Hawaiian Liverworts and Hornworts:
A Bryologists' Notebook, Vol. 1 of 5:
Introduction, Leafy Liverworts (Acrobolbus-Cylindrocolea)

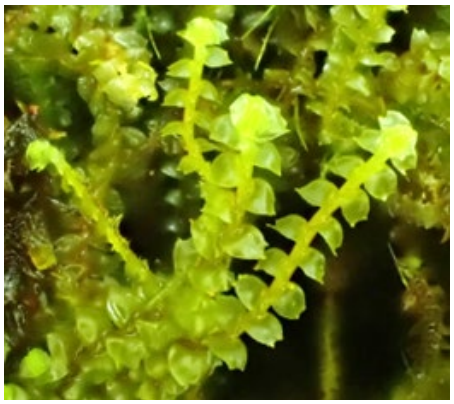
A. Virginia Freire and Emmet J. Judziewicz, May 2025

With photographs by the authors, Miles K. Thomas, Kevin Faccenda, Kenneth R. Wood, Zach Pezzillo, Susan Fawcett, Mike Ross and others









Hawaiian Liverworts and Hornworts:
A Bryologists' Notebook, Vol. 1 of 5:
Introduction, Leafy Liverworts (*Acrobolbus-Cylindrocolea*)

May 2025

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

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

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Contact us with comments and corrections to both of us at calypogeia@gmail.com (Virginia) and judzemmet@gmail.com (Emmet).

Cover photos

Top: *Anastrophyllum fissum* (National Tropical Botanical Garden/K.R. Wood, Kaua'i) and *Chiastocaulon combinatum* (E.J. Judziewicz, Hawai'i Island).

Middle: *Cryptolophocolea ciliolata* (A.V. Freire, Hawai'i Island), *Calypogeia cuspidata* (A.V. Freire, Hawai'i Island), and *Cuspidatula robusta* (E.J. Judziewicz, Hawai'i Island).

Bottom: *Bazzania patens* (K. Faccenda, Kaua'i) and *Anastrepta orcadensis* (M.K. Thomas, O'ahu).

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RESULTS OF SURVEYS ON MANY ISLANDS

Hawaiian Liverworts and Hornworts: A Bryologists' Notebook

May 2025
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Distinguished Affiliates, Bernice P. Bishop Museum

Liverworts and hornworts are the exquisite but neglected jewels of Hawaiian land plants. They are as diverse as pteridophytes and favor much the same ecological niches: Wet montane forests, with maximum diversity from 3,000-6,000 feet elevation on the windward sides of the larger islands. They can grow in pure stands, creeping on bark or rock; or they can be intermixed with other liverworts, mosses, cyanobacteria, fungi, and algae, in complex interwoven "mats" with ten or more bryophyte species present. Some are terrestrial, while others favor canopy branches and even living leaves.

When fresh, some leafy liverworts are translucent with crystalline bulging cells (*Fuscocephaloziopsis connivens*); others, the freshest, brightest green (*Lepidozia australis*); most *Frullania* species have indescribably rich brownish-mahogany pigments; *Lopholejeunea* is a shiny ebony black in color, almost like little kūkaenēnē berries.

Thalloid liverworts include *Dumortiera hirsuta*, the largest and most conspicuous liverwort in Hawai'i; and in contrast, the tiny, translucent and fragile-looking *Metzgeria furcata*, as well as the ruffled, terrestrial *Fossombronia* and the large, colorful, charismatic, and possibly carnivorous *Pleurozia conchifolia*. Hornworts have their own charms, including beautiful colorful spores (brown, vivid yellow or bright green) that aid in their identification. Some have attractive crispate thalli (*Dendroceros crispus*); others look as if perpetually covered by frost (*Megaceros flagellaris*) and yet others have the look of a tiny feather covered by flowing pāhoehoe lava (*Folioceros fusiformis*).

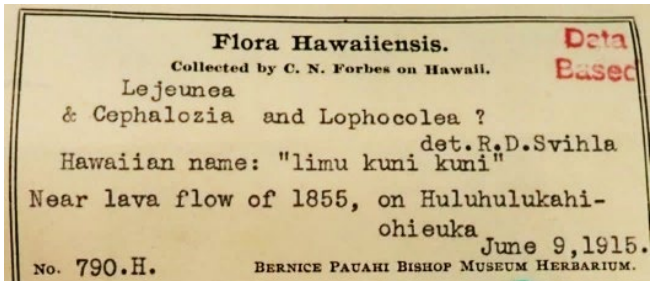
These are our current notes on the approximately 250 (our estimate is a range of 240-258) species of Hawaiian liverworts and hornworts (LH) in our illustrated research notebook. **It is not a complete floristic account of Hawaiian LH, nor is it intended to be one; full descriptions and synonymies are not included, not all types have been examined, not all taxa are assigned to species, and many of them are only tentatively assigned to species**. Generic treatments, at this point, are at different "stages of maturity". However, we wish to give biologists, land managers, and anyone interested in the flora of Hawai'i the tools to *begin* to become acquainted *now* with these wonderful plants, and not to have to wait for ten years or a generation for an accessible guide. We invite comments and corrections.

Most species are illustrated with photographs of Hawaiian material. Forty-nine names represent changes from the Staples and Imada (2006) checklist of Hawaiian LH, and an additional 39 species are reported as new to Hawai'i.

If you become deeply interested in Hawaiian LH, please consider choosing a genus or family that needs a "friend" – *Bazzania, Cephaloziella, Cololejeunea, Drepanolejeunea, Lejeunea, Plagiochila, Radula*, *Riccia, Riccardia, Scapania, Symphyogyna* or one of many others – that needs field work and revision using a combination of morphological and molecular techniques. Our "Bryologists' Notebook" is merely a starting point for this immense task. We think that many more species of liverworts, and some hornworts, remain to be described from Hawai'i.

HAWAIIAN NAMES (Nā inoa Hawai‘i)

Waite (2007) searched Pukui & Elbert (1986) and found the following names applied to liverworts, alone or included with other groups of plants: limu ahi (“a tree moss or liverwort”), limu kaha (“a kind of liverwort”), and limu kau lā‘au (“all tiny ferns (filmy ferns), lichens, liverworts, mosses growing on trees”). After examining over 5,000 herbarium specimens of Hawaiian liverworts and hornworts, the only name for them we have been able to find on collection labels is “limu kuni kuni”, from a BISH specimen made in 1915 on Hawai‘i Island in the mountainous saddle between Mauna Loa and Mauna Kea by Charles N. Forbes (below). “Kuni” can apparently denote “burning”; could “limu kuni kuni” allude to the frequently bright orange or red colors of common cloud forest liverwort genera such as *Anastrophyllum, Cuspidatula, Herbertus, Odontoschisma, Pleurozia,* and *Scapania*? Or to the black, burnt coloration of *Frullania apiculata, Lopholejeunea nigricans*, or *Odontoschisma denudatum* subsp. *denudatum*?


Flora Hawaiiensis. Data Based
Collected by C. N. Forbes on Hawaii.
Lejeunea
& Cephalozia and Lophocolea ?
det. R. D. Svihla
Hawaiian name: "limu kuni kuni"
Near lava flow of 1855, on Huluhulukahi-
ohieuka
June 9, 1915.
No. 790.H. BERNICE PAUAHI BISHOP MUSEUM HERBARIUM.

OUR WORK

We began work in October 2019 with collections around our residence (the Freire-Judziewicz Bryological Laboratory) at 3,435 ft. in ‘Ōhi‘a Estates, Volcano, Hawai‘i Island, and for four years we enjoyed living in a *Metrosideros polymorpha-Cibotium glaucum* forest that receives 120 inches of rain per year. We studied liverworts and hornworts there daily, ending our surveys in January 2024, and found 60 species of LH in an area of just three hectares. Our first year of work was conducted here and in and around Hawai‘i Volcanoes National Park; the reader will notice that we have a bias towards citing habitat preferences for the Kīlauea area of Hawai‘i Island. Within a few weeks of our arrival, we made our first discoveries in Volcano – the first record for *Isopaches bicrenatus* in Hawai‘i, and of *Fossombronia* on Hawai‘i Island – and realized that there was much more exploration to be done on the island. On our first visit to Bishop Museum in May 2021, the very first specimen that the first author examined turned out to be *Tritomaria exsecta*, a genus and species new to Hawai‘i.

Through 2024 we have collected 4,209 hepatics and hornworts; 3,660 were made on Hawai‘i Island, 135 from Maui, 228 from Lāna‘i, 146 from O‘ahu, and 40 from Kaua‘i; of these, about 2,000 (all from Hawai‘i Island) are still under study by us and have not yet been dispersed to Bishop Museum (Table 1). Of 89 confirmed Hawaiian LH genera, we have seen 74 in the field. We’ve spent about 8,000 hours in field, herbarium, library, and laboratory work on this project. Through field and herbarium research, we published the first documentation of Hawaiian occurrences of these 18 genera: *Aneura, Asperifolia* (as a segregate), *Cryptolophocolea* (as a segregate), *Cylindrocolea, Diplasiolejeunea, Fuscocephaloziopsis* (as a segregate), *Gymnomitrion, Isopaches, Kahakuloa, Leptoscyphus* (as a segregate), *Lophozia, Mannia, Marsupella, Myriocoleopsis* (as a segregate), *Sphenolobus, Telaranea, Tritomaria*, and *Vitalianthus* (as a segregate).

Published reports include a survey of the liverworts and hornworts of Lāna‘i (Judziewicz, Freire & Bogner, 2023); new state records and name changes (Judziewicz & Freire, 2023), new island records (Judziewicz, Freire & Thomas, 2024), and a survey of the Kaua‘i Summits (Judziewicz, Faccenda & Freire, 2025). Unpublished reports are available for our surveys (all will be summarized in Volume 5) of Hawai‘i

Volcanoes National Park (Freire & Judziewicz, 2022a), the Kahuku Unit of that Park (Freire & Judziewicz, 2022b), the Puʻu Makaʻala, Manukā, Puʻu o ʻUmi, and Laupāhoehoe Natural Area Reserves on Hawaiʻi Island (Judziewicz & Freire 2022c, 2022d, 2024b, and 2024c), The Nature Conservancy's Kaiholena Reserve on Hawaiʻi Island (Freire & Judziewicz, 2020), The Nature Conservancy's Waikamoi Preserve on Maui (Judziewicz & Freire 2023a), and Hakalau Forest National Wildlife Refuge (Judziewicz & Freire 2023b). Collections made in Hawaiʻi Volcanoes National Park have been deposited, following the terms of our research permit, at their herbarium (acronym HAVO), while all others have or will be deposited at the Herbarium Pacificum (BISH), Bishop Museum.

We have examined about two-thirds of the 5,649 Hawaiian collections of hepatics and hornworts at Bishop Museum, about 95% of the 1,038 collections at the National Tropical Botanical Garden (PTBG) on Kaua'i, all 1,654 collections at the Hawaiʻi Volcanoes National Park Herbarium HAVO, all ca. 25 collections at the Haleakalā National Park Herbarium (HALE), all 75 collections in the Joseph Rock Herbarium (HAW) at the University of Hawaiʻi at Mānoa, about 500 of the 2,714 collections at the Willard Sherman Turrell Herbarium (MU) at Miami University in Oxford, Ohio, 166 collections by James R. Shevock & Wenzhang Ma at the California Academy of Sciences (CAS), and John B. Hall's personal collection of 77 Hawaiian specimens, since donated to Bishop Museum.

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Left: A.V. Freire (far right) during bryophyte field trip to the summit of Puʻu Kaʻala, Oʻahu, 9 Nov. 2022; with Barbara Kennedy (far left), Susan N. Ching and Miles K. Thomas (seated, rear), and students. Photo by E.J. Judziewicz. Right: E.J. Judziewicz (far left) on Puʻu Kaʻala, Oʻahu, 6 May 2023. Photo, A.V. Freire.

We conducted two workshops on the identification of Hawaiian liverworts and hornworts, the first at Bishop Museum (sponsored by them) in November 2021, and the second at the University of Hawaiʻi at Mānoa in May 2023 (sponsored through the assistance of Tim Chambers of the US Army Natural Resources Program on Oʻahu, and by Bishop Museum). At the latter workshop, first drafts of our guide were shared with participants to encourage the study of Hawaiian liverworts and hornworts. We also presented a talk to the Hawaiian Native Plant Society at Makawao, Maui in February 2023.

TABLE 1. Liverwort and hornwort holdings by island in various herbaria.

Right: Depository. **Below: Islands.**	**Bernice P. Bishop Museum (BISH), B. Kennedy, 24 Nov. 2024**	**National Tropical Botanical Garden (PTBG), 19 Feb. 2025**	**Miami University Herbarium (MU), Aug. 2022**	**Hawai‘i Volcanoes National Park Herbarium (HAVO), L. Pratt, 11 Apr. 2025**	**TOTAL**
Kaua‘i	929	832	294	0	2,055
O‘ahu	1,574	10	613	0	2,197
Lāna‘i	236	0	9	0	245
Moloka‘i	198	29	271	2	500
Maui	1,563	139	461	40	2,203
Hawai‘i	3,112*	28	351	1,612	5,103
Island not specified	37	0	693	0	730
TOTAL	7,649	1,038	2,692	1,654	13,033

* - Includes about 2,000 of our collections yet to be dispersed from us to Bishop Museum.

FIGURES

For photography we used a variety of cameras and microscopes, but mainly (since 2021) an Olympus Tough TG-6 model IM-015 camera, several dissecting and compound (Lab Binocular) AmScopes, and an Olympus SZ51 dissecting microscope. Of the photographs in Volume 1, 1,081 were taken by us, including all photos of our own collections, and no photo credits are specified. For collections by contributors, photo credits are specified. The following people generously lent us images to use: Miles K. Thomas (26 photos), Kevin Faccenda (22), Kenneth R. Wood (15), Zachary Pezzillo (7), Mike Ross (5), Susan Fawcett (3), W. Cuyler Bleecker (2), and Tim Flynn (1).

DISTRIBUTION MAPS

The distribution maps for species of hornworts and liverworts were compiled from these sources:

Our collections
We made 4,209 LH collections (87% of these from Hawai‘i Island), as previously summarized in the previous section (“Our Work”).

Literature
We used specimens cited by Miller (1963), mainly from the Stockholm Herbarium (S), and published revisions of Hawaiian genera such as *Frullania* (So & Wang, 2006), *Plagiochila* (Inoue, 1976), *Radula* (So, 2005), and others.

Herbarium specimens
See previous discussion in "Our Work" section.

iNaturalist
We used inaturalist.org to map several dozen island records. The second author (avatar = judziewicz) has examined the majority of Hawaiian liverwort and hornworts (4,034 as of 1 May 2025) on this site. For critical reports, such as an island or mountain range record, we include the link so that readers can judge the accuracy of the determination for themselves.

Location markers
For the islands of Kauaʻi, Lānaʻi, and Kahoʻolawe, we mapped just one occurrence, not differentiating between different island localities. For Oʻahu, Molokaʻi, and Maui we mapped up to two sites, differentiating between the western and eastern ranges of each of these islands. For much larger Hawaiʻi Island we mapped up to about ten different localities.

FORMAT OF OUR PRELIMINARY TAXONOMIC TREATMENTS

Genus
Genera are arranged in alphabetical order. For each genus, its authority and family are given, along with the number of species known from Hawaiʻi (including both identified and possible novel taxa), followed by the worldwide estimate of species given by Brinda & Atwood (2025). In this section, distinguishing characters of the genus may be presented, sometimes with brief discussions of similar genera. If the genus name has changed since the Staples & Imada (2006) checklist, this is also noted. A key to Hawaiian species is then presented, if more than one species occurs here; the key includes unidentified species for which we have assigned a numerical designation (e.g. "*Bazzania* species 1, *B.* species 2, …").

Species
The accepted name of the species is given along with the authority(s), according to Brinda & Atwood (2025). This is followed by its status in Hawaiʻi – Indigenous (naturally occurring, but not endemic), endemic (found only in Hawaiʻi), or naturalized (accidentally introduced to the islands), as well as a brief summary of its worldwide distribution. If the species was treated under some other name by Staples & Imada in their 2006 checklist, that name is also given. If researchers have postulated affinities with non-Hawaiian species, this information is presented, as is the species' infra-generic classification as given by Söderström et al. (2016) or more recent authors. A description of the species then follows, based on material that we have been able to examine, and as our time permitted; note that numerous aspects of the plants' morphology may be absent, including, but not limited to, sexuality, sexual structures, and sporophyte and spore morphology, as well as vegetative features such as slime papillae and oil bodies.

Species that appear to us to differ from named species accepted from Hawaiʻi we have denominated as (for example) "*Bazzania* species 1". This indicates that we regard "*Bazzania* species 1" as either a novel species (perhaps endemic to Hawaiʻi), or a non-Hawaiian species with an already existing name that we have not yet been able to ascertain.

HABITAT PREFERENCES

As the default, users of this guide can assume (in the absence of any specific mention of habitat preference) that liverwort species grow as epiphytes on the bark of trunks and branches. One hornwort genus, *Dendroceros*, also consistently grows as an epiphyte, and another (*Megaceros*) is occasionally epiphytic on the bases of trees and tree ferns. ʻŌhiʻa (*Metrosideros polymorpha*), the dominant tree of Hawaiian wet forests, often has a rich liverwort flora growing at its base and in crevices of its bark, while koa (*Acacia koa*) has its own, less diverse liverwort flora that sometimes includes spectacular growth of the colorful thalloid *Pleurozia inflata*. Certain smaller indigenous tree species such as olomea (*Perrottetia sandwicensis*) also have diverse liverwort bark floras, while exotic trees such as *Eucalyptus* species and gymnosperms rarely harbor hepatics.

Many species of liverworts grow on the decaying (decorticating) logs of woody plants in shaded, moist forests. *Odontoschisma denudatum* subsp. *sandvicense* is perhaps the most common species with this habitat preference. The thalloid liverwort *Riccardia* also often grows in this habitat but is often also terrestrial.

Epiphylls

Compared with tropical mainland areas, Hawaiian liverworts and hornworts are poorly represented as epiphylls on vascular plants. Smith et al. (1997) list just seven species as facultative epiphylls: the hornwort *Dendroceros crispus* and liverworts *Cololejeunea ceatocarpa, C. hillebrandii, C. kapingaensis, C. lanciloba* (= *C. planissima*)*, C.* aff. *planissima*, and *Drepanolejeunea micholtzii* Steph. (= *D. pentadactyla*); Miller (unpublished) also notes that *Radula cavifolia* can be epiphyllic. The dominant Myrtaceous tree ʻōhiʻa (*Metrosideros polymorpha*) has leaves that are nearly always devoid of epiphylls, and the phyllodes of koa (*Acacia koa*) are similarly impoverished, except in exceptionally wet areas, where the tiny leafy liverworts *Colura tenuicornis, Drepanolejeunea anderssonii,* and *Metalejeunea cucullata* may colonize canopy phyllodes, as in the Volcano area. In the Kīlauea area of Hawaiʻi Island, kāwaʻu (*Ilex anomala*) and kōlea (*Myrsine lessertiana*) often harbor epiphylls, as does the exotic shrub *Camellia*, and even coffee plants. The Myrtaceous genera *Eugenia* and *Syzygium* (both indigenous and exotic species) seem to be "liverwort magnets", attracting species of epiphylls such as *Cololejeunea planissima*.

Epiphylls usually occur at elevations below 4,000 ft. We've observed these 17 liverwort species and one hornwort species growing as epiphylls on vascular plants in Hawaiʻi; doubtlessly there are more:

Cololejeunea ceatocarpa
Cololejeunea planissima
Colura tenuicornis
Dendroceros species (a hornwort)
Drepanolejeunea anderssonii
Drepanolejeunea pentadactyla
Drepanolejeunea ungulata
Frullania meyeniana
Jubula javanica
Lejeunea adpressa
Lejeunea flava (naturalized)
Lejeunea laetevirens (naturalized)
Lejeunea pacifica
Lopholejeunea nigricans
Metalejeunea cucullata
Microlejeunea lunulatiloba
Myriocoleopsis minutissima

Smaller ferns and their allies can also harbor small leafy liverworts as epiphylls on both their stipes and fronds. Examples of such pteridophytes include species of *Adenophorus* (*A. pinnatifidus* and *A. tamariscinus*)*, Asplenium* (substrate for several collections of *Jubula javanica*), *Blechnum* (which reportedly harbored the only Hawaiian collection of a species of the liverwort genus *Leptolejeunea*)*,*

Elaphoglossum paleaceum, E. pellucidum, Hymenophyllum obtusum, H. recurvum, Schizaea robusta, *Selaginella deflexa*, and *Vandenboschia davallioides*.

High elevation bog sedges such as *Carex montis-eeka, C. meyenii*, *Rhynchospora chinensis* subsp. *spiciformis*, *R. rugosa* subsp. *lavarum*, and especially *Oreobolus furcatus* can host small leafy liverworts twining among their stems and leaves; the enigmatic leafy liverwort *Protolophozia perssoniana* grows only amongst the leaves of the latter species on Maui and Molokaʻi. We have examined collections of most of the bog sedges listed above at BISH and MU, to glean "incidental" liverwort collections from them.

In wet forests, common mosses such as *Leucobryum* species, *Aerobryopsis* species, and *Acroporium fuscoflavum* often harbor small, leafy twining liverworts such as *Cephaloziella*, and *Pyrrhobryum pungens* is recorded as the host of the rare liverwort *Drepanolejeunea pentadactyla*. Yet *Pyrrhobryum spiniforme*, one of the dominant moss species of Hawaiian montane forests, only rarely hosts liverworts, and the common exotic moss *Hypnum plumaeforme* appears to be similarly "hepatic-phobic".

Some hornworts, thalloid liverworts (such as *Dumortiera hirsuta* and *Pleurozia* species), and larger leafy liverworts (*Bazzania cordistipula, Chiloscyphus laceratus, Cuspidatula* species, and *Herbertus* species) can themselves be host to smaller epiphyllic, often twining leafy liverworts such as *Blepharostoma trichophyllum, Drepanolejeunea s*pecies, *Lophocolea spinosa, Metalejeunea cucullata*, and *Microlejeunea lunulatiloba*.

Terrestrial

Most hornworts (except *Dendroceros*), most thalloid liverworts, and a minority of Hawaiian leafy liverworts share a terrestrial habitat preference. Liverworts that prefer to grow terrestrially in partial or full sun include the thalloid genera *Fossombronia, Kahakuloa,* and *Riccia,* and the leafy taxa *Cephaloziella, Isopaches bicrenatus, Odontoschisma denudatum* subsp. *denudatum*, and *Solenostoma micranthum*; the last species often grows in pure stands on trailside or roadside clay embankments. It is possible that the apparently extirpated genus *Schistochila* was also terrestrial. Several hornworts (*Anthoceros punctatus, Notothylas breutelii, N. orbicularis,* and *Phaeoceros carolinianus*) grow in partial to full sun.

Aquatics

Aquatic liverworts are rarely encountered. The few with this habit appear to be exotic species occurring in lowland agricultural areas, namely the thalloids *Riccia fluitans* and *Ricciocarpos natans*; however, the possibility that these species naturally colonized irrigated areas via migrating birds cannot be discounted. Unlike mosses, which can be rheophytes such as *Limbella tricostata* (Sull.) Müll. Hal. ex E.B. Bartram growing in streams on Kauaʻi (Shevock et al., 2019) and elsewhere, we have encountered no truly aquatic hornworts or leafy liverworts in Hawaiʻi. We have seen the hornwort *Phaeoceros* and the leafy liverwort *Lophocolea hawaica* growing on the margins of artificial ponds in the Volcano area.

Rocky areas – Outcrops, cave mouths, and streamsides

Moist, shaded rock outcrops in wet forests are often dominated by the complex thalloid liverwort *Dumortiera hirsuta*, the "monarch" of Hawaiian hepatics because of its large size and dominance at the entrance to lava tubes such as Nāhuku in Hawaiʻi Volcanoes National Park. Smaller liverworts such as the thalloid *Riccardia* and the leafy *Calypogeia* often seem to be associated with *Dumortiera*. Such sites may also harbor a diversity of hornworts (such as *Megaceros flagellaris*) and other thalloid liverworts. The walls of higher elevation moist, shaded gulches may also harbor uncommon leafy liverworts such as *Cephalozia*

lucens, Diplophyllum exiguum, Notocyphus lutescens, Porella acutifolia, and species of *Radula* and *Scapania.*


Left: *Lophocolea spinosa* twining on the liverwort *Herbertus aduncus*, Freire & Judziewicz 21-792, Hawai‘i Island. Right: *Drepanolejeunea pentadactyla* epiphyllic on the moss *Pyrrhobryum pungens*, Ko‘olau Range, O‘ahu, May 2023, photo by Miles K. Thomas.

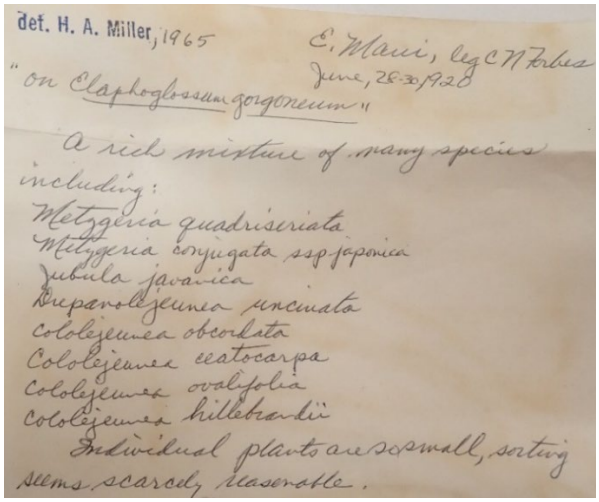

Left: Liverwort-rich wet montane forest on Kaua‘i. The dominant taxa are the larger leafy liverworts *Bazzania, Cuspidatula, Herbertus,* and the thalloid *Pleurozia*. February 2024 photo by Kevin Faccenda. Right: This bryologically rich site on the Munro Trail, Lāna‘i, at the head of Kunoa Gulch, el. 3,000 ft., 25 March 2022, is the most diverse liverwort site on the island, with 39 species. Yet nearly all host plants are exotic: Cook pine (*Araucaria columnaris*), strawberry guava (*Psidium cattleianum*), and mānukā (*Leptospermum scoparium*). Photo by E.J. Judziewicz.


Above: Excellent liverwort habitat at 5,800 ft. in Pu‘u Maka‘ala Natural Area Reserve, Hawai‘i Island. Left, habitat of *Scapania javanica*. Right: *Acacia koa* with thick growths of *Pleurozia subinflata* on trunk and branches. Photos by E.J. Judziewicz.


