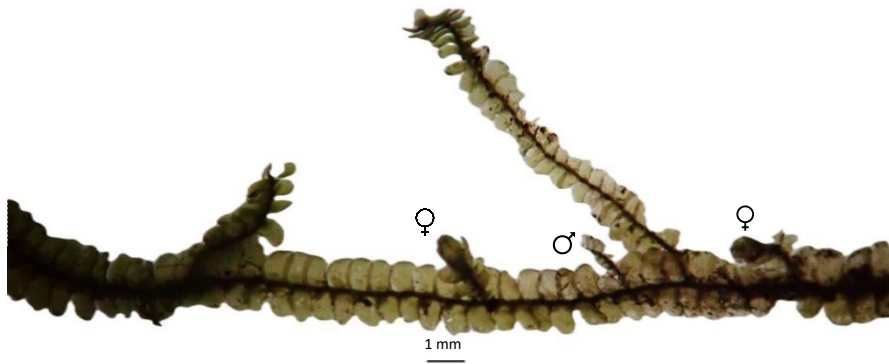
When compared with *L. eulopha* from Japan (Yamaguchi 30607, BISH), the Hawaiian plant has thinner cell walls with smaller trigones and smaller underleaves, but they are within the range of variation according to Zhu & Gradstein (2005). This species is considered as one of the most variable within the genus by the same authors. This variation may account for some discrepancies when we compare our plants with the published description by Zhu & Gradstein (2005).



Lopholejeunea eulopha. Growing on lava rock. Note its loose attachment to the substrate. Manukā N.A.R., Hawai‘i Island, Freire & Judziewicz 22-57 (BISH).



Left: Plants are long and pendant, loosely attached to their substrate, with apices often curving up. Note the olive-green color. Right: Scale in mm. Freire & Judziewicz 22-57 (BISH).



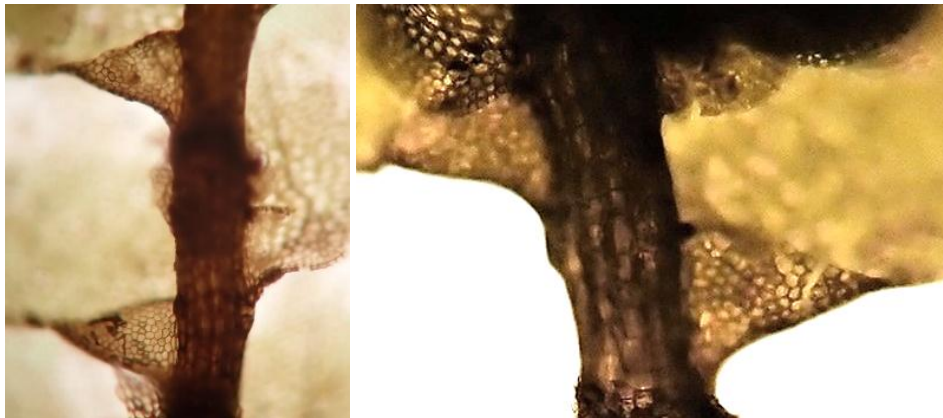
Plants are monoicous, with sexual organs in separate short intercalary branches. Freire & Judziewicz 22-57 (BISH).



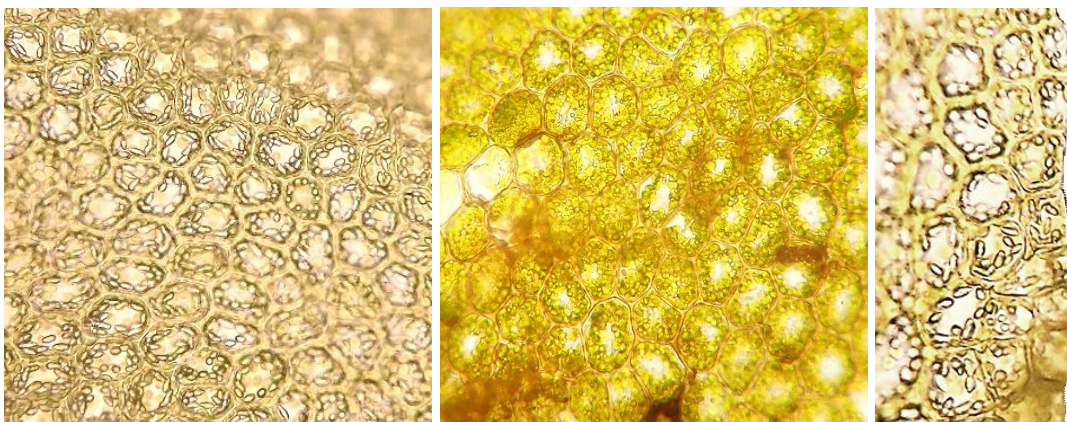
Lopholejeunea eulopha. Plants are olive green (left), with occasional lateral branches; these are intercalary and of the *Lejeunea* type (left and right). Manukā N.A.R., Hawai'i Island, Freire & Judziewicz 22-57 (BISH).



Left: Leaves overlap and spread from the stem at right angles. They are ligulate, slightly falcate, and rounded at their apex. Center and right: Underleaves are large, 4-5 times the stem width and frequently inflated (right, see arrows). Note the incurved leaf apices (right). Freire & Judziewicz 22-57 (BISH).



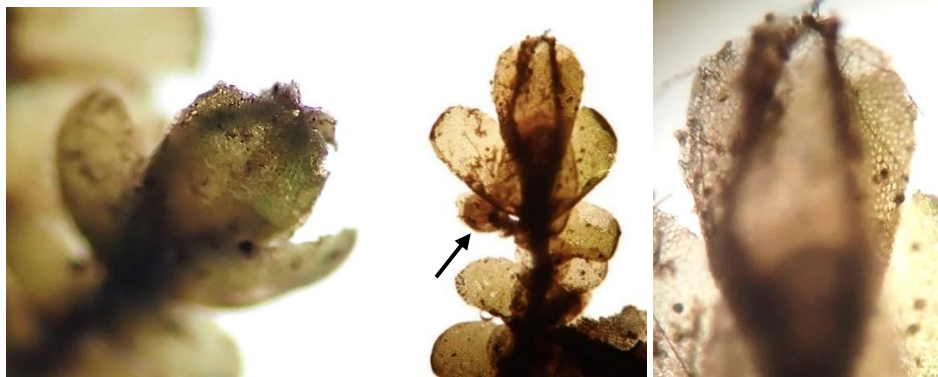
Leaf lobules are triangular, small and inflated (left), or sometimes flat (right). Freire & Judziewicz 22-57 (BISH).



Lopholejeunea eulopha. leaf cells with numerous, elongated oil bodies (left). Cell walls are colored, thin, with small trigones (center). Marginal cells are rectangular (right). Manukā N.A.R., Hawai'i Island, Freire & Judziewicz 22-57 (BISH).



Detail of short branch bearing two perianths that are obovate and keeled. Freire & Judziewicz 22-57 (BISH).



Perianths are four keeled, with no or just a very small wing (left), obovate, or occasionally with a small basal innovation (center, arrow). Gynoeceal bracts are not clearly dentate, but may have a few, irregular, tiny teeth. The keels have a few irregular short teeth (right). Freire & Judziewicz 22-57 (BISH).

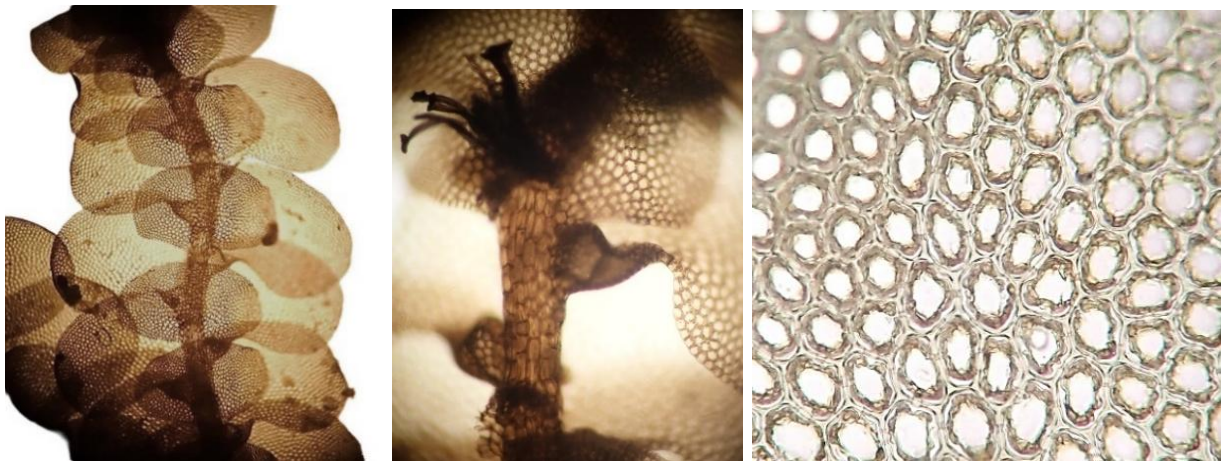


Lopholejeunea eulopha. Left and center: Older leaves are often eroded, perhaps as a type of asexual propagation by fragmentation (arrows). Left, center and right: Androecial branches are long, with modified leaves that exhibit a very reduced lobe, lobules and underleaves. Note antheridia housed in some of the bracts. Manukā N.A.R., Hawai'i Island, Freire & Judziewicz 22-57 (BISH).

The photos below are from a specimen identified as *Lopholejeunea eulopha* from Japan (Yamaguchi 30607, BISH). We place them here for the sake of comparison with the Hawaiian individuals. Photos by A.V. Freire.

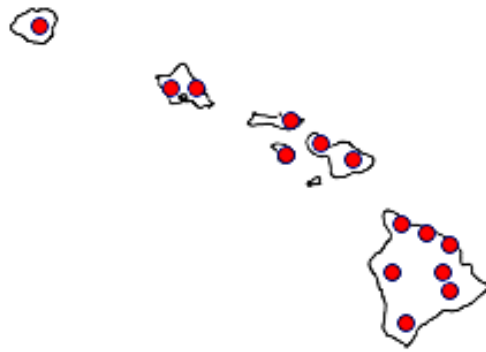


Plants are 1.2-1.7 mm wide and at least 1 cm long. Note the darker color on the older plant section, the large underleaves, and the small, triangular lobules. Scale in mm.



Lopholejeunea eulopha from Japan. Left: Plants have broader underleaves than the Hawaiian collection, over five times the width of the stem. Center: Rhizoids are clustered and dark purple and lobules are triangular, but unlike the Hawaiian plants, they are kinked on the upper middle. Right: Median leaf cells are slightly elongated, with evident trigones.

2. *Lopholejeunea nigricans* (Lindenb.) Schiffn. **Indigenous.** Found on all major islands (750-5,100 ft.); pantropical. Synonyms: *Lopholejeunea proxima* Steph. (Judziewicz et al., 2025b: 138), *Lopholejeunea subnuda* (Mitt.) Steph. Plants creeping on bark of trees or sometimes on rock, at the edges of wet forests where partially exposed to sun. This species is a large member of the Lejeuneaceae; it is easily recognized by its shiny, ebony color with light green or brown-green growing tips, and by their overlapping, concave leaves that give them an inflated, worm-like look.



Populations form dense, creeping rosettes on bark of trees or rock. Plants are closely to loosely attached; about 2 mm wide by 1 cm long; shiny, blackish-brown, with light brown-green new growth. Leaves are imbricate, oblong-ovate, entire, with incurved round apices and projecting at around 45° angles with the stem. The lobules are inflated on their lower half and flattened above, horizontally elongated, about 1/2 as long as the lobe, and 1/5-1/6 its size. Underleaves are contiguous, sub-orbicular, slightly broader than long with a rounded and entire apex and 3-6 times the stem width. Leaf cells are isodiametric or slightly elongated, with slightly thickened brown or reddish walls and with small to large trigones; marginal cells subquadrate. Perianths obovate, with four lacinate and winged keels. Gynoecial bracts can be entire to crenulate or slightly dentate. Antheridia are produced on intercalary branches.



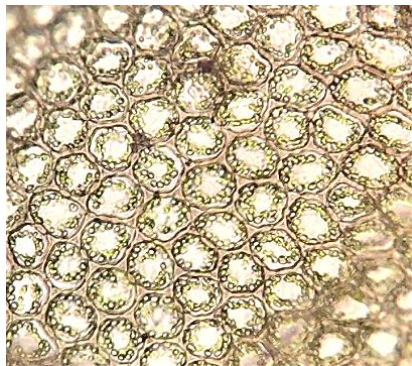
Lopholejeunea nigricans. Left: Plants form dense mats on exposed tree trunks in areas with high humidity. Right: Plants are blackish with brown-green growing tips, (here with light green *Lophocolea hawaica* growing intermixed), 'Ōla'a Tract, Wright Road, Hawai'i Volcanoes National Park, Hawai'i Island, Freire & Judziewicz 21-150 (HAVO).



Leaves incubous and highly imbricate. The concave leaves give the plants a slightly inflated appearance. O'ahu. Photos by Miles K. Thomas, with permission.

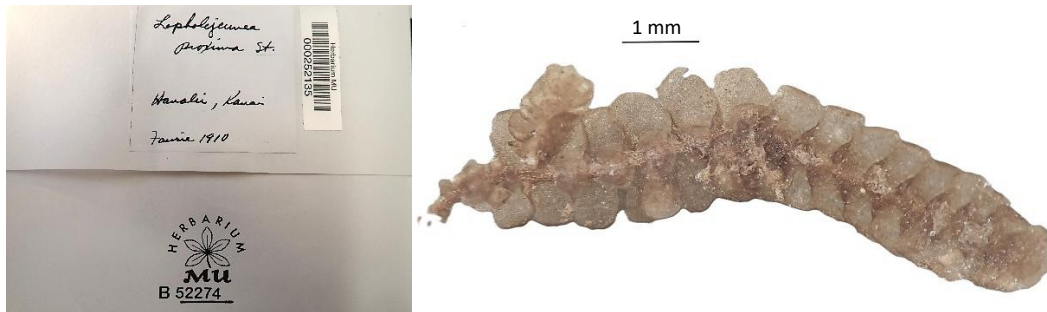


Left: Leaves ovate-oblong, incurved, underleaves large and rounded. Lobules elongated and inflated. Perianth keels lacinate. Right: Leaves with rounded apices and quadrate marginal cells. Freire & Judziewicz 20-702 (BISH).



Lopholejeunea nigricans. Median leaf cells are isodiametric, with thickened walls and prominent trigones. Note the reddish-brown cell walls. Hale Alema, Volcano, Freire & Judziewicz 20-702 (BISH).

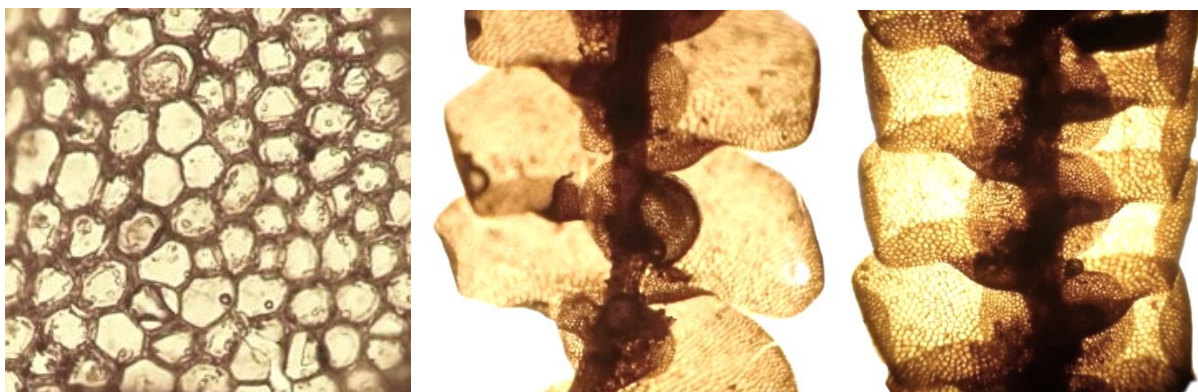
Lopholejeunea proxima Steph. is apparently known only from the type collection made by Urbain Faurie in 1909 from the vicinity of Hanalei, Kaua‘i. The type is in the Geneva Herbarium (G). We studied an isotype at MU. Given the very high variability of *L. nigricans*, we consider *L. proxima* a synonym of it (Judziewicz et al., 2025b: 138). This form of *L. nigricans* has tiny trigones, and very lacinate and winged perianth keels with entire bracts.