Some ferns seem to be attractive to certain epiphytic and epiphyllic liverworts. The decaying stipes of hāpu‘u (*Cibotium* species) frequently harbor the thalloid *Riccardia,* the leafy liverwort *Calypogeia cuspidata,* many Lejeuneaceae, and the rare Hawaiian endemic leafy liverwort *Cephaloziella* aff. *microphylla*, el. 3,800 ft., Volcano, Hawai‘i Island. Photos by E.J. Judziewicz.

Subalpine heathlands

At elevations above tree line (roughly 6,000 ft.) on Maui and Hawai‘i Island, liverwort diversity declines quickly; however, the species that occur there are of great interest. These liverworts often occur in pūkiawe (*Leptecophylla tameiameiae*) heathlands at the bases of shrubs, or terrestrially, and include *Cephaloziella heteroica, C. kilohanensis, Fossombronia pusilla, Gymnomitrion* cf. *laceratum* (Maui only)*, Isopaches bicrenatus, Odontoschisma denudatum,* several species of *Scapania, Solenostoma exsertum, S. micranthum, Sphenolobus minutus* (Maui only)*, Symphyogyna* species, and *Targionia hypophylla.* An unusual liverwort, tentatively identified by us as a species of *Acrobolbus*, was collected in this habitat on Mauna Kea, Hawai‘i Island, in 2024 by Daniel Tucker.



Left: Leafy liverworts often grow in interwoven mats with complex mixtures of species and probably involve unknown fungal and cyanobacterial symbionts. Saddle Road, 4,500 ft., Hawai‘i Island: With *Diplophyllum exiguum* (A), *Mnioloma fuscum* (B), *Kurzia hawaica* (C), and minute *Cephaloziella kiaeri* (D). *Asperifolia arguta* is also present in this mixture but is not visible in the photo. Photo by E.J. Judziewicz. On other Hawaiian Islands, *Acromastigum intergrifolium* is a characteristic species of such “mixtures”. Right: In 1965, bryologist Harvey A. Miller noted the difficulty of dealing with a diverse collection of tiny liverworts growing as epiphylls on the fern *Elaphoglossum aemulum* (from Maui, gathered by Charles N. Forbes in 1920 shortly before his death).

DECLINING SPECIES

Based on our herbarium and field surveys, and on historic intensity of collecting, the (apparently mainly) terrestrial species *Bazzania patens* and *Jubula javanica* have declined in abundance. We speculate that trampling by exotic ungulates, mainly feral pigs and axis deer, may be a causal factor in their apparent decline. We wonder whether the apparent extirpation of the genus *Schistochila* from Hawai‘i resulted from this cause. Ungulates can also have an indirect effect on the abundance of non-terrestrial species. We observed a striking decline in the abundance of the bark epiphyte leafy liverwort *Lopholejeunea nigricans* in a forest in Hawai‘i Volcanoes National Park, on the Nāulu Trail south of Makaopuhi Crater. On 22 Nov. 2019 the species was frequent on the bark of ‘ōhi‘a along the shaded trail. Soon afterwards, feral pigs invaded this forest, opening the understory and allowing more sunlight to penetrate, and on a return visit (13 Apr. 2021) we found just one remnant population of *Lopholejeunea*.

Climate change will be a major driver of change in liverwort and hornwort communities (Maul et al., 2023), presumably including those in Hawai‘i.

DIVERSITY

A total of 240-258 species of liverworts and hornworts are now known from Hawai‘i, an increase from 180 and six species, respectively, in the Staples and Imada (2006) literature survey. The uncertainty in this figure derives from our uncertainty of the number of species in many genera, especially the thalloid *Riccardia*. Table 2 presents a summary, along with an island-by-island comparison with the respective moss floras (from data in Staples et al., 2004) and vascular plant floras (from data in Gustafson et al., 2014). “All major islands” signifies Kaua‘i, O‘ahu, Moloka‘i, Lāna‘i, Maui and Hawai‘i. The table also attempts to break down the floras of geographically discrete parts of major islands – for example, the eastern and western mountain ranges on both O‘ahu, Moloka‘i, and Maui.

Hawai‘i Island has the largest flora of liverworts and hornworts (185 species), followed by Kaua‘i and Maui (both 169), O‘ahu (154), Moloka‘i (117), and Lāna‘i (82). Although our extensive field work on Hawai‘i Island is partly responsible for that island’s apparently greater floristic richness than other islands, there may be other contributing factors. The first liverwort has recently been found on Kaho‘olawe (*Frullania sandvicensis*), by Paul Higashino, William Bleecker, and David Beilman, and it is plausible that species may occur on Ni‘ihau.

Curiously, pteridophyte and liverwort/hornworts floras tend to be somewhat comparable in size, with LH slightly more diverse; the ratio of LH/pteridophytes varies from 1.18-1.41/1 on major islands, and 1.45-1.64/1 for the entire archipelago. On most islands and parts of islands the two groups tend to occupy the same general habitats: Moist, shaded montane forests. Since pteridophytes (Palmer, 2003) are more well-surveyed than hepatics, it is tempting to use these ratios as surrogates to predict which islands (or parts of islands) require more hepatic surveys. So, based on these ratios, the islands particularly need more LH surveys are Lāna‘i (0.75) and Moloka‘i (0.97). Note that the ratio of liverworts and hornworts to vascular plants is 0.31-0.34 (0.48 for Hawai‘i Island) for all major islands; thus, liverworts and hornworts constitute a significant part of the Hawaiian land plant flora.

The hepatic flora of Hawai‘i is still incompletely known. Given that we have found two novel species within just 100 meters of the Freire-Judziewicz Bryological Laboratory in Volcano, together with other novelties that we have encountered in the field and in the herbarium, it seems possible that the number of liverworts and hornworts known will increase from the current estimate of 240-258 species. For comparison, Fiji, about the same size and latitude as Hawai‘i, although geologically older and closer to mainland biotic source areas, has 291 species of liverworts and hornworts (Söderström et al., 2011). In particular, the large leafy liverwort family Lejeuneaceae requires more survey effort in Hawai‘i. 45% (131 species) of the Fijian liverwort flora belongs to this family, compared with only 18% (44 species) of the Hawaiian flora. In Hawai‘i, the Lejeuneaceae appear to be more diverse in wet, lower elevation forests rather than in montane sites. These wet lowland areas, even if host to exotic forests, require more exploration for hepatics. Some rare Lejeuneaceae recorded from wet, lowland areas in Hawai‘i include *Diplasiolejeunea* sp. (undescribed), *Drepanolejeunea pentadactyla*, *Lejeunea cocoes* and *L. laetevirens* (both perhaps introduced), *Leptolejeunea* sp., and *Lepidolejeunea involuta* and *Marchesinia brachiata.* The latter two species are each known from a 19th century collection of uncertain island provenance. It appears that more species of *Cheilolejeunea, Cololejeunea, Drepanolejeunea* and *Lejeunea* remain to be documented from Hawai‘i.

There are 89 genera of LH in Hawai‘i; of these, five are naturalized, and four indigenous genera are of uncertain island provenance. Therefore, 80 genera are both indigenous, and have at least one known specific island of occurrence. The number of indigenous genera on each island is therefore: Kaua‘i (61), O‘ahu (55), Moloka‘i (49), Lāna‘i (39), Kaho‘olawe (1), Maui (68), and Hawai‘i (62).

TABLE 2 (1 of 2, part two on facing page). Comparison of liverworts and hornworts as part of the land plant flora. of the Hawaiian Islands, from west to east. Maui Nui includes Maui, Molokaʻi, Lānaʻi, and Kahoʻolawe, which were joined into one island during the Pleistocene. On Oʻahu, the western Waiʻanae Range has 120 species of LH, while the eastern Koʻolau Range has 126 species; on Maui, the western part of the island has 126 species, while the eastern part (Haleakalā) has 156 species. We also include three large areas on Hawaiʻi Island (Kohala, Puʻu Makaʻala Natural Area Reserve, and Hawaiʻi Volcanoes National Park) with extensive land plant surveys. Data for vascular plants is from Gustafson et al. (2014); moss data from Staples et al. (2004) and (for Kauaʻi) Shevock et al. (2019).

	Kauaʻi	**Oʻahu**	**Lānaʻi**	**Molokaʻi**	**Maui Nui**	**Maui**
Liverworts-Hornworts (Staples & Imada, 2006)	106	110	8	86	141	134
Liverworts-Hornworts (Apr. 2025); includes unpublished species	**169**	**154**	**82**	**117**	**172**	**169**
Mosses	170	152	57	83	221	208
Total Bryophytes	337	306	139	200	393	377
Pteridophytes	136	130	108	121	141	138
Angiosperms	493	457	254	373	564	491
TOTAL LAND PLANTS	968	893	501	694	1,098	1,006
Ratio, Liverworts-Hornworts (2025): Pteridophytes	**1.25**	**1.18**	**0.75**	**0.97**	**1.23**	**1.22**
Liverwort-Hornwort species added, 2006-2025	**63**	**43**	**74**	**31**	**31**	**35**
Ratio, Liverworts-Hornworts (2025): Angiosperms	0.34	0.34	0.32	0.31	0.30	0.34

TABLE 2 (2 of 2, part one on facing page). Comparison of land plant floras of the Hawai‘i.

	Hawai‘i	Hawai‘i (Kohala)	Hawai‘i (Pu‘u Maka‘ala N.A.R.)	Hawai‘i Volcanoes National Park	TOTAL
Liverworts-Hornworts (Staples & Imada, 2006)	110	n/a	n/a	n/a	186
Liverworts- Hornworts (Apr. 2025)	**185**	**103**	**78**	**131**	**240-258**
Mosses	179	n/a	n/a	110	273
Total Bryophytes	364	100	78	241	513-531
Pteridophytes	131	97	83	101	163
Angiosperms	389	231	93	236	1,044
TOTAL	884	n/a	n/a	578	1,720-38
Ratio, Liverworts-Hornworts (2025): Pteridophytes	**1.41**	**1.03**	**0.94**	**1.30**	**1.45-1.64**
Liverwort- Hornwort species added, 2006-2025	**75**				**321 island records, 39 state records**
Ratio, Liverworts-Hornworts (2025): Angiosperms	0.48	0.43	0.44	0.56	0.23-0.26

Hawai‘i has approximately 3.1-3.3% of the world’s liverwort diversity and roughly 5-7% of its hornwort diversity. For comparison, the state has 2.3% of the world’s moss diversity and about 3.3% of its vascular plant diversity.

TABLE 3. Progress towards complete documentation of "island species records" and "state records" of liverwort and hornwort species in Hawai'i. The number of "island species records" has increased from 554 (Staples & Imada, 2006) to 864, an increase of 310 records (56% higher). State records have increased from 186 to 225, 21% higher.

Paper	Reference	Year	New island records	New Hawai'i records
Lāna'i survey	Judziewicz, Freire & Bogner	2023	72	9
New state records	Judziewicz & Freire	2023	23	20
Kahakuloa operculispora	Freire, Judziewicz, Cargill, Forrest, Gradstein, Oppenheimer, Pezzillo & Sepsenwol	2023	1	1
New island records	Judziewicz, Freire & Thomas	2024	106	0
Kaua'i summits	Judziewicz, Faccenda & Freire	2025	7	5
More new state and island records (in preparation)	Judziewicz, Freire, Pezzillo, Faccenda, Christianson, Fawcett & Bleecker	2025	27	7
Subtotal: Our contributions so far	Freire, Judziewicz et al.		236	39
Checklist of Hawaiian liverworts and hornworts	Staples & Imada	2006	554	186
Total			790	225
Species not yet assigned names	Freire & Judziewicz	in prep.	84	0
Grand total		in prep.	864	

Diversity by elevation

To form an approximate idea of leafy liverwort diversity by elevation, we extracted elevation data for 171 species of Hawaiian leafy liverworts from the September 2022 BISH collections spreadsheet (provided by curator Barb Kennedy), the August 2022 PTBG collections spreadsheet (provided by curator Tim Flynn), our own collections, and published data cited in revisions of Hawaiian taxa.

The graph below is a summary of our back-of-the-envelope survey; we looked at the data in 500-foot elevational increments. It gives a rough idea of liverwort diversity in Hawai'i (orange line), which peaks and plateaus between 3,000-6,000 feet. The highest elevation occurrences (7,000-8,500 feet) were nearly all from the north rim of Haleakalā, Maui.

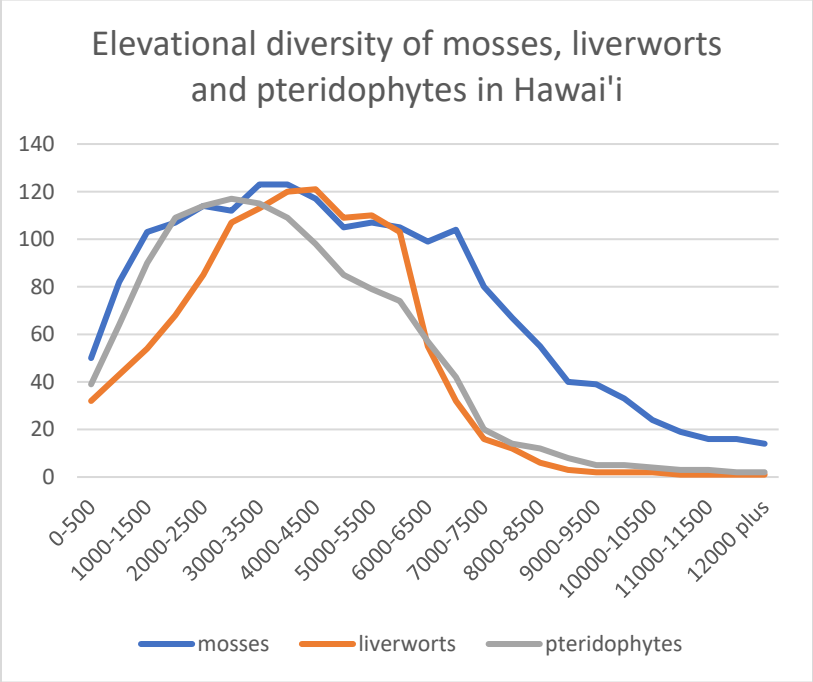
For comparison, we plotted the same data for 145 species of indigenous Hawaiian pteridophytes using the data in Palmer (2003). Pteridophytes and leafy liverworts occupy the same ecological habitat – most preferring moist to wet, shady montane forest understories – yet pteridophyte diversity peaks at lower elevations, roughly 2,000-4,000 feet (gray line).

In September 2022, we canvassed 8,890 Hawaiian moss records in the Consortium of Bryophyte Herbaria database. There are many caveats - first, nomenclature (Staples et al. 2004; needs updating); secondly, many of the database entries did not give elevations. But, overall, the curve indicates that: 1) Mosses (blue line) are much more diverse at higher elevations (above 6,000 ft.; elevations found only on Maui and Hawai'i Island) than liverworts and ferns; 2) At low elevations (below 2,500 ft.) moss and fern diversity is higher

than for liverworts; and 3) both mosses and liverworts have a somewhat higher peak of diversity (3,000-6,000 ft.) than ferns (1,500-4,000 ft.)

Maul et al. (2023) confirm that "liverworts show a globally consistent mid-elevation richness peak". Their graph appears to show a global peak between 1,000-3,000 m (ca. 3,000-10,000 ft.).

Hawaiian leafy liverwort (orange) versus mosses (blue) and pteridophyte (gray) diversity by elevation. September 2022 iteration.



Low elevation liverworts and hornworts

The liverwort and hornwort floras of the lowlands, even in the wettest areas such as around Hilo, Hawai'i Island, are less diverse when compared to mountainous areas. Only a few rare species are known: *Cheilolejeunea* sp. 3, *Diplasiolejeunea* sp., perhaps a species of *Leptolejeunea*, and *Plagiochila corticola*. It seems possible that *Lepidolejeunea involuta* and *Marchesinia brachiata*, two Lejeuneaceous liverworts collected only in the 18th and 19th centuries and not seen since, were also low elevation species. Below are species that are often encountered at elevations below 2,000 feet in Hawai'i.

Acrolejeunea sandvicensis
Bazzania cordistipula
Calypogeia tosana
Cheilolejeunea intertexta
Cololejeunea ceatocarpa
Cololejeunea planissima
Colura tenuicornis
Cuspidatula labrifolia
Cuspidatula robusta
Dendroceros crispus
Folioceros fuciformis
Frullania apiculata
Frullania hypoleuca
Frullania meyeniana
Frullania oahuensis
Frullania sandvicensis
Lejeunea cocoes (exotic; rare)
Lejeunea flava (exotic)
Lejeunea laetevirens (exotic)
Lejeunea pacifica
Metalejeunea cucullata
Myriocoleopsis minutissima
Odontoschisma denudatum
Phaeoceros carolinianus
Radula javanica
Riccardia species
Solenostoma micranthum
Spruceanthus planiusculus
Spruceanthus polymorphus

High elevation liverworts and hornworts

The highest elevation record for any liverwort in Hawai‘i that we have examined is the leafy *Cephaloziella kilohanensis*, made by Amy Greenwell in 1952 (MU) at 13,000 ft. on Mauna Kea. The highest thalloid liverwort collection is *Targionia hypophylla*, from 10,300 ft. above Hale Pohaku on Mauna Kea, Hawai‘i Island, made by Constance E. Hartt in 1952 (BISH). The highest hornwort record is a collection of a *Dendroceros* species made at 6,750 ft. by Lani Stemmermann (2467, BISH) in 1977 from Wai‘ānapanapa, Haleakalā, Maui.

EXOTIC AND NATURALIZED SPECIES

Three hornworts and 12 liverwort species (five leafy, seven thalloid) appear to be exotic and naturalized in Hawai‘i. We believe that the evidence indicates this because they either 1) grow only in highly disturbed sites, and/or 2) were not documented until the 21st century:

Exotic Leafy Liverworts

Geocalyx graveolens. A Holarctic species known from collections by H.A. Miller (Hawai‘i Island, 1953) and Maui (Zach Pezzillo, 2024). It grows in disturbed areas and we presume it to be exotic.

Lejeunea cocoes. A tiny Asian species collected by E.J. Judziewicz in the Hilo Nursery Arboretum in 2023.

Lejeunea flava. A cosmopolitan leafy liverwort first documented at Foster Botanical Garden in Honolulu (1977), it is now the dominant lowland liverwort in Hawai‘i, with first records from Kaua‘i (1993), Hawai‘i Island (2019), Maui (2021) and Lāna‘i (2022). The first iNaturalist record is from October 2019; it is now the “most observed” Hawaiian leafy liverwort on that website (161 records). We suspect that it may pose a threat to bryodiversity by outcompeting indigenous bryophytes – for example, we offer the speculation that species of *Spruceanthus* may be affected by competition with this species.

Lejeunea laetevirens. A widespread American species found sparingly on tree trunks in botanical gardens by us on Hawai‘i Island (2019 and 2024) and O‘ahu (2021 and 2024), based on our collections and later observations by Kevin Faccenda in the Honolulu area. It is apparently spreading.

Telaranea nematodes. This species is widespread in the Americas, Africa, and western Europe. It was first collected in 1983 on Hawai‘i Island from the remote East Rift Zone kīpuka by Higashino and Pratt and is now common on most islands in wet forests from sea level to 6,000 ft., often along trails but also in forests away from trails. It is mainly terrestrial. First records from these islands: Kaua‘i (2014), Maui (2016), O‘ahu (2022), and Lāna‘i (2022). While this is an inconspicuous species and could have been overlooked by early collectors, it is readily found in recent (post-2000) mixed collections, but never in mixes until the late 20th century, suggesting its absence in Hawai‘i until the last few decades. In the Volcano area we suspect that it may pose a threat to bryodiversity by outcompeting indigenous bryophytes.

Exotic Thalloid Liverworts

Fossombronia pusilla. This weedy, subcosmopolitan species was first collected on Kaua‘i in 1993 by Tim Flynn (also the first record of the genus in Hawai‘i), then in 1998 along roadsides and trails in heavily visited Haleakalā National Park on Maui by Tatsuwo Furuki (Krayeski et al., 2005), and several times by us on Hawai‘i Island beginning in 2021.

Lunularia cruciata. This cosmopolitan, weedy complex thalloid liverwort is occasionally found in and near greenhouses. First collected by William Hoe in 1969 on Hawai‘i Island (Yoshida & Smith, 1997).

Marchantia polymorpha. Another cosmopolitan, large, weedy complex thalloid liverwort that is found in and near human habitation, especially greenhouses. It is much more common than *Lunularia cruciata* and was first collected on Maui in 1875 by David D. Baldwin.

Riccia fluitans. A cosmopolitan, aquatic complex thalloid species that is reportedly sometimes cultivated for aquarium use. First collected from a watercress pond in lowland Oʻahu, by Steven Fukuda (Hall et al., 1995); also known from an artificial pond on Kauaʻi, where collected by Martin and Karen Hutten in 2024.

Riccia rechingeri. A complex thalloid species collected in 1954 in dry ground in Hawaiʻi Volcanoes National Park by Edith Bohrer Scott (1928-2009), a student of H.A. Miller.

Riccia sorocarpa. A cosmopolitan complex thalloid species first found in open, weedy ground at 4,400 ft. on Haleakalā, Maui, by William Hoe in 1977.

Ricciocarpos natans. A cosmopolitan, aquatic complex thalloid species collected once by Marie Neal and Constance Hartt in a taro patch in Mānoa, Oʻahu in 1934.

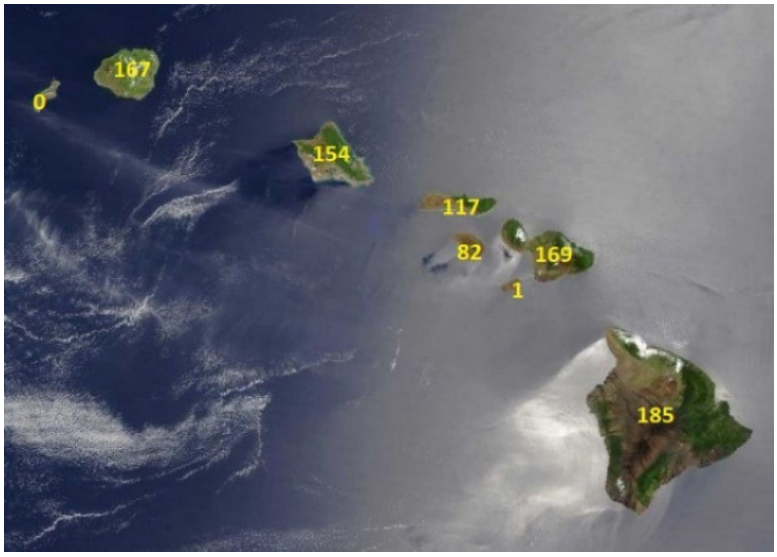
Exotic Hornworts

Anthoceros punctatus. A cosmopolitan hornwort that is known from lawns in campgrounds and picnic areas in Hawaiʻi Volcanoes National Park (first record: 2020), based on our collections. Also found on the leeward side of Haleakalā, Maui in 2024 by Zach Pezzillo.

Nothothylas breutelii. A mainly neotropical (but also found in the Philippines) terrestrial hornwort known from several urban sites on Oʻahu and perhaps other islands; first collected on the UH-Mānoa campus in 1952 by general botany students there (Miller's notes) and re-discovered there by us in 2022.

Nothothylas orbicularis. This subcosmopolitan hornwort was collected at low elevations on Kauaʻi (in 1948 by M.L. Lohman) and Maui (in 1953 by H.A. Miller and A.R.H. Lamberton) but has not been seen since.

ISLAND-BY-ISLAND SUMMARIES



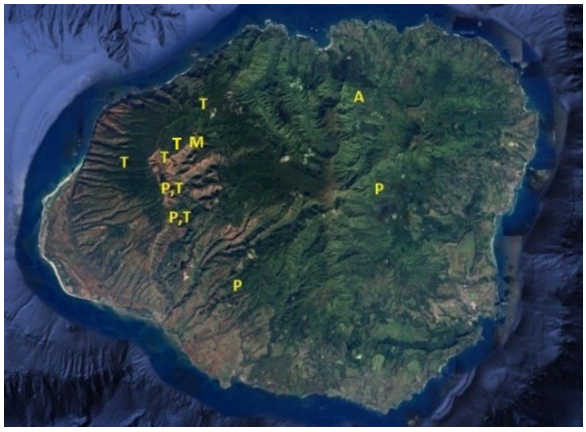
Number of liverwort and hornwort species on each of the major Hawaiian Islands.

Northwestern Hawaiian Islands and Niʻihau

No LH have been documented from the Northwestern Hawaiian Islands or Niʻihau. However, we think it likely that liverworts occur on Niʻihau in the deeper gulches on the northern end of the central plateau.

Kauaʻi

Kauaʻi has 169 species of liverworts and hornworts, this high diversity is not surprising for this oldest and most topographically dissected island. Endemics include *Lophocolea* sp. (related to the more widespread *L. spinosa*) and a possible new species of *Porella* from the Kalalau Valley (but also known from Maui). The island is relatively rich in species of the genera *Bazzania, Cololejeunea, Plagiochila* and *Radula*. The northeastern Makaleha Mountains have 28 species of LH; the southern Hāʻupu (Hoary Head) Range has 27 species, and the Kanaele (Wahiawā) Bog area has 33 species. The complex thalloid *Mannia californica* is known in Hawaiʻi only from Poʻomau Canyon. In recent decades Kauaʻi has been well-collected by Tim Flynn and Ken Wood of the National Tropical Botanical Garden, but much of the island is rugged and remote and we can expect many more liverwort surprises. The adjacent headwaters of the North Fork of the Wailua River (the "Blue Hole") to the east has 23 documented species of LH, but certainly more are to be expected. Recently, Kevin Faccenda of Bishop Museum made a productive foray to the Alakaʻi Plateau, as well as two forays to the summit area of Waiʻaleʻale; the "Kauaʻi Summits" including Kawaikini now has 73 documented species (Judziewicz, Faccenda & Freire, 2025). These summit bogs include two new endemics, *Cheilolejeunea* sp. 2, *Leptoscyphus* sp., *Marsupella* aff. *stoloniformis*, and *Calypogeia aeruginosa*, disjunct from Asia and known in Hawaiʻi (and Oceania) only from a 1938 collection made in the summit bog of Waiʻaleʻale and not recollected since; the rare Holarctic disjunct *Anastrepta orcadensis* also occurs there. The summit bogs will likely yield more interesting species; we agree with Miller (1963: 500) that "The summit of Waiʻaleʻale is cool and windswept as well as being one of the wettest spots in the world. The presence of a Himalayan species [the disjunctive leafy liverwort *Calypogeia aeruginosa*] in this situation suggests that the high, cool, and fog-shrouded bogs of Hawaiʻi may reveal similar disjunct distributions when they are carefully explored bryologically…"



Distribution of some rare and uncommon complex thalloid liverworts on Kauaʻi. Kauaʻi, especially the upper reaches of Waimea Canyon, seems to have the richest complex thalloid liverwort flora in the state. A = *Asterella innovans* (all collections were made in the Hanalei River valley); M = *Mannia californica*; P = *Plagiochasma japonicum*; T = *Targionia hypophylla*. The middle reaches of the canyon also has noteworthy leafy liverworts such as *Cylindrocolea planifolia*. James R. Shevock writes about the bryophyte flora: "There needs to be a lot more sampling in Waimea Canyon… It is a massive area with lots of microhabitats to explore."

Oʻahu

Oʻahu has 154 species of LH. They are concentrated in the Waiʻanae Range in the west and the Koʻolau Range in the east.

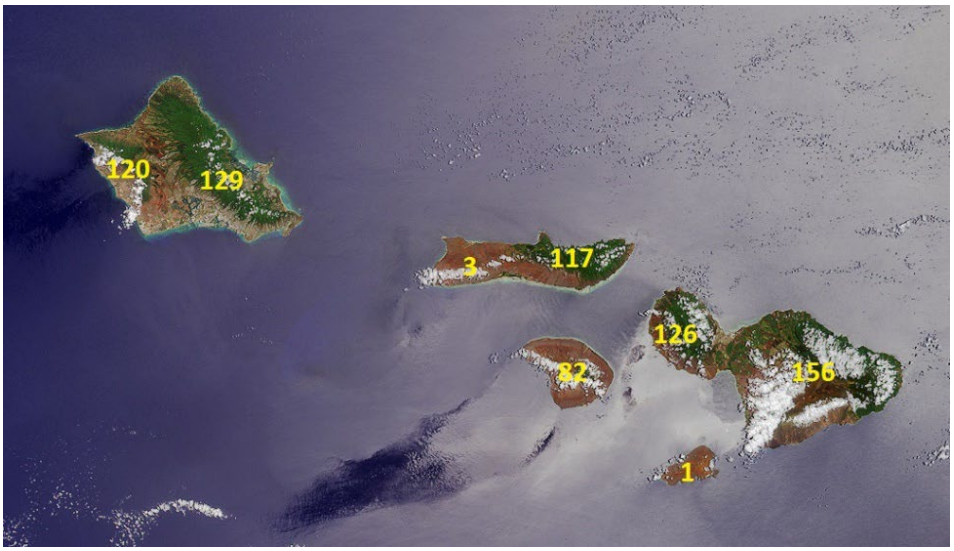
The western Waiʻanae Range has 120 species of LH. The range is only about one-fourth as large as the wetter, windward-facing Koʻolaus, but it culminates in Puʻu Kaʻala, at 4,025 feet the highest point on Oʻahu. Puʻu Kaʻala has a very diverse LH flora with over 90 species documented, the richest single site so far documented in Hawaiʻi. Noteworthy species include the hornwort *Anthoceros angustus* (disjunct from Asia), a new species of the hornwort *Folioceros*, the Holarctic disjunct leafy liverwort *Anastrepta orcadensis*, *Chiloscyphus* sp. with prominent leaf teeth, and a variable, unusual population of *Porella acutifolia* for which different species names have been proposed. The southern Waiʻanae Range has less than 50 species of LH, but the area around Palikea (elevation 3,098 ft.) is diverse. No Hawaiian or Oʻahu endemic LH species are known from the Waiʻanae Range.

The eastern Koʻolau Range has 129 species of liverworts, and although it is lower than the Waiʻanae Range, it benefits from more moisture from prevailing winds, and a larger area. The highest point, Kōnāhuanui, is 3,150 feet high and is the only site for the Hawaiian and Oʻahu endemic leafy liverwort *Radula hawaiica*, and the only Hawaiian record of the cosmopolitan *Metzgeria leptoneura* (or perhaps a distinct species). The rugged Koʻolaus are difficult to access in many places and more LH discoveries can be expected from the central and northern parts of the range.

A.V. Freire near the summit of Puʻu Kaʻala, 3,950 ft., Waiʻanae Range, Oʻahu, 9 Nov. 2022. Photo by E.J. Judziewicz.

Mokoliʻi Islet

This island of approximately 5 ha lies about 0.5 km offshore of the eastern, windward coast of Oʻahu, in Kāneʻohe Bay; it harbors *Acrolejeunea sandvicensis* (Charles R. Long, s.n., 5 May 1964, MU).



Liverwort/hornwort floras of Oʻahu and Maui Nui (Molokaʻi, Lānaʻi, Kahoʻolawe, and Maui), and their major mountain ranges.

Maui Nui

The number of LH found on Maui Nui (Molokaʻi, Lānaʻi, Kahoʻolawe and Maui combined) is 172 species, with six endemic species: *Kahakuloa operculispora, K.* sp., *Porella hoeana, Protolophozia perssoniana, Schistochila cookei,* and *Trichocolea gracillima.* Of these five species, two (*Kahakuloa operculispora* and *Protolophozia perssoniana*) have no evident close mainland relatives.

Molokaʻi

Molokaʻi has 117 species of LH, nearly all found on the wetter, higher eastern end of the island, which is rugged and must have more liverwort surprises. The austral genus *Schistochila* is purportedly known in Hawaiʻi only from *S. cookei*, known from just one collection made by C.M. Cooke, Jr. in 1903. At 3,600-4,100 feet elevation, the Pēpēʻōpae Bog and forest has the most interesting LH flora on the island: the austral genus *Protolophozia* is known from *P. perssoniana*, which occurs here and from a bog in West Maui. Three species of liverworts, *Cheilolejeunea intertexta, Frullania sandvicensis*, and a *Riccardia* (Miller & Lamberton 3907, 3908, and 3913 respectively, all at MU), have been collected near Maunaloa on the much drier western end of the island.

Mōkapu Islet

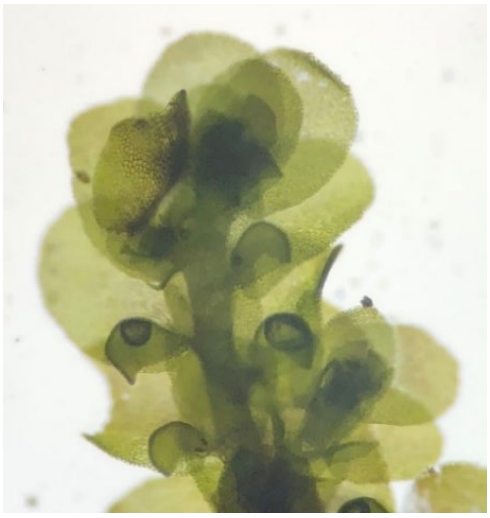
This 4 ha island lies about 1 km offshore of the north side Molokaʻi, east of the Kalaupapa Peninsula. It harbors *Acrolejeunea sandvicensis* and *Frullania oahuensis* (Wood 12194, PTBG).

Lānaʻi

Lānaʻi has 82 species of LH, most of them added to the island's flora during our March 2022 collecting foray with Kari K. Bogner (Judziewicz, Freire & Bogner, 2023). About 65 species are found on the windswept, foggy summit ridge, Lānaʻihale, at elevations between 3,000-3,370 feet. Among these are *Cephaloziella* sp. 1, a tiny new leafy liverwort species also found from several locations in the Volcano, Hawaiʻi Island area. A few additional species are found in deep mesic gulches running northeast from the summit ridge, and in intermittently wet Maunalei Gulch, explored by Bogner in June 2022.

Kahoʻolawe

One liverwort species, the xero-tolerant *Frullania sandvicensis,* is known from under an overhang on "Bell Rock" on Puʻuomoaʻula Iki, near the summit of the island (ca. 1,450 ft.), where it was discovered in 2022 by Paul Higashino, Dave Beilman, and W. Cuyler Bleecker (his photos below); they also report the species on other parts of the island. It would not be surprising if more liverworts (in genera such as *Acrolejeunea, Cololejeunea, Frullania, Lejeunea,* and *Spruceanthus*) occur in the deeper gulches on the northern and western sides of Kahoʻolawe. Below: Puʻuomoaʻula Iki, near the summit of Kahoʻolawe, 1,400 ft., habitat of *Frullania sandvicensis*. Photos by W. Cuyler Bleecker, with permission.



Maui

Maui has 169 species of LH. Of these, 126 species have been documented known from West Maui, while Haleakalā (East Maui) has 156 species. *Trichocolea gracillima* is the only Hawaiian and Maui endemic found on both West Maui and Haleakalā; *Scapania ornithopoides*, a cosmopolitan species, is known in Hawaiʻi only from West Maui and Haleakalā. Of note are species found on both Maui and Hawaiʻi Island but nowhere else in the archipelago: *Diplophyllum exiguum, Kurzia mauiensis, Isopaches bicrenatus, Lophozia silvicola,* and *Plagiochila* sp.

West Maui has been the focus of intensive LH collecting, especially in 1875-1876 (by David D. Baldwin) and 1938 (the Hawaiian Bog Survey (HBS) led by Carl Skottsberg; Miller, 1963), focusing on the summit bog on Puʻu Kukui (5,788 feet), with 110 documented species of LH. A Hawaiian endemic species occurring here is *Protolophozia perssoniana.* Two miles north lies the larger, somewhat lower (4,500 feet) ʻEke Bog, with a very interesting liverwort flora, including the 2023 collection of a new species and genus of simple thalloid liverwort, *Kahakuloa operculispora*, by Zach Pezzillo and Hank Oppenheimer, and a probable new, diminutive species of *Symphyogyna*. One mile northeast of ʻEke is the Keahikauō Bog (3,200 feet), with 25 species documented in a 1980 foray by Derral R. Herbst (1934-2023) including *Kahakuloa* along with several Lejeuneaceae that we have not yet been able to identify. A curious tiny, gemmiferous species of *Riccardia*, perhaps related to the tropical American *R. digitiloba*, is found at Hanaʻula.

Haleakalā includes the entirety of East Maui and has seen collecting beginning with D.D. Baldwin and then Charles Forbes (1910s), continuing with Harvey A. Miller, Ruth Svihla, William Hoe, Lani Stemmermann, Paul Higashino, Linda Pratt (née Cuddihy), Hank Oppenheimer, and Zach Pezzillo. However, the northern and eastern sides of the Haleakalā caldera are rugged and remote and much more work remains to be done

there. In 2024, we found an herbarium specimen (at MU) of a second species of *Kahakuloa*, distinct from *K. operculispora*, in these forests. Asian and Holarctic disjuncts *Anastrepta orcadensis, Gymnomitrion* cf. *laceratum*, *Lophozia silvicola, Marsupella emarginata*, *Southbya organensis*, and *Sphenolobus minutus* are also found at higher elevations on Haleakalā. Hawai‘i. Maui endemics *Porella hoeana*, another undetermined *Porella* species, and two species of *Radula* are known only from Haleakalā, while Hawaiian endemic *Radula curvilobula* is known only from Haleakalā and Kaua‘i. The high elevation bogs of Haleakalā, East Maui, are poorly known bryologically (Selling, 1948; Loope et al., 1991).

TABLE 4. Comparison of liverwort and hornwort diversity in sites on the two volcanoes on Maui. It is difficult to generate an accurate list for Haleakalā National Park (HNP), since it is uncertain whether early collectors such as Baldwin and Forbes collected within the present boundaries of the Park.

	Liverwort & Hornwort Species	Collectors
WEST MAUI	126	
Keahikauō Bog	25	D.L. Herbst (1980)
Waihe‘e Valley	39	Z. Pezzillo, H. Oppenheimer (2023-2024)
‘Eke Bog	29	Z. Pezzillo, H. Oppenheimer (2023); Faccenda (2025)
Pu‘u Kukui	110	Many beginning with Baldwin (1875); arbitrarily defined here as from Haela‘au (4,000 ft.) to the summit.
Violet Lake (part of Pu‘u Kukui)	16	D.L. Herbst (1980)
Hana‘ula	32	L.R. Stemmermann (1977), Z. Pezzillo (2024)
EAST MAUI	156	
Haleakalā National Park	99	Many
Waikamoi Preserve & Drainage (in the wide sense, including Olinda its flume and pipeline, and down to 2,000 ft.)	100	Many beginning with Forbes (1919-1920), Svihla (1935 and 1956), Miller (1953), Oppenheimer (2015-2023), Pezzillo (2023), Freire & Judziewicz (2023)
Hanawī Natural Area Reserve	19	Z. Pezzillo (2024)
Makapipi Valley	37	H.A. Miller (1953)
Waiho‘i Valley	43	Page Hiller (1972, MU), Z. Pezzillo (2024)
Kīpahulu Valley (part of HNP)	75	G.Y. Daida (1977), Higashino & Cuddihy (Pratt) (1983-1984), Pezzillo (2023, 2024)
Kula Forest Reserve	12	Z. Pezzillo (2024)
Leeward Haleakalā (Kahikinui and Kanaio)	23	Z. Pezzillo (2024)
All of MAUI	169	
MAUI NUI	174	

A.V. Freire, Hank Oppenheimer, and E.J. Judziewicz, Waikamoi Preserve, 6,200 ft., Haleakalā, Maui, 23 Feb. 2023. Photo by Zach Pezzillo, with permission.

Hawai‘i Island

Hawai‘i Island has 185 species (included in this total are taxa that we are unable to name), substantially more than any other island. Areas that are well-surveyed include parts of the eastern, windward sides of the island: Hawai‘i Volcanoes National Park (131 species), including the Park’s disjunct Kahuku Unit (72 species); the Pu‘u Maka‘ala Natural Area Reserve (78 species); and Saddle kīpuka and Hakalau Forest National Wildlife Refuge (63 species), including possible new species *Acrobolbus* sp. 1, *Bazzania* spp. 1, 2, 3 and 4*, Cheilolejeunea* sp. 3*, Cololejeunea* sp. 1, *Diplasiolejeunea* sp., *Lejeunea* sp., *Lophocolea* sp., and two species of *Radula*. The higher elevation (5,000-6,600 ft.) forests on this side of the island are also noteworthy for the presence of Holarctic disjuncts such as *Anastrepta orcadensis, Blepharostoma trichophyllum, Lophozia silvicola, Plagiochila caduciloba, Scapania verrucosa,* and *Tritomaria exsecta*, as well as *Diplophyllum exiguum*.

Kohala Mountain, in the far northwestern part of the island, was surveyed by the Hawaiian Bog Survey (HBS) of 1938 (Miller, 1963), which documented 70 species including the Hawai‘i Island endemic *Chiloscyphus skottsbergianus*, and *Diplophyllum exiguum*, a Hawaiian endemic also found on windward Mauna Kea and on Haleakalā, Maui. The HBS worked just a few miles north of Waimea along the Upper Hāmākua Ditch on the forested plateau above the headwall of Alakahi Stream, at elevations of 3,800-4,000 feet. The higher, wetter parts of Kohala to the northwest, exceeding 5,000 feet elevation, have never been well-surveyed and are likely to be very rich. Our foray to ‘Eke (5,300 ft.) on 5 Sept. 2023 with Joshua VanDeMark yielded an additional 16 species to the Kohala flora, including *Lophozia silvicola* and several species of *Scapania*. A total of 103 LH are now known from these rugged, wet, forested mountains. Other large, forested parts of Hawai‘i Island remain inadequately surveyed, especially the high forests of South Kona and Ka‘ū; the western flanks of Hualālai volcano; and remnant forests on the northern and eastern flanks of Mauna Kea. In particular, the very wet, rugged, trackless forests at elevations from 3,000-4,000 ft. on the eastern flanks of Mauna Loa seem likely to yield surprises, if they could be accessed. On the eastern, windward flank of Mauna Kea, Waipāhoehoe Gulch runs makai (oceanward) from the NW to SE, with forest patches extending up to 2,930 m (9,600 ft.) elevation, some of the highest “forests” in Hawai‘i. The Ka‘ali‘ali Trail/Road crosses this gulch from north to south. We speculate on the possibility of

interesting liverworts in moist ledges in this gulch such as Dan Tucker and Randall Mindell's unusual *Acrobolbus* species (?), as well as the possibility of island records of *Gymnomitrion* cf. *laceratum*, *Sphenolobus minutus*, and perhaps some Holarctic disjuncts that we can't anticipate. Only three xero-tolerant species are known from the Kaʻū desert (elevation 2,800-4,000 feet), where they occur mostly on seasonal moist ash embankments: *Cephaloziella heteroica*, *Isopaches bicrenatus*, and *Odontoschisma denudatum* subsp. *denudatum* (the latter also in moist rock crevices).

TABLE 5. Hawaiʻi Island liverwort/hornwort flora by volcano. Our estimates are based on areal and altitudinal ranges of moist to wet forests on each volcano. Mauna Loa and Kīlauea forests are contiguous.

Volcano(s)	Documented species	Total species (our estimate)
Kohala	103	130-140
Hualālai	56	80-100
Mauna Kea	105	150-175
Mauna Loa + Kīlauea	159	180-200

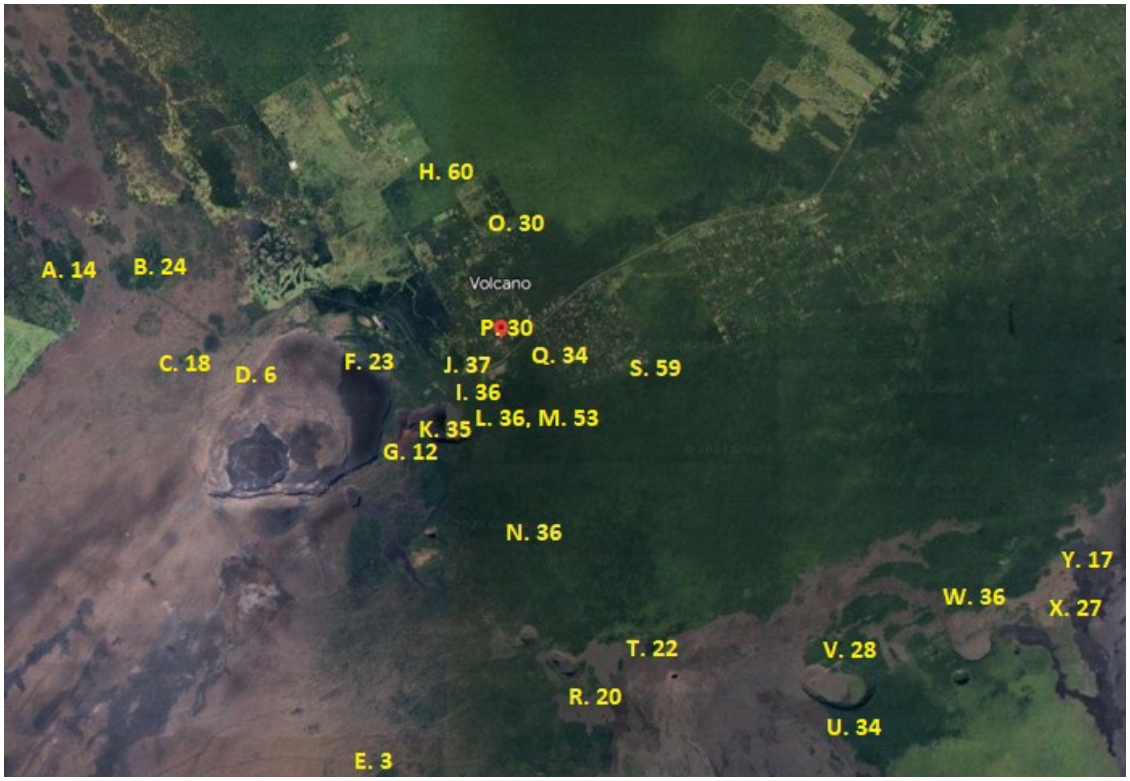
Nāuhi Gulch, 5,300 ft., Hakalau Forest National Wildlife Refuge, Hawaiʻi Island, 25 March 2023. Habitat of *Porella acutifolia* on rock face on left side of gulch. Note feral pig damage. Photo by E.J. Judziewicz.

ʻEke summit, 5,200 ft., looking towards summit of Kohala Mountain, Puʻu o ʻUmi Natural Area Reserve, Hawaiʻi Island, 5 Sept. 2023. Photo by E.J. Judziewicz.

Widely spreading roots of mānele (*Sapindus saponaria*) in mesic forest, 4,200 ft., Kīpukakī, Hawai‘i Volcanoes National Park, 18 Dec. 2023. The leafy liverworts *Frullania sandvicensis, Lejeunea pacifica, Lophocolea autoica,* and *Radula acutangula* are common here and cover the roots; *Frullania oahuensis* and *Cylindrocolea planifolia* are also present. Photo by E.J. Judziewicz.

Ephemeral ponds, with *Isopaches bicrenatus* and *Lophozia silvicola* growing on pond margins, 6,000 ft., 9 August 2022, Kahuku Unit, Hawai‘i Volcanoes National Park. Photo by E.J. Judziewicz.

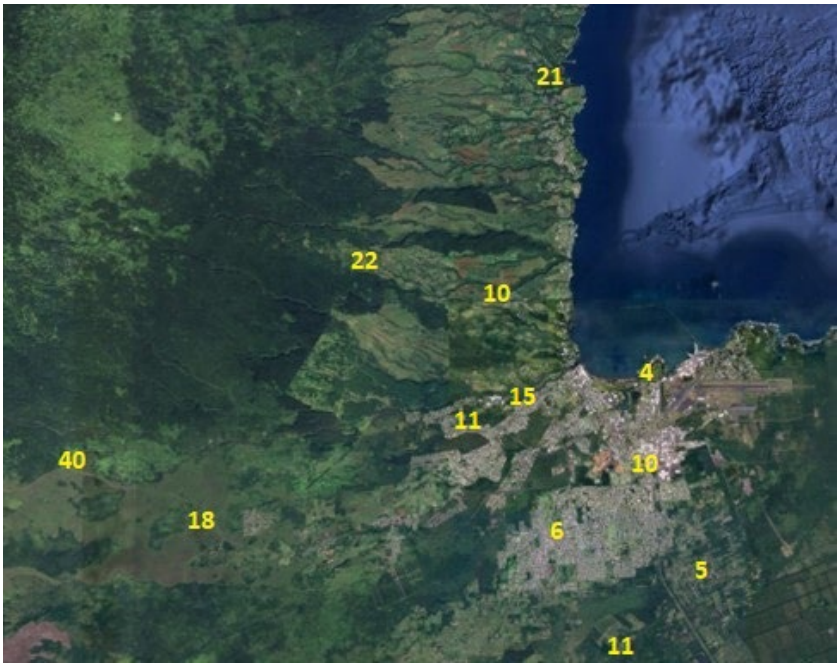
Diversity of liverworts and hornworts in the Kīlauea-Volcano area of Hawai‘i Island. Rainfall increases dramatically from west to east. See legend below.



Site	Species	Site	Species
A. Kīpukakī, HAVO	14	N. Pua Po‘o, HAVO	36
B. Kīpukapuaulu, HAVO	24	O. Spencer-Chavez ‘Āina on Wright Road	30
C. Nāmakanipaio Campground, HAVO	18	P. Maluhia Nature Trail, Kīlauea Lodge	30
D. Kīlauaea Overlook Crevices, HAVO	6	Q. Hoverson Tract, Mauna Loa Estates	34
E. Kīpukabihopa, Hilina Pali Road, HAVO	3	R. Mauna Ulu Parking Lot, HAVO	20
F. Halema‘uma‘u Trail, HAVO	23	S. Freire-Judziewicz Bryology Lab, 11-3733 Ala ‘Ōhi‘a St., ‘Ōhi‘a Estates	59
G. Devastation Parking Lot Pit, HAVO	12	T. Pu‘u Huluhulu, trail to summit, HAVO	22
H. ‘Ōla‘a Tract along Wright Road, HAVO	60	U. Makaopuhi Crater, kīpuka S of, HAVO	34
I. Escape Road Tunnel Pit, HAVO	36	V. Kānenuiohamo, HAVO	28
J. Niaulani Rain Forest	37	W. Nāpau Crater, kīpuka north of, HAVO	36
K. Kīlauea Iki Trail to Nāhuku, HAVO	35	X. Pu‘u ‘Ō‘ō, kīpuka northwest of, HAVO*	27
L. Twin Pit Craters, HAVO	36	Y. Boundary Kīpuka, HAVO*	17
M. Nāhuku Lava Tube, HAVO	53		

* Destroyed by lava in 1980s eruptions. Sites U-Y were largely surveyed by Linda Pratt and Paul Higashino in 1982-1983, before the Pu‘u ‘Ō‘ō eruption; we also collected in Site U south of Makaopuhi Crater. HAVO = Hawai‘i Volcanoes National Park.

Diversity of hornworts and liverworts in the wet, mostly lowland Hilo area, Hawai‘i Island, mostly surveyed by A.V. Freire and E.J. Judziewicz. Most sites have low diversity; the exception is the “40 species” site in the west, at Mile 12 on the Saddle Road (2,900 ft.), surveyed by Daniel Tucker and Randal Mindell in 2024, based on iNaturalist records.



ENDEMISM

It is difficult to evaluate endemism in the Hawaiian liverwort flora. Staples and Imada (2006) have pointed out that “…A number of species that were described as endemic to the Hawaiian Islands were later found to be synonyms of widespread tropical species. This trend will likely continue as additional revisionary and floristic research further clarifies the status of Hawaiian hepatics…” Sun et al. (2018) concur and emphasize the need for molecular studies.

Nevertheless, using the status given for each species by Staples and Imada (2006), there are 102 endemic species out of a total of 186 Hawaiian leafy liverwort and hornwort species, an endemism rate of 55%; however, we believe that this figure will fall significantly with further research.

There are currently no endemic hornworts known, but that could change with more research into this challenging group. We do not treat the thalloid liverwort genus *Riccardia* in the list below since its taxonomy is so uncertain. We also recognize that additional field work will add more island records for many species. The preponderance of new species on Hawai‘i Island is perhaps due to our intense collecting there; Maui and Kaua‘i, and perhaps O‘ahu, will also yield new species with more intensive exploration. There are just two endemic genera of Hawaiian bryophytes: The moss *Baldwiniella* M. Fleisch. (Staples et al., 2004), and *Kahakuloa*, our new genus of simple thalloid liverworts from Maui.

While *Kahakuloa operculispora* is certainly the most taxonomically isolated endemic Hawaiian liverwort, two other endemic species appear to be at morphologically anomalous within their respective genera and particularly merit molecular analysis: *Acromastigum integrifolium* and especially the anomalous *Protolophozia perssoniana.*

Hawaiian single-island endemic hornwort and liverwort species (tentatively new species are **bolded**). This tentative list has 27 species; 20 are found on Maui and Hawai‘i, the richest islands.