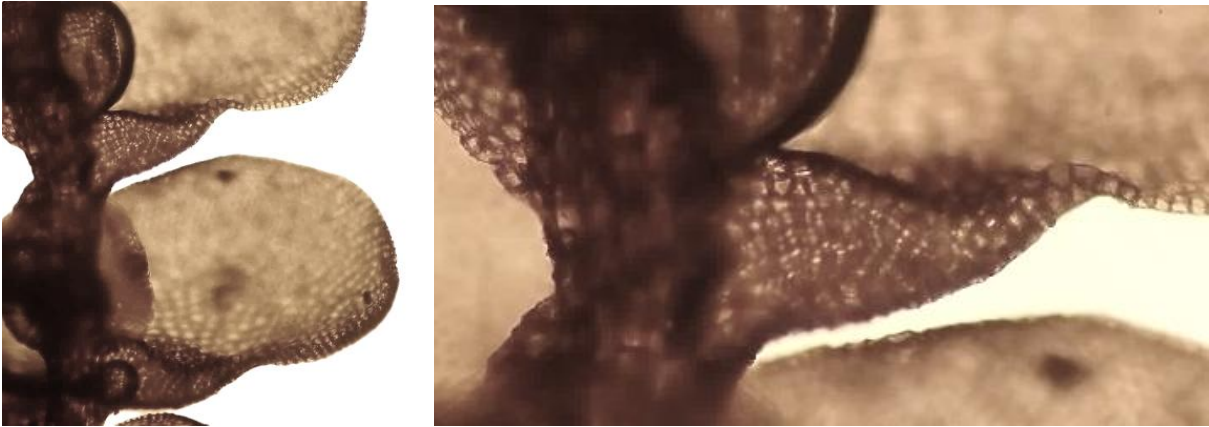
Left: Isotype at MU. Right: Image of dry plant. Kaua‘i, Faurie s.n. Photos by A.V. Freire.



Left: Leaves are slightly falcate, with round apices and horizontally elongated lobules. Center: Underleaves are 3-5 times the stem width. Right: Branching is commonly observed. Faurie s.n. (MU). Photos by A.V. Freire.



Lopholejeunea proxima, a synonym of *L. nigricans*. Left: Leaf cells are isodiametric, thin-walled, with tiny trigones, if any. Center and right: Underleaves vary from obovate to orbicular but are slightly broader than tall. Leaves are incurved. Vicinity of Hanalei, Kaua‘i, Faurie s.n. (MU). Photos by A.V. Freire.



Leaf lobules are inflated but flattened above (left), and are single celled in width at the very apex (right), a characteristic of subgenus *Eulophae*. Faurie s.n. (MU). Photos by A.V. Freire.



Male branches are short and stout, with lobules; here seen with antheridia. Faurie s.n. (MU). Photo by A.V. Freire.



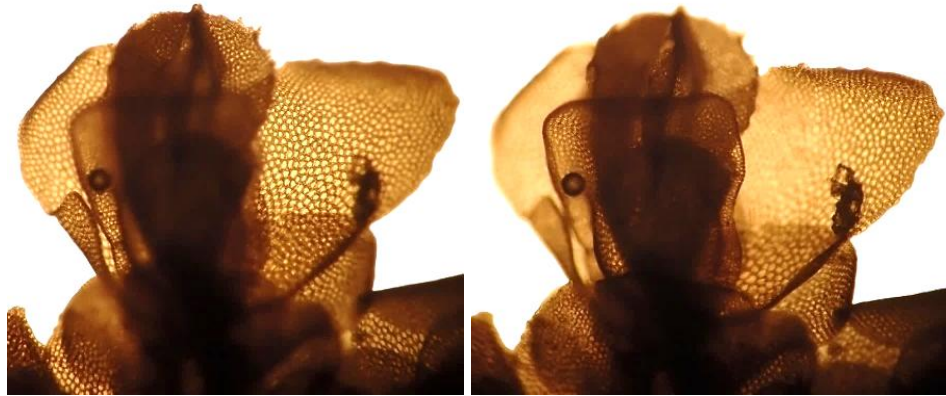
Perianths are 4-keeled, winged, with large and lacinate teeth. Gynoecial bracts are entire. Vicinity of Hanalei, 1909, Kaua'i, Faurie s.n. (MU). Photos by A.V. Freire.

***Lopholejeunea subnuda* (Mitt.) Steph., a synonym of *L. nigricans*:**

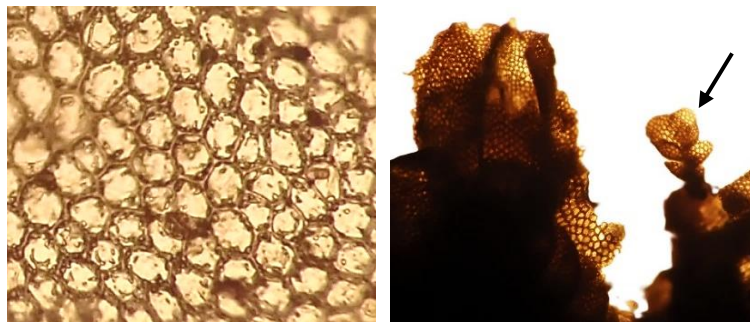
According to Tropicos, *Lopholejeunea subnuda* is a synonym of *L. nigricans* (Bardat et al., 2021; Staples & Imada, 2006; Zhu & Gradstein, 2005). We studied a specimen collected on O'ahu by Miller & Hathaway 1570 (MU; all photos below) and agree with this reduction. The packet has an annotation by H.A. Miller stating that *L. subnuda* is not the same as *L. proxima* but we think these are both synonyms of *L. nigricans*.



Left: H.A. Miller wrote on the label that perianths are smooth to armed. Center: As in *L. nigricans*, plants are around 2 mm wide. Right: Leaves are round and incurved; lobules are elongated and about half the length of the lobe; underleaves are large, 6 or more times as broad as the stem. Photos by A.V. Freire.



Perianths are strongly keeled; the keels have lacinate margins. The gynoecial bracts have crenulate-dentate margins. Note enlarged, rectangular underleaf (right). Miller & Hathaway 1570 (MU). Photos by A.V. Freire.



Lopholejeunea subnuda (Mitt.) Steph., a synonym of *L. nigricans*. Left: Leaf cells have thin, colored walls and small trigones. Right: Plants have leaf propagules (arrows). Perianths are keeled and with obvious lacinate teeth. O'ahu, Miller & Hathaway 1570 (MU). Photos by A.V. Freire.

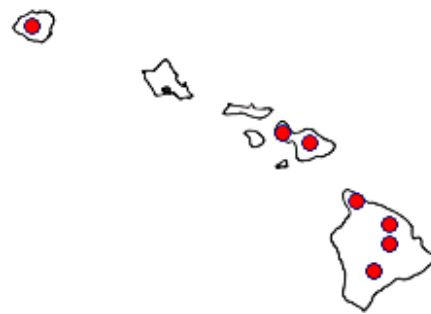
***Lophozia* (Dumort.) Dumort. (Lophoziaceae)**

At least one species in Hawai‘i, 27 species worldwide.

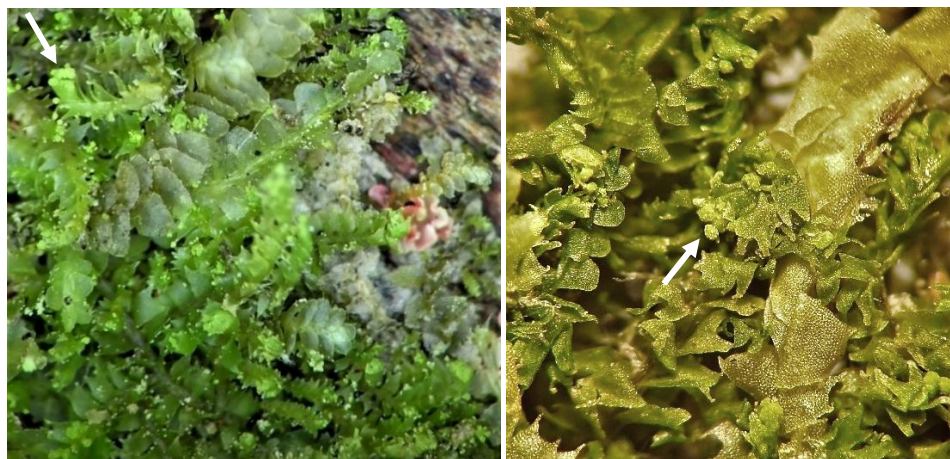
In wet, montane forests. The genus is characterized by bifid leaves of nearly transverse insertion that produce large clusters of yellow-green gemmae at the tip of the lobes of younger leaves. *Lophozia* in Hawai‘i differs from *Marsupella* in its pointed rather than rounded leaf lobes and in the production of gemmae (not observed in the latter genus). It differs from *Tritomaria* in having yellow-green polygonal rather than red or orange-brown ellipsoidal gemmae and in having bifid rather than trifid leaves (but there are exceptions for both genera). *Lophozia perssoniana* H.A. Mill. (Staples & Imada, 2006) is now placed in the genus *Protolophozia*, (Judziewicz & Freire, 2023c: 171). while *Lophozia bicrenata* is now placed in *Isopaches* (see entry in this notebook).

***Lophozia silvicola* H. Buch. Indigenous.**

First report for Hawai‘i: Judziewicz & Freire (2023c: 171). Uncommon; usually terrestrial, on soil, rocks or logs, in moist high elevation (4,300-8,020 ft.) forests on Kaua‘i (Waimea Basin, west side, Forbes 1648K, BISH), Maui, Z. Pezzillo (<https://www.inaturalist.org/observations/255142928>), and Hawai‘i Island (Kohala, Mauna Kea, and Mauna Loa).



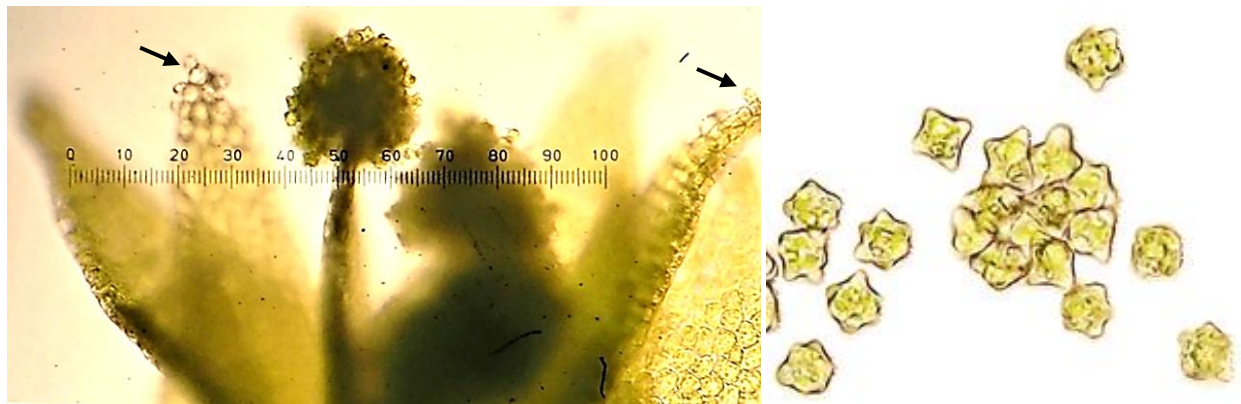
It often grows with *Tritomaria exsecta* on Hawai‘i Island. Plants are fragile looking, yellow-green, prostrate to ascending, (1)1.5(2) mm wide. The leaves are rectangular to slightly ovate and canaliculate, transversely inserted, spreading at 45-90° from the stem, bilobed, with a rounded sinus to about 1/3-1/4 the leaf length and with triangular, acute, slightly divergent lobes. Clusters of gemmae with angular, rounded protuberances are produced at the leaf lobe apices, at the tip of the plants. Lower leaves may have some remaining gemmae still attached, but they are released early. Median leaf cells are rectangular to quadrate, thin-walled, with concave to triangular trigones.



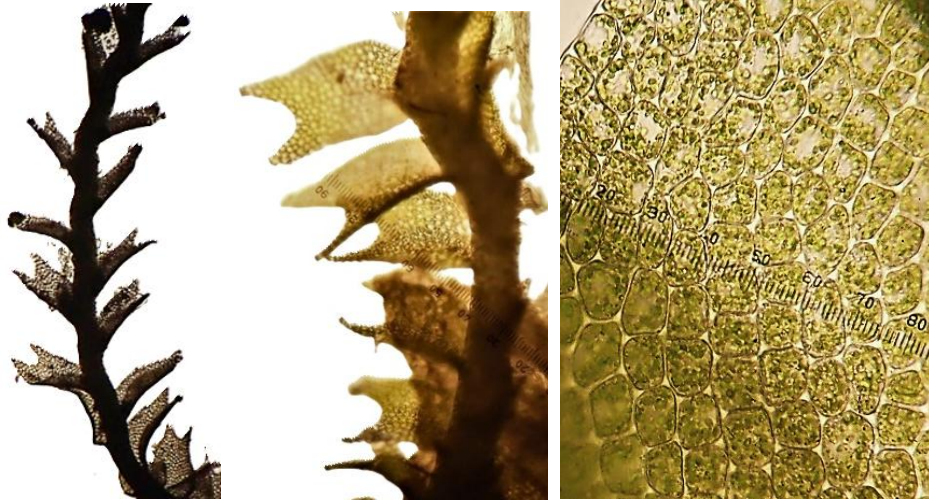
Lophozia silvicola. Left: On bark of ‘ōhi‘a (*Metrosideros polymorpha*); note abundant yellow-green clusters of gemmae at leaf lobe apices (arrows); here with *Bazzania nuuanuensis*. Saddle area, Hawai‘i Island, 5,700 ft., Freire & Judziewicz 22-957 (left), 21-1067 (right) (BISH).



Left: Leaves with large clusters of yellow-green gemmae. Hawai'i Island, Freire & Judziewicz 22-957 (BISH). Right: Plant with transversely inserted, canaliculate, bifid leaves. Note the clusters of gemmae on leaf lobe tips at its apex. Hawai'i Island, Freire & Judziewicz 21-1067 (BISH).

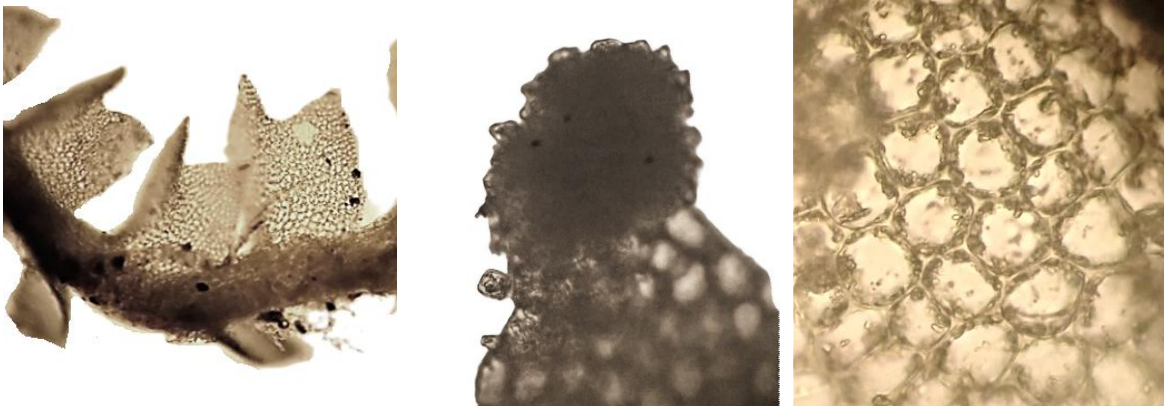


Lophozia silvicola. Left: Detail of clustered gemmae at the apex of leaf lobes (scale = 10 μ m). Note some isolated gemmae still remaining attached on lower leaves (arrows). Hawai'i Island, Freire & Judziewicz 21-1067 (BISH). Right: Gemmae are angular with several rounded protuberances. Kohala Mountain, Hawai'i Island, Freire & Judziewicz 23-531a (BISH).



Leaves are nearly transversely inserted, bilobed to about 1/3-1/4 of their length, lobes separated by a rounded sinus; lobes are acute and slightly divergent. Right: Median leaf cells are quadrate to rectangular, thin-walled, with concave to triangular trigones. Left: Kohala Mountain, Hawai'i Island, Freire & Judziewicz 23-531a (BISH). Center and right: Hawai'i Island, Freire & Judziewicz 21-1067 (BISH).

Photos below are of *Lophozia silvicola* (Nimtofte 13 (BISH), Denmark). We briefly studied this specimen to corroborate the identity of our specimens. Plants do match in leaf morphology and the presence of quadrate cells with triangular trigones. The gemmae are angular on both. From this study and ample literature research, we conclude that *Lophozia silvicola* is present in Hawai'i.

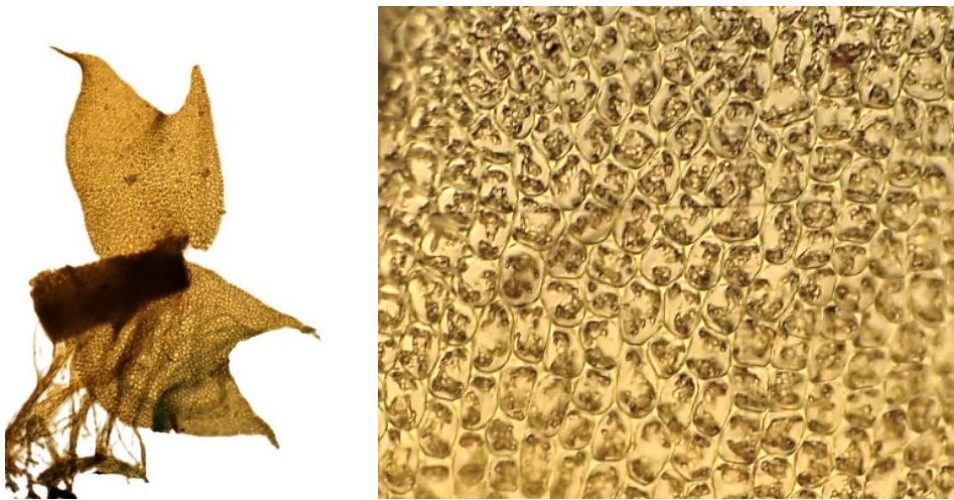


Lophozia silvicola: Plant with bifid leaves (left); angular clustered gemmae at leaf lobe apex (center); and thin-walled quadrate leaf cells with mainly concave trigones. Photos by A.V. Freire.

The specimen below is from Maui and was collected at the shaded base of a grass clump, in a *Deschampsia cespitosa* grassland at 8,020 ft., on Kalapawili Ridge on the north side of Haleakalā (Hoe 4554, BISH). It differs somewhat from typical *L. silvicola* in its leaf morphology. The leaves are bifid, canaliculate, and rectangular as in our concept of *Lophozia silvicola*, but with narrower lobe tips that are sometimes acuminate. Leaf lobes can be rather asymmetrical. Median leaf cells are quadrate to rectangular, thin-walled, and have triangular trigones as in *L. silvicola*. No gemmae were observed.



Plants 1.5 mm wide (left), leaves are concave, transverse, projecting at approximately 90° (right). Photos by A.V. Freire.



Lophozia silvicola. Leaves are asymmetrically bifid to about 1/3 their length. Leaf lobes are narrow, often acuminate (left). Median leaf cells are rectangular to quadrate, thin-walled and with concave to triangular trigones (right). Photos by A.V. Freire.

Marchesinia Gray (Lejeuneaceae)

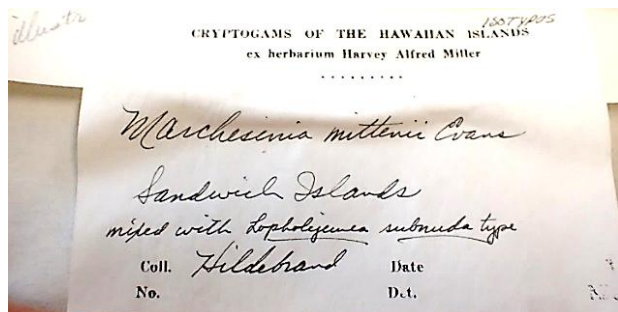
One species in Hawai‘i, ten species worldwide.

Marchesinia brachiata (Sw.) Schiffn. **Indigenous.** A member of subgenus *Marchesiniopsis* R.M. Schust. (Söderström et al., 2016: 409). Common in tropical America. Treated as *M. mittenii* by Staples & Imada (2006); but reduced to *M. brachiata* by Gradstein (2012: 73) upon his examination of Hawaiian material at NY; see Judziewicz & Freire (2023c: 164). Rare, collected by William Hillebrand in the 19th century somewhere in Hawai‘i, mixed with *Lopholejeunea nigricans*. No island information, location or habitat is provided (see labels below). We have not seen this species in the field but did examine an isotype of *M. mittenii* at MU (photos below); the very deeply arched insertion of the underleaves is diagnostic.

Marchesinia brachiata resembles *Lopholejeunea nigricans* but differs from it in having small, triangular lobules, with 3-4 small teeth (according to Gradstein, 2012), that are hidden by the underleaves (*L. nigricans* has horizontally elongated lobules that protrude from the underleaves, and do not have conspicuous teeth or may have a single one); in its auriculate-decurrent obovate underleaves with a deep, arched insertion; in its mostly flattened leaves that may be toothed (*L. nigricans* has concave leaves that are rarely toothed); and in its flat, non-keeled and obovate-oblong perianths (Gradstein, 2012: 73).

Other Hawaiian specimens are perhaps members of this species. We’ve seen some with the conspicuously arched leaf insertion (but not as dramatic as some illustrations in the literature), but either failed to see the teeth on the lobule, the decurrency on the underleaf, or were not able to perform a detailed study. We recommend revisiting the specimens labelled as *Lopholejeunea nigricans* and *Sprucenthus* deposited at BISH, PTBG and HAVO, paying particular attention to cell shape and wall thickness as a possible diagnostic character in combination with others. Seemingly, the cells in *Marchesinia brachiata* are polygonal, with firm, trigonous walls that form a well-defined and “rigid” net-like pattern.

Plants are large, about 3 mm wide, with imbricate, horizontally spreading, oblong leaves with rounded apices that may bear a small apiculum or a few small and irregular teeth (see drawing on NY specimen). Leaves arch on the dorsal side, obscuring the stem. Leaf lobules are small, triangular, and have three teeth (based on NY drawing). Underleaves are large, more than five times as broad as the stem; they are obovate, slightly reflexed above, narrowing at their base to form a decurrency. The long, arched insertion occupies almost half of the underleaf length. Leaf cells are isodiametric and polygonal, with thickened walls that bear long and almost continuous trigones with some intermediate thickenings. No sexual organs were studied by us; however, Gradstein (2012) did find a perianth in Hawaiian material.



Specimen from Hawai‘i (MU), collected by Hillebrand [note misspelling on label] and lacking specific location information. The plants have large underleaves and small lobules hidden under them.



Left: Dorsal view; the stem is obscured by the overarching leaf upper margins. Scale in mm. Center and right: Underleaves are obovate, decurrent, with a long and arched insertion line that resembles the door of a hobbit's house. Hawai'i, Hillebrand s.n. (MU). Photos by A.V. Freire.



Leaf cells are isodiametric, polygonal, with thick walls and rectangular, almost contiguous trigones, with intermediate thickenings. Hawai'i, Hillebrand s.n. (MU). Photo by A.V. Freire.



Marchesinia brachiata, Hawaiian specimen collected by Hillebrand at New York Botanical Garden (NY) (lectotype of *M. mittenii*). From the line drawing at the upper right corner (left), enlarged (right), the leaf apices may have teeth; these were not observed by us on the isotype at MU.

Marsupella Dumort. (Gymnomitriaceae)

Two very dissimilar and rare species in Hawai‘i, 38 species worldwide.

This genus is characterized by small, stoloniferous plants that form dense mats; by the long and transverse leaf insertion, and lack of underleaves; by the small median leaf cell size; and by the small and inconspicuous perianths that remain hidden by tubular bracts. In Hawai‘i, the two species belonging to this genus are rare and quite dissimilar. Both species are new reports for Hawai‘i (Judziewicz & Freire, 2023c; Judziewicz et al., 2025b).

1. Plants at least 1 mm wide, reddish to brown or olive green; leaves bifid; Haleakalā, Maui.. *M. emarginata*
1. Plants much less than 1 mm wide (0.1 – 0.45 mm wide), blackish; leaves entire or a few bifid; Wai‘ala‘ale, Kaua‘i *M. stoloniformis*



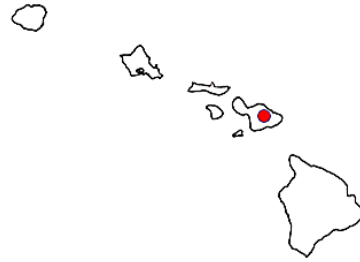
Marsupella emarginata



Marsupella stoloniformis

1. *Marsupella emarginata* (Ehrh.) Dumort. Indigenous.

First report for Hawai‘i: Judziewicz & Freire (2023c: 162). Rare. A worldwide (but mainly Holarctic) species found in wet montane forests. In Hawai‘i, found at high altitudes (5,350-7,200 ft.) on Haleakalā, Maui. Vegetatively, the rounded leaves with shallow sinuses and mainly rounded lobes, together with the nodulose trigones, are enough to separate *Marsupella* from other bifid Hawaiian liverworts.



Marsupella emarginata resembles *Lophozia*, *Anastrophyllum* and *Sphenolobus*; for the contrast with *Lophozia*, see that genus. It differs from *Anastrophyllum* and *Sphenolobus* in having a transverse rather than succubous leaf insertion; in its small perianths that remain enclosed and hidden by large, tubular bracts. Other vegetative characters can be more problematic but *Marsupella emarginata* has orbicular rather than rectangular leaves (*Anastrophyllum* can have rounded leaves); mostly rounded rather than pointed leaf lobes (*Anastrophyllum* can have rounded lobes); prominent nodulose trigones (*Anastrophyllum* has much thicker cell walls, while *Sphenolobus* and *Lophozia* have smaller trigones or none at all) and in the lack of gemmae (but gemmae are sometimes observed in *Anastrophyllum*).

Anastrophyllum is then the most problematic genus to separate vegetatively from *Marsupella emarginata*, but the former is succubous, stouter, and the leaf cells are larger with much thicker walls, and branching is more commonly observed. Judziewicz & Freire (2023) erroneously identified Stemmermann 7034 (HAVO) from ‘Eke Bog, West Maui and Flynn 3021 (PTBG) from Nāmōlokama, Kaua‘i as *Marsupella emarginata*, but both are members of the genus *Anastrophyllum*.

Plants are erect, mostly unbranched or with few branches, forming dense mats; they are rigid, 0.7-0.8(?) and cm long 1.5-1.7 mm wide. Stolons may be present. Color can vary from olive green, brown, orange-brown, or pink to red. Leaves are canaliculate; transversely inserted, obscuring the stem midline; semi-erect to spreading, overlapping above, contiguous to distant below; occasionally caducous; orbicular but may be slightly broader than long. Leaf apices bear two broadly obtuse and mostly rounded lobes, but some acute lobes may be intermixed; sinuses are broad, obtuse, to about 1/5-1/4(1/3) the leaf length. Marginal cells are rectangular, thick-walled, and transversely oriented, forming a distinct and thickened border. Leaf margins are sometimes recurved. Leaf cells are small, 22-26 µm long, thick-walled, with prominent nodular trigones, and the basal mid-portion of the leaf usually has larger cells. Oil bodies are large, elliptical, granulose, and usually 2-3(4) per cell. Gemmae are never produced. Perianths are globose, small, remaining hidden by enveloping tubular bracts. Innovations are present at the base of gynoecia. Spores are tiny, 10-12.5 µm in diameter, brown, finely papillose (or spinulose?) on the distal face, with a strong tri-radiate ridge. Elaters are approximately 100 µm long and 10 µm wide, with 2(3) spirals. The capsule wall has annular thickenings (the only capsule available to us was immature).

We studied a fresh collection made by Pezzillo 368, eastern Waikamoi Preserve, 6,300 ft., Haleakalā, Maui (BISH). The specimen was determined using the key in Bakalin et al. (2019) and was compared to several descriptions (Lee & Gradstein, 2021; Schuster, 1969; Paton, 2014). The specimen fits our concept of *Marsupella emarginata*. The recurved lateral leaf margins, an important character reported in the literature, was observed on older leaves and was thus more evident in mature plants.



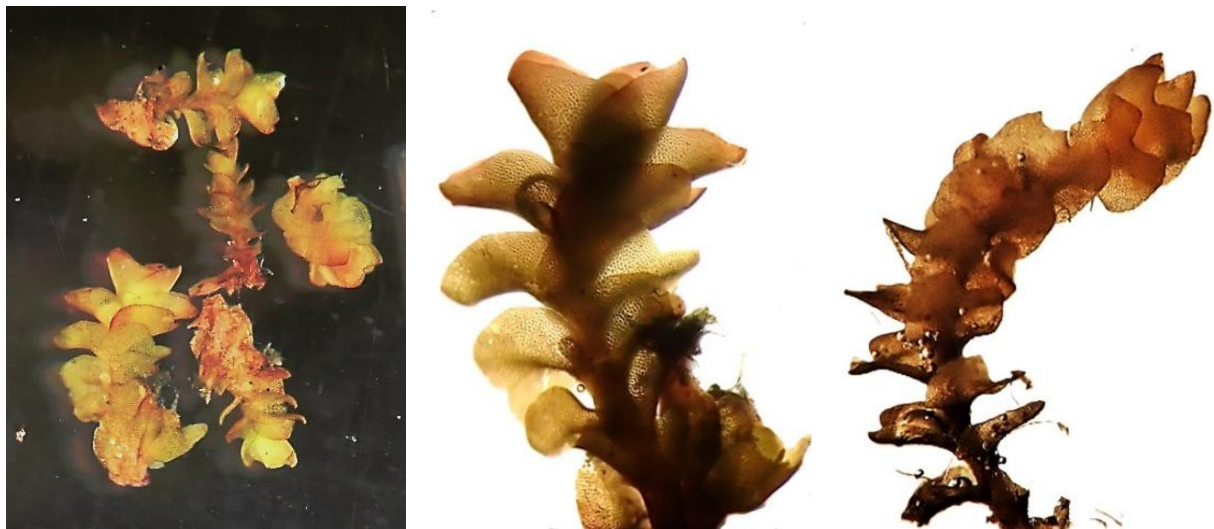
Plants form dense erect mats. Note the color variation. Waikamoi Preserve, Haleakalā, Maui, *in situ* photos by Z. Pezzillo, with permission. <https://www.inaturalist.org/observations/214743946>.



Marsupella emarginata. Left: Cropped portion of previous picture, note the rounded leaf lobes (yellow arrows) and reflexed leaf margins. Waikamoi Preserve, Haleakalā, Maui, *in situ* photos by Z. Pezzillo, with permission. <https://www.inaturalist.org/observations/214743946>. Right: Scale in mm. Note fragment of stolon at plant base. East Maui, Pezzillo 1250 (BISH). Photo by A.V. Freire.