KAUA‘I (3): ***Leptoscyphus* sp., *Lophocolea* sp.*, Nothoceros* sp.**
O‘AHU (2): ***Folioceros* sp.,** *Radula hawaiica.*
MOLOKA‘I (2): ***Cheilolejeunea* sp. 4,** *Schistochila cookei.*
MAUI (8): ***Chiloscyphus* sp. 1, *Kahakuloa operculispora*, *Kahakuloa* sp.,** *Porella hoeana,* ***Radula* (2 spp.), *Symphyogyna* sp.**, *Trichocolea gracillima.*
MAUI NUI (10): ***Cheilolejeunea* sp. 4, *Chiloscyphus* sp. 1, *Kahakuloa operculispora*, *Kahakuloa* sp.,** *Porella hoeana, Protolophozia perssoniana*, ***Radula* (2 spp.),** *Schistochila cookei*, *Trichocolea gracillima.*
HAWAI‘I (12): ***Bazzania* spp. 1, 2, 3, 4, *Cheilolejeunea* sp. 3,** *Chiloscyphus skottsbergianus,* ***Diplasiolejeunea* sp., *Fossombronia* sp., *Lejeunea* sp., *Lophocolea* sp.,** and ***Radula* (2 spp.).**

Hawaiian indigenous/endemic liverworts found on just two islands (or also found on Moloka‘i, a part of Maui Nui). The island pairs with the closest similarities appear to be Kaua‘i-Maui (both have extensive high elevation summit bogs) and Maui-Hawai‘i.

Kaua‘i – O‘ahu
Cololejeunea ovalifolia

Kaua‘i – Moloka‘i – Maui
Asterella innovans (East Maui)
Southbya organensis (West & East Maui)

Kaua‘i – Maui
Cephalozia aff. *otaruensis* (West Maui)
Cephaloziella species 3 (West Maui)
Kurzia tayloriana (tentative; West & East Maui)
Porella species (East Maui)
Radula curvilobula (East Maui)
Syzygiella eatonii (West Maui)
Temnoma setigerum (West Maui)

Kaua‘i – Hawai‘i
Cheilolejeunea species 1 and 2
Cheilolejeunea raduliloba?
Cylindrocolea planifolia

O‘ahu - Moloka‘i – Maui
Chiloscyphus lambertonii (East Maui)

O‘ahu - Maui
Bazzania species 3 (East Maui)
Solenostoma hawaiicum (West Maui)

Moloka‘i – Maui
Protolophozia perssoniana (West Maui)

Lāna‘i – Hawai‘i
Cephaloziella species 1 aff. *microphylla*

Maui (both West and East)
Kahakuloa operculispora
Scapania ornithopoides
Trichocolea gracillima

Maui – Hawai‘i
Cheilolejeunea hawaica (West Maui)
Isopaches bicrenatus (East Maui)
Diplophyllum exiguum (East Maui)
Jubula pennsylvanica (East Maui)
Kahakuloa species (East Maui)
Plagiochila species (East Maui)

Widespread species found on all major islands [Lāna‘i excluded] - except absent on the one specified:

Acromastigum integrifolium – absent on Hawai‘i (but possible on Kohala Mountain there?).
Lepidozia australis, Scapania grossidens – absent on O‘ahu.

BIOGEOGRAPHY

Tables 6-11 compare the diversity of liverwort and hornwort floras of Hawai‘i and other Pacific archipelagoes with mainland areas, or near-mainland archipelagoes, on the Pacific rims of both Asia and tropical America. Hawai‘i is richer than French Polynesia or the Galapágos Islands, but is much poorer than Fiji, New Caledonia or any tropical continental or near-continental areas. Especially striking is the low percentage (18%) of the Lejeuneaceae (the largest liverwort family) compared with other Pacific floras (Fiji: 45%; French Polynesia, 29%). Yet, we discovered a new genus record for *Diplasiolejeunea* on Hawai‘i Island and the addition of *Vitalianthus* (formerly *Drepanolejeunea* in part), which hints that perhaps these tiny epiphylls and bark epiphytes may have been overlooked in the wet, lowland forests of windward Hawai‘i; areas now largely lacking indigenous trees but with suitable exotic species.

There is a small component whose affinities appear to be mainly Austral (eastern Australia, New Caledonia, Aotearoa/New Zealand, and Chile): *Cephalozia lucens, Lophocolea muricata, Protolophozia perssoniana*, *Radula hawaiica, R. mauiensis, Schistochila cookei, Southbya organensis,* and *Temnoma setigerum.* There is also evidence for some American affinities: *Vitalianthus pseudoneurus* (Asia-South America, the Hawaiian species perhaps closer to American species); *Leptoscyphus baldwinii;* (affinity American); and *Gymnomitrion* cf. *laceratum* and *Sphenolobus minutus* (affinities Holarctic).

Of interest is the addition of three more genera of Holarctic liverworts, perhaps dispersed to Hawai‘i as gemmae on the feet or feathers of kōlea (Pacific golden plovers) or other migratory shorebirds: *Isopaches bicrenatus*, *Lophozia silvicola*, and *Tritomaria exsecta*. Lewis et al. (2014) present evidence for such dispersal (although not specifically citing any Hawaiian liverworts as dispersed by this method). A complete list of these disjuncts, possibly brought southwards to Hawai‘i by birds (all are gemmiferous except *Geocalyx graveolens, Herbertus hawaiiensis*, and *Marsupella emarginata*) include:

Anastrepta orcadensis
Blepharostoma trichophyllum
Diplophyllum albicans
Fuscocephaloziopsis connivens
Geocalyx graveolens
Herbertus hawaiiensis
Isopaches bicrenatus
Liochlaena subulata
Lophozia silvicola
Marsupella emarginata
Scapania verrucosa
Sphenolobus minutus
Tritomaria exsecta

Of these 13 Holarctic taxa that have “made it” to Hawai‘i, only *Blepharostoma trichophyllum, Isopaches bicrenatus, Marsupella emarginata,* and *Tritomaria exsecta* have dispersed farther south to another island group, in each case to Aotearoa/New Zealand (gbif.org). *Fuscocephaloziopsis connivens* subsp. *sandvicensis*, a mainly Holarctic species, is also found in French Polynesia (Bardot et al., 2021: 81).

TABLE 6. Holarctic gemmae-producing liverwort species in the Hawaiian flora. See discussion.

Island	**species**
Kaua‘i	6
O‘ahu	4
Moloka‘i	2
Lāna‘i	1
Maui	9
Hawai‘i Island	7
Hawai‘i	10

TABLE 7. Largest liverwort and hornwort components in Pacific Oceanic floras. Common and characteristic families and genera were selected for this comparison. The final column is our subjective comparison of Hawai‘i with Fiji; both archipelagoes have about the same area and flora size.

Taxonomic group	**New Caledonia (**Thouvenot et al., 2011, 2023)	**Fiji (**Söderström et al., 2011)	**French Polynesia** (Bardot et al., 2021)	**Hawai‘i** (this study)	**Richness of the Hawaiian flora compared with Fiji**
HORNWORTS	14	10	6	11--15	Richer
THALLOID LIVERWORTS (*Riccardia* excluded)	27	14	13	30	Richer
Bazzania	18	13	6	17	Slightly richer
Cheilolejeunea	12	11	5	8	Slightly poorer
Cololejeunea	41	36	6	10	Much poorer
Colura	9	14	3	1	Much poorer
Frullania	44	26	9	6	Much poorer
Lejeuneaceae	146	131	48	44	Much poorer
Lejeunea	18	22	11	7	Much poorer
Lophocoleaceae	44 (27)	10	5	18-19	Somewhat richer
Plagiochila	23	12	12	18	Somewhat richer
Radula	21	12	8	13	Average
Riccardia	19	7	5	"18"	Taxonomy uncertain
TOTAL	464	291	166	240-258	Somewhat poorer

TABLE 8. Jaccard Coefficient of Similarity between four Pacific Oceanic archipelagoes. Note the very low similarity between Hawai‘i and other archipelagoes. We suggest that further taxonomic work will result in more synonyms and anticipate that these similarity indices will then increase.

Jaccard similarity (species in common in parentheses)	**New Caledonia (**Thouvenot et al., 2011)	**Fiji (**Söderström et al., 2011)	**French Polynesia** (Bardot et al., 2021)
Fiji	“45%” (but perhaps not equivalent to Jaccard similarity)		
French Polynesia	14% (75 spp.)	11% (77 spp.)	
Hawai‘i (this study)	8% (46 spp.)	9% (41 spp.)	8% (31 spp.)

A late addendum: Cocos Island, Costa Rica (550 km from the mainland) has 126 species of LH (Dauphin et al. 2025), with seven species in common with Hawai‘i: *Lejeunea flava, L. laetevirens* (but both are exotic in Hawai‘i), *Lepidolejeunea involuta, Lopholejeunea eulopha, L. nigricans, Metalejeunea cucullata*, and *Radula javanica*. This yields a Jaccard similarity of only 4%, about one-half of the New Caledonia, Fiji, and French Polynesia indices.

TABLE 9. **Comparison of liverwort/hornwort diversity in Hawai‘i, Oceania, Pacific Asia, and Tropical America.** Note that rates of endemism are poorly known for many islands. The 55% rate of endemism for Hawai‘i is surely inflated and will drop with more research. Conversely, Hawaiian Lejeuneaceae need much more work and the number of members in this family will probably increase.

Archipelago	Liverwort and hornwort species	Endemic species (% endemism)	Lejeuneaceae (% of flora)	Reference
Hawai‘i, 2006	**186**	**102 (55%)**	**28 (15%)**	Staples & Imada, 2006
Hawai‘i, 2025	**240-258**	**not given**	**44 (18%)**	this study
OCEANIA				
French Polynesia	166	1 (0.7%)	48 (29%)	Bardat et al. 2021
Fiji	291	not given	131 (45%)	Söderström et al., 2011
New Caledonia	464	("13-39%") [= 62-185 species]	146 (31%)	Thouvenot et al. 2021
Aotearoa/New Zealand	665	not given	76 (11%)	Gibb et al., 2017
PACIFIC ASIA				
Malaysia	773	not given	312 (40%)	Lee et al., 2022
Taiwan	512	25 (5%)	121 (23%)	Wang et al., 2011
Japan	655	not given		Katagiri & Furuki, 2018
TROPICAL AMERICA				
Galápagos Islands	126	10 (8%)	33 (26%)	Gradstein, 2021
Colombia	720	26 (3.5%)	330 (39%)	Gradstein, 2021
Ecuador	720	44 (6%)	Not given	Gradstein, 2021

TABLE 10. **Geographic affinities of named indigenous Hawaiian leafy liverwort and hornwort species** (July 2024 iteration). This table explores the possible geographic affinities of named Hawaiian leafy liverwort and hornwort species listed by Staples & Imada (2006). This comparison is *very* preliminary since in many cases the most recent speculations on these affinities are those of Evans (1900) or Cooke (1904).

Suggested Affinities of All Indigenous Species (excluding endemics)	Number of species	Percent of indigenous flora
Widespread (cosmopolitan, sub-cosmopolitan, or pantropical)	44	42
Asia, Oceania, or Australia	39	37
Warm temperate or tropical America	7	7
Boreal (Northern Eurasia and boreal to cold temperate North America)	13	12
Austral (Aotearoa/New Zealand, Chile)	1	1
Endemic to Hawai‘i	86	n/a
TOTAL	190	100

TABLE 11. **Geographic affinities of putatively endemic Hawaiian leafy liverwort and hornwort species** (July 2024 iteration). This table explores the possible geographic affinities of species listed by Staples & Imada (2006) as endemic. This comparison is *very* preliminary since in many cases the most recent speculations on these affinities are those of Evans (1900) or Cooke (1904).

Affinities of Endemic Species Only	Number of species	Percent of flora
Widespread (cosmopolitan, sub-cosmopolitan, or pantropical)	7	8
Asia, Oceania, or Australia	30	35
Warm temperate or tropical America	6	7
Boreal (Northern Eurasia and boreal to cold temperate North America)	6	7
Austral (Aotearoa/New Zealand, Chile)	3	3
Affinities not yet suggested	34	40
TOTAL	86	100

The combined data from Tables 10 and 11 suggest that about 42% of the flora is derived from tropical Asian sources; 19% are widespread taxa occurring on both the eastern and western rims of the Pacific Ocean; 6% derive from tropical American sources; 5% derive from boreal Eurasian and American source areas; and up to 3% from Austral areas. For the remaining 25% of the flora, even speculative source areas have not yet been suggested.

TABLE 12. **Largest Liverwort Families in Hawai‘i.** With numbers of species.

Lejeuneaceae	44
Lepidoziaceae	27
Lophocoleaceae	18-19
Plagiochilaceae	18
Aneuraceae	ca. 11-12
Scapaniaceae	8-10

TABLE 13. **Largest Liverwort Genera in Hawai‘i.** With numbers of species.

Plagiochila	18
Bazzania	17
Radula	13
Cololejeunea	10
Riccardia	Ca. 10
Lophocolea	9

SPECIES WE WISH WE COULD REDISCOVER

1. ***Schistochila cookei***. **Moloka‘i**. A large distinctive plant from a mainly Austral genus, it was collected once in Hawai‘i, by Charles M. Cooke, Jr. in 1903; its congener ***Schistochila aligera*** has also been collected from somewhere in Hawai‘i.

2. ***Protolophozia perssoniana***. **Molokaʻi** and **West Maui,** occurring on mountain-top bogs, this is the only tropical species in an otherwise North and South temperate genus; but its generic placement is uncertain. The most recent collection was made in 1972 by John M. Gillett.

3. ***Chiloscyphus skottsbergianus.*** **Hawaiʻi Island.** Collected in a sedge bog on Kohala Mountain in 1938 by Lucy Cranwell and the Hawaiian Bog Survey (Miller, 1963), it has not been seen since. It might belong to a different genus in the Lophocoleaceae, perhaps *Cryptolophocolea*.

4. ***Gymnomitrion* cf. *laceratum.*** **East Maui**. This mostly alpine, cosmopolitan genus is known in the Pacific area only from Aotearoa/New Zealand and one collection made on the rim of Haleakalā by Marko Lewis in 1981. The species determination is provisional; the species may prove to be endemic.

5. ***Lepidolejeunea involucrata*.** **Collected from somewhere in Hawaiʻi**. Known only from an 18th century Archibald Menzies specimen. This is otherwise a tropical American species; Hawaiian material could represent a separate, endemic species (Heinrichs et al., 2015). We have not examined specimens.

6. ***Calypogeia aeruginosa.*** **Kauaʻi.** Collected in that island's summit bogs in 1938 by Lucy Cranwell and the Hawaiian Bog Survey and not seen since. Disjunct from Asia (Sun et al., 2018); Miller believed it to be a separate species, *C. waialealeensis*, and Bakalin et al. (2020) question whether it is conspecific with the Asian taxon.

7. ***Marchesinia brachiata***. **Collected from somewhere in Hawaiʻi**. This widespread tropical American species, superficially somewhat resembling *Lopholejeunea nigricans*, was collected by William Hillebrand in the 19th century and not since.

8. ***Mannia californica.*** **Kauaʻi.** Collected once by Tim Flynn et al. in 1993 in a side canyon of Waimea Canyon. This is the first record of this subcosmopolitan complex thalloid genus from any Pacific Island.

9. ***Temnoma setigerum* var. *hawaiicum.*** **Kauaʻi, West Maui,** and perhaps **Hawaiʻi Island.** A rare Asian species, last collected in 1980 (by Derral Herbst on Maui), 2006 (by Ken Wood on Kauaʻi), and 2014 (James Shevock et al. on Kauaʻi).

WHAT STILL NEEDS TO BE DONE

We are well-aware that our "Bryologists' Notebook" falls well short of what we would wish to see in a formally published document: An integrated molecular and morphological analysis of all taxa, including a detailed study of types, will be essential.

More field exploration is needed throughout Hawaiʻi, concentrating on these areas: Kauaʻi: High elevation bogs; steep wet canyons and waterfalls islandwide. Oʻahu: Summits and leeward slopes of the central and northern Koʻolau Range. Molokaʻi: Steep wet canyons and waterfalls in the northeastern part of the island. Maui: High-elevation forests, grasslands, and shrublands and bogs of windward Haleakalā; the pitted summit of Mauna ʻEʻeka in West Maui. Hawaiʻi: High and mid-elevation very wet forests on the leeward slopes of Mauna Kea; the wettest forests on the leeward side of Hualālai; high elevation kīpuka on the saddle between Mauna Loa and Mauna Kea; and the highest elevations of the Kaʻū Forest Reserve.

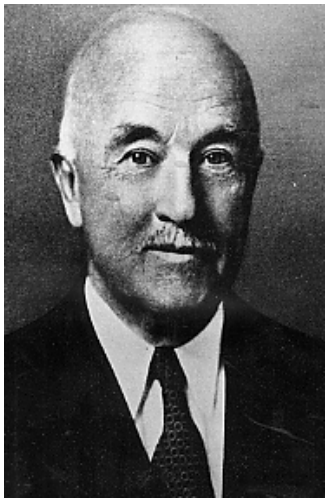
COLLECTING HISTORY, WITH EMPHASIS ON RECENT EXPLORATION

It appears that Archibald Menzies (1754-1842) was the first Western botanist to collect liverworts in Hawai‘i. He collected on several islands and found species such as *Lepidolejeunea involuta* that have never been re-collected in Hawai‘i.

Briefly, some of the most prolific collectors of Hawaiian liverworts and hornworts over the last 150 years have been (in approximate chronological order, with number of collections in selected herbaria): William Hillebrand (1821-1886); Charles Gaudichaud (1789-1854); Horace J. Mann (1844-1868) and William T. Brigham (1841-1926); David D. Baldwin (1831-1912; mostly from Maui in 1874-1875; 123 collections at BISH); A. Arthur Heller (1867-1944); Urbain Faurie (1847-1915); Matthias Newell (1854-1939); Charles M. Cooke, Jr. (1874-1948), mostly from Kaua‘i and O‘ahu, ca. 1900; 420 collections at BISH; also contributed treatments of many genera of leafy liverworts (1904); Charles N. Forbes (1883-1920; all islands, 706 collections at BISH); the Hawaiian Bog Survey of 1938, by Carl Skottsberg (1880-1963), Olof H. Selling (1917-2012), Lucy M. Cranwell (1907-2000; from Aotearoa/New Zealand), and Folke Fagelind (1907-1996), their work summarized by Miller (1963), and including about 3,000 collections, with the first set housed at the Stockholm Herbarium (S); Ruth D. Svihla (1897-1974; all islands, in the years 1935 and 1956, 735 collections at BISH; she also apparently curated Forbes’ bryophyte collections; we sincerely regret that we have been unable to locate an image of this pioneering bryologist), and Otto Degener (1899-1988; 53 collections at MU). Alexander W. Evans (1868-1959) never collected in Hawai‘i, but contributed a treatment of the Lejeuneaceae (Evans, 1900) that remains relevant today.

David D. Baldwin

Charles M. Cooke, Jr.

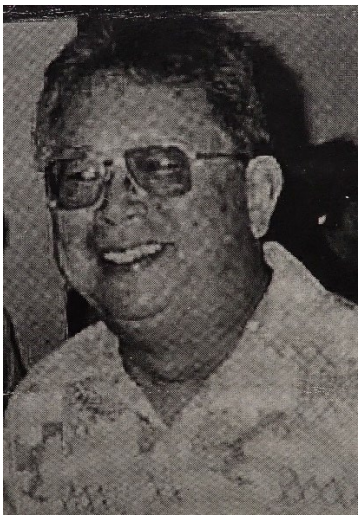


Alexander W. Evans

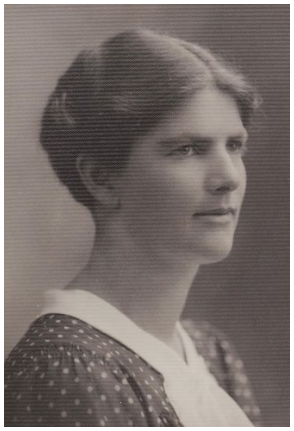
In the latter half of the 20th century and this century, important collectors include William J. Hoe (1941-2000; all islands, 179 collections at BISH), Lani Stemmermann (1952-1995; Maui and Hawai‘i, collections at BISH); Linda W. Pratt (née Cuddihy; Maui and Hawai‘i, ca. 150 collections at HAVO); John B. Hall (b. 1934), who gave us his collections to identify, which we then conveyed to Bishop Museum; Paul K. Higashino (b. 1955, Maui and Hawai‘i, ca. 150 collections at HAVO); Hank Oppenheimer (Maui Nui, collections at BISH and PTBG); Kenneth R. Wood (mostly Kaua‘i, 288 collections at PTBG); Timothy W. Flynn (mostly Kaua‘i, 754 collections at PTBG); Miles K. Thomas (Kaua‘i and O‘ahu, BISH); Zach Pezzillo (Maui); Kevin Faccenda (Kaua‘i, O‘ahu, and Hawai‘i Island); James R. Shevock and Wenzhang Ma (Kaua‘i), California Academy of Sciences; and Randal Mindell (Hawai‘i Island) and Daniel Tucker (Hawai‘i Island), from the University of Victoria, British Columbia.

Charles N. Forbes

Otto Degener

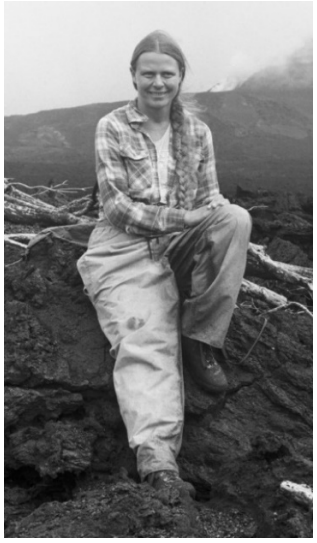


William “Bill” J. Hoe

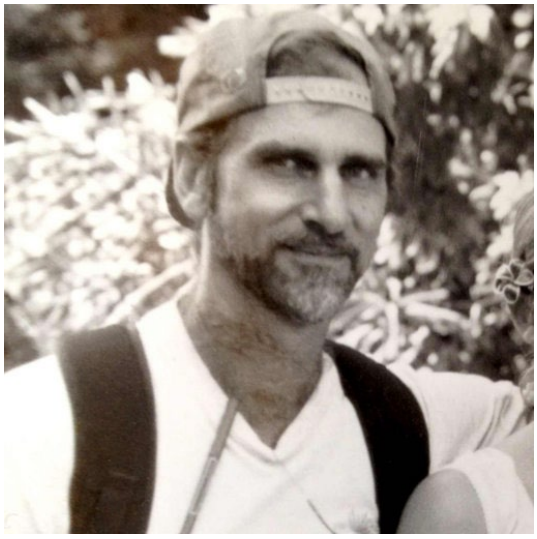


The Swedish Hawaiian Bog Expedition of 1938: Carl Skottsberg, Lucy M. Cranwell, and Olof H. Selling.

Paul K. Higashino



Ruth Leilani “Lani” Stemmermann



Kenneth R. Wood

Timothy W. Flynn

Hank Oppenheimer

Linda W. Pratt (née Cuddihy)

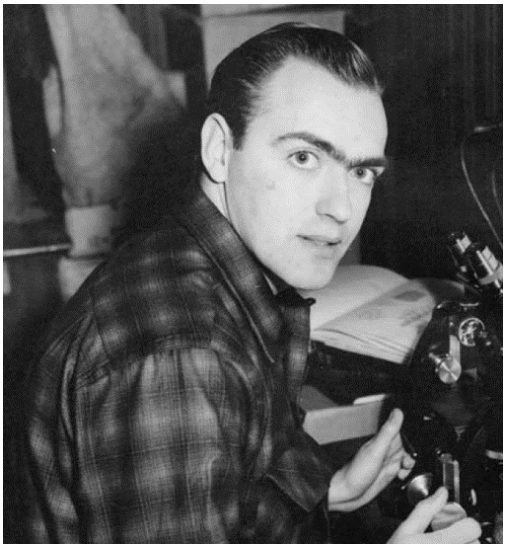
Kevin Faccenda

Miles K. Thomas

Zach Pezzillo

Mashuri Waite

Daniel Tucker, Randal Mindell



Harvey A. ("Al") Miller (1928-2020), contributed significantly to the knowledge of Hawaiian bryophytes. Collecting there intensively from 1950-1953, he wrote an unpublished draft key to Hawaiian liverwort genera (1960) that we found essential at the beginning of our research in 2019. His unpublished camera lucida drawings and notes on many genera exist at Bishop Museum and elsewhere. Photo courtesy of Gretchen Meier, Willard Sherman Turrell Herbarium (Miami University, MU).

TABLE 12. Harvey A. Miller's Hawaiian bryophyte collection itineraries, 1950-1953, compiled from his notebooks at MU by E.J. Judziewicz, comprising 3,915 collections. Perhaps about one-half of these are liverworts and hornworts; the remainder are mosses. His 1953 Molokaʻi, Maui, and Hawaiʻi Island collections were made with Alastair R.H. Lamberton (1931-2008), for whom *Chiloscyphus lambertonii* is named. Note that some collection ranges are out of chronological sequence.