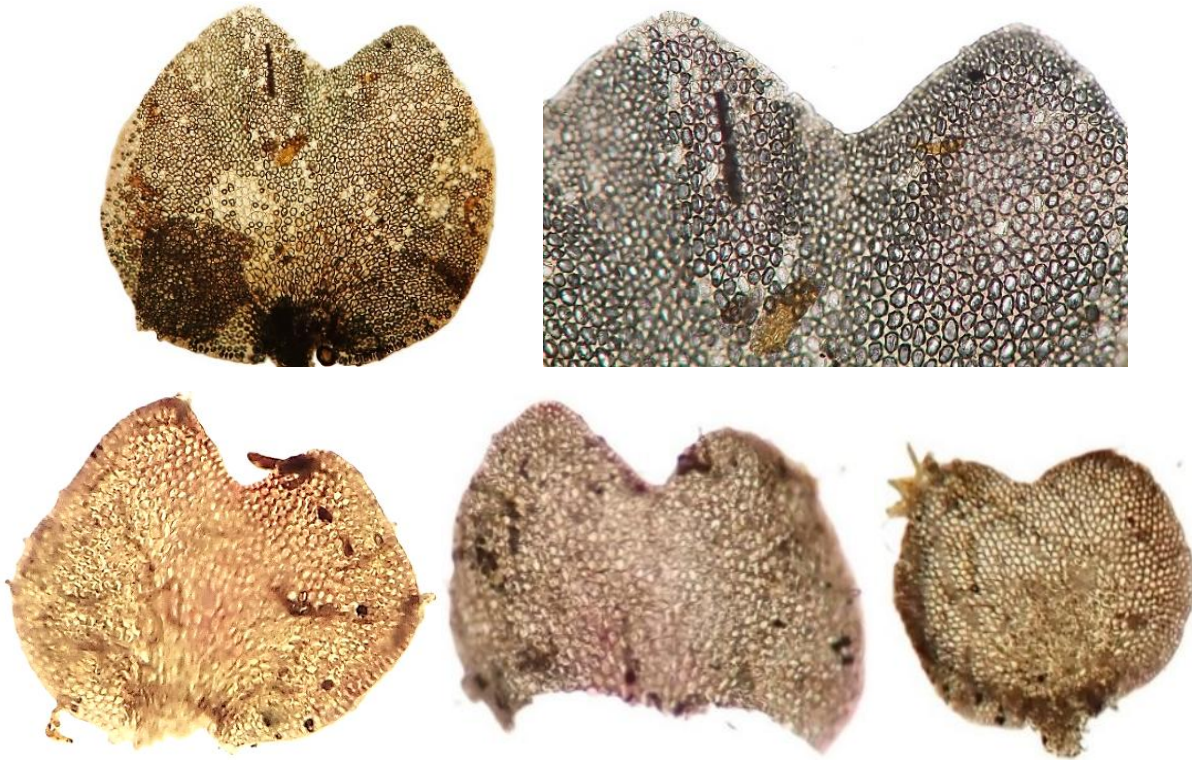
Left: Plants are erect and densely arranged. Note the stolon at the base (arrow). Center: Gynoecia; the perianths are obscured by large tubular bracts (arrows). Innovations are produced at the base of gynoecia. Right: Gynoecial bracts are removed revealing a short, globose, inconspicuous perianth (arrow). Note the erect, microphyllous branch we interpret as a stolon. Pezzillo 368 (BISH).



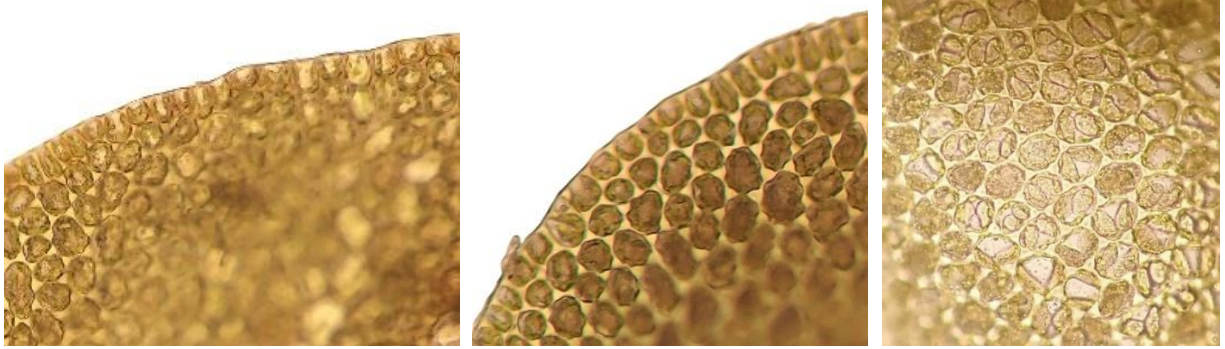
Marsupella emarginata. Plants showing spreading, rounded and bifid leaves. Left and center: Eastern Waikamoi Preserve, 6,300 ft., Haleakalā, Maui, Pezzillo 368 (BISH). Plants are up to 1.7 mm wide. Right: 'Ukulele, Haleakalā, Maui. Forbes 1462 (BISH). Plant is 1.5 mm wide. Photos by A.V. Freire.



Left: Plant with recurved lateral leaf margins (arrows). Pezzillo 368 (BISH), photos by A.V. Freire.



Marsupella emarginata: Orbicular leaflets with rounded lobes and obtuse, shallow sinuses. Note prominent nodular trigones. Haleakalā, Maui, Pezzillo 368 (BISH). Photos by A.V. Freire.



Left and center: Examples of leaf borders with rectangular to square cells and thickened walls. Right: Leaf cells with prominent nodular trigones and large, elliptical, and granular oil bodies. Eastern Waikamoi Preserve, 6,300 ft., Haleakalā, Maui, Pezzillo 368 (BISH). Photo by A.V. Freire.

We also studied two specimens collected by C.N. Forbes 1462 (BISH), in 1919, at ‘Ukulele, Haleakalā, Maui (BISH), and initially identified by R.D. Svihla as *Marsupella* in 1935. We agree with her generic determination. Based on the round leaves and rounded leaf lobes, the conspicuous trigones and border of rectangular cells laterally thickened, we identify them as *M. emarginata*.



Marsupella emarginata. Plants are 1-1.4 mm broad. Leaves are erect to spreading, rounded, and transversely inserted. Leaf lobes are mainly rounded and obtuse, with a broad, shallow sinus. Trigones are very prominent, and the leaves have a distinct border. ‘Ukulele, Haleakalā, Maui, Forbes 1462 (BISH). Photos by A.V. Freire.

2. *Marsupella stoloniformis* M. Kitag. **Indigenous.** Kauaʻi (Waiʻaleʻale), extremely wet area near summit rim, open, exposed area in bog, terrestrial on soil, south facing aspect, forming a blackish mat on bog floor, 5,070 ft., 18 Jun 2024, K. Faccenda 3505a (BISH, PTBG). This tiny plant represents a new state record for Hawaiʻi and is also the first record of *Marsupella* Sect. *Stolonicaulon* (N. Kitag.) Váňa (Kitagawa, 1967b; Schuster, 1996: 68-74; Bakalin et al. 2022; Lee et al., 2022) for the state (Judziewicz et al., 2025b). We thank Frank Müller for suggesting the correct identification.



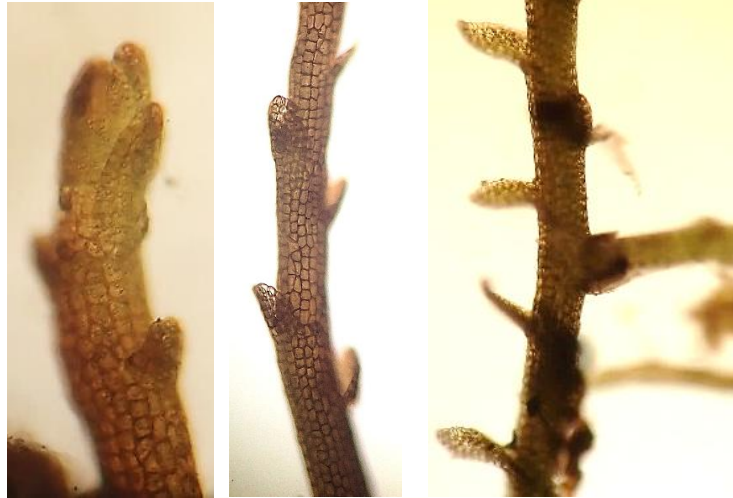
Marsupella stoloniformis is known from montane China (including Taiwan), Vietnam, Malaysia (Mt. Kinabalu, Sabah), and Papua New Guinea (Mt. Wilhelm). This tiny, blackish mat-forming plant superficially resembles species of *Cephaloziella* or *Cylindrocolea*. Unlike either one, the perianths are inconspicuous, the leaf cells are tiny, and most leaves are entire rather than bifid.

Populations form wiry, tangled blackish mats on the bog floor. Plants are stoloniferous, tiny, sterile shoots mostly 100-125 µm wide (female branches up to 450 µm wide). The stems have moderately thick-walled epidermal cells (sometimes with trigones) and are frequently branched. Leaves on sterile branches are tiny, entire, ovate-triangular, subacute to rounded, sometimes emarginate, distant, about as wide as the stem, appressed or spreading; with thin-walled cells, these quadrate and only around 15 µm wide; each cell has several large (6–8 µm in diameter) smooth oil bodies. A few larger, concave, imbricate, bifid leaves are present on female branches; these are gradually larger towards the gynoeceum where the plant width can be up to 0.45 mm wide; the sinus is narrowly acute above and slit-like below, to ½ the leaf length or sometimes deeper. Lobes are acute to acuminate and parallel, sometimes asymmetrical; leaf cells are moderately thick, reddish, with some trigones, up to 15-27(30) µm long by 10-17.5 µm wide. Gynoeceum terminal on branches, with large and bifid gynoeceal bracts 0.7–1 mm, and no obvious perianth (however, Schuster, 1996 and Kitagawa, 1967 describe a perigynium and a vestigial perianth). Androeceum terminal, 0.4–0.5 mm long, with 5-9 concave androeceal bracts subtending antheridia.

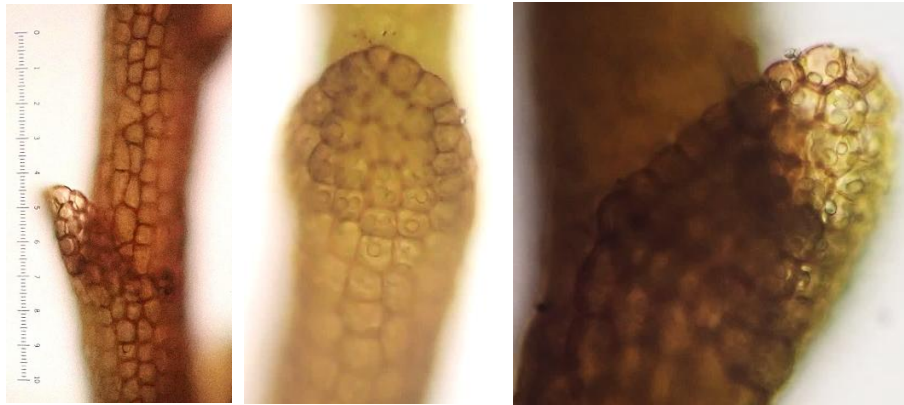
Schuster's description (1996) and illustrations of this species match the Hawaiian material very well, except that he describes and illustrates much thicker-walled leaf cells than we observed in our material.



Marsupella stoloniformis. Plants form a dense creeping mat. Waiʻaleʻale summit, K. Faccenda 3505a (BISH). Photo by K. Faccenda, <https://www.inaturalist.org/observations/224264671>, with permission.



Left: Stem apex. Center: Section of stem with slightly spreading ligulate leaves. Right: Leaves spreading at a broad angle. Faccenda 3505a (BISH, PTBG). Photos by A.V. Freire & E.J. Judziewicz.



Marsupella stoloniformis. Leaves (ca. 100 μm wide) are about as wide as stem and are not bifid (but see below); leaf cells thin-walled. Note smooth, spherical oil bodies. Left: Scale units = 2.5 μm . Faccenda 3505a (BISH, PTBG). Photos by A.V. Freire & E.J. Judziewicz.



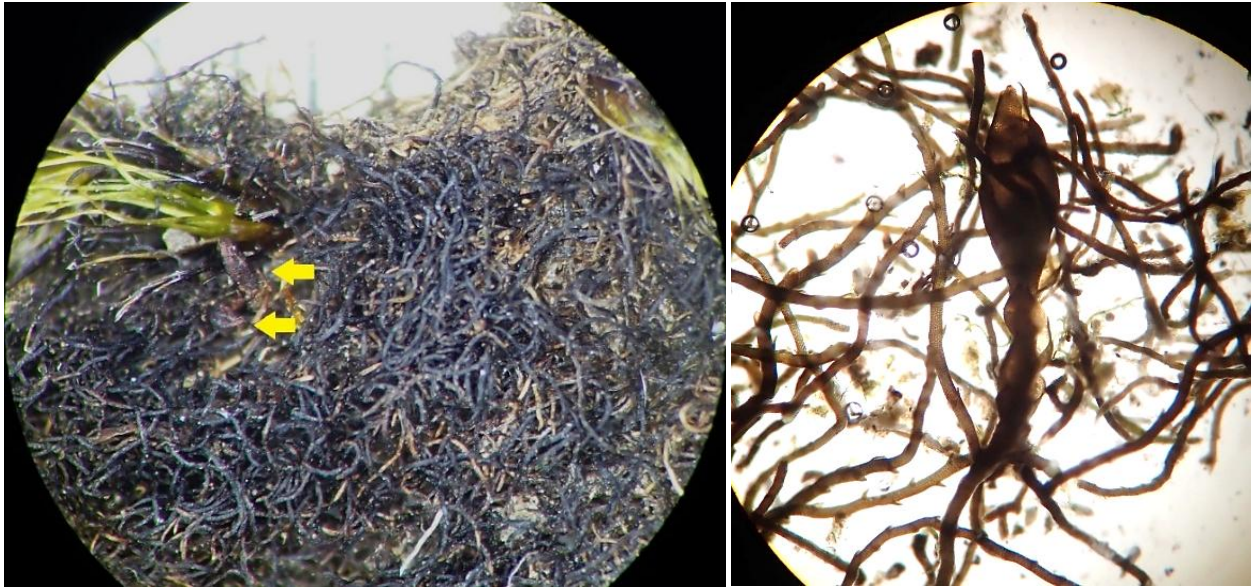
The “entire” leaves on sterile shoots sometimes have a rudimentary lobe. Scale units = 2.5 μm . Wai‘ale‘ale summit, Kaua‘i, K. Faccenda 3505a (BISH, PTBG). Photos by A.V. Freire.



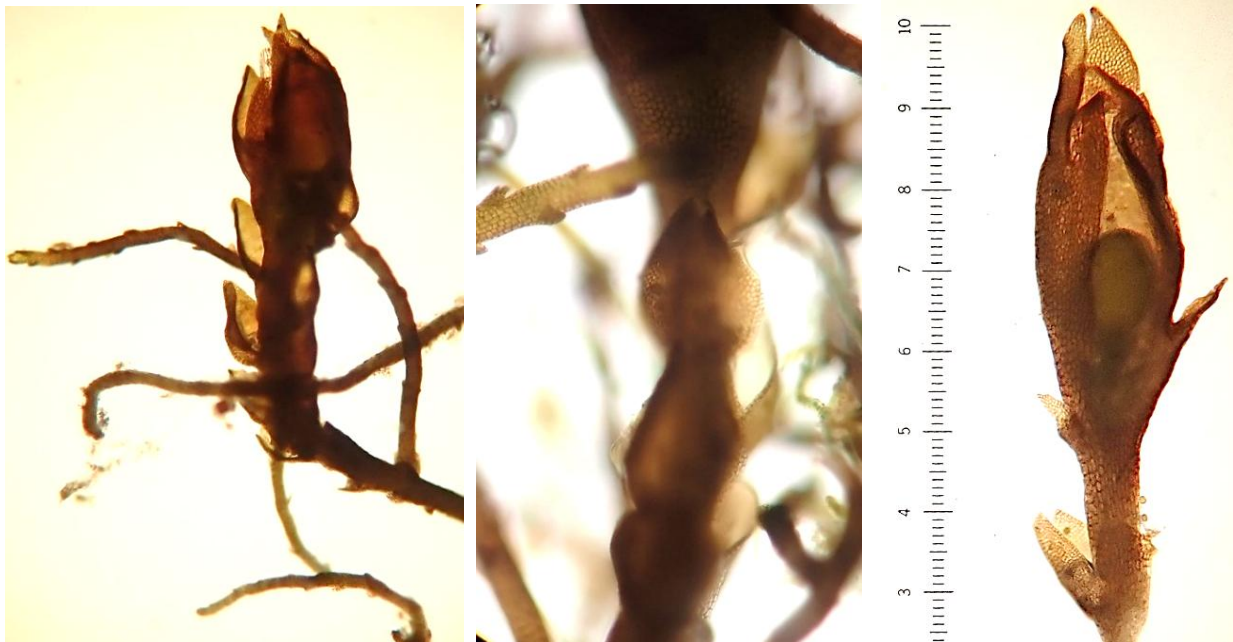
Bifid leaves on female branch are larger and concave/canaliculate, with acute to acuminate lobes that can be asymmetrical. Faccenda 3505a (BISH, PTBG). Photos by A.V. Freire.



Marsupella stoloniformis. Leaf cells are tiny, have moderately thickened walls, and have small trigones. Scale units = 2.5 μm . Wai'ale'ale summit, Kaua'i, Faccenda 3505a (BISH, PTBG). Photos by A.V. Freire.



Left: Gynoecia are 0.7-0.8 mm long (yellow arrows). Scale in mm. Photo by E.J. Judziewicz. Right: Gynoecium, note the enlarged leaves at its base. Photo by A.V. Freire.



Left and center: Gynoecium subtended by larger bifid leaves. Right: Section through gynoecium; no obvious perianth is observed. Note the fused lower half. Wai'ale'ale summit, Kaua'i, Faccenda 3505a (BISH, PTBG). Photos by A.V. Freire.



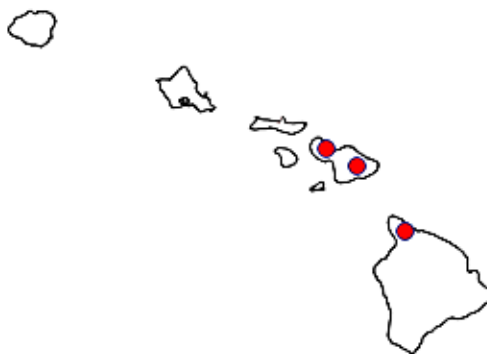
Marsupella stoloniformis. Androecial branch ca. 0.5 mm long (red arrow). Wai‘ale‘ale summit, Kaua‘i, K. Faccenda 3505a (BISH, PTBG). Photos by E.J. Judziewicz & A.V. Freire.

Metacalypogeia (S. Hatt.) Inoue (Calypogeiaceae)

One species in Hawai‘i, three species worldwide.

Metacalypogeia alternifolia (Nees) Grolle. **Indigenous.**

A temperate Asian and North American genus (Schuster, 1995b; Lee & Gradstein, 2021: 55); related to *Calypogeia*. It supposedly occurs on all major islands except Lāna‘i (Miller, 1983: 220, later cited by Staples & Imada, 2006). However, we have not collected any Hawaiian material, and it appears that Miller initially confounded this species with *Mnioloma fuscum* and that many of his reports (Miller, 1963: 499-500) of *Calypogeia alternifolia* (= *Metacalypogeia alternifolia*) from many islands should be referred to *Mnioloma fuscum*. See discussion in Judziewicz et al. (2025b: 135).



Zach Pezzillo and Remy Henderson (1995, BISH) recently collected this species several times from Waikamoi Preserve, Maui (photos below) and Pezzillo once from Pu‘u Kukui, West Maui (1074, BISH), at elevations from 3,600-5,600 ft.; in 2026, Miles K. Thomas and Pezzillo collected it from near Pu‘u ‘Eke, West Maui (BISH). There are also two other possible authentic Hawaiian records of this species, both from Kohala, Hawa‘i Island, reported by Miller (1963: 500-501) as *Metacalypogeia montana* (Horik.) Inoue var. *verruculosa* (Hatt.) H.A. Mill.: “Upper Hāmākua Ditch Trail between Koiawe and Waima Valleys, Selling 5405; [and] above Waima, in cave, Selling 5371” (both collections in S, the Stockholm Herbarium, and not examined by us). Miller cites Yukinobu Kuwahara as the determiner of these specimens; presumably Kuwahara would have been familiar with this species, which is common in Japan (Yamada & Iwatsuki, 2006).

Metacalypogeia alternifolia differs from the common Hawaiian species of *Calypogeia* in the entire rather than bifid underleaves (although the rare *C. aeruginosa* has very broad entire leaves and is heavily pigmented). It is also related to *Mnioloma fuscum* but is turquoise greenish (never fuscous brownish) in color and has pointed leaves that have small trigones. The underleaves of *Metacalypogeia* are chlorophyllous, much larger, and mostly perfectly rounded at the apex, whereas in *Mnioloma* the underleaves lack chlorophyll, are much smaller, and have an apex that is often very slightly irregular with a minute indentation about one cell layer deep (underlined by very unique elongated convergent cells not observed in *Metacalypogeia*). It is apparently much less common than *Mnioloma*; we had not seen any material at BISH, MU, or PTBG. *Metacalypogeia* resembles some species of *Bazzania*, differing from that genus in its lack of ventral microphyllous branches.

Plants are turquoise green, at least 1-1.5 cm long and up to 3 mm wide. They creep loosely attached to their substrate. Stems are stout, dark in color, with some branching, sometimes with long microphyllous apical sections. No gemmae were observed. Leaves distant to slightly imbricate, incubous, spreading at 45°, ligulate, concave, inserted beyond the stem midline on the dorsal side; with pointed apices that may have a shallow notch, curled towards the ventral side. Leaf cells are elongate, thin-walled, and bear small trigones. Underleaves are large, reniform, about twice as wide as they are long, and about 2.5-3 times as broad as the stem; they bear trigones and colorless rhizoids at their base. Sexual organs not observed.



Pu'u near 'Eke, West Maui, 29 Jan. 2026, M.K. Thomas & Z. Pezzillo s.n. (BISH); photo by Miles K. Thomas, with permission: <https://www.flickr.com/photos/mileskt/55258152534/in/dateposted/>.



Metacalypogeia alternifolia. Note turquoise-green color of fresh plants. Scale in mm. Waikamoi Preserve, East Maui, 4,600 ft., Pezzillo & Henderson 995 (BISH). Photo by E.J. Judziewicz.



Left: Dorsal view showing long insertion line of leaves. Right: Ventral view showing distant leaves and large underleaves. West Maui, Thomas & Pezzillo s.n. (BISH). Photos by A.V. Freire.



Metacalypogeia alternifolia. Left: Waikamoi Preserve, Maui, 4,600 ft., Pezzillo & Henderson 995 (BISH). Photo by E.J. Judziewicz. Right: West Maui, Thomas and Pezzillo s.n. (BISH). Photo by A.V. Freire. Scales in mm.



Metacalypogeia alternifolia. Top: Leaf apices vary from rounded to acute, to one-cell-notched. Underleaves are large and reniform, with entire apices. Bottom: Leaf cells showing small trigones. Waikamoi Preserve, Maui, 4,600 ft., Pezzillo & Henderson 995 (BISH). Photos by E.J. Judziewicz.

REFERENCES

Includes citations for both the present volume as well as future volumes in progress. **Citations new to Volume 2 are bolded.**

- Ackerman, C., S. Anderson and C. Anderson. 2008. Extremophilic eukaryote life in Hawaiian fumaroles. American Geophysical Union, Fall Meeting 2008. Abstract identification BSI-D-0422.
- Alam, A. and S.C. Srivastava. 2009. Current status of genus *Plagiochasma* in Nilgiri and Palni hills with SEM details of spores. Indian Journal of Forestry 32(4): 623-634.
- Álvaro-A., W.R. and J. Uribe-M. 2017. Revisión taxonómica del género *Anastrophyllum* (Marchantiophyta, Anastrophyllaceae) para Colombia. Caldasia 39(2): 269-291.
- Amakawa, T. 1960. Family Jungermanniaceae of Japan. II. Journal of the Hattori Botanical Laboratory 22: 1-90.
- Amakawa, T. and S. Hattori. 1955. A revision of the Japanese species of the Scapaniaceae. III. Journal of the Hattori Botanical Laboratory 14: 71-90.
- Amélio, L. de, A.M. de Souza, D.F. Peralta and E. de B. Valente. 2021. A taxonomic review of Brazilian *Dendroceros* Nees (Dendrocerotaceae). Pesquisas, Botânica 75: 237-251.
- Anonymous (H.A. Miller? W.A. Weber?). Nov. 1985. Checklist of bryophytes of Hawai'i Volcanoes National Park. Unpublished 4 pg. list, deposited at Hawai'i Volcanoes National Park Herbarium.
- Aranda, S.C., S.R. Gradstein, J. Patiño, B. Laenen, A. Désamaré and A. Vanderpoorten. 2014. Phylogeny, classification and species delimitation in the liverwort genus *Odontoschisma* (Cephaloziaceae). Taxon 63(5): 1008-1025.
- Asakawa, Y. 2008. Recent advances of biologically active substances from the Marchantiophyta. Natural Product Communications 3(1): 77-92.
- Asthana, G. and Murti. 2009. *Geocalyx lancistipulus* (Geocalycaceae), a marsupiate liverwort new to the Indian bryoflora. The Bryologist 112(2): 359-362.
- Austin, C.F. 1869. Characters of some new Hepaticae (mostly North American), together with notes on a few imperfectly described species. Proceedings of the Academy of Natural Sciences of Philadelphia 21(4): 218-234.
- Austin, C.F. 1874. Sandwich Island Hepaticae, collected by H. Mann and W.T. Brigham, and named by C.F. Austin. Bulletin of the Torrey Botanical Club 5(3): 14-16.
- Bączkiewicz, A., M. Szczecińska, J. Sawicki, A. Stebel and K. Buczkowska. 2017. DNA barcoding, ecology and geography of the cryptic species of *Aneura pinguis* and their relationship with *Aneura maxima* and *Aneura mirabilis* (Metzgeriales, Marchantiophyta). PLoS One 512: e0188837.
- Bakalin, V.A., V.E. Federov, A.V. Fedorova and V.S. Nguyen. 2019. Integrative taxonomic revision of *Marsupella* (Gymnomitriaceae, Hepaticae) reveals neglected diversity in Pacific Asia. Cryptogamie, Bryologie 40(7): 59-85.
- Bakalin, V.A., K.G. Klimova and V.S. Nguyen. 2020a. A review of *Calypogeia* (Marchantiophyta) in the eastern Sino-Himalaya and Meta-Himalaya based mostly on types. PhytoKeys 153: 111-154.
- Bakalin, V.A., A.A. Vilnet, S.S. Choi and V.S. Nguyen. 2020b. *Blepharostoma trichophyllum* s.l. (Marchantiophyta): The complex of sibling species and hybrids. Plants 2020, 9, 1423. doi:10.3390/plants9111423.
- Bakalin, V.A., Y.D. Maltseva, K.G. Klimova, V.S. Nguyen, S.S. Choi and A.V. Troitsky. 2022a. The systematic position of puzzling Sino-Himalayan *Lophocolea sikkimensis* (Lophocoleaceae, Marchantiophyta) is identified. PhytoKeys 206: 1-24.

- Bakalin, V.A., Y.D. Maltseva, F. Müller, K.G. Klimova, V.S. Nguyen, S.S. Choi and A.V. Troitsky. 2022b. *Calypogeia* (Calypogeiaceae, Marchantiophyta) in Pacific Asia: Updates from molecular revision with particular attention to the genus in north Indochina. *Plants* 2022(11), 983: 1-56.
- Bakalin, V.A., A.A. Vilnet, Y.S. Mamontov, A. Schäfer-Verwimp, Y.D. Maltseva, K.G. Klimova, V.S. Nguyen and S.S. Choi. 2022c. *Stolonicaulon*: A section-puzzle within *Marsupella* (Gymnomitriaceae, Marchantiophyta). *Plants* 11(12): 1596. DOI: [10.3390/plants11121596](https://doi.org/10.3390/plants11121596)
- Bakalin, V.A., Y.D. Maltseva, K.G. Klimova, V.S. Nguyen, S.S. Choi and A.V. Troitsky. 2024. New insight into the taxonomy of Cephaloziellaceae (Marchantiophyta): The family of the smallest higher plants on earth. *Frontiers in Plant Science* 15: 1326810.
- Bakalin, V.A. and A.A. Vilnet. 2018. A review of the genus *Diplophyllum* (Marchantiophyta) in North and East Asia with the description of a new species (*D. sibiricum*) based on integrative taxonomy. *Plant Systematics and Evolution* 304: 1269-1287.
- Bakalin, V.A. and Y. Xiong. 2015. *Lophozia silvicola* (Scapaniaceae, Hepaticae) – An unexpected record of a boreal species in the subtropical forest of Guizhou (southern China). *Herzogia* 28(1): 44-49.
- Bardat, J., L. Söderström, A. Hagborg, S. Leblond and S.R. Gradstein. 2021. Checklist of the liverworts and hornworts of French Polynesia. *Cryptogamie, Bryologie* 42(6): 73-116.
- Barthlott, W., E. Fischer, J.P. Frahm and R. Seine. 2000. First experimental evidence for zoophagy in the hepatic *Colura*. *Plant Biology (Stuttgart)* 2: 93-97.
- Bartram, E.B. 1933. Manual of Hawaiian mosses. Bernice P. Bishop Museum Bulletin 101: 1-275.
- Bell, D. 2020. Systematics of deep and recent lineages of bryophytes using phylogenomic approaches. Phd Thesis, University of British Columbia. 272 Pages.
- Benitez, D.M., T. Belfield, R. Loh, L. Pratt and A.D. Christie. 2008. Inventory of vascular plants of the Kahuku Addition, Hawai'i Volcanoes National Park. Pacific Cooperative Studies Unit University of Hawai'i at Mānoa Technical Report 157: 1-115.
- Bischler, H. 1964. Le genre *Drepanolejeunea* Steph. en Amérique Centrale et Méridionale. *Revue Bryologique et Lichenologique* 33: 15-179.**
- Bischler, H. 1967 [1968]. Le genre *Drepanolejeunea* Steph. en Amérique Centrale et Méridionale. Part II. *Revue Bryologique et Lichenologique* 35: 95-134.**
- Bischler-Causse, H. 1979. *Plagiochasma* Lehm. et Lindenb. III. Les taxa d'Asie et d'Océanie. *Journal of the Hattori Botanical Laboratory* 45: 25-79.
- Bischler-Causse, H. 1989. *Marchantia* L., the Asiatic and Oceanic taxa. *Bryophytarum Bibliotheca* 38: 317 pages.
- Bischler-Causse, H., S.R. Gradstein, S. Jovet-Ast, D.G. Long and N. Salazar Allen. 2005. Marchantiidae. *Flora Neotropica Monograph* 97: iv + 262 pp.
- Brinda, J.C. and J.J. Atwood (eds.) 2025. The Bryophyte Nomenclator, 7 Apr. 2025. <https://www.bryonames.org/>
- Briscoe, L., J. Engel, L. Söderström, A. Hagborg and M. Von Konrat. 2015. Notes on early land plants today. 66. Nomenclatural notes on Acrobolbaceae. *Phytotaxa* 202(1): 58-62.
- Brown, E.A. and J.E. Braggins. 1989. A revision of the genus *Riccardia* S.F. Gray in New Zealand with notes on the genus *Aneura*. *Journal of the Hattori Botanical Laboratory* 66: 1-132.
- Burghardt, M. and S.R. Gradstein. 2008. A Revision of *Tylimanthus* (Acrobolbaceae, Marchantiophyta) in Tropical America, Africa, and Macaronesia. *Fieldiana Botany*, 2008(47): 199-210.
- Campbell, D.H. 1933. The Flora of the Hawaiian Islands. *Quarterly Review of Biology* 8(2): 164-184.
- Chandini, V. K. & T. Pócs & C. N. Manju. 2021. The genus *Diplasiolejeunea* (Lejeuneaceae, Porellales) new to India, with records of two species from the Western Ghats. *Acta Botanica Hungarica* 63(3-4): 285-296.**
- Chantanaorrapint, S. and K. Sridith. 2014. The genus *Plagiochasma* (Aytoniaceae, Marchantiopsida) in Thailand. *Cryptogamie, Bryologie* 35(2): 127-132.