Range	Year	Month	Day(s)	Island	Locality	Elevation (ft.)	Co-collectors(s)
1409-1522	1950	Sept.	9 & 10	Oʻahu	Dupont Trail and on the summit of Mt. Kaʻala, Waiʻanae Mts.	[not given]	W.H. Hatheway
1523-1582	1950	Sept.	15	Oʻahu	East branch, East Makaleha Valley, Waiʻanae Mts.	1,900	W.H. Hatheway
1583-1597	1950	Sept.	26	Oʻahu	Mt. Tantalus, along forest trail number 2, Koʻolau Mts.	1,800	
1598-1652	1950	Oct.	15	Oʻahu	West branch, East Makaleha Valley, Waiʻanae Mts., relict dry type forest.	1,280	W.H. Hatheway
1653-1753	1950	Oct.	22	Oʻahu	Kolekole Pass, Puʻu Hapapa, Waiʻanae Mts.	1,800-2,883	M.S. Doty, W.H. Hatheway, O. Degener, Silva
1754-1765	1950	Nov.	11	Oʻahu	Mt. Tantalus, along forest trail number 2, Koʻolau Mts.	1,800	M.S. Doty, D. Strassburg
1766-1799	1950	Dec.	9	Oʻahu	Mānoa Valley west of Mānoa Falls, Koʻolau Mts.	800	M.S. Doty, M.L. Lohman
1800-1883	1950	Nov.	24	Maui	Haleakalā, Red Hill to Kahikinui House.	600-10,000	With Otto Degener, students
1884-1911	1950	Nov.	27	Maui	Above Lahaina in ʻōhiʻa and koa forest, West Maui.	1,800	With Otto Degener, students
1912-1961	1950	Dec.	17	Oʻahu	Poamoho Trail, Koʻolau Mts.	1,600	M.S. Doty
1962-1977	1950	Dec.	22	Oʻahu	Aiea Trail, Koʻolau Mts.	1,600	M.L. Lohman

1978-1998	1950	Dec.	24	Oʻahu	Ridge in Wailupe Valley, between Wiliwilinui and Hawaiʻi Loa Ridge, Koʻolau Mts.	1,800	W.H. Hatheway
1999-2007	1951	Jan.	27	Oʻahu	Cliff 1.7 miles north of Makapuʻu Light.	300	M.L. Lohman
2008-2022	1951	Jan.	27	Oʻahu	Along stream in Maunawili Valley near Girl Scout Camp.	400	M.L. Lohman
2023-2037	1951	Jan.	30	Oʻahu	On Diamond Head side of Koko Head in bottoms and sides of gulches.	100	M.L. Lohman
2038-2067	1951	Feb.	4	Oʻahu	East Makaleha Valley, Waiʻanae Mts., dry type relict forest.	1,300	
2068-2084	1951	Feb.	17	Oʻahu	Eastern West Mānoa Falls, Koʻolau Mts.	800	
2085-2136	1951	Feb.	25	Oʻahu	South Kīpapa Ridge trail, Koʻolau Mts.	1,200-2,500	
2137-2167	1951	Mar.	18	Oʻahu	Puʻu Kaua firebreak trail, Waiʻanae Mts.	1,800-3,113	
2168-2195	1951	Apr.	1	Oʻahu	Waiāhole Ditch Trail, windward Koʻolau Mts.	800	
2196	1951	Apr.	24	Oʻahu	Trail to West Mānoa Falls, Koʻolau Mts.	600	
2197-2208	1951	Apr.	29	Oʻahu	West branch, East Makaleha Valley, Waiʻanae Mts., in gulch below Hatheway's 1,280 ft. quadrat.	1,100	
2209	1951	Apr.	30	Oʻahu	On rock, 2111 McKinley St., Honolulu.	200	
2210-2216	1951	June	9	Oʻahu	Dupont Trail to Puʻu Kaʻala, Waiʻanae Mts.		
2217	1951	July	1	Oʻahu	Sacred Falls, windward Koʻolau Mts., in falls above pool level.	200	
2218-2220 at least	1951	Aug.	2	Oʻahu	Pupukea and summit trail, Koʻolau Mts.	1,800	M.L. Lohman
GAP							
xxxx-2259-2277					Collections perhaps not made in Hawaii.		
2288-2347	1953	Jan.	18	Oʻahu	Kaiwaiiki Ditch Trail, Koʻolau Mts.	1,000	
2348-2393	1953	Feb.	1	Oʻahu	Kaipapau Valley, windward Koʻolau Mts.	1,100-1,500	
2394-2405	1953	Feb.	8	Oʻahu	Tantalus Mt., trail number 2, Koʻolau Mts.	2,000	
2406	1953	Feb.	21	Oʻahu	Behind St. Louis Heights, Trail No. 2, Koʻolau Mts.	1,100	
2407-2414	1953	Mar.	?	Oʻahu	Mānoa Valley, gulch on west side, Koʻolau Mts.	800	
2415-2424	1953	Mar.	17	Oʻahu	Pohakea Pass, Waiʻanae Mts.	2,170 +-200	
2425-2453	1953	Mar.	22	Oʻahu	Pupukea Kahuku summit, Koʻolau Mts.	1,800	
2454-2486	1953	Mar.	29	Oʻahu	Waiahole Ditch Trail, Koʻolau Mts.	800	
2487-2499	1953	Apr.	24	Oʻahu	Mt. Tantalus summit, Koʻolau Mts.	1,984	
2500-2537	1952	Sept.	18	Oʻahu	Kaʻawa Gulch, Kamananui ahupuaʻa, Puʻu Kaʻala, Waiʻanae Mts.	1,300-2,200	
2538-2561	1952	Oct.	5	Oʻahu	Kealia Trail, Kealia, Waiʻanae Mts.	1,000-1,800	
2562-2567	1952	Oct.	2	Oʻahu	Regent P.E. Spalding home, Makiki Heights, Honolulu.	600	
2568-2571	1952	Sept.	20	Oʻahu	Mt. Tantalus summit, Koʻolau Mts.	1,800	
2572-2578	1952	Nov.	16	Oʻahu	West Mānoa Falls, Mānoa Valley, Koʻolau Mts.	800	
2579-2632	1952	Oct.	26	Oʻahu	Papali Gulch, Hauʻula, Koʻolau Mts.	1,200-1,800	
2633	1952	Nov.	12	Oʻahu	Mt. Tantalus summit, Koʻolau Mts.	1,600	

2634-2700	1952	Nov.	30	Oʻahu	Along left branch of main stream, Makaha Valley, Waiʻanae Mts.	1,600	
2701-2758	1952	Nov.	23	Oʻahu	South Ridge, Kīpapa Gulch, Koʻolau Mts.	1,800-2,500	
2759	1952	Dec.	13	Oʻahu	University of Hawaiʻi Campus, under bush on north side of Dean Hall.		
2760-2765	1952	Dec.	10	Oʻahu	University of Hawaiʻi Campus.		
2766-2808	1952	Dec.	14	Oʻahu	Halawa Trail, North Halawa, South Halawa Ridge, Koʻolau Mts.	1,152-2,400	
2809-2810	1952	Dec.	13	Oʻahu	Mānoa Valley, Koʻolau Mts.	600	
2811-2812	1952	Dec.	22	Oʻahu	Campus of Mānoa Valley.	200	
2813-2844	1952	Dec.	24	Kauaʻi	Kalalau Lookout.	4,000	
2845-2961	1952	Dec.	25	Kauaʻi	Waimea ahupuaʻa, Alakaʻi Swamp Trail, Kilohana Lookout, Kawaikoa Stream.	3,700-4,000	
2962-2990	1952	Dec.	26	Kauaʻi	Long Nualolo Trail, Kōkeʻe [down] to Nā Pali Coast (2962-2975 at 2800-3500 ft., 2976-2990 at 1000 ft.).	3,500-700	
2991-3010	1952	Dec.	27	Kauaʻi	Kōkeʻe Camp.	3,700	
3011-3034	1952	Dec.	28	Kauaʻi	Kōkeʻe area, Halemanu Cliff Lookout, Waiahulu Stream, Waimea.	3,000	
3035-3055	1952	Dec.	28	Kauaʻi	Second stop along trail parallel to Kōkeʻe Stream near junction with Maluapopoki Stream, Waimea.	3,000	
3056-3101	1952	Dec.	29	Kauaʻi	Pass east of Hauipu, Kipu (3056-3067 at 1500 ft., 3068-3092 at 1000 ft., 3093-3101 at 750 ft.).	1,500-750	
3102-3103	1952	Dec.	30	Kauaʻi	Between Kōkeʻe and Hanalei. 3 stops. Stop 1: Along wet streambank 6 miles from Kapaʻa.	500	
3104-3112	1952	Dec.	30	Kauaʻi	Between Kōkeʻe and Hanalei. 3 stops. Stop 2: Around house of McBride Plantation above powerhouse. Wainiha Valley ca. 1.5 miles from beach on right side of valley.	200	
3113-3119	1952	Dec.	30	Kauaʻi	Between Kōkeʻe and Hanalei. 3 stops. Stop 3: Fern grotto, Wailua offshore of Wailua River.	10 to 25	
3120-3217	1952	Dec.	31	Kauaʻi	Wainiha Valley below Hono o Nā Pali at 750 ft., in thicket of *Hibiscus tiliaceus* (3125-3217), and Haʻena Caves (20 ft.).	20-750	
3218-3219	1953	Jan.	2	Kauaʻi	Honokoa Valley, along trail at main stream, Na Pali Cliffs Trail.	400	
3220-3288	1953	Jan.	3	Kauaʻi	Wainiha Valley, 0.5 miles below water intake.	750	
3289-3303	1953	Apr.	29	Oʻahu	Mt. Tantalus, along forest trail number 2, Koʻolau Mts.	1,800	
3304	1953	May	1	Oʻahu	In shaded court of chemistry building, watered bushes [University of Hawaiʻi].		
3305-3327	1953	May	3	Oʻahu	Makaha Valley, Waiʻanae Mts., along main stream.	2,000	Earl Ozaki
3328-3338	1953	May	10	Oʻahu	Along trail to Sacred Falls, Hauʻula Forest Reserve.	300	
3339	1953	May	16	Oʻahu	University of Hawaiʻi campus, on *Calophyllum inophyllum*.		
3340-3387	1953	June	5	Maui	Honokawai Gulch, West Maui.	1,500	A.R.H Lamberton
3388-3399	1953	June	5	Maui	Kaulaewelewe, Mauhinahina, West Maui.	2,980	A.R.H Lamberton

3400-3502	1953	May	29	Molokaʻi	Northwest of Puʻu Kolekole, Kawela ahupuaʻa.	3,800	A.R.H Lamberton
3503-3613	1953	May	30	Molokaʻi	Molokaʻi Swamp below Kaunuohua, Kawela ahupuaʻa.	4,200	A.R.H Lamberton
3614-3697	1953	May	31	Molokaʻi	Above Kamuela, near Kolekole.	3,800	A.R.H Lamberton
3698-3762	1953	June	1	Molokaʻi	Along trail from west side of head of Waikolu Canyon to Kolekole about one mile from Waikolu.	4,000	A.R.H Lamberton
3763-3854	1953	June	2	Molokaʻi	Pipeline Trail at the head of Waikolu Canyon.	4,000	A.R.H Lamberton
3855-3856	1953	June	2	Molokaʻi	Under cabin floor at junction of Waikolu-Kolekole Trail and pipeline road.	4,000	A.R.H Lamberton
3857-3880	1953	June	3	Molokaʻi	Road to Waikolu pipeline.	2,000	A.R.H Lamberton
3881-3900	1953	June	3	Molokaʻi	Kalaupapa Trail in kukui grove.	300	A.R.H Lamberton
3901-3914	1953	June	3	Molokaʻi	Mauna Loa, 200 ft. below summit in a gulch, West Molokaʻi.	[1,000?]	A.R.H Lamberton
3915-3942	1953	June	6	Maui	Hanakahau Valley Trail to ʻEke, West Maui.	2,000	A.R.H Lamberton
3943-4067	1953	June	7	Maui	Trail from Haelaʻau to Puʻu Kukui, West Maui, 4,000 ft. to summit.	4,000-[5,788]	A.R.H Lamberton
4068-4176	1953	June	9	Maui	Trail to Kukui, near Haelaʻau, West Maui.	3,250	A.R.H Lamberton
4177-4211	1953	June	10	Maui	Road to Haelaʻau, West Maui.	2,500	A.R.H Lamberton
4212-4307	1953	June	13	Maui	Koʻolau Gap, Haleakalā.	7,500	A.R.H Lamberton
4308-4316	1953	June	14	Maui	Old trail up face of rim up Haleakalā Crater, near Koʻolau Gap.	8,500	A.R.H Lamberton
4317-4321	1953	June	15	Maui	Trip around lee side of Haleakalā, several stops: Above Hokuhano, Auwahi.	1100	A.R.H Lamberton
4322-4349	1953	June	15	Maui	Trip around lee side of Haleakalā, several stops: Alelelele Stream.	200	A.R.H Lamberton
4350-4351	1953	June	15	Maui	Trip around lee side of Haleakalā, several stops: Kaupō Village.	none given	A.R.H Lamberton
4352-4481	1953	June	12	Maui	Olinda Ditch Trail.	none given	A.R.H Lamberton
4482-4550	1953	June	16	Maui	9 miles west of Hānā	1,500	A.R.H Lamberton
4551-4668	1953	June	17	Maui	East branch of Makapipi Gulch, 9 miles west of Hānā.	1,500-3,500	A.R.H Lamberton
4669-4672	1953	June	20	Hawaiʻi	Mauna Kea Truck Trail, Kamuela to Pōhakuloa: 5 miles out from Kamuela.		A.R.H Lamberton
4673	1953	June	20	Hawaiʻi	Mauna Kea Truck Trail, Kamuela to Pōhakuloa: 6.5 miles out from Kamuela.		A.R.H Lamberton
4674-4679	1953	June	20	Hawaiʻi	Mauna Kea Truck Trail, Kamuela to Pōhakuloa: 7 miles out from Kamuela.		A.R.H Lamberton
4680-4692	1953	June	20	Hawaiʻi	Mauna Kea Truck Trail, Kamuela to Pōhakuloa: 7.1 miles out from Kamuela.		A.R.H Lamberton
4693-46-94	1953	June	20	Hawaiʻi	Mauna Kea Truck Trail, Kamuela to Pōhakuloa: 9 miles out from Kamuela.		A.R.H Lamberton
4695	1953	June	20	Hawaiʻi	Mauna Kea Truck Trail, Kamuela to Pōhakuloa: 15 miles out from Kamuela.		A.R.H Lamberton
4696-4727	1953	June	20	Hawaiʻi	Mauna Kea Truck Trail, Kamuela to Pōhakuloa: 2 miles below Umiloa.		A.R.H Lamberton
4728-4747	1953	June	20	Hawaiʻi	ʻAkaka Falls State Park.		A.R.H Lamberton
4748-4784	1953	June	20	Hawaiʻi	12 miles out from Kamuela.		A.R.H Lamberton
4785-4800	1953	June	19	Hawaiʻi	Kohala Mts. behind Kamuela.	4,000	A.R.H Lamberton
4801-4807	1953	June	19	Hawaiʻi	Kohala Mts. behind Kamuela.	3,000	A.R.H Lamberton

4808-4821	1953	June	19	Hawai‘i	Kohala Mts., forest gate above Waimea.	not given	A.R.H Lamberton
4822-4895	1953	June	19	Hawai‘i	Kohala Mts., forest reserve.	4,000	A.R.H Lamberton
4896-4933	1953	June	21	Hawai‘i	Above tree line, Mauna Kea above Pōhakuloa: Vicinity of Lake Waiau.	13,000	A.R.H Lamberton
4934-4948	1953	June	21	Hawai‘i	Above tree line, Mauna Kea above Pōhakuloa: To about 500 ft. below Lake Waiau.	[12,500]	A.R.H Lamberton
4949-4955	1953	June	21	Hawai‘i	Above tree line, Mauna Kea above Pōhakuloa: To about 1,200 ft. below Lake Waiau.	[11,800]	A.R.H Lamberton
4956-4962	1953	June	21	Hawai‘i	Above tree line, Mauna Kea above Pōhakuloa: To about 1,700 ft. below Lake Waiau.	[11,300]	A.R.H Lamberton
4963-4974	1953	June	21	Hawai‘i	Above tree line, Mauna Kea above Pōhakuloa: To about 2,000 ft. below Lake Waiau.	11,000	A.R.H Lamberton
4975-4980	1953	June	22	Hawai‘i	Hale Pōhaku.	9,000	A.R.H Lamberton
4981-4989	1953	June	23	Hawai‘i	Mauna Kea truck trail from Humu‘ula, 1 mile out.	[7,000?]	A.R.H Lamberton
4990-4996	1953	June	23	Hawai‘i	On exposed lava soil at roadside, Hawai‘i saddle road summit.	ca. 7,000	A.R.H Lamberton
4997-5056	1953	June	23	Hawai‘i	In kīpuka in old lava flow (1843 flow), saddle road ca. 15 miles from Hilo.	[ca 3,000?]	A.R.H Lamberton
5057-5084	1953	June	23	Hawai‘i	Keau‘ohana Forest Reserve near Kalapana.	1,000	A.R.H Lamberton
5085-5089	1953	June	23	Hawai‘i	On beach - rocks or coconut trunks at Kalapana.	sea level	A.R.H Lamberton
5090-5150	1953	June	22	Hawai‘i	Mauna Kea Truck Trail from Kamuela, 13 miles out in deep shaded gulch.	6,500	A.R.H Lamberton
5151-5192	1953	June	22	Hawai‘i	Same gulch as previous, but in exposed areas.	6,500	A.R.H Lamberton
5193-5195	1953	June	23	Hawai‘i	Kalapana Village.	[ca. 30]	A.R.H Lamberton
5196-5239	1953	June	24	Hawai‘i	12 miles below Kūlani Prison.	[ca. 1,500]	A.R.H Lamberton
5240-5245	1953	June	25	Hawai‘i	Mauna Loa truck trail 21 miles above Kūlani Prison.	above 11,000	A.R.H Lamberton
5246-5255	1953	June	25	Hawai‘i	Kīpuka of weathered pahoehoe, 15 miles above Kūlani Prison.	8,100	A.R.H Lamberton
5256-5259	1953	June	25	Hawai‘i	12 miles above Kūlani Prison, on trees in old pahoehoe flow.	7,800	A.R.H Lamberton
5260-5279	1953	June	25	Hawai‘i	6 miles below Kūlani Prison.	[3,200?]	A.R.H Lamberton
5280-5284	1953	June	25	Hawai‘i	6.7 miles below Kūlani Prison.	[3,000?]	A.R.H Lamberton
5285-5308	1953	June	25	Hawai‘i	2 miles above Kulani Prison.	[5,500+?]	A.R.H Lamberton
5309-5322	1953	June	26	Hawai‘i	In spruce patch at English home near Kīlauea Crater.	4,000	A.R.H Lamberton
5323-5357	1953	June	26	Hawai‘i	Kūlani area 3 miles above lower end of road - ‘Ōla‘a Forest Reserve.	[800?]	A.R.H Lamberton
5358-5361	1953	June	30	Hawai‘i	Pu‘u Wa‘awa‘a Ranch.	2,000	A.R.H Lamberton
5362-5371	1953	June	30	Hawai‘i	Greenwell Ranch above Captain Cook.	2,500-3,000	A.R.H Lamberton
5372-5374	s.d.			Hawai‘i	Punalu‘u.		
5375-5377	s.d.			Hawai‘i	Kona.		
5378-5382	s.d.			Hawai‘i	Kīlauea.		

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Clyde Imada (front), Tim Gallaher, Miles K. Thomas, and Barbara Kennedy, November 2021.

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NOMENCLATURE

We follow the synonymy in Staples & Imada (2006), updated through Söderström et al. (2016), papers since 2016, and the current versions of Tropicos.org (April 2025) and the Bryophyte Nomenclator (Brinda & Atwood, 2025); note that Söderström et al. (2016) omitted the Hawaiian species *Frullania hawaiiensis, Lophocolea spinosa,* and *Marchantia marginata* from their paper. We also largely follow the "Dubious Records" and "Excluded Records" status of species given in Staples & Imada (2006), except that we confirm the presence of *Cololejeunea planissima, Heteroscyphus argutus, Lophocolea pusilla*, and *Notheroceros vincentians* (as *Megaceros vincentianus*) in Hawai'i. Numbers of species in each genus follow Brinda & Atwood (bryonames.org, 7 Apr. 2025).

NAME CHANGES SINCE 2006

Staples & Imada 2006 name	**Name in this notebook** (see species entry for reference)
Anthoceros spongiosus	*Folioceros fuciformis*
Archilejeunea planiuscula	*Spruceanthus planiusculus*
Asterella parva	*Asterella innovans*
Calypogeia arguta	*Asperifolia arguta*
Cephalozia sandvicensis	*Fuscocephaloziopsis connivens* subsp. *sandvicensis*
Cephaloziella baldwinii	*Fuscocephaloziopsis baldwinii*
Cephaloziella lilae	*Cephaloziella kiaeri*
Cheilolejeunea pyriflora	*Cheilolejeunea intertexta*
Chiloscyphus autoicus	*Lophocolea autoica*
Chiloscyphus baldwinii	*Leptoscyphus baldwinii*
Chiloscyphus bartlettii	*Cryptolophocolea bartlettii*
Chiloscyphus biscuspidatus	*Lophocolea biscuspidata*
Chiloscyphus ciliolatus	*Cryptolophocolea ciliolata*
Chiloscyphus hawaicus	*Lophocolea hawaica*
Chiloscyphus kilauensis	*Lophocolea kilauensis*
Chiloscyphus muricata	*Lophocolea muricata*
Chiloscyphus spinosus	*Lophocolea spinosa*
Cololejeunea cookei	*Myriocoleopsis minutissima* subsp. *myriocarpa*
Cololejeunea hoeana	*Cololejeunea kapingaensis*
Cololejeunea lanciloba	*Cololejeunea planissima*
Drepanolejeunea pseudoneura	*Vitalianthus pseudoneurus*
Frullania ericoides	*Frullania sandvicensis*
Frullania neurota	*Frullania sandvicensis*
Fulfordistria cookei	*Schistochila cookei*
Herbertus sanguineus	*Herbertus aduncus*
Hygrolejeunea pacifica	*Cheilolejeunea intertexta*
Jamesoniella labrifolia	*Cuspidatula labrifolia*
Jamesoniella robusta	*Cuspidatula robusta*
Jubula hutchinsiae subsp. *javanica*	*Jubula javanica*
Jungermannia hawaica	*Solenostoma exsertum* and *S. hawaiicum*
Jungermannia micrantha	*Solenostoma micranthum*
Lejeunea anisophylla	*Lejeunea adpressa*
Lopholejeunea proxima	*Lopholejeunea nigricans*

Lophozia perssoniana	*Protolophozia perssoniana*
Marchesinia mittenii	*Marchesinia brachiata*
Metahygrobiella lucens	*Cephalozia lucens*
Metahygrobiella maxima	*Cephalozia maxima*
Odontoschisma sandvicense	*Odontoschisma denudatum* subsp. *sandvicense*
Odontoschisma subjulaceum	*Odontoschisma denudatum* subsp. *denudatum*
Plagiochilion combinatum	*Chiastocaulon combinatum*
Scapania hawaiica	*Scapania ciliata* subsp. *hawaiica*
Scapania mauiana	*Scapania verrucosa*
Scapania paucidens	*Scapania javanica*
Southbya grollei	*Southbya organensis*
Trocholejeunea sandvicensis	*Acrolejeunea sandvicensis*
Tylimanthus integrifolius	*Acrobolbus integrifolius*

POSSIBLE NEW SPECIES OF HAWAIIAN LIVERWORTS AND HORNWORTS

In our research we have encountered numerous liverworts (and some hornworts) that we are unable to satisfactorily assign to known species that have been reported from Hawai‘i. These could either be undescribed endemic species, or conspecific with described species known from elsewhere in the world. Since we do not have a comprehensive knowledge of world liverworts, we are presently unable to decide between these two possibilities, and in this study we have assigned them arbitrary numbers (e.g., "***Bazzania* species 1**"). We leave other researchers to resolve these questions.

NEW HAWAI‘I RECORDS since Staples & Imada (2006) (leafy liverworts unless noted)

Acromastigum cf. *cavifolium*
Aneura maxima (thalloid liverwort)
Aneura pinguis (thalloid)
Anthoceros angustus (hornwort)
Anthoceros punctatus (hornwort)
Cephalozia aff. *otaruensis*
Cephaloziella cf. *microphylla*
Cololejeunea kapingaensis
Cololejeunea raduliloba
Cylindrocolea planifolia
Diplasiolejeunea species
Drepanolejeunea pentadactyla
Geocalyx lancistipulus
Gymnomitrion cf. *laceratum*
Isopaches bicrenatus
Kahakuloa operculispora (thalloid)
Jubula pennsylvanica
Lejeunea cocoes (exotic)
Lejeunea flava (exotic)
Lejeunea laetevirens (exotic)
Lepidozia holorhiza
Lopholejeunea eulopha
Lophozia silvicola
Mannia californica (thalloid)
Marsupella emarginata
Marsupella cf. *stoloniformis*
Myriocoleopsis minutissima ssp. *minutissima*
Myriocoleopsis minutissima ssp. *myriocarpa*
Nothoceros vincentianus (hornwort)
Notothylas orbicularis (hornwort)
Plagiochasma cordatum (thalloid)
Plagiochila caduciloba
Plagiochila aff. *corticola*
Plagiochila cf. *recurvata*
Riccardia aff. *digitiloba*
Schistochila aligera
Solenostoma exsertum
Sphenolobus minutus
Telaranea nematodes (exotic)
Tritomaria exsecta

PHYLOGENETIC ARRANGEMENT

The following phylogenetic list of Hawaiian hornwort and liverwort families and genera follows the classification of Brinda & Atwood (2025). Estimated number of Hawaiian species in each genus are in parentheses. Genera in which all species are exotic and naturalized are denoted by an asterisk. There are an estimated 11-15 hornwort species, and 229-243 liverwort species in the Hawaiian flora; thalloid liverworts are represented by 41-44 species. We must give ranges for numbers of species for many groups because of possible unidentified species and unresolved species delimitations – most evident in *Riccardia*!

Nineteen genera and at least 71 (possibly up to 77) species of liverworts are treated in this volume.