- Cooke, C.M. 1904. The Hawaiian Hepaticae of the tribe Trigonantheae. Transactions of the Connecticut Academy of Arts and Sciences 12: 1–44.
- Costa, D.P. 2008. Metzgeriaceae (Hepaticae). Flora Neotropica 102: 1–169.
- Crandall-Stotler, B., R. Stotler and D.G. Long. 2009. Phylogeny and classification of the Marchantiophyta. Edinburgh Journal of Botany 66: 155–198.
- Cuddihy [now Pratt], L.W., S.J. Anderson, C.P. Stone and C.W. Smith. 1986. A botanical baseline study of forests along the East Rift of Hawai'i Volcanoes National Park adjacent to Kahauale'a. Cooperative National Park Resources Studies Unit, University of Hawai'i at Mānoa. NPS Contract CA 8002-2-0001.
- Daniels, A.E.D., K.C. Kariyappa and R. Sreebha. 2014. On the occurrence of *Calycularia crispula* Mitt. (Calyculariaceae) in the Western Ghats, India. Acta Botanica Hungarica 56(3-4): 293–297.
- Dauphin, G., L. Söderström, A. Hagborg, N. Salazar Allen, A.M. Sierra, T. Pócs, J. Gudiño L., M.E. Pérez, J.C. Villarreal, Y. Rodríguez, M. von Konrat and A. Whittemore. 2025. Catalog of liverworts (Marchantiophyta) and hornworts (Anthocerotophyta) from Central America and Cocos Island. Smithsonian Contributions to Botany 119: 1–449.
- Deepa, K.M., B. Mufeed and C.N. Manju. 2019. *Wiesnerella denudata* (Mitt.) Steph. (Marchantiales; Marchantiophyta), a rare species in the western Ghats of India.
- Degenkolbe, W. 1938. Brutorgane bei beblätterten Lebermoosen. Annales Bryologici 10: 43–96.**
- Dey, M., D. Singh and D.K. Singh. 2011. *Jubula pennsylvanica* (Hepaticae: Jubulaceae) new to Asia. Taiwania 56(1): 66–70.
- Engel, J.J. 2010. Austral Hepaticae 45. A monograph of the genus *Chiloscyphus* Corda (Lophocoleaceae) for Australasia. Fieldiana Botany, 2010(48): 1–206.
- Engel, J.J. and D. Glenny. 2008. A flora of the liverworts and hornworts of New Zealand. Volume 1. Monographs in Systematic Botany from the Missouri Botanical Garden 110: 1–897.
- Engel, J.J. and D. Glenny. 2019a. A flora of the liverworts and hornworts of New Zealand. Volume 2. Monographs in Systematic Botany from the Missouri Botanical Garden 134: 1–739.
- Engel, J.J. and D. Glenny. 2019b. A flora of the liverworts and hornworts of New Zealand. Volume 3. Monographs in Systematic Botany from the Missouri Botanical Garden 135: 1–672.
- Evans, A.W. 1891. A provisional list of the hepaticae of the Hawaiian Islands. Transactions of the Connecticut Academy of Arts and Sciences 8(15): 253–261.
- Evans, A.W. 1900. The Hawaiian hepaticae of the tribe Jubuloideae. Transactions of the Connecticut Academy of Arts and Sciences 10: 387–460 + plates.
- Evans, A.W. 1915. The genus *Plagiochasma* and its North American species. Bulletin of the Torrey Botanical Club 42: 259–308.
- Faubert, J. 2015. Aneuraceae. Bryophyte Flora of North America, Provisional Publication, Missouri Botanical Garden. <https://www.mobot.org/plantscience/bfna/V3/Aneuraceae.htm>.
- Feldberg, K., J. Vána, J. Hentschel and J. Heinrichs. 2010. Currently accepted species and new combinations in Jamesonielloideae (Adelanthaceae, Jungermanniales). Cryptogamie, Bryologie 31(2): 141–146.
- Flores, J.R. and G.M. Suárez. 2015. *Plagiochasma intermedium* Lindenb. & Gottsche (Aytoniaceae, Marchantiophyta), the third species of *Plagiochasma* for southern South America. Cryptogamie, Bryologie 36(1): 1–6.
- Forrest, L.L., N. Salazar Allen, J.A. Gudiño, H. Korpelainen, and D.G. Long. 2011. Molecular and morphological evidence for distinct species in *Dumortiera* (Dumortieraceae). Bryologist 114: 102–115.
- Freire, A.V. 2002. A Revision of the Genus *Fossombronina* in Latin America. Doctoral Dissertation, Southern Illinois University, Carbondale, IL. 275 pages.
- Freire, A.V. and E.J. Judziwicz. 2020. Bryophytes of the Kaiholena Unit of The Nature Conservancy's Ka'ū Preserve. Report to The Nature Conservancy.

- Freire, A.V. and E.J. Judziewicz. 2022a. Liverworts and hornworts of Hawai‘i Volcanoes National Park. Report to the National Park Service.
- Freire, A.V. and E.J. Judziewicz. 2022b. Liverworts and hornworts of the Kahuku Unit of Hawai‘i Volcanoes National Park. Report to the National Park Service.
- Freire, A.V., E.J. Judziewicz, D.C. Cargill, L.L. Forrest, S.R. Gradstein, H.L. Oppenheimer, Z. Pezzillo and S. Sepsenwol. 2023. *Kahakuloa operculispora*, a new Hawaiian simple thalloid liverwort in a new genus and family, Kahakuloaceae, Fossombroniales. *Bryophyte Diversity and Evolution* 46: 10-34.
- Furuki, T. 1991. A taxonomical revision of the Aneuraceae (Hepaticae) of Japan. *Journal of the Hattori Botanical Laboratory* 70: 293-397.
- Garcia, C. C. Sérgio, J.C. Villareal, N. Sim-Sim and F. Lara. 2012. The hornworts *Dendroceros* Nees and *Megaceros* Campb. in São Tomé e Príncipe (Africa, Gulf of Guinea) with the description of *Dendroceros paivae* sp. nov. *Cryptogamie, Bryologie* 33(1): 3-21.
- Gibb, E.S. et al. 2017. Checklist of the New Zealand Flora – Hornworts, liverworts, and mosses. Lincoln, Manaaki Whenua-Landcare Research.
- Glime, J.M. 2025. Bryophyte Ecology: <https://digitalcommons.mtu.edu/bryophyte-ecology>.
- Gottsche, C.M., Lindenberg, J.B.W. & C.G.D. Nees von Esenbeck. 1844. Synopsis Hepaticarum. 834 pp. Meissner, Hamburg.**
- Gradstein, S.R., S.P. Churchill and N.S. Allen. 2001. Guide to the Bryophytes of Tropical America. *Memoirs of the New York Botanical Garden* 86: i-viii + 1-577.
- Gradstein, S.R. and D.P. Costa. 2003. The Hepaticae and Anthocerotae of Brazil. *Memoirs of the New York Botanical Garden* 87: i-xviii + 1-318.
- Gradstein, S.R. and A.L. Ilkiu-Borges. 2009. Guide to the plants of Central French Guiana. Part 4. Liverworts and hornworts. *Memoirs of the New York Botanical Garden* 76: i-iv + 1-140.
- Gradstein, S.R. 2012. An overview of the genus *Marchesinia* (Marchantiophyta: Lejeuneaceae), with special attention to the species described from Asia and Oceania. *Polish Botanical Journal* 57(1): 69–79.
- Gradstein, S.R. and A.L. Ilkiu-Borges. 2015. Taxonomic monograph of the genus *Odontoschisma* (Cephaloziaceae) based on molecular and morphological evidence. *Nova Hedwigia* 100: 15–100.
- Gradstein, S.R. 2017. *Bazzania* (Marchantiophyta) in South America. *Nova Hedwigia* 105 (1-2): 243-266.
- Gradstein, S.R. 2018. Amphi-tropical Pacific disjunctions in the bryophyte flora of Asia and the New World. *Philippine Journal of Systematic Biology* 12(1): 1-11.
- Gradstein, S.R. and C. Reeb. 2018. The genus *Riccardia* (Aneuraceae) in Colombia and Ecuador. *Cryptogamie, Bryologie* 39(4): 515–540.
- Gradstein, S.R. and E.L. Bernard. 2020. An evaluation of the endemic bryophyte flora of Guadeloupe. *Cryptogamie, Bryologie* 41: 205-214.
- Gradstein, S.R. 2021. The Liverworts and Hornworts of Colombia and Ecuador. *Memoirs of New York Botanical Garden* 121: 1-723.
- Grolle, R. and S. Piippo. 1986. Bryophyte flora of the Huon Peninsula, Papua New Guinea. XVI. Pallaviciniaceae (Hepaticae). *Acta Botanica Fennica* 133: 59–79.
- Grolle, R. 1988. *Miscellanea Hepaticologica* 261–270. *Journal of the Hattori Botanical Laboratory* 65: 403–410.
- Grolle, R. 1991. *Miscellanea Hepaticologica* 281–290. *Journal of the Hattori Botanical Laboratory* 69: 185–194.
- Grolle, R. and M.L. So. 2000. Notes on *Plagiochila* Section *Firmae* (Hepaticae). *Systematic Botany* 25: 5-14.
- Grolle, R. and H. Persson. Die Gattung *Tylimanthus* auf den Atlantischen Inseln. *Svensk Botanisk Tidskrift* 60: 164–174.
- Guerke, W.R. 1978. Monograph of the genus *Jubula*. *Bryophytarum Bibliotheca* 17: 1-114.
- Gustafson, R.J., D.R. Herbst and P.W. Rundel. 2014. *Hawaiian Plant Life: Vegetation and Flora*. University of Hawai‘i Press. 336 pages.
- Haerida, I., S.R. Gradstein and S.S. Tjitrosoedirdjo. 2010. Lejeuneaceae subfamily Ptychanthoideae (Hepaticae) in West Java. *The Gardens’ Bulletin Singapore* 62(1): 53-103.

- Hall, J.B., S. Fukuda and W.J. Hoe. 1995. *Riccia fluitans* (Hepaticae, Ricciaceae): first observation in Hawai'i. *Fragmenta Floristica et Geobotanica* 40(1): 233–234.
- Hawaii, DLNR. 2013. Pu'u Maka'ala Natural Area Reserve (NAR) Management Plan. 2013. Report to Hawaii DLNR. 86 pages.
- Heinrichs, J., K. Feldberg, J. Bechteler, A. Scheben, A. Czumaj, T. Pócs, H. Schneider and A. Schäfer-Verwimp. 2015. Integrative taxonomy of *Lepidolejeunea* (Jungermanniopsida: Porellales): Ocelli allow the recognition of two neglected species. *Taxon* 64(2): 216–228.
- Hess, S., J.-P. Frahm and I. Theisen. 2005. Evidence of zoophagy in a second liverwort species, *Pleurozia purpurea*. *The Bryologist*. 108(2): 212–218.
- Hewson, H.J. 1970. The family Aneuraceae in Australia and New Guinea: II. The genus *Riccardia*. *Proceedings of the Linnean Society of New South Wales* 95(1): 60–121 + 4 plates.
- Higashino, P.K., L.W. [Pratt] Cuddihy, S.J. Anderson and C.P. Stone, 1988. Bryophytes and vascular plants of Kīpahulu, Haleakalā National Park. PCSU Technical Report 65: 1-63.
- Hobdy, R. 1993. Lāna'i - A case study: The loss of biodiversity on a small Hawaiian Island. *Pacific Science* 47: 201-210.
- Hodgetts, N.G., L. Söderström, T.L. Blockeel, S. Caspari, M.S. Ignatov, N.A. Konstantinova, N. Lockhart, B. Papp, C. Schröck, M. Sim-Sim, D. Bell, N.E. Bell, H.H. Blom, M.A. Bruggeman-Nannenga, M. Brugués, J. Enroth, K.I. Flatberg, R. Garilleti, L. Hedenäs, D.T. Holyoak, V. Hugonnot, I. Kariyawasam, H. Köckinger, J. Kučera, F. Lara and R.D. Porley. 2020. An annotated checklist of bryophytes of Europe, Macaronesia and Cyprus. *Journal of Bryology* 42(1): 1-116.
- Hoe, W.J. 1978. *Riccia sorocarpa* Bisch. in Hawai'i. *Miscellanea Bryologica et Lichenologica* 8: 52– 53.
- Huang, S.-F. and S.-H. Lin. 2009. Materials to [sic] the bryophyte flora of Taiwan (I): *Cephaloziella microphylla* (Steph.) Douin (Cephaloziellaceae). *Taiwania* 54(1): 97-99.
- Hürlimann, H. 1976. Hepaticae aus dem Gebiete des südlichen Pazifik. IV. Aneuraceae. *Bauhinia* 5: 191-213.
- Hürlimann, H. 1986. *Riccia hawaiiensis* Hürl., species nova. *Phytologia* 61(5): 339–342.
- Inoue, H. 1962. Notes on *Plagiochila eatonii* Austin, a Hawaiian liverwort. *Journal of Japanese Botany* 37(12): 357–360.
- Inoue, H. 1964. The genus *Plagiochilon*. *Journal of the Hattori Botanical Laboratory* 27: 51-72.
- Inoue, H. 1966. A monograph of the hepatic genus *Syzygiella* Spruce. *Journal of the Hattori Botanical Laboratory* 29: 171-213.
- Inoue, H. 1974a. Illustrations of Japanese Hepaticae – 1. Tsukiji Shokan, Tokyo. 189 pages.
- Inoue, H. 1974b. *Temnoma setigerum* (Lindenb.) Schust. from the Hawaiian Islands. *Bulletin of the National Science Museum, Tokyo* 17(3): 227– 231.
- Inoue, H. 1976a. Illustrations of Japanese Hepaticae – 2. Tsukiji Shokan, Tokyo. 193 pages.
- Inoue, H. 1976b. Notes on the Plagiochilaceae, V. studies in the genus *Plagiochila* (Dumort.) Dumort. in the Hawaiian Islands. *Journal of the Hattori Botanical Laboratory* 40: 411–440.
- Inoue, H. 1976c. Illustrations of Japanese Hepaticae – 2. Tsukiji Shokan, Tokyo. 193 p.
- Inoue, H. 1982. Speciation and distribution of *Plagiochila* in Australasia and the Pacific. *Journal of the Hattori Botanical Laboratory* 52: 44–56.
- Judziewicz, E.J. and A.V. Freire. 2022a. Liverworts and hornworts of the Pu'u Maka'ala Natural Area Reserve. Report to the Hawai'i Department of Land and Natural Resources.
- Judziewicz, E.J. and A.V. Freire. 2022b. Liverworts and hornworts of the Manukā Natural Area Reserve. Report to the Hawai'i Department of Land and Natural Resources.
- Judziewicz, E.J. and A.V. Freire. 2023a. Liverworts and hornworts of The Nature Conservancy's Waimakoi Preserve, Maui. Report to The Nature Conservancy.
- Judziewicz, E.J. and A.V. Freire. 2023b. Liverworts and hornworts of the Hakalau Forest National Wildlife

- Refuge. Report to the U.S. Fish and Wildlife Service.
- Judziewicz, E.J. and A.V. Freire. 2023c. Updates to the Hawaiian hornwort (Antherocerotophyta) and liverwort (Marchantiophyta) floras: Species new to Hawai‘i and name changes. Bishop Museum Occasional Papers: 155: 167-176.
- Judziewicz, E.J., A.V. Freire and K.K. Bogner. 2023. A survey of Lāna‘i hornworts and liverworts, including 63 new island records. Bishop Museum Occasional Papers: 155: 9-38.
- Judziewicz, E.J., A.V. Freire and M.K. Thomas. 2024a. New Hawaiian bryophyte records from Herbarium Pacificum for 2024: 106 new island records for Hawaiian liverworts and hornworts. Bishop Museum Occasional Papers 156: 3-22.
- Judziewicz, E.J. and A.V. Freire. 2024b. Liverworts and hornworts of the Pu‘u o ‘Umi Natural Area Reserve. Report to the Hawai‘i Department of Land and Natural Resources.
- Judziewicz, E.J. and A.V. Freire. 2024c. Liverworts and hornworts of the Laupāhoehoe Natural Area Reserve. Report to the Hawai‘i Department of Land and Natural Resources.
- Judziewicz, E.J., K. Faccenda and A.V. Freire. 2025a. Liverworts (Marchantiophyta) of the Kaua‘i Summits, Hawai‘i, with two new state records and four new island records. Bishop Museum Occasional Papers 160: 55-95.
- Judziewicz, E.J., A.V. Freire, Z. Pezzillo, K. Faccenda, S. Fawcett, P. Christianson and W.C. Bleecker. New Hawaiian bryophyte records from Herbarium Pacificum for 2025: 30 new island records and seven new state records for Hawaiian liverworts and hornworts. Bishop Museum Occasional Papers 163: 131-147 (2025). <https://hbs.bishopmuseum.org/pubs-online/pdf/op163p131-147.pdf>.**
- Juslén, A. 2004. Bryophyte flora of Hunan Province, China. 7. *Herbertus* (Herbertaceae, Hepaticae). *Annales Botanici Fennici* 41: 393–404.**
- Juslén, A. 2006. Revision of Asian *Herbertus* (Herbertaceae). *Annales Botanici Fennici* 43: 409–436.
- Katagiri T., T. Yamaguchi and H. Deguchi. 2010. Taxonomic studies on the liverwort *Jubula* Dumort. (Marchantiophyta: Jubulaceae) in Japan. *Hikobia* 15: 463–472.
- Katagiri, T. and T. Furuki. 2018. Checklist of Japanese liverworts and hornworts, *Hattoria* 9: 53-102.
- Katagiri, T., A. Sadamitsu, H. Miyauchi, H. Tsubota and H. Deguchi. 2013. Taxonomic studies of the Trichocoleaceae in Southeast Asia. III. The genus *Trichocolea* Dumort. *Hattoria* 4: 1-42. 2013.
- Khotimperwati, L., R.S. Kasiamdari, Santose and B.S. Daryono. 2018. *Bazzania* Gray (Lepidoziaceae, Marchantiophyta) in Central Java, Indonesia. *Biodiversitas* 19(2): 875-887.
- Kitagawa, N. 1967. Marsupellae of Mt. Kinabalu, Borneo. *Journal of the Hattori Botanical Laboratory* 30: 199-204.
- Khotimperwati, L., R.S. Kasiamdari, Santose and B.S. Daryono. 2018. *Bazzania* Gray (Lepidoziaceae, Marchantiophyta) in Central Java, Indonesia. *Biodiversitas* 19(2): 875-887.
- Kitagawa, N. 1967a. Studies on the Hepaticae of Thailand. I. The genus *Bazzania*, with general introduction. *Journal of the Hattori Botanical Laboratory* 30: 249-270.
- Kitagawa, N. 1972. Miscellaneous notes on little-known species of Hepaticae, 1-25. *Journal of the Hattori Botanical Laboratory* 36: 444-454.
- Kitagawa, N. 1973. A new species of *Southbya*, Hepaticae. *Acta Phytotaxonomica et Geobotanica* 25: 127-130.
- Klazenga, N. 2017. Report of the nomenclature committee for bryophytes: 13. *Taxon* 66(3): 745–746.
- Krayesky, D.M., B. Crandall-Stotler and R.E. Stotler. 2005. A revision of the genus *Fossombronina* Raddi in East Asia and Oceania. *Journal of the Hattori Botanical Laboratory* 98: 1–45.
- Laaka-Lindberg, S, T.A. Hedderson and R.E. Longton. 2000. Rarity and reproductive characters in the British hepatic flora. *Lindbergia* 25: 78–84.**
- Lee, G.E., 2013. A systematic revision of the genus *Lejeunea* Lib. (Marchantiophyta: Lejeuneaceae) in Malaysia. *Cryptogamie, Bryologie* 34: 381-484.
- Lee, G.E., J. Bechteler, T. Pócs, A. Schäfer-Verwimp, H.Y. Tang and P.W. Chia. 2022. Integrative taxonomy reveals a new species of the genus *Lejeunea* (Marchantiophyta: Lejeuneaceae) from

- peninsular Malaysia. *Plants* 11(13): 1642 [1-12].
- Lee, G.E. and S.R. Gradstein. 2021. Guide to the Liverworts and Hornworts of Malaysia. Hattori Botanical Laboratory. 234 pages.
- Lee, G.E., S.R. Gradstein, E. Pesiu and N. Norhazrina Binti Nik Mohamed Kamil. 2022. An updated checklist of liverworts and hornworts of Malaysia. *PhytoKeys* 199: 29-111.
- Lee, G.E., J. Bechteler, T. Pócs, A. Schäfer-Verwimp, X. He, C. Ah-Peng and L. Zhang. 2026a. **Species delimitation in genus *Lejeunea* (Marchantiophyta: Lejeuneaceae) through molecular phylogeny, morphology and biogeography, and the discovery of a new species from Fiji.** *Plant Systematics and Evolution* 312(1).
- Lee, G.E., S.R. Gradstein, X. He, J. Bechteler, A. Schäfer-Verwimp and T. Pócs. 2026b. **An infrageneric classification of the genus *Lejeunea* (Marchantiophyta: Lejeuneaceae) using molecular phylogeny and morphology.** *Plant Ecology and Evolution* 159(1): 123-141.
- Lewis, L.R., E. Behling, H. Gouse and E. Qian. 2014. First evidence of bryophyte diaspores in the plumage of transequatorial migrant birds. *PeerJ* 2(1): e424.
- Long, D.G. and R. Grolle. 1990. Hepaticae of Bhutan II. *Journal of the Hattori Botanical Laboratory* 68: 381-440.
- Long, D.G. 2005. Studies on the genus *Asterella* (Aytoniaceae) VI: Infrageneric classification of *Asterella*. *Journal of the Hattori Botanical Laboratory* 97: 249-261.
- Long, D.G. 2006. Revision of the genus *Asterella* P. Beauv. In Eurasia. *Bryophytarum Bibliotheca* 63: 299 pp.
- Loope, L.L., A.C. Medeiros and B.H. Gagne. 1991. Studies in montane bogs of Halekalā National Park: Aspects of the history and biology of the montane bogs. Cooperative National Park Resources Studies Unit, University of Hawai'i at Mānoa. Technical Report 76.
- Lorence, D.H. and K.R. Wood. 1994. *Kanaloa*, a new genus of Fabaceae (Mimosoideae) from Hawai'i. *Taxon* 4(2): 137-145.
- Mamontov, Y.S., A.A. Vilnet, N. Konstantinova and V.A. Bakalin. 2019. Two new species of Gymnomitriaceae (Marchantiophyta) in the North Pacific. *Botanica Pacifica* 8(1): 70.
- Maul, K., Y.-M. Wei, E.A.P. Iskandar, S. Chantanaorrapint, B.-C. Ho, D. Quandt and M. Kessler. 2023. Liverworts show a globally consistent mid-elevation richness peak. *Ecology and Evolution*, 13, e9862. <https://doi.org/10.1002/ece3.9862>.
- Meagher, D.A. 2015. Studies on *Bazzania* (Marchantiophyta: Lepidoziaceae) 8. *Bazzania wooroonooran* sp. nov. and seven other rare species from tropical Australia. *Nova Hedwigia* 100: 535-552.
- Miller, H. A. 1953. Notes on Hawaiian Hepaticae: Frullaniaceae. *The Bryologist* 56(1): 40-48.
- Miller, H. A. 1956. A Phytogeographical Study of Hawaiian Hepaticae. Doctoral dissertation, Stanford University. 123 pages.
- Miller, H. A. 1963. Notes on Hawaiian Hepaticae. V. Collections from recent Swedish expeditions. *Arkiv för Botanik* 5(2): 489-531.
- Miller, H.A. 1965. A review of *Herberta* in the tropical Pacific and Asia. *Journal of the Hattori Botanical Laboratory* 28: 299-412.
- Miller, H. A. 1967. Oddments of Hawaiian bryology. *Journal of the Hattori Botanical Laboratory* 30: 271-276.
- Miller, H.A. 1970. Some circum-Pacific Schistochilaceae. *Phytologia* 20(5): 314-323.
- Miller, H. A., H.O. Whittier and B.A. Whittier. 1983. *Prodromus Florae Hepaticarum Polynesiae*. J. Cramer, Vaduz. 423 pp.
- Mizutani, M. and K.C. Chang 1986. A preliminary study of Chinese Lepidoziaceae flora. *Journal of the Hattori Botanical Laboratory* 60: 419-437.
- Oliveira da Silva, F.R., S.R. Gradstein and A.L. Ilkiu-Borges. 2021. The genus *Radula* Dumort. (Radulaceae, Marchantiophyta) in Brazil. *Nova Hedwigia Band* 112 (Heft 1-2): 69-163.
- Palmer, D.D. 2003. *Hawai'i's Ferns and Fern Allies*. University of Hawai'i Press. 324 pages.
- Paton, J.A. 2014. *Liverwort Flora of the British Isles*. Brill Academic Publications. 626 pp.

- Patzak, S. D. F., M. A. M. Renner, A. Schäfer-Verwimp, K. Feldberg, M. M. Heslewood, D. F. Peralta, A. M. de Souza, H. Schneider and J. Heinrichs. 2016. A phylogeny of Lophocoleaceae-Plagiochilaceae-Brevianthaceae and a revised classification of Plagiochilaceae. *Organismal Diversity and Evolution* 16(3): 481–495.
- Peng T. and Zhu R.-L. 2013. A revision of the genus *Anthoceros* in China. *Phytotaxa* 100: 21–35.
- Piippo, S. 1985a. Bryophyte flora of the Huon Peninsula, Papua New Guinea. XII. Geocalycaceae (Hepaticae). *Acta Botanica Fennica* 131: 126–167.
- Piippo, S. 1985b. Bryophyte flora of the Huon Peninsula, Papua New Guinea. XIII. *Arachniopsis* and *Kurzia* (Lepidoziaceae, Hepaticae). *Acta Botanica Fennica* 131: 169–179.**
- Piippo, S. 1986. A monograph of the genera *Lepidolejeunea* and *Luteolejeunea*. *Acta Botanica Fennica* 132: 1–69.
- Piippo, S. 1991. Bryophyte Flora of the Huon Peninsula, Papua New Guinea. XXXIX. *Fossombronia* (Fossombroniaceae) and *Metzgeria* (Metzgeriaceae, Hepaticae). *Acta Botanica Fennica* 143: 1–22.
- Pócs, T. 1969. A short survey of the *Bazzania* of North Vietnam. *Journal of the Hattori Botanical Laboratory* 32: 79–94.
- Pócs, T. 1976. Correlations between the tropical African and Asian bryofloras, I. *Journal of the Hattori botanical laboratory* 41: 95–106.
- Pócs, T. 2006. Bryophyte colonization and speciation on oceanic islands: An overview. *Lindbergia* 31: 54–62.
- Pócs, T. and J. Eggers. 2007. Bryophytes from the Fiji Islands, II. An account of the genus *Colura* with a description of *C. vitiensis* sp. nov. *Polish Botanical Journal* 52: 81–92.
- Pócs, T. 2023. New or little-known epiphyllous liverworts, XXVI. Records of last century Vietnam collections. *Frahmia* 34: 1–10.
- Pócs T., Mizutani M. and Koponen T. 2019. Bryophyte flora of the Huon Peninsular, Papua New Guinea. LXXX. *Cheilolejeunea* and *Drepanolejeunea*, with contributions to *Ceratolejeunea*, *Cololejeunea*, *Diplasiolejeunea*, *Lejeunea*, *Leptolejeunea*, *Metalejeunea* and *Microlejeunea* (Lejeuneaceae, Marchantiophyta). *Acta Bryolichenologica Asiatica* 8: 41–84.**
- Potemkin, A.D. 2002. Phylogenetic system and classification of the family Scapaniaceae Mig. emend. Potemkin (Hepaticae). *Annales Botanici Fennici* 39: 309–334.
- Printarakul N., P. Sukkharak and S. Chantanaorrapint S. 2020. The genus *Calycularia* (Calyculariaceae, Marchantiophyta) in Thailand. *Thai Forest Bulletin (Botany)* 47: 108–112.
- Pukui M.K. and S.H. Elbert. 1986. *Hawaiian Dictionary*. University of Hawai‘i Press, Honolulu. xi + 572 pp.
- Reeb. C. and J. Bardat. 2014. Studies on African *Riccardia* types and related material. *Cryptogamie, Bryologie* 35(1): 47–75.
- Renner, M.A.M. 2014. *Radula* subg. *Radula* in Australasia and the Pacific (Jungermanniopsida). *Telopea* 17(1):107–167.
- Roberts, T.L. 1986. A taxonomic study of Hawaiian *Marchantia*. Master’s Thesis, University of Central Florida.
- Sass-Gyarmati, A., N.G. Hodgetts, J.C. Brinda, G.-A. Abalo-Loko, E. Lavocat-Bernard, A. Vanderpoorten, E. Boucheron-Dubuisson, A. Allard, L. Kervran, R. Lala Andriamiarisoa and C. Reeb. 2023. Checklist and distribution of the liverworts of the Andasibe (Périnet) Region (Madagascar). *Acta Biologica Plantarum Agriensis*. 11(1): 333–395.
- Schill, D.B. 2007. Taxonomy and phylogeny of the liverwort genus *Mannia* (Aytoniaceae, Marchantiales). PhD Dissertation, University of Edinburgh. 361 pp.
- Schuster, R.M. 1971. Studies of antipodal Schistochilaceae and Scapaniaceae. *Bulletin of the National Science Museum, Tokyo. Series B, Botany* 14: 609–660.
- Schuster, R.M. 1969. The Hepaticae and Anthocerotae of North America east of the hundredth meridian. Volume II. Columbia University Press, New York, 1,062 pp.
- Schuster, R.M. 1974. The Hepaticae and Anthocerotae of North America east of the hundredth meridian. Volume III. Columbia University Press, New York, 880 pages.