MARCHANTIOPHYTA (Liverworts) (229-243 species)

JUNGERMANNIIDAE (Leafy liverworts) (188-197 species)

Acrobolbaceae
- *Acrobolbus* Nees (2-3)

Adelanthaceae (4)
- *Cuspidatula* Steph. (3); perhaps to be transferred to *Syzygiella*.
- *Syzygiella* Spruce (1)

Anastrophyllaceae (5-6)
- *Anastrepta* (Lindb.) Schiffn. (1)
- *Anastrophyllum* (Spruce) Steph. (2-3)
- *Isopaches* H. Buch (1)
- *Sphenolobus* (Lindb.) Berggr. (1)

Blepharostomataceae
- *Blepharostoma* (Dumort.) Dumort. (1)

Calypogeiaceae (7)
- *Asperifolia* Troizk., Bakalin & Maltseva (1)
- *Calypogeia* Raddi (4)
- *Metacalypogeia* (S. Hatt.) Inoue (1)
- *Mnioloma* Herzog (1)

Cephaloziaceae (6)
- *Cephalozia* (Dumort.) Dumort. (3)
- *Fuscocephaloziopsis* Fulford (2)
- *Odontoschisma* (Dumort.) Dumort. (1)

Cephaloziellaceae (8-10)
- *Cephaloziella* (Spruce) Schiffn. (6-7)
- *Cylindrocolea* R.M. Schust. (1-2)
- *Protolophozia* (R.M. Schust.) Schljakov (1)

Frullaniaceae
- *Frullania* Raddi (6)

Geocalycaceae
- *Geocalyx* Nees (2)

Gymnomitriaceae (3)
- G*ymnomitrion* Corda (1)
- *Marsupella* Dumort. (2)

Herbertaceae
Herbertus Gray (4-5)
Jubulaceae
Jubula Dumort. (2)
Jungermanniaceae
Liochlaena Nees (1)
Lejeuneaceae (44)
Acrolejeunea (Spruce) Steph. (1)
Cheilolejeunea (Spruce) Steph. (8)
Cololejeunea (Spruce) Steph. (10)
Colura (Dumort.) Dumort. (1)
Diplasiolejeunea (Spruce) Schiffn. (1)
Drepanolejeunea (Spruce) Steph. (5)
Lejeunea Lib. (7)
Lepidolejeunea R.M.Schust. (1)
Leptolejeunea (Spruce) Steph. (1?)
Lopholejeunea (Spruce) Steph. (2)
Marchesinia S.F. Gray (1)
Metalejeunea Grolle (1)
Microlejeunea (Spruce) Steph. (1)
Myriocoleopsis Schiffn. (1)
Spruceanthus Verd. (2)
Vitalianthus R.M. Schust. & Giancotti (1)
Lepidoziaceae (27)
Acromastigum A. Evans (2)
Bazzania Gray (17)
Kurzia G. Martens (3)
Lepidozia (Dumort.) Dumort. (4)
Telaranea Schiffn. (1*)
Lophocoleaceae (19-21)
Chiloscyphus Corda (5-6); some or all may be transferred to other genera.
Cryptolophocolea L. Söderstr., Crand.-Stotl., Stotler & Váňa (2-3)
Heteroscyphus Schiffn. (1)
Leptoscyphus Mitt. (2)
Lophocolea (Dumort.) Dumort. (9)
Lophoziaceae (2)
Lophozia (Dumort.) Dumort. (1)
Tritomaria Schiffn. ex Loeske (1)
Notoscyphaceae
Notoscyphus Mitt. (1)
Plagiochilaceae (18)
Chiastocaulon Carl (1)
Plagiochila (Dumort.) Dumort. (17)
Porellaceae
Porella L. (3)
Pseudolepicoleaceae
Temnoma Mitt. (1)

Radulaceae
Radula Dumort. (13)
Scapaniaceae (8-10)
Diplophyllum (Dumort.) Dumort. (2-4)
Scapania (Dumort.) Dumort. (6)
Schistochilaceae
Schistochila Dumort. (2)
Solenostomataceae
Solenostoma Mitt. (3)
Southbyaceae
Southbya Spruce (1)
Trichocoleaceae
Trichocolea Dumort. (1)

THALLOID LIVERWORTS (41-44 species)

MARCHANTIIDAE (Complex Thalloid Liverworts) (16 species)

Aytoniaceae (4)
Asterella P. Beauv. (1)
Mannia Opiz (1)
Plagiochasma Lehm. & Lindenb. (2)
Dumortieraceae
Dumortiera Nees (1)
Lunulariaceae
Lunularia Adans. (1*)
Marchantiaceae
Marchantia L. (3)
Ricciaceae (5)
Riccia L. (4)
Ricciocarpos Corda (1*)
Targioniaceae
Targionia L. (1)
Wiesnerellaceae
Wiesnerella Schiffn. (1)

METZGERIIDAE (Simple Thalloid Liverworts) (18-19 species)

Aneuraceae (ca. 11-12)
Aneura Dumort. (1-2)
Riccardia Gray (ca. 10?)
Metzgeriaceae
Metzgeria Raddi (4)
Pleuroziaceae
Pleurozia Dumort. (3)

PELLIIDAE (Simple Thalloid Liverworts) (7-9 species)

Fossombroniaceae
Fossombronia Raddi (2)

Kahakuloaceae
Kahakuloa A.V. Freire, Judz., D.C. Cargill, L.L. Forrest & Gradst. (2)
Pallaviciniaceae (3-5)
Pallavicinia Gray (1-2)
Symphyogyna Nees & Mont. (2-3)

ANTHOCEROTOPHYTA (Hornworts) (11-15 species)

Anthocerotaceae (4)
Anthoceros L. (2)
Folioceros D.C. Bharadwaj (2)
Dendrocerotaceae (4-7)
Dendroceros Nees (2-3)
Megaceros Campb. (1-2)
Nothoceros (R.M. Schust.) Hasegawa (1-2)
Notothyladaceae (3-4)
Notothylas Sull. (2*)
Phaeoceros Prosk. (1-2)

BASIC TERMINOLOGY

We present some basic terminology to aid with the use of our keys. Here we emphasize leafy liverworts, the group treated in the first three volumes (including this volume) of our Bryologist's Notebook. This is not intended as a complete glossary.

Thalloid versus leafy plants.

1. **Thalloid plants do not have leaves**. They can be either thalloid liverworts or hornworts (Exceptions: *Fossombronia* and *Pleurozia* are thalloid liverworts that appear leafy). Examples of thalloid plants (left to right): *Kahakuloa operculispora* (male), photo by Zach Pezzillo; *Riccardia* sp. (note branching but no leaves); *Dendroceros* sp. (a hornwort).

2. **Leafy liverworts have well-defined leaves.** They are arranged in two lateral rows on the stem. Examples of leafy liverworts (left to right): *Anastrophyllum esenbeckii*, *Calypogeia cuspidata*, *Cololejeunea planissima*.

Dorsal (upper) vs. ventral (lower) sides.

1. **The dorsal side is the upper surface exposed to the environment.** To determine if leaves are incubous or succubous, plants need to be studied on the dorsal side.

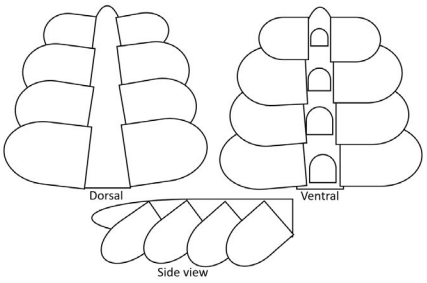
2. **The ventral side is the lower surface that faces the substrate.** The ventral surface is nearly always the most taxonomically informative side. In leafy liverworts it may exhibit lobules and underleaves. Rhizoids are also found on this side.

Example of dorsal vrs. ventral sides (left to right): tardigrade toy; endemic thalloid liverwort *Kahakuloa operculispora* (note rhizoids on the ventral side); *Chiloscyphus laceratus* dorsal view showing succubous leaf arrangement (photo by Susan Fawcett); *Chiloscyphus laceratus* ventral view showing underleaves with prominent teeth (photo by Miles K. Thomas).

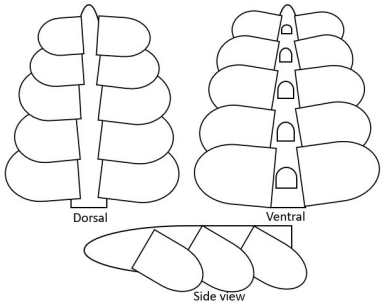
It is harder to find dorsal and ventral sides for vertical plants (especially if you just have a specimen with plant fragments!). Look for pieces of bark or clumps of dirt attached to the plant (substrate), rhizoids, lobules and/or underleaves. Any of these would indicate the ventral side.

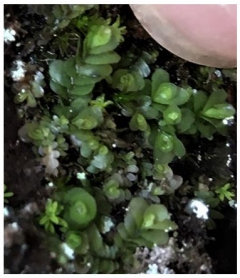
Leaf orientation – Four possible orientations (there are many intermediate states).

1. **Incubous** – In dorsal view, the leaf margins facing the apex of the plant are visible. Most Hawaiian leafy liverworts have this orientation, for example the common family Lejeuneaceae and the common genera *Bazzania, Calypogeia, Frullania* (pictured on dorsal side), *Lepidozia,* and *Radula*. Underleaves are lacking in some incubous genera.

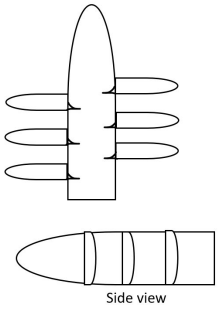


2. **Succubous** – In dorsal view, the leaf margins facing the base of the plant are visible. A significant minority of Hawaiian leafy liverworts have this orientation, for example the genera *Cuspidatula, Chiloscyphus, Cryptolophocolea, Leptoscyphus, Lophocolea, Odontoschisma*, and *Plagiochila*. Underleaves are lacking in some succubous genera.



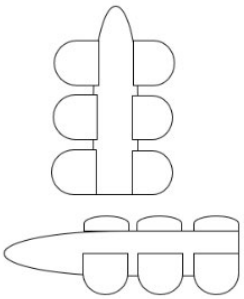
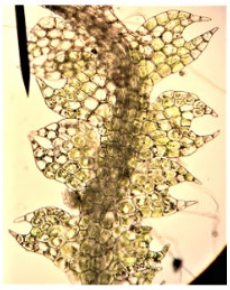


3. **Transverse –** Leaves inserted perpendicular to the stem's axis. A minority of Hawaiian leafy liverworts have this orientation, for example *Kurzia, Cephaloziella,* and some species of *Solenostoma* (all pictured). Underleaves may be present.





4. **Horizontal –** Leaves inserted parallel to the main axis of the stem. A small minority of Hawaiian leafy liverworts have this orientation, for example *Fuscocephaloziopsis connivens* (pictured). Underleaves are usually absent.


Side view


Leaf arrangement: leaves can be opposite or alternate.

1. **Opposite. Leaves side by side.** This state is much less common than alternate. The only Hawaiian genera with this arrangement are *Chiastocaulon combinatum* (left photo, by Miles K. Thomas), *Cryptolophocolea ciliolata* (right photo), *Chiloscyphus* species, *Southbya organensis*, and *Syzygiella eatonii*.

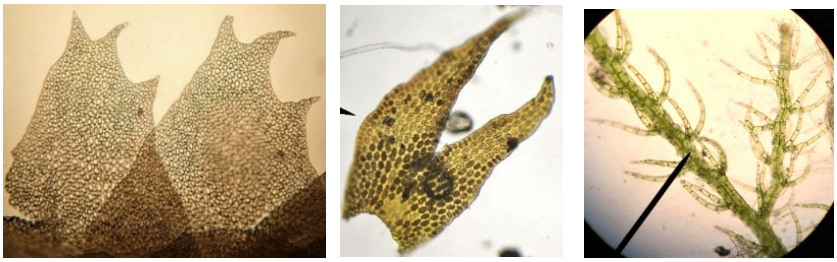

2. **Alternate.** Most leafy liverworts have this arrangement. Here, *Anastrepta orcadensis* and *Cololejeunea ceatocarpa*.

Leaf lobing/teeth. Leaves can be entire, lobate or toothed.

1. **Entire leaves have undivided margins.** Example below: *Acromastigum integrifolium*. First photo by Zach Pezzillo.

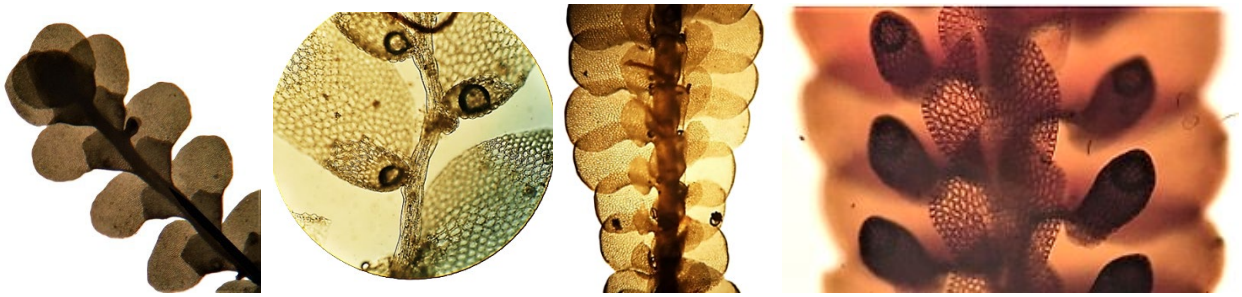
2. **Lobate leaves have broad lobes, not well-defined as teeth.** Toothed leaves can sometimes be called lobate. Examples (left to right): *Acrobolbus integrifolius*, *Marsupella emarginata*, and *Anastrepta orcadensis*

3. **Leaves with well-defined triangular or linear teeth.** Examples below (left to right): Tridentate leaves (*Bazzania praerupta*), bifid leaves (*Herbertus*), and bifid or trifid leaves with uniseriate segments (*Telaranea nematodes*).



Caducous leaves – Leaves that fall easily from the plant for asexual reproduction. Naked stem segments are observed. Photos below: *Plagiochila convoluta*, *Radula gracilis* (lobes only caducous, the lobules persistent), and *Plagiochila grossispina*.

Leaves complicate-bilobed. Leaves with a portion of the lamina folded into a pocket-like lobule**.** Common genera: *Frullania, Radula, Scapania*, and all Lejeuneaceae. Below: *Radula cordata, Cololejeunea, Porella* species with both underleaves and lobules, and *Frullania apiculata* with underleaves and stalked lobules.

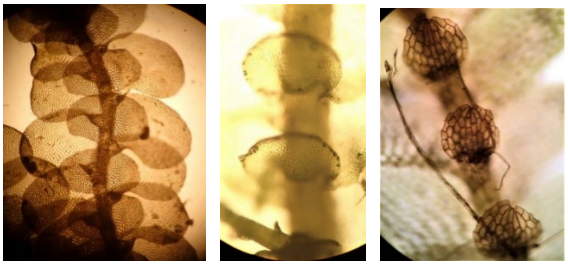


Julaceous leaves/plants – Leaves are curved or folded appearing inflated. Plants with this type of leaves are not flat; instead they appear fleshy, resembling a stonecrop plant.

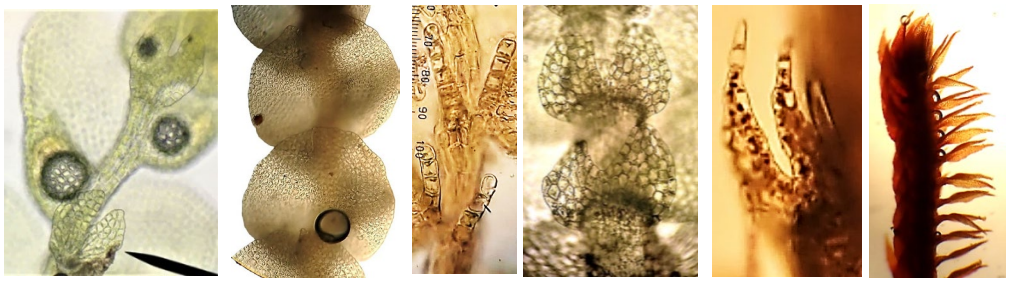
Pleurozia conchifolia, julaceous aspect (photo by Miles K. Thomas).

Underleaves. These are ventral, and usually of different shape and much smaller than the leaves (which are lateral). They form a third "leafy" rank. A minority of Hawaiian leafy liverworts lack well-developed underleaves, including the common genera *Cuspidatula, Odontoschisma, Plagiochila*, *Radula, Scapania,* and *Solenostoma.*

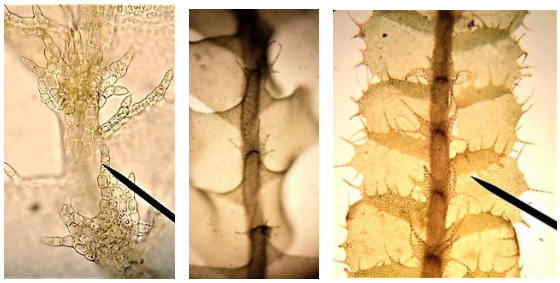
1. **Underleaves present, but unlobed (holostipous) –** Common Hawaiian genera with unlobed, unnotched underleaves include *Acrolejeunea, Bazzania, Lopholejeunea, Mnioloma,* and *Spruceanthus*. Below (left to right): *Lopholejeunea eulopha, Bazzania didericiana,* and *Mnioloma fuscum.*



2. **Underleaves present, but with a sinus separating two lobes (schizostipous) –** Common Hawaiian genera include *Calypogeia, Cheilolejeunea, Drepanolejeunea, Frullania,* and *Lejeunea.* Below (left to right): *Metalejeunea cucullata*, *Cheilolejeunea stenoschiza* (nearly holostipous; with only a tiny apical slit)*, Diplasiolejeunea* species, *Calypogeia tosana*, *Geocalyx lancistipulus,* and *Herbertus aduncus*.

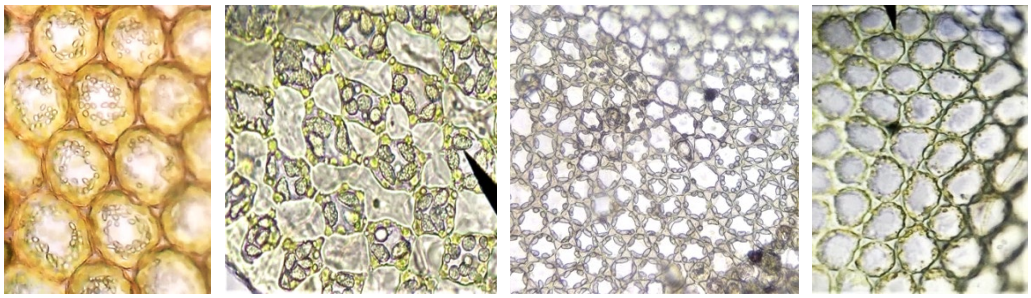


3. **Underleaves with teeth/lobes.** They may have 2-8 teeth - Common Hawaiian genera include *Chiloscyphus, Cryptolophocolea, Leptoscyphus, Lophocolea,* and occasionally *Calypogeia*. Photos (left to right): *Lophocolea spinosa*, *Chiloscyphus* cf. *greenwelliae*, and *Leptoscyphus baldwinii.*

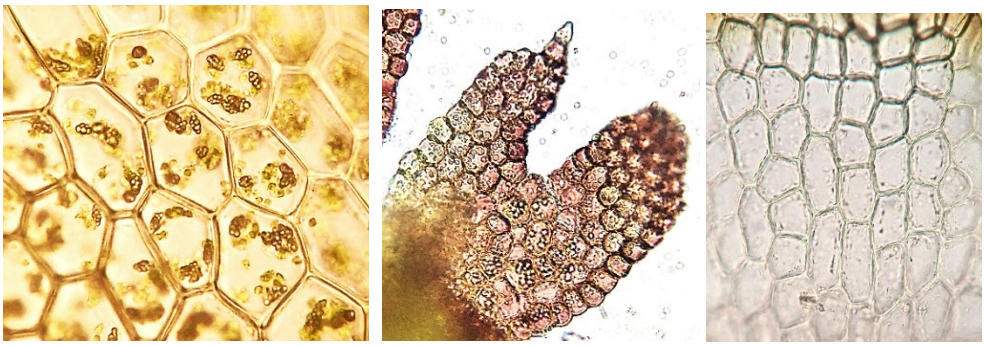


Trigones: Thickened portions of unevenly-thickened cell walls. They appear as angles or various thickened shapes that are easily observed under a microscope.

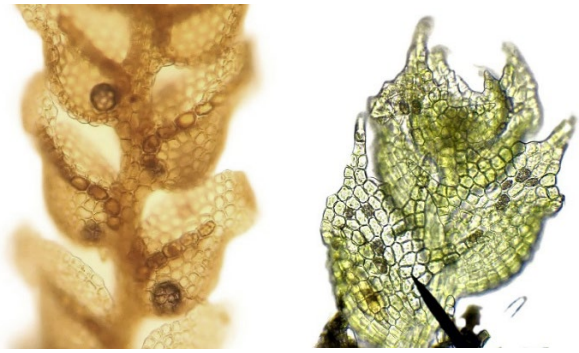
1. **Trigones present.** Photos from left to right: *Acrolejeunea sandvicensis*, with small cordate trigones and intermediate thickenings; *Cuspidatula labrifolia*, with large, confluent trigones equal in size to the cells; *Chiloscyphus laceratus* (photo by Miles K. Thomas), with nodular trigones, and *Lejeunea flava* (also with intermediate thickenings).



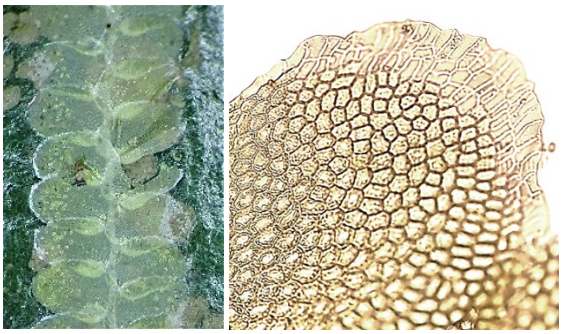
2. **Trigones absent.** Leaf cells with no trigones present. Left to right: *Calypogeia tosana*, *Cylindrocolea* aff. *planifolia* (with inflated cells), and *Cephalozia maxima*.



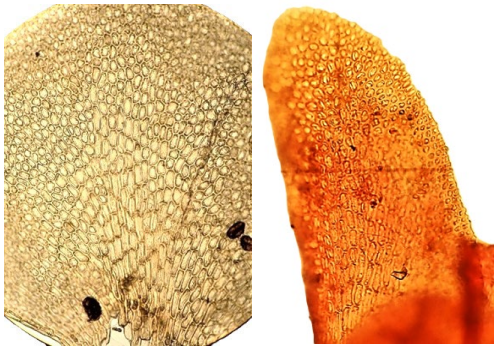
Ocelli. Leaf cells with contents that confer a different color or in some cases also shape. Left: Golden-brown ocelli in a row, *Vitalianthus pseudoneurus*. Right: Lobes with scattered dark ocelli, *Drepanolejeunea ungulata*.



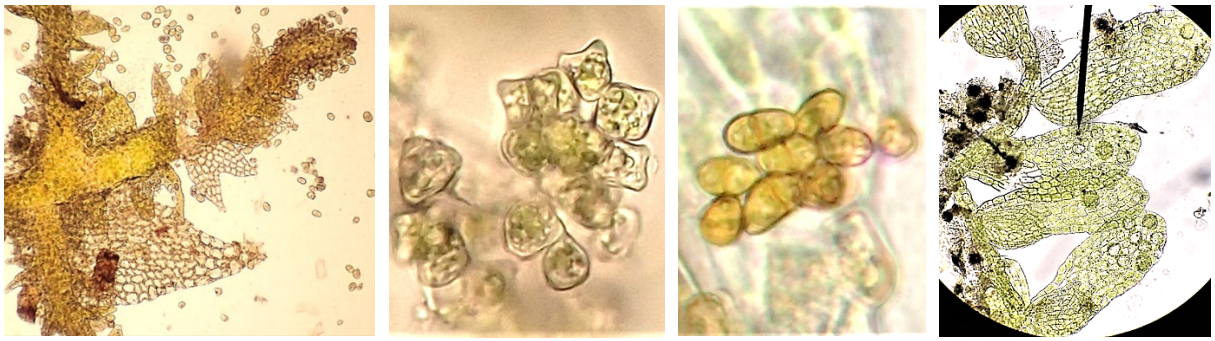
Hyaline leaf margins. Leaf marginal cells lack chloroplasts and form a clear border. Example below: *Cololejeunea planissima*.



Vittae - Vittate area (of elongated cells) at base of leaf of *Plagiochila hoei* (left) and in median area of ventral lobe of *Diplophyllum exiguum* (right). Some species of *Bazzania* also have leaf vittae.

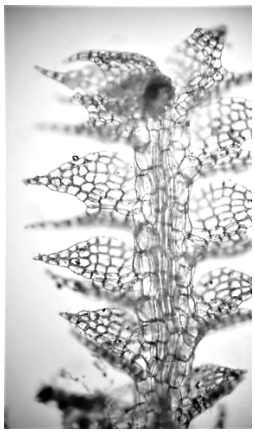


Gemmae – Asexual, often 1-2-celled propagules produced from various parts of the plant. From left to right: *Cephaloziella* aff. *heteroica* showing abundant **bicellular ellipsoidal gemmae** from the shoot apex; *Lophozia silvicola* (**angular gemmae**); *Tritomaria exsecta* (ellipsoidal 2-celled gemmae); and **discoid gemmae** produced from the surface of the lobes - characteristic of the genus *Cololejeunea*, here represented by *C.* aff. *hillebrandii.*



Gemmiferous shoots bearing clusters of gemmae. Left: *Liochlaena subulata.* Right: *Odontoschisma denudatum* subspecies *sandvicense*; photo by Zach Pezzillo, with permission.


Hyalodermis. Type of stem with large cortical (outer) cells contrasting with smaller medullary (inner) cells. It appears as two clear strips on either side of the stem. Example below: *Cephalozia lucens.*



Microphyllous branches. Branches with reduced leaves, also called flagelliform branches. Left to right: *Acromastigum* cf. *cavifolium, Bazzania nuuanuensis,* and *Anastrophyllum esenbeckii*.



DIFFERENTIATING HORNWORTS, LEAFY LIVERWORTS AND THALLOID LIVERWORTS

1. Plants thalloid, lacking well-defined leaves ……..…. **2**
   2. Cells with 1 or 2(4) large chloroplasts; plants producing persistent horn-shaped sporophytes that gradually split longitudinally from the top down ……...……..…… **HORNWORTS**
   2. Cells with many small chloroplasts; plants not producing horns but instead sporophytes with fragile stalks bearing round to ellipsoidal capsules that split at once …….. **THALLOID LIVERWORTS***
1. Plants with discrete, well-defined leaves ……...……..…….……..…… **3**
   3. Plants resembling stonecrops (fleshy-looking), erect or semi-erect, robust, reddish (but green when in shade); leaves complicate-bilobed, with large, mostly inflated leaf lobules …….. ……..... ***Pleurozia*** **(a thalloid liverwort)**
   3. Plants not as above, lacking well-defined leaves…….…… **4**
      4. Plants with purple rhizoids and crispate or undulate leaves ..… ***Fossombronia*** **(a thalloid liverwort)**
      4. Plants not with purple rhizoids (exception: *Solenostoma micranthum*, which has plane and not crispate or undulate leaves) ……..……..…...…... **LEAFY LIVERWORTS**

* Fern gametophytes in Hawai‘i are abundant and are easily mistaken for simple thalloid liverworts. More about this topic and about the morphology of thalloid liverworts will be found in Volume 4.

LEAFY LIVERWORTS (7,310 liverwort species worldwide; Brinda & Atwood, 2025).

KEY TO THE GENERA OF LEAFY LIVERWORTS OF HAWAI‘I

(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)

1. Leaves complicate-bilobed (with dorsal lobe and ventral lobule) …….…….. **KEY 1**
1. Leaves simple, not complicate-bilobed (without a ventral 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 along the lower margin of the lobe forming a long fold or keel (hornlike in *Colura*), inflated or plane, plants light green or blackish, rarely reddish-tinged; mainly on tree bark, or some epiphyllous ……..……...….. **LEJEUNEACEAE (see KEY 4)**
         4. Lobule attached at the lobe’s base or along its lower margin, but not forming a long fold or keel (*Frullania sandvicensis* have some ligulate lobules with short keels intermixed), mostly inflated, plants often forming reddish-black mats appressed to smooth tree bark, or projecting from it …**5**

5. Lobule attached at the base of the lobe's lower margin, usually from a short stalk, galeate (helmet-shaped), or cylindrical (sausage-shaped), some with occasional ligulate (tongue-shaped), and flattened lobules intermixed (*Frullania sandvicensis*); common ……... ***Frullania***
5. Lobule attached at the middle of the lobe's lower margin, always cylindrical; 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*** (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 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 (vittae) ……. ***Diplophyllum***
10. Leaves with lobe and lobule ± round, the cells of lobe and lobule homogenous, lacking a central band of elongated cells (vittae) ……..……..……..…… ***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.** ***hawaiicum***
3. Filiform segments arising near the leaf base, blade absent or very small ……. **4**
4. Leaves compoundly dissected into numerous segments, fringed; 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 short, not needlelike, 75-150 μm long, 2-3 cells wide at the base, usually concave; stem hyalodermis absent ……..…….……..…... ***Kurzia***
6. Lobes long, needlelike, 150-250 μm long, 2 cells wide at the base, not concave; stem hyalodermis present ……..……..…….... ***Telaranea nematodes***

1. Leaves undivided, or divided to much less than ½ their length …… **7**
7. Leaves succubous ……. **8**
8. Underleaves bifid, with parallel lobes ……..…… **9**
9. Leaves bifid; rare……..……..……..……... ***Geocalyx***
9. Leaves rounded to slightly retuse, not bifid; common ……...…..……. ***Notoscyphus lutescens***
8. Underleaves quadrifid (occasionally 6-8-fid), the lobes often divergent (all Lophocoleacae) ….... **10**

10. Leaf margins with 7-10 ciliate teeth; plants tending to turn yellowish-brown with age; perianth bucket-like……..…….……..…… ***Leptoscyphus baldwinii***
10. Leaf margins with 0-5 teeth or cilia; plants remaining greenish with age; perianth tubular, or rarely broad and bucket-like …….…… **11**
11. Leaves inrolled, opposite; underleaves fused to both adjacent leaves; trigones present; leaf teeth 2-3…….…… ***Cryptolophocolea***
11. Leaves flat, not inrolled, opposite or alternate; underleaves fused to both adjacent leaves or not; trigones present or absent; leaf teeth 0-5 ……..…… **12**
12. Trigones prominent, nodular; underleaves with 6-8 equal-sized teeth …… ……..……...…… ***Chiloscyphus laceratus***
12. Trigones small or absent; underleaves usually with 4 unequally-sized teeth (6 similar-sized in *Chiloscyphus skottsbergianus*) ……..……..… **13**
13. Leaves with 3-5 teeth, not bilobed; rare …….……... ***Heteroscyphus argutus***
13. Leaves consistently with 0-2 teeth, bilobed or not …….…..…. **14**
14. Leaves alternate; perianth 3-keeled; underleaves fused to just one of the adjacent Leaves, or unfused to either leaf; plants 0.5-4 mm wide …….…… ***Lophocolea***
14. Leaves opposite or subopposite; perianth round in cross-section; underleaves fused to both adjacent leaves; plants generally 3-6 mm wide ……..…… **15**
15. Leaves bilobed or not, but if bilobed then the lobes lacking additional teeth … ……..……..…. ***Chiloscyphus***
15. 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 …… **16**
16. Leaves minute (< 0.2 mm long) ……..……..… ***Cephaloziella heteroica***
16. Leaves larger (> 0.3 mm long) ……..…….. **17**
17. Leaves transversely inserted …… **18**
18. Leaves entire, unlobed ……..……..……..…. ***Acromastigum***
18. Leaves 2-4-lobed ……..……..… **19**
19. Leaves bilobed ……..…..… ***Herbertus***
19. Leaves 3-4-lobed ……..……..… ***Lepidozia***
17. Leaves incubous …….……..…… **20**
20. Plants with ventral microphyllous branches (both Lepidoziaceae) ….…… **21**
21. Leaves often 2-3(4) dentate to much less than ½ their length (occasionally without teeth); underleaves rounded to erose …...…....……..… ***Bazzania***
21. Leaves 3-4-lobed to at least ½ their length; underleaves 3-4 lobed ……..… ***Lepidozia***
20. Plants without ventral microphyllous branches (all Calypogeiaceae) ……..…. **22**
22. Underleaves deeply bifid (occasionally slightly quadrifid) ……..…… **23**
23. Stems with a partial hyalodermis; leaves distant, clearly decurrent, bordered …….. ……..……..……..…….. ***Asperifolia arguta***
23. Stems lack a hyalodermis; leaves imbricate, not decurrent or bordered …***Calypogeia***
22. Underleaves rounded or minutely retuse, not bifid …….…….…… **24**
24. Underleaves 5 times as wide as the stem; rare Kaua‘i …….. ***Calypogeia aeruginosa***
24. Underleaves barely wider than the stem; widespread ……..…… **25**
25. Leaves acute at the apex; plants bluish-green ..….. ***Metacalypogeia alternifolia***
25. Leaves rounded at the apex; plants green, often with a brownish cast ……. …..…...…….…….. ***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 at most 1 mm wide ……..……. ***Southbya organensis***
      4. Leaves slightly longer than wide; plants at least 2 mm wide ……..…..…..… ***Syzygiella eatonii***
  2. Leaves alternate …….…… **5**
    5. Leaves transversely inserted, plants minute, 0.1 mm wide; rare, summit bogs, Kaua‘i ……...
    ……. ***Marsupella* aff. *stoloniformis***
    5. Leaves succubous, plants much wider than 0.1 mm; common or rare ……..…….…… **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 shoots …….……..**9**
            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 shoots …….……..**10**
            10. Plants often reddish; leaf trigones very large; rhizoids clear …… ***Cuspidatula***
            10. Plants never reddish; leaf trigones absent or small; rhizoids clear or purplish …….
            ……...…….…..……...……. ***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 tiny, less than 0.5 mm wide, leaves transversely inserted ……. ***Cephaloziella***
      14. Plants at least 0.5 mm wide, leaves succubous or transversely inserted ……..……. **15**
        15. Plants wormlike, with very densely overlapping leaves; gray, green or reddish …...…. **16**
          16. Plants grayish; leaves symmetrically bifid; gemmae absent; rare, Haleakalā, Maui ….
          …..……..……..……..…… ***Gymnomitrion* cf. *laceratum***
          16. Plants green to slightly red or brown; leaves asymmetrically bifid; gemmae may be present; Haleakalā, Maui and Hawai‘i Island ……...…....…… ***Isopaches bicrenatus***
        15. Plants not wormlike, with leaves not densely overlapping, green, brown, or red ….…. **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, 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 (conspicuous on either side of the stem in longitudinal view); 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. Leaves flat to somewhat concave, not canaliculate; moist high elevation forests, Maui and Hawai‘i Island …… ***Lophozia silvicola***
21. Leaves canaliculate (folded into almost a tube over most of their length); 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; 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) …… ***Acrolejeunea sandvicensis***
                     9. Leaf trigones absent/poorly defined, never cordate …… ***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 …… ***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 acute …….. **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. Lobe ocelli scattered; common ……...……..… ***Drepanolejeunea***
            14. Lobe ocelli in a line 4-7 cells long down the middle of the lobe; rare …….. ……..…….… ***Vitalianthus pseudoneurus***
    12. Leaves rounded ……...…….. **15**
        15. Leaves erect or erect-spreading; plants < 0.5 mm wide …….. **16**
            16. Lobes lacking ocelli; leaves erect-spreading; stem straight; lobes of underleaves 3-5 cells wide ……..… ***Metalejeunea cucullata***
            16. Lobes with 1-3 ocelli near base; leaves erect; stem slightly zigzag; lobes of the underleaves 1-2 cells wide ……..…… ***Microlejeunea lunulatiloba***
        15. Leaves obliquely spreading; plants often at least 1 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; underleaves at least twice as wide as stem, roundish ..……..… ***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; underleaves usually less than twice as wide as stem, usually "V"-shaped ……..….. ***Lejeunea***

KEY TO BRIGHTLY COLORED LEAFY LIVERWORTS

Genera of leafy liverworts of Hawai'i that *may* exhibit a pronounced orangish, reddish, purplish, or blackish color. Many of these genera occur at higher elevations. Could these bright colors be a response to increased insolation? In shaded habitats, many of them exhibit a normal green color.

1. Leaves complicate-bilobed (with dorsal lobe and ventral lobule) ……..... **2**
    2. Underleaves present …….. **3**
        3. Underleaves bifid; lobules stalked…….……..…… ……..…..….. ***Frullania***
        3. Underleaves entire; lobules not stalked …… ….…...….. ***Lopholejeunea***
    2. Underleaves absent ……...…… **4**
        4. Plants juleaceous, very large and robust (actually not a leafy liverwort)**,** erect or semi-erect, resembling a stonecrop; lobule inflated, sacklike ……. ***Pleurozia*** (actually a thalloid liverwort)
        4. Plants not juleaceous, not robust, usually prostrate, procumbent, or in few cases erect, not resembling a stonecrop; lobule not inflated, never sacklike ……...…..……. **5**
            5. Leaves with lobe and lobule narrowly elliptical, with a ± well-developed central band of elongated cells (vittae); Maui and Hawai'i Island ……..…….……..… ***Diplophyllum***
            5. Leaves with lobe and lobule ± round, the cells of lobe and lobule homogenous, lacking vittae; widespread ……..……...…… ***Scapania***
1. Leaves simple, not complicate-bilobed ……. **6**
    6. Plants 0.1 mm wide; summit bogs, Kaua'i …… ***Marsupella* aff. *stoloniformis***
    6. Plants at least 0.3 mm wide ……...…….…….. **7**

7. Underleaves present and well-developed ……. **8**
8. Leaves bifid, the margins lacking cilia ……..……..……*Herbertus*
8. Leaves not bifid, the margins with 7-10 cilia ……,……..……***Leptoscyphus baldwinii***
7. Underleaves absent or rudimentary ……..…….. **9**
9. Leaves unlobed ……...…….…….**10**
10. Leaves opposite; Kaua‘i and Maui ……..… ***Syzygiella eatonii***
10. Leaves alternate …….…….……...…… **11**
11. Plants not producing gemmae on reduced-leafy shoots …….……..……..… ***Cuspidatula***
11. Plants producing gemmae on reduced-leafy shoots ……..… ***Odontoschisma denudatum***
9. Leaves bifid or trifid ……...…. **12**
12. Plants 2-2.5 mm wide ……..……..……....…… ***Anastrophyllum fissum***
12. Plants < 1.5 mm wide ……...……. **13**
13. Leaf lobes rounded; rare, Maui ……..……. ***Marsupella emarginata***
13. Leaf lobes acute to acuminate …….. **14**
14. Hyalodermis well-developed; cells large and thin-walled ……...…….. ***Cephalozia***
14. Hyalodermis absent or poorly developed; cells small, thin- to thick-walled ……..…. **15**
15. Leaves 0.5-1 mm long …… ***Anastrophyllum esenbeckii***
15. Leaves 0.1-0.3(-0.5) mm long …… **16**
16. Leaves unconstricted at base, transversely inserted …… ***Cephaloziella***
16. Leaves slightly constricted at base, horizontally inserted ..…….. ***Cylindrocolea***

KEY TO LIVERWORTS WITH PURPLE RHIZOIDS

1. Plants thalloid; rare, Maui ……..…….. ***Kahakuloa***
1. Plants leafy or appearing leafy ……. **2**
2. Leaves crispate; uncommon, always terrestrial ……..……..…….. ***Fossombronia***
2. Leaves plane or cupped; terrestrial or epiphytic ……...… **3**
3. Plants complicate-bilobed, with small dorsal lobes; large (6-8 mm wide); rare….……... ***Schistochila***
3. Plants not complicate-bilobed, < 3 mm wide; common ……..…… ***Solenostoma micranthum***

Acrobolbus Nees (Acrobolbaceae)

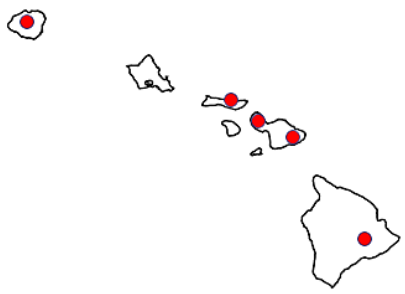
Two or three species in Hawai‘i, 36 species worldwide. Plants are erect, stoloniferous; with succubous, caducous leaves, and a swollen pouch or marsupium at their apex, where sporophytes are produced. Rhizoids can be observed at some leaf margins (those leaves will likely separate from the plant for asexual reproduction). Vegetatively, the genus *Acrobolbus* resembles *Plagiochila* in its long decurrent leaf insertion and robust stems. Unlike the latter, no prominent trigones are present on leaf cell walls. Occasionally, vestigial underleaves are present (see photo, page 92).

The plants have been described as papillose or rarely smooth (Burghardt & Gradstein, 2008; Gradstein, 2021) with a pendent marsupium at the stem apex. The Hawaiian plants are not papillose, and we did not observe a single marsupium. However, plants fit the rest of the characters attributed to the genus.

Daniel Tucker and Randal Mindell collected what may be a third species of *Acrobolbus* from 7,300 ft. at the base of northern Loaloa on the southern flank of Mauna Kea, Hawai‘i Island, in Dec. 2024 (https://www.inaturalist.org/observations/255838305). It has variably toothed leaves and does not resemble any congeners we have seen in Hawai‘i; based on the description and illustration in E.A. Hodgson (1957, Transactions of the Royal Society of New Zealand 85: 572-575), Tucker (pers. comm.) suggests that it may be related to the Australasian *Tylimanthus diversifolius* E.A. Hodgs. (=*Acrobolbus tenellus* (Taylor ex Lehm.) Trevis. var. *diversifolius* (E.A. Hodgs.) Briscoe); he is conducting further studies of this collection.

1. Leaves without teeth, often with a shallow sinus on the apical portion of the lower margin; leaf marginal rhizoids sometimes present; stems tough and wiry……..……..... ***Acrobolbus integrifolius***
1. Leaves with 1-3 sharp teeth, without a sinus on the apical portion of the lower margin; leaf marginal rhizoids not observed; stems soft and fleshy, not wiry ……..…….…….…... ***Acrobolbus* sp. 1**

1. *Acrobolbus integrifolius* (A. Evans) Briscoe. **Endemic.** Treated as *Tylimanthus intregrifolius* by Staples & Imada (2006); see Briscoe et al. (2015: 59) and Judziewicz & Freire (2023c: 159). Possible affinity: *A. laxus* (Lehm. & Lindenb.) Briscoe, tropical America, eastern Africa, and Macaronesia (Burghardt & Gradstein, 2008). An uncommon species of wet forests in the East Rift Zone kīpuka on Hawai‘i Island; also on Kaua‘i, Moloka‘i and Maui (2,500-8,000 ft.).



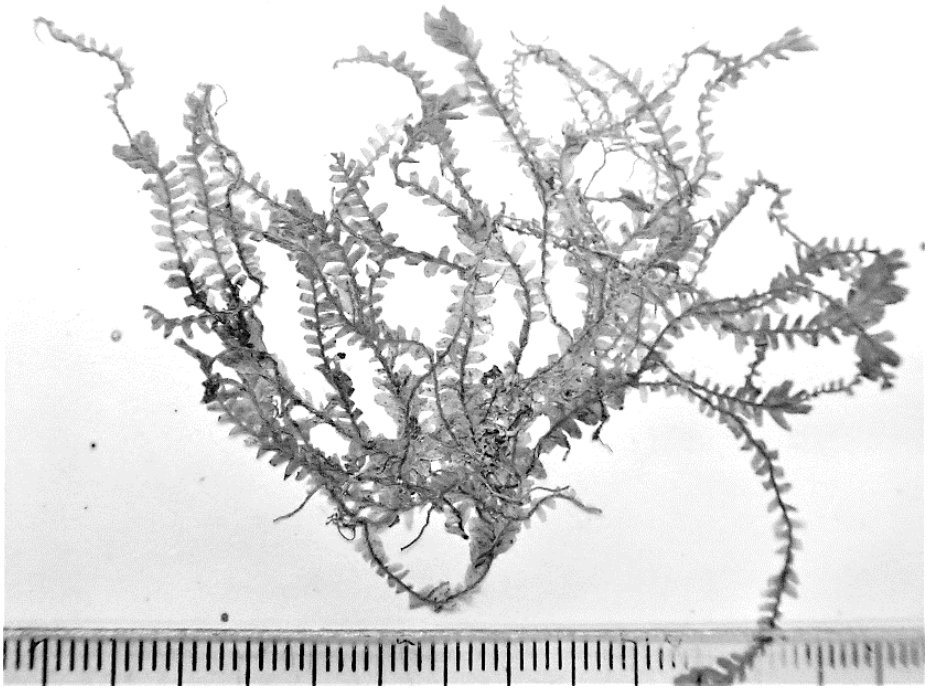
Acrobolbus integrifolius forms dense mats of erect or procumbent green to white-green plants with distant to contiguous, succubous, oblong-rectangular leaves that are caducous for asexual propagation; the leaves have an oblique and truncate tip, sometimes with a shallow sinus (but no teeth) and may appear asymmetrically bilobed. Leaf cells have evenly thickened walls, with or without very small triangular trigones. Oil bodies are brown, large, granular, and elliptical. Plants resemble those of the genus *Plagiochila* in their long leaf insertion, tough appearance of the stem, and lateral branching. No teeth are observed, unlike in Hawaiian species of *Plagiochila* who have them on at least a portion of the leaf margin. Long hyaline rhizoids, resembling hairs, are produced from leaf margins of at least some populations. No sexual structures were observed by us.

Because of the presence of leaf marginal rhizoids, *A. integrifolius* belongs to Grolle’s section *Anisodon* Grolle (Grolle & Persson, 1966; Burghardt & Gradstein, 2008). Burghardt & Gradstein (2008) suspect that *A. integrifolius* may be conspecific with *A. laxus*, noting that “We have not studied [*A. integrifolius*] but would expect it to belong to *T. laxus* as well.”

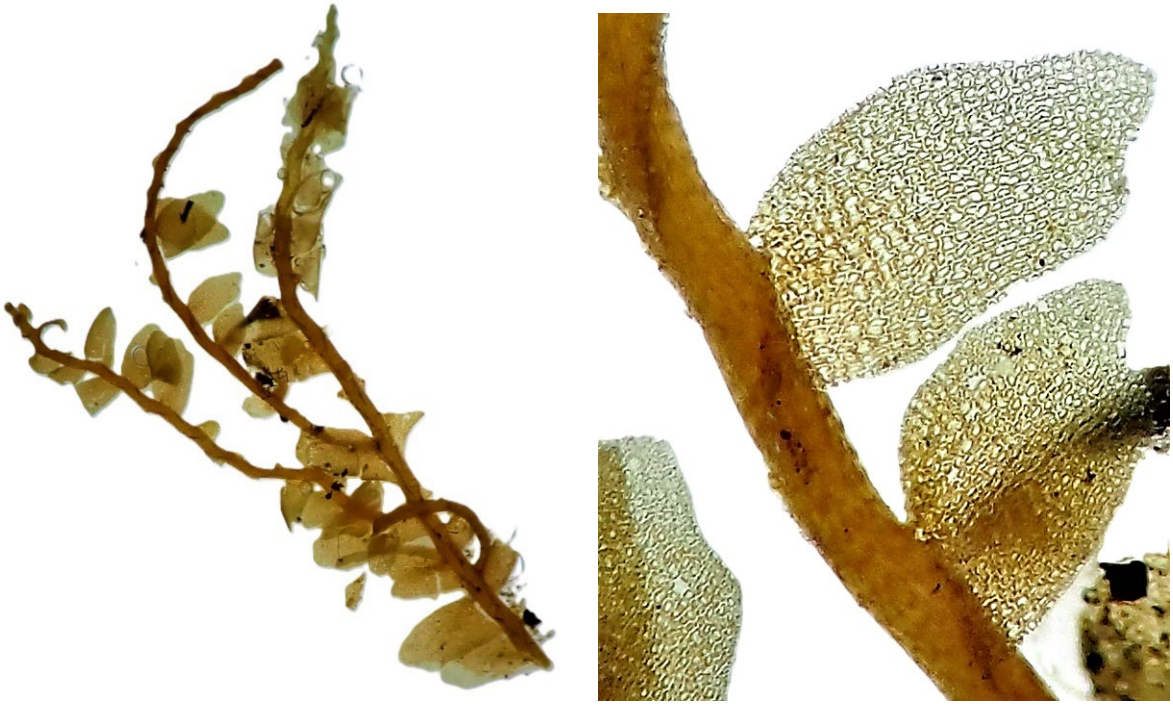
Plants are green and form dense mats, here growing hanging from rock. Kahikinui (4,760 ft.), south side of Haleakalā, Maui, collected by Pezzillo 656 (BISH). Photos by Z. Pezzillo, with permission. (https://www.inaturalist.org/observations/202131338).

Acrobolbus integrifolius. Note the milky white color of fresh plants and abundant community associates. Waiʻaleʻale, Kauaʻi, K. Faccenda 3522a (BISH), photo by Kevin Faccenda, with permission. (https://www.inaturalist.org/observations/224266223).


Plants have distant to contiguous oblong rectangular leaves with truncate apices and entire margins. Right: Note the long leaf insertion that curves on the ventral side and the milky white color of fresh plants. Wai‘ale‘ale, Kaua‘i, K. Faccenda 3522a (BISH), his photos, with permission. Photo by Faccenda (https://www.inaturalist.org/observations/224266223) , with permission.

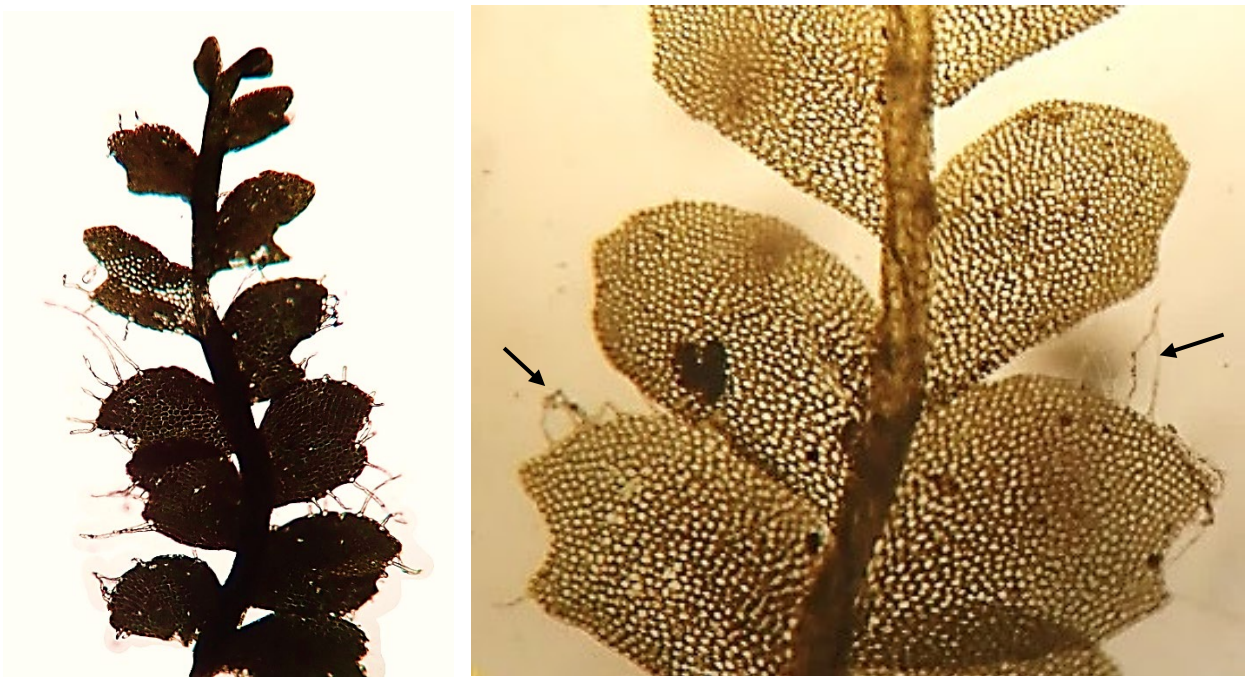


Acrobolbus integrifolius. Plants are large, with distant leaves (scale in mm). Maui, Baldwin 280 (BISH).

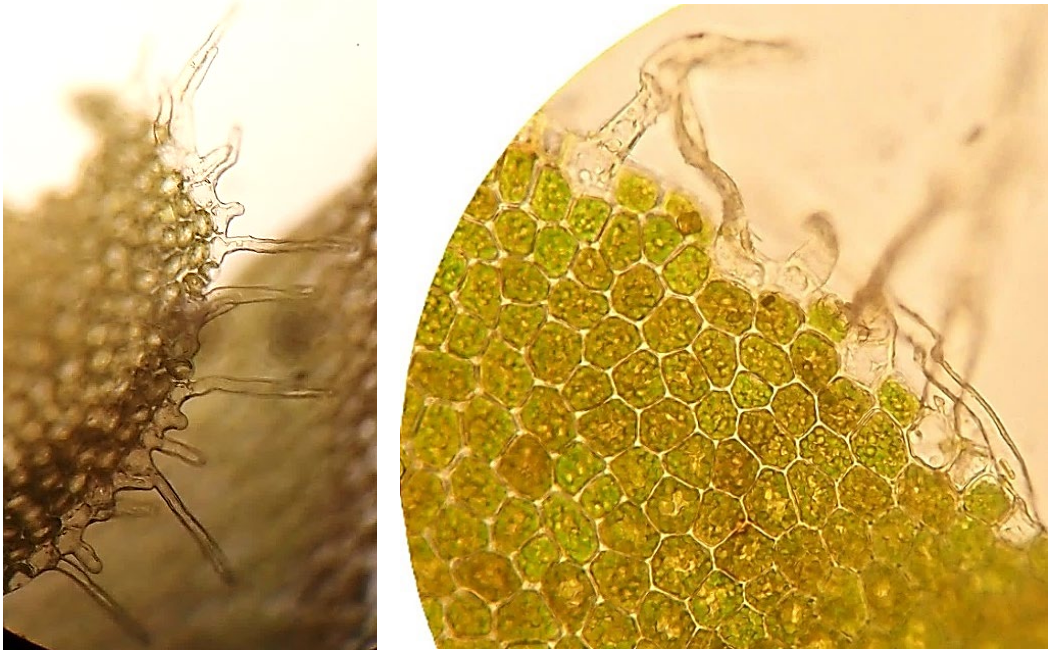


The plants resemble *Plagiochila* in their branching, thick "wiry" stems, and caducous leaves with a long insertion on the dorsal side (right). Hawai'i Volcanoes National Park, Hawai'i Island, Pratt 1748 (HAVO). Photos by E.J. Judziewicz.