- Schuster, R.M. 1982. Studies on Hepaticae, LIX. On *Sandeothallus* Schust., gen. n. and the classification of the Metzgeriales. *Nova Hedwigia* 36: 1-16.
- Schuster, R.M. 1995a. On a new species of *Gymnomitrium*, *G. mucrophorum* Schust., sp. n. *The Bryologist* 98(2):242-245.
- Schuster, R.M. 1995b. Phylogenetic and taxonomic studies of Jungermanniidae, III: Calypogeiaceae. *Acta Fragmenta Floristica et Geobotanica* 40: 825-888.
- Schuster, R.M. 1996. Studies on Antipodal Hepaticae. XII. Gymnomitriaceae. *Journal of the Hattori Botanical Laboratory* 80: 1-147.**
- Schuster, R.M. 2000. Austral Hepaticae, Part I. Beiheft zur *Nova Hedwigia* 118: 1-524.
- Schuster, R.M. 2002. Austral Hepaticae, Part II. Beiheft zur *Nova Hedwigia* 119: 1-606.
- Schuster, R.M. 2021. Austral Hepaticae, Part III. Beiheft zur *Nova Hedwigia* 120: 1-721.
- Schuster, R.M. and J.J. Engel. 1975. Austral Hepaticae, IV. Notes on *Lophozia* subgenus *Protolophozia* Schust., with a diagnosis of a new South American species. *Journal of Bryology* 8: 465-474.
- Scott, E.B. and H.A. Miller. 1959. Notes on Hawaiian Hepaticae. IV. *Herberta herpocladoides* sp. nov. *The Bryologist* 62: 116-117.
- Selling, O.H. 1948. Studies in Hawaiian pollen statistics. Part III. On the late Quaternary history of the Hawaiian vegetation. B.P. Bishop Museum Special Publication 39.
- Shevock, J.R., T.W. Flynn, J.C. Game, W.Z. Ma, A. Williams, D.R. Toren, B.C. Tan and J.R. Spence. 2019. New additions, range extensions and nomenclatural updates for the Hawaiian moss flora, island of Kaua'i, USA. *Acta Musei Silesiae, Scientiae Naturales*: 68: 105-122.
- Shi, X.-Q., S. Gradstein and R.-L. Zhu. 2015. Phylogeny and taxonomy of *Archilejeunea* (Marchantiophyta: Lejeuneaceae) based on molecular markers and morphology. *Taxon* 64: 881-892.
- Singh, D. and D.K. Singh. 2023. Liverwort and Hornwort flora of Sikkim. 2 volumes. Botanical Survey of India, Kolkata. 1222 pages.
- Singh, D.K. and D. Singh. 2008. Rediscovery of *Calypogeia aeruginosa* Mitt. (Hepaticae: Calypogeiaceae) – a long, lost liverwort from Sikkim, India. *Journal of Bryology* 30: 229-231.
- Sinton, J.M. 2012. Geologic history of Maui. http://www.soest.hawaii.edu/Library/Sinton_Maui.pdf.
- Smith, C.W., D.E. Gardner and W.J. Hoe. 1997. Follicolous Hawaiian cryptogams. *Abstracta Botanica* 21(1): 163-167.
- So, M.-L. 2001a. Recognised species of *Plagiochila* in Australasia and some island groups of the Pacific Ocean. *New Zealand Journal of Botany* 39: 395-421.
- So, M.-L. 2001b. *Plagiochila* (Hepaticae, Plagiochilaceae) in China. *Systematic Botany Monographs* 60: 1-214.
- So, M.-L. 2002. The genus *Porella* (Porellaceae, Hepaticae) in Australasia and the South Pacific. *Systematic Botany* 27: 4-13.
- So, M.-L. 2002. *Metzgeria* (Hepaticae) in Australasia and the Pacific. *New Zealand Journal of Botany* 40: 603-627.
- So, M. L. 2005a. A synopsis of *Radula* (Radulaceae, Marchantiophyta) in New Zealand and Tasmania. *Journal of the Hattori Botanical Laboratory* 98: 149-174.
- So, M.-L. 2005b. *Radula* (Radulaceae, Marchantiophyta) in Hawai'i. *Journal of the Hattori Botanical Laboratory* 98: 175-191.
- So, M.-L. 2006. *Radula* (Radulaceae, Marchantiophyta) in the South Pacific. *Journal of the Hattori Botanical Laboratory* 99: 207-232.
- So, M.-L. and R. Grolle. 2000. Studies on *Plagiochila* (Hepaticae) in Australasia and the Pacific. I. Cryptogamie, *Bryologie* 21: 7-18.
- So, M.-L. and J. Wang. 2006. *Frullania* (Frullaniaceae, Marchantiophyta) in Hawai'i. *Journal of the Hattori Botanical Laboratory* 100: 419-430.
- Söderström, L., A. Hagborg, M. Von Konrat, S. Bartholomew-Began, D. Bell, L. Briscoe, E. Brown, D. C. Cargill, D. P. Costa, B. J. Crandall-Stotler, E. D. Cooper, G. Dauphin, J. J. Engel, K. Feldberg, D. Glenny, S. R. Gradstein, X. He, J. Heinrichs, J. Hentschel, A. L. Ilkiu-Borges, T. Katagiri, N. A. Konstantinova, J. Larraín,

- D. G. Long, M. Nebel, T. Pócs, F. Puche, E. Reiner-Drehwald, M. A. M. Renner, A. Sass-Gyarmati, A. Schäfer-Verwimp, J. G. Segarra Moragues, R. E. Stotler, P. Sukkharak, B. M. Thiers, J. Uribe, J. Vána, J. C. Villarreal, M. Wigginton, L. Zhang and R.-L. Zhu. 2016. World checklist of hornworts and liverworts. *PhytoKeys* 59: 1–828.
- Söderström, L., A. Hagborg, T. Pócs, A. Sass-Gyarmati, E. Brown, M. Von Konrat and M. Renner. 2011. Checklist of hornworts and liverworts of Fiji. *Telopea* 13(3): 405–454.
- Söderström, L., A. Hagborg and M. Von Konrat. 2012. The Friendly Islands — A checklist of hornworts and liverworts of Tonga. *Polish Botanical Journal* 57(1): 129–135.
- Söderström, L., B. Crandall-Stotler, R.E. Stotler, J. Vána, A. Hagborg and M. Von Konrat. 2013a. Notes on early land plants today. 36. Generic treatment of Lophocoleaceae (Marchantiophyta). *Phytotaxa* 97(2): 36–43.
- Söderström, L., J. Vána, B. Crandall-Stotler, R.E. Stotler, A. Hagborg and M. Von Konrat. 2013b. Notes on early land plants today. 43. New combinations in Lophocoleaceae (Marchantiophyta). *Phytotaxa* 112(1): 18–32.
- Söderström, L., J. Vána, A. Hagborg and M. Von Konrat. 2013c. Notes on early land plants today. 35. Notes on Lophoziaceae (Marchantiophyta). *Phytotaxa* 97(2): 27–35.
- Söderström, L., A. Hagborg, T. Pócs and F. Barrie. 2023. Proposal to conserve the name *Colurolejeunea tenuicornis* (*Colura tenuicornis*) against *Lejeunea ceratophora* (*Colura ceratophora*) (Marchantiophyta: Lejeuneaceae). *Taxon* 72(4): 926–927.
- Staples, G.W. and C.T. Imada. 2006. Checklist of Hawaiian anthocerotites and hepatics. *Tropical Bryology* 28: 15–47.
- Staples, G.W., C.T. Imada, W.J. Hoe and C.W. Smith. 2004. A revised checklist of Hawaiian mosses. *Tropical Bryology* 25: 35–69.
- Stephani, F. 1898–1924. *Species Hepaticarum* 1–6. Genève, Bale.
- Stevens, P.F. "Begoniaceae". Angiosperm Phylogeny Website. 2011. Retrieved 2023-11-27.
<http://www.mobot.org/MOBOT/Research/APWeb/orders/cucurbitalesweb.htm#Begoniaceae>
- Stone, B.C. 1967. A review of the endemic genera of Hawaiian plants. *Botanical Review* 33: 216–259.
- Stotler, R. E. and B. J. Crandall-Stotler. 2017. A synopsis of the liverwort flora of North America north of Mexico. *Ann. Missouri Bot. Gard.* 102(4): 574–709.
- Sukkharak, P. 2013. *Jubula hutchinsiae* subsp. *javanica* (Hepaticae, Jubulaceae): a genus and species new for Thailand. *Polish Botanical Journal* 58(2): 585–587.
- Sun, L.-W., S. R. Gradstein, Z. Dai, W.-Z. Ma, R.-P. Shi, Q.-Q. Wei, X.-D. Gao and J. Wang. 2018. Notes on the distribution of *Acrolejeunea sandvicensis* (Gottsche) Steph., a liverwort species disjunctive between East Asia and Hawai'i. *Phytotaxa* 367(2): 158–164.
- Sun, Y. and X. He. 2019. On the identity of *Herbertus aduncus* (Dicks.) Gray, a taxonomic update. *Acta Bryolichenologica Asiatica* 8: 145–161.
- Thiers, B. M. 1993. A monograph of *Pleurozia* (Hepaticae; Pleuroziaceae) *Bryologist* 96: 517–554.
- Thomas, M.K. 2022. New Hawaiian bryophyte records from Herbarium Pacificum for 2022. *Bishop Museum Occasional Papers* 148: 9–11.
- Thouvenot L., S.R. Gradstein, A. Hagborg A., L. Söderström and J. Bardat. 2011. Checklist of the liverworts and hornworts of New Caledonia. *Cryptogamie, Bryologie* 32(4): 287–390.
- Thouvenot L. 2023. A Taxonomic Revision of the Lophocoleaceae Vanden Berghen (Marchantiophyta) of New Caledonia. *Cryptogamie, Bryologie* 44(1): 1–60.
- Tixier, P. 1985. Contribution à la connaissance des Cololejeunoideae. *Bryophytarum Bibliotheca* 27: 1–439.
- Vána, J. 1975. Studien über die Jungermannioideae (Hepaticae). 9. Jungermannia Subg. *Plectocolea* and Subg. *Solenostoma* in Hawai'i *Ergänzungen und Synopsis der Gattung Jungermannia. Folia Geobotanica et Phytotaxonomica, Praha* 10: 357–382.
- Vána, J. 1988. *Cephalozia* (Dum.) Dum. In Africa, with notes on the genus (Notes on some African hepatic genera 10). *Beihefte zur Nova Hedwigia* 90: 179–198.

- Váňa, J. and S. Piippo. 1989. Bryophyte flora of the Huon Peninsula, Papua New Guinea. XXXI. Cephaloziaceae subfam. Alobielloideae, Cephaloziellaceae, Antheliaceae and Lophoziaceae (Hepaticae). *Annales Botanici Fennici* 26: 263-290.
- Váňa, J. and D. G. Long. 2009. Jungermanniaceae of the Sino-Himalayan region. *Nova Hedwigia* 89(3-4): 485-517.
- Váňa, J., J. Hentschel and J. Heinrichs. 2010. New combinations in Jungermanniales: transfer of 32 taxa to *Solenostoma* Mitt. *Cryptogamie, Bryologie* 31(2): 135-139.
- Váňa, J., R. Grolle and D. G. Long. 2012. Taxonomic realignments and new records of *Gongylanthus* and *Southbya* (Marchantiophyta: Southbyaceae) from the Sino-Himalayan region. *Nova Hedwigia* 95(1-2): 183-196.
- Váňa, J., R. Ochrya, M. Lebouvier and B. Cykowska-Marzencka. 2014. Bryophytes of Île Amsterdam in the south Indian Ocean: 1. Liverworts. *Cryptogamie, Bryologie* 35(4): 335-371.
- Váňa, J., L. Söderström, A. Hagborg and M. Von Konrat. 2013a. Notes on early land plants today. 17. Transfers of some taxa in Adelanthaceae (Marchantiophyta). *Phytotaxa* 76(3): 35-36.
- Váňa, J., L. Söderström, A. Hagborg and M. Von Konrat. 2013b. Notes on early land plants today. 40. Notes on Cephaloziellaceae (Marchantiophyta). *Phytotaxa* 112(1): 1-6.
- Váňa, J., L. Söderström, A. Hagborg and M. Von Konrat. 2013c. Notes on early land plants today. 24. What is *Protolophozia*? (Cephaloziellaceae, Marchantiophyta). *Phytotaxa* 76(3): 50-54.
- Váňa, J., L. Söderström, A. Hagborg and M. Von Konrat. 2013d. Notes on early land plants today. 41. New combinations and synonyms in Cephaloziaceae (Marchantiophyta). *Phytotaxa* 112(1): 7-15.
- Váňa, J., L. Söderström, A. Hagborg and M. Von Konrat. 2013e. Notes on early land plants today. 30. Transfer of some taxa from *Anastrophyllum* (Anastrophyllaceae, Marchantiophyta). *Phytotaxa* 81(1): 15-18.
- Verdoorn, F. 1930. Die Frullaniaceae der Indomalesischen inseln (De Frullaniaceis VII). *Annales Bryologici, Supplement 1: 1-187.***
- Villareal, J.C., B. Goffinet, R.J. Duff and D.C. Cargill. 2010. Phylogenetic delimitation of *Nothoceros* and *Megaceros*. *The Bryologist* 113: 106-113.
- Villarreal, J.C., C. Cargill, L. Söderström, A. Hagborg and M. Von Konrat. 2015. Notes on early land plants today. 70. Nomenclatural notes in hornworts (Anthocerotophyta). *Phytotaxa* 208(1): 92-96.
- Vilnet, A.A., N.A. Konstantinova and A.V. Troitsky. 2011. Taxonomical rearrangements of Solenostomataceae (Marchantiophyta) with description of a new family Endogemmataceae based on trnL-F cpDNA analysis. *Folia Cryptog. Estonica, Fasc.* 48: 125-133.
- Von Konrat, M. and J. E. Braggins. 2001. Notes on five *Frullania* species from Australia, including typification, synonyms, and new localities. *Journal of the Hattori Botanical Laboratory* 91: 229-263.**
- Waite, M. 2007. Mosses of Hawai'i Volcanoes National Park. Pacific Cooperative Studies Unit, University of Hawai'i at Mānoa, Department of Botany. PCSU Technical Report 153.
- Waite, M. and L.W. Pratt. 2007. Plant inventory of the 'Ōla'a Trench at Hawai'i Volcanoes National Park. PCSU Technical Report 139: 1-55.
- Wang, J., M.-J. Lai and R.L. Zhu. 2011. Liverworts and hornworts of Taiwan: An updated checklist and floristic accounts. *Annales Botanici Fennici* 48(5): 369-395.
- Wang, J., R.-L. Zhu and S. R. Gradstein. 2016. Taxonomic revision of Lejeuneaceae subfamily Ptychanthoideae (Marchantiophyta) in China. *Bryophytarum Bibliotheca* 65: 4-141.
- Wigginton, M. J. 2018. Checklist and distribution of the liverworts and hornworts of sub-Saharan Africa, including the East African Islands. *Tropical Bryology Research Reports* 9: 1-138.
- Wood, K. et al. 2008. Floristic survey of the Kaiholena Unit, TNC Ka'ū Preserve, Big Island, Hawai'i. Report to The Nature Conservancy.
- Wyatt, R., E.S.J. Harris and I.J. Odrzykoski. 2021. The pantropical moss *Plagiomnium rhynchophorum* (Mniaceae) disjunct to the Southern Appalachians and Hawai'i. *The Bryologist* 124(3): 343-351.

- Xiang, Y.-L., C. Shen, W.-Z. Ma and R.-L. Zhu. 2024. Molecular phylogenetics and the evolution of morphological complexity in Aytoniaceae (Marchantiophyta). *Plants* 2024 (13): 1053.
- Yamada, K. 1979. A revision of the Asian taxa of *Radula*, Hepaticae. *Journal of the Hattori Botanical Laboratory* 45: 201-322.
- Yamada, K. and Z. Iwatsuki. 2006. Catalog of the hepatics of Japan. *Journal of the Hattori Botanical Laboratory* 99: 1–106.
- Yang, J.D. and S.H. Lin. 2009. *Calypogeia aeruginosa* Mitten, a newly recorded liverwort to Taiwan. *Endemic Species Research*. 11: 93–99.
- Yoshida, L. and C.W. Smith. 1976. Two recent thalloid liverworts introduced to Hawai'i. *Bulletin of the Pacific Tropical Botanical Garden* 6(1): 18–20. So, M.-L. 2002a.
- Yu, Y., Pócs. T., Schäfer-Verwimp, A., Heinrichs, J., Zhu, R.-L. and H. Schneider. 2013. Evidence for rampant homoplasy in the phylogeny of the epiphyllous liverwort genus *Cololejeunea* (Lejeuneaceae). *Systematic Botany* 38 (3): 553–563. doi: 10.1600/036364413X670304.
- Yu, Y., T. Pócs and R.-L. Zhu. 2014. Notes on early land plants today. 62. A synopsis of *Myriocoleopsis* (Lejeuneaceae, Marchantiophyta) with special reference to transfer of *Cololejeunea minutissima* to *Myriocoleopsis*. *Phytotaxa* 183(4): 293–297.
- Zhu, R.-L. and M.-J. Lai. 2005. *Cheilolejeunea decursiva* (Sande Lac.) R.M. Schuster and *Cheilolejeunea ventricosa* (Schiffn.) X.L. He (Lejeuneaceae, Hepaticae), new to Australia. *Journal of the Hattori Botanical Laboratory* 98: 193–203.
- Zhu, R.-L. and S.R. Gradstein. 2005. Monograph of *Lopholejeunea* (Lejeuneaceae, Hepaticae) in Asia. *Systematic Botany Monographs* 74: 1–98.
- Zhu R.L. and Grolle R., 2003. Taxonomy and distribution of *Lejeunea exilis* (Lejeuneaceae, Hepaticae). *Annales Botanici Fennici* 40: 101-106.
- Zhu, R.-L., L. Shu and H. Mohamed. 2018. *Vitalianthus lamyii* (Marchantiophyta: Lejeuneaceae), a new species from the lowland rainforests of Brunei Darussalam. *Cryptogamie, Bryologie* 39(2): 293-299.