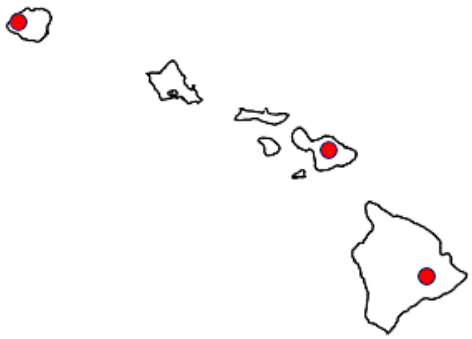
Acrobolbus integrifolius. Left and Center: Plants with contiguous to distant leaves. Leaves are oblong-rectangular, with a characteristic shallow sinus on the apical portion of the lower margin. Left: scale = 1 mm; Pezzillo 648c, East Maui (BISH). Right: Underleaves are rarely present. Pezzillo 656, East Maui (BISH). Photos by A.V. Freire.



Plants with rhizoids on leaf margins. East Maui, Pezzillo 656 (BISH). Photos by A.V. Freire.



Acrobolbus integrifolius. Left: Detail of rhizoids growing from leaf marginal cells. East Maui, Pezzillo 656 (BISH). Right: Leaf cells have thin, evenly-thickened walls. Small, triangular trigones can be present. Note the marginal rhizoids on the leaf margin. East Maui, Pezzillo 648c (BISH). Photos by A.V. Freire.



2. *Acrobolbus* species 1. Differing from *A. integrifolius* in its toothed leaves that lack a sinus and in the absence of rhizoids on leaf margins. Found in montane forests on Kauaʻi, Maui (Waikamoi) and in the Puʻu Makaʻala N.A.R. on Hawaiʻi Island, elevation 4,000-6,000 ft. The lack of leaf marginal rhizoids places this species in the *Tylimanthus* section of *Acrobolbus*, according to Grolle & Persson (1966). The plants grow on tree trunks, fallen logs, and occasionally on soil. They are light green, erect, projecting horizontally when on vertical substrates, forming dense mats that spread through long stolons. The younger portions of stems are often zigzagged. The leaves are succubous, caducous, or fragmented, rounded or elongated, with a few sharp teeth. The round shape could be the result of elongate leaves losing their upper half for asexual propagation. Leaf cells without trigones, oil bodies elliptical and brown.

The authors and other collectors have collected this species in Maui and Hawaiʻi Island. A collection made by Charles M. Cooke, Jr., on 28 Oct. 1903 at the Kalalau Flats, Kauaʻi (BISH) also appears to be this species; it was long filed as an undetermined *Plagiochila*. This taxon needs more work. A full morphological characterization and molecular work are needed to determine whether this is a new species.

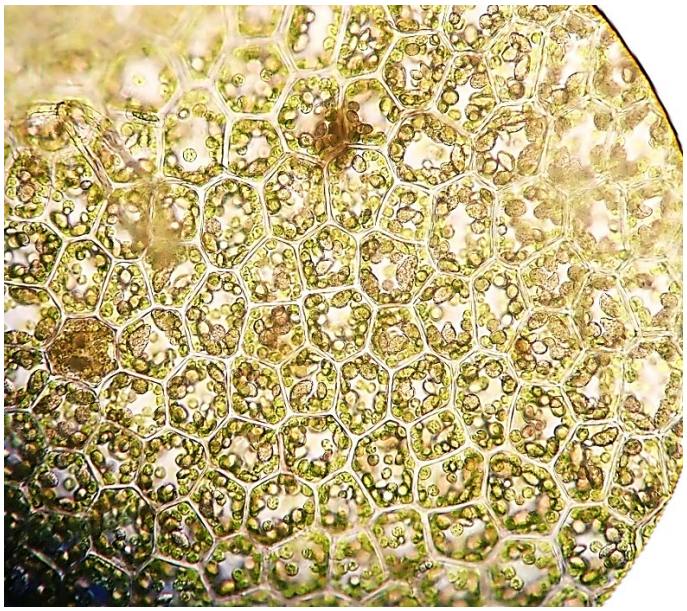
Acrobolbus sp. 1. Population found on fallen *Metrosideros* log. Right: Plants project horizontally. Puʻu Makaʻala N.A.R. on Hawaiʻi Island, Freire & Judziewicz 22-237 (BISH).

Dense mat of light green, horizontally projecting plants. Freire & Judziewicz 22-237 (BISH).

Acrobolbus sp. 1. Plants form dense mats that spread through long stolons (arrows). Puʻu Makaʻala N.A.R., Hawaiʻi Island, Freire & Judziewicz 22-237 (BISH).

Detail of stoloniferous growth. Pu‘u Maka‘ala N.A.R., Hawai‘i Island, Freire & Judziewicz 22-237 (BISH).

Acrobolbus sp. 1. Plants have zigzag stems. Leaves are rounded and caducous, with some teeth. Left: Scale in mm. Center: Leaves fragment, losing their upper portion. Right: Some teeth are present. Pu‘u Maka‘ala N.A.R., Hawai‘i Island, Freire & Judziewicz 22-224 (BISH).



Cells are isodiametric, thin-walled, and lack trigones. Oil bodies are large, elliptical, and granular. Pu‘u Maka‘ala N.A.R., Hawai‘i Island, Freire & Judziewicz 22-224 (BISH).

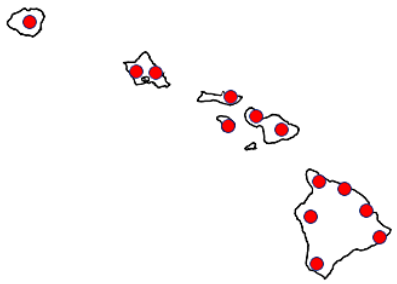
Acrobolbus sp. 1. Plants with stolons. Leaves can be elongated. Note plant to the far left with rounded leaves. Scale = 1 mm. Pu‘u Maka‘ala N.A.R., Hawai‘i Island, Freire & Judziewicz 22-601 (BISH).

Leaves can be elongated, caducous, and with few sharp teeth. Cells thin-walled, without trigones. The oil bodies are large, brown, and elliptical. Note the sharp marginal tooth. Puʻu Makaʻala N.A.R., Hawaiʻi Island, Freire & Judziewicz 22-608 (BISH).

Acrobolbus sp. 1. Plants with stolons, zigzag stems, and caducous leaves with teeth. Kalalau Flats, Kauaʻi, Cooke 103 (BISH). Photos by A.V. Freire.

Acrolejeunea (Spruce) Steph. (Lejeuneaceae)

One species in Hawai‘i, 23 species worldwide.



Acrolejeunea sandvicensis (Gottsche) Steph. **Indigenous.** Treated as *Trocholejeunea sandvicensis* in Staples & Imada (2006); see Wang *et al.* (2016) and Judziewicz & Freire (2023c: 163). This is a member of subgenus *Acrolejeunea* (Söderström et al., 2016). Found on all major islands (0-6,100 ft., but mostly below 2,000 ft., where often weedy); it is disjunct from subtropical eastern Asia and previous reports from other Pacific Islands are erroneous (Sun et al., 2018).

A common, mostly low elevation, wet forest species that is epiphytic on both exotic and indigenous trees, it can also grow on rocks and in partial sun. On iNaturalist, it is the most observed indigenous leafy liverwort species in Hawai‘i, with 123 observations (81 were made on O‘ahu). Populations from higher elevations appear to be somewhat smaller; perhaps more than one taxon is present.

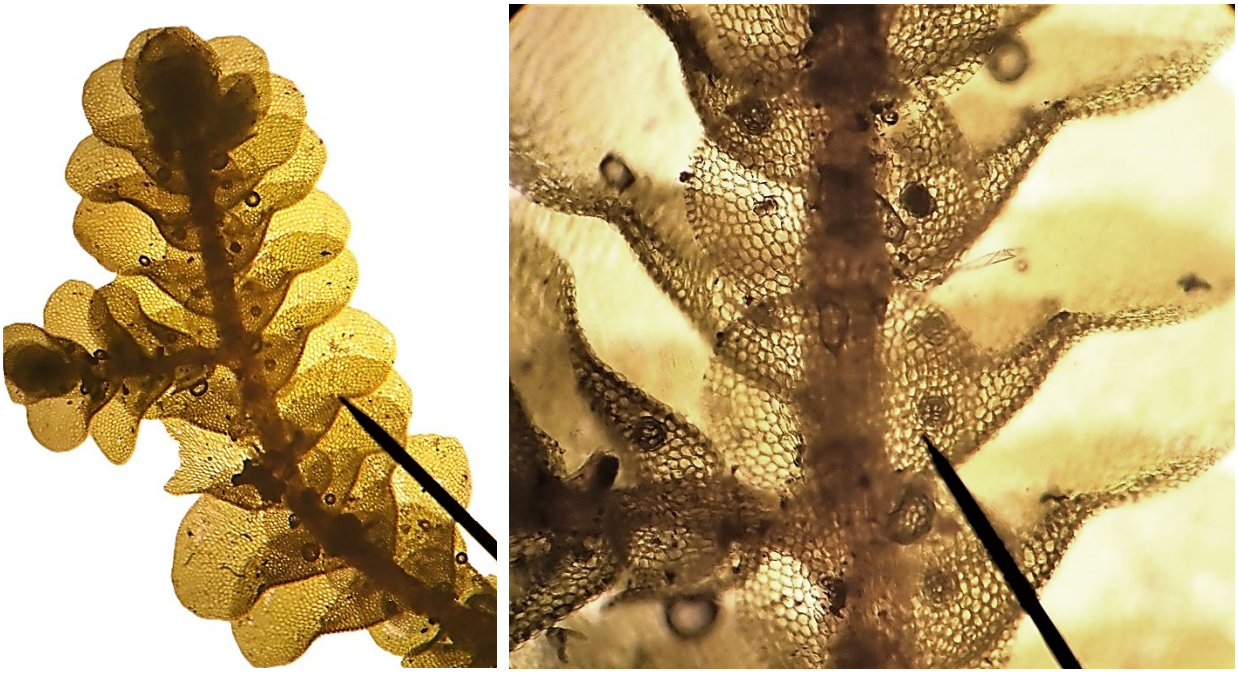
Plants grow closely appressed to their substrate; they are green, olive-green or brownish-green, 1-2(2.5) mm wide. They are frequently branched; the branches are terminal and of the *Frullania*-type. Leaves are incubous, entire, rounded, concave, imbricate, obscuring the stem on dorsal view, squarrose when wet but appressed when dry, with slightly reflexed margins, more pronounced on older plants that may also have hyaline margins. Leaf cells are isodiametric to slightly elongated; marginal cells smaller and square, forming a border; cell walls thin, with cordate trigones and intermediate thickenings. Oil bodies are numerous, small, smooth, and elongated. Lobules large, horizontally elongated, to slightly over half the leaf length; inflated below but flattened above, with 3-4 small and blunt teeth on their upper margin. Underleaves are large, more than 3 times the stem width, entire, rounded, kidney-shaped, contiguous to imbricate, concave and with reflexed upper margins. Brown rhizoids are often observed clustered at the underleaf bases. Perianths are keeled; sporophytes shortly exerted, and capsules dehisce in four valves. Elaterophores are present. *Acrolejeunea sandvicensis* resembles *Spruceanthus*, but it is much less often fertile; the leaves lack teeth; and it has small, distinctly cordate trigones between its leaf cells. The leaves in *Acrolejeunea* “flair” a bit at the apex (especially in older plants), like frayed shirt cuffs.

Acrolejeunea sandvicensis. Plants grow appressed to their substrate and often branch. Note dehisced sporophyte (left). Wai‘alae Ridge, Kaua‘i, Wood 18178 (PTBG). Photo courtesy of National Tropical Botanical Garden/Ken Wood.

Plants have imbricate, incubous, overlapping leaves with reflexed margins. Wai‘alae Ridge, Kaua‘i, Wood 18178 (PTBG). Photo courtesy of National Tropical Botanical Garden/Ken Wood.

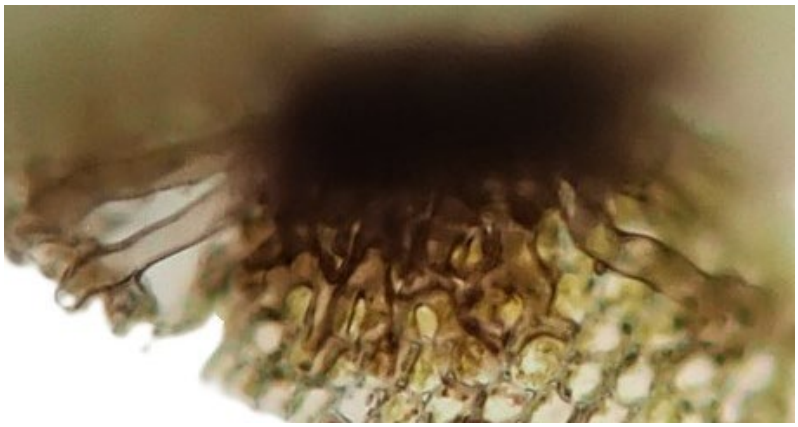
Acrolejeunea sandvicensis. Plants are 1-2(2.5) mm wide. Left: Scale in mm. Right: Scale = 1 mm. ‘Akoni Pule Hwy. across Waikama Gulch, Hawai‘i Island, Judziewicz & Faccenda 17,121 (BISH). Photos by A.V. Freire.

Left: Plants creep on their substrate. Right: Detail of plant with squarrose leaves. Note the keeled perianth and shortly exerted sporophyte bearing a dehisced capsule. Photos by Miles K. Thomas, with permission.



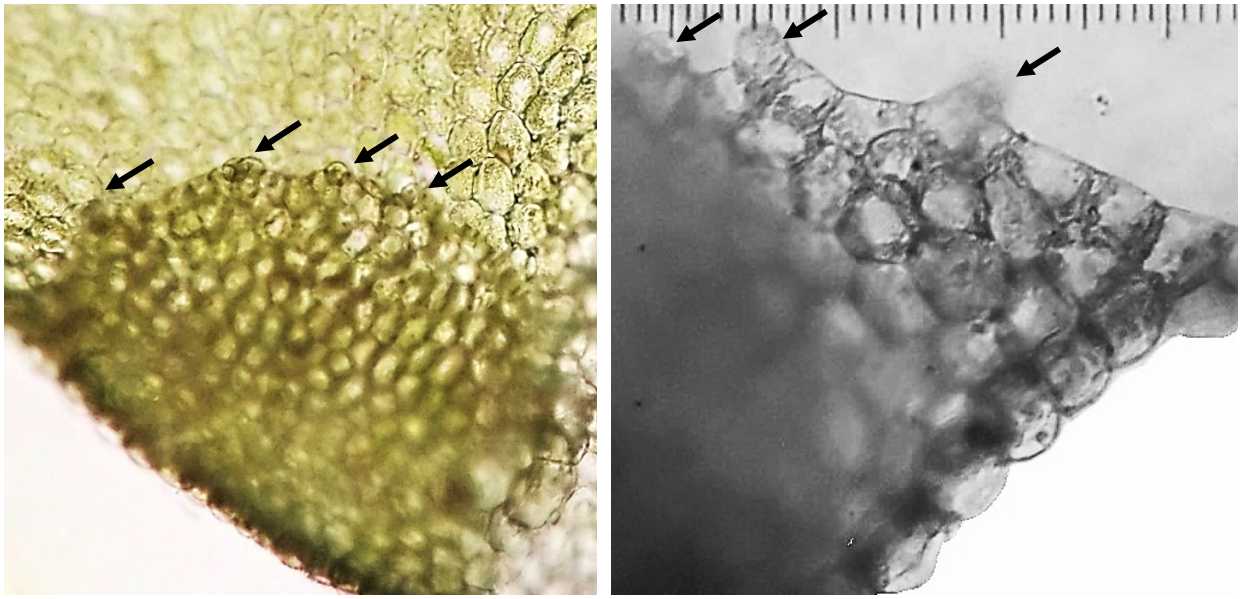
Acrolejeunea sandvicensis. Branching is terminal, of the *Frullania* type. Note branch taking the place of the water sac. The leaves are rounded and imbricate. Right: The underleaves are slightly imbricate, orbicular, over three times the stem width. Hilo, Hawai‘i Island, Freire & Judziewicz 20-693 (BISH).

Leaves are squarrose and concave. Water sacs are large, horizontally elongated, up to about ½ the leaf length. They are inflated below and flattened above. Judziewicz & Faccenda 17,121 (BISH). Photo by A.V. Freire.

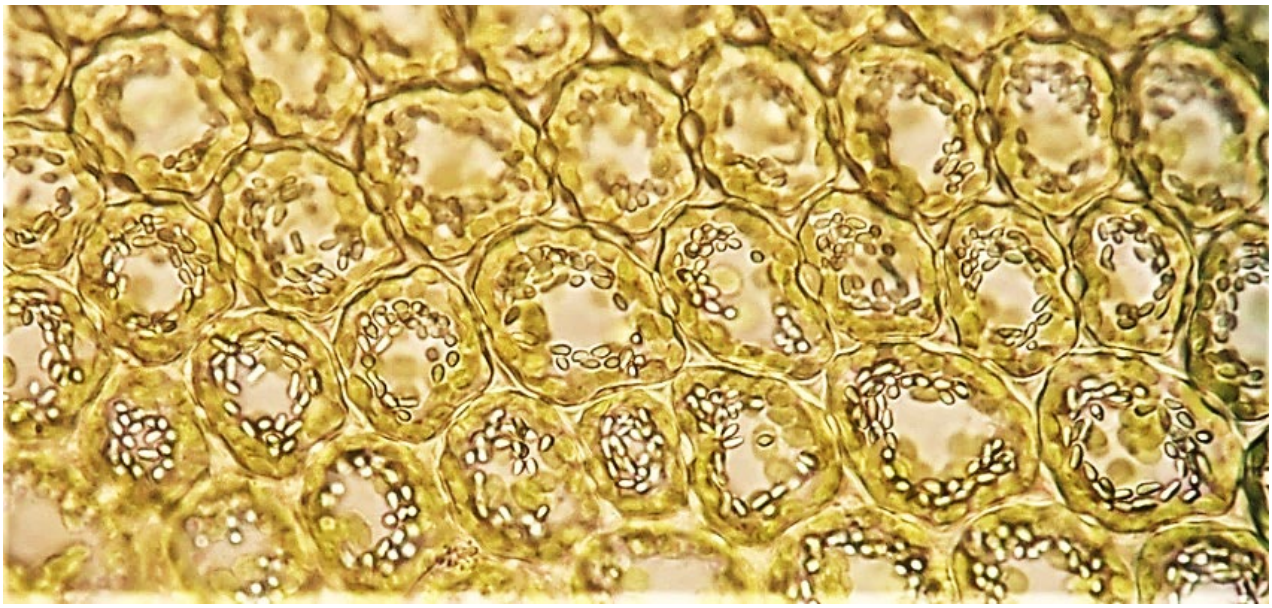


Acrolejeunea sandvicensis. Tinted rhizoids form clusters at the base of some underleaves. ʻAkoni Pule Hwy. at Waikama Gulch, Hawaiʻi Island, Judziewicz & Faccenda 17,121 (BISH). Photo by A.V. Freire.

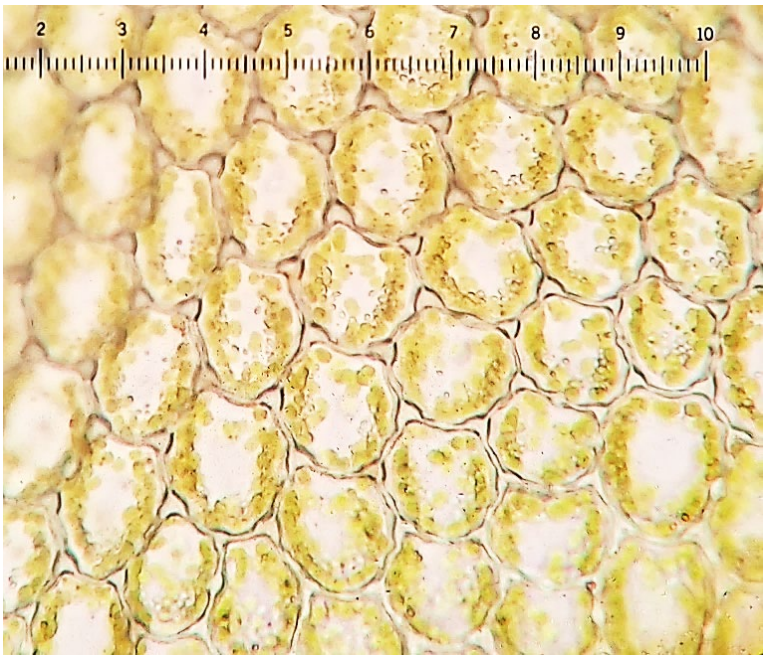
Left: Leaf with lobule. Note the round shape of the leaf and the large lobule. Judziewicz & Faccenda 17,121 (BISH). Photo by A.V. Freire. Right: Leaf lobes are bordered by smaller, square marginal cells; note the cordate trigones. Hilo, Hawai‘i Island, Freire & Judziewicz 20-693 (BISH).

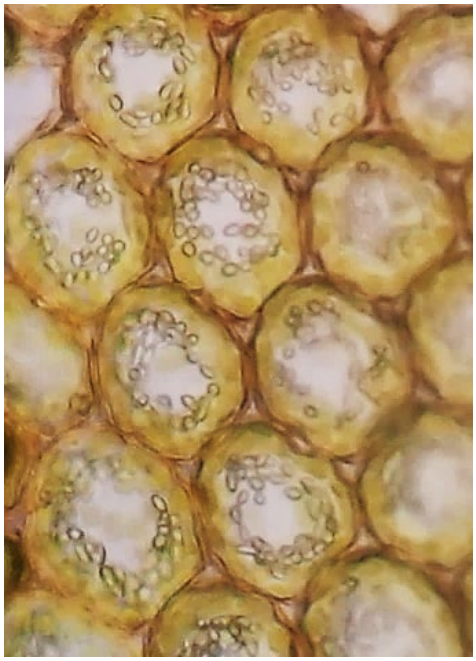


Acrolejeunea sandvicensis. Free margin of lobule with 3-4, single-celled, small, blunt teeth (arrows). Left: ‘Akoni Pule Hwy. across Waikama Gulch, Hawai‘i Island. Judziewicz & Faccenda 17,121 (BISH), photo by A.V. Freire. Right: Each scale subunit = 5 µm. Note inflated cells on lobule keel. Onomea, Hawai‘i Island, Freire & Judziewicz 21-513 (BISH).



Leaf cells have small, elongate, smooth and numerous oil bodies. Note the cordate trigones and intermediate thickenings. Hilo, Hawai‘i, Freire & Judziewicz 22-917 (BISH).





Acrolejeunea sandvicensis. Leaf cells have thin walls with cordate trigones. Intermediate thickenings are sometimes present. Left: Each scale subunit = 2.5 µm. ‘Akoni Pule Hwy. across Waikama Gulch, Hawai‘i Island. Judziewicz & Faccenda 17,121 (BISH), photo by A.V. Freire. Right: National Tropical Botanical Garden, Kalāheo, Kaua‘i, 5 April 2022, photo by E.J. Judziewicz.

Acrolejeunea sandvicensis. Top: Note keeled perianth. Bottom: Dehisced capsule. Note four valves and elaterophores at valve tips. ʻAkoni Pule Hwy. across Waikama Gulch, Hawaiʻi Island, Judziewicz & Faccenda 17,121 (BISH), photos by A.V. Freire.

Acrolejeunea sandvicensis. Campanulate, keeled perianth with shortly exserted sporophyte. Elaterophores are present at capsule valve tips. ʻAkoni Pule Hwy. across Waikama Gulch, Hawaiʻi Island, Judziewicz & Faccenda 17,121 (BISH), photo by A.V. Freire.

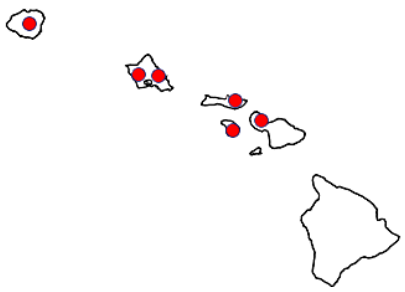
Acromastigum A. Evans (Lepidoziaceae)

One or possibly two species in Hawai‘i, 48 species worldwide. This is a largely Austral and Tropical Asian genus related to *Bazzania* and *Lepidozia*. The type for the genus is the Hawaiian *Acromastigum integrifolium*. Hawaiian representatives of the genus belong to the subgenus *Acromastigum* A. Evans, with transverse leaf insertion, entire leaves and underleaves (although 2-3 small teeth may be present on leaf apices; Schuster, 2000). Plants are pale, yellow to brown; stems are strong and wiry. Leaves are entire or only very shallowly bifid, spreading, with thickened cells and bulging nodulose trigones. Underleaves spread at 45˚-90˚ angles. Branching is abundant and complex; ventral flagelliform branches can be of the *Bazzania*-type (at the underleaf axis and bearing a collar) or more commonly of the *Acromastigum*-type (the branch replaces half of the underleaf; no collar is present). Lateral branches are of the *Frullania*-type. The genus has been confirmed from all major islands, except Hawai‘i.

1. Leaves squarrose, widely spreading, distant, entire, leaf apices mainly acute …….. ***A. integrifolium***

1. Leaves not squarrose, obliquely spreading at 45˚ angles (sub-erect), imbricate, entire or shallowly bifid, leaf apices obtuse but sometimes acute ……..……..….. ***A.* cf. *cavifolium*?**

1. *Acromastigum integrifolium* (Austin) A. Evans. **Endemic. Rare.** Confirmed for Kaua‘i and West Maui (not yet recorded from East Maui), probably also found in O‘ahu, Lāna‘i and Moloka‘i (but herbarium specimens need to be carefully confirmed to species). A small, pale yellowish plant creeping among other liverworts in wet, windswept, summit cloud forests (3,000-5,800 ft.). Although Schuster (2000: 296) reports its possible occurrence in New Caledonia, Thouvenot (2011: 296) attributes reports of this species there to *Acromastigum homodictyon* (Herz.) Grolle.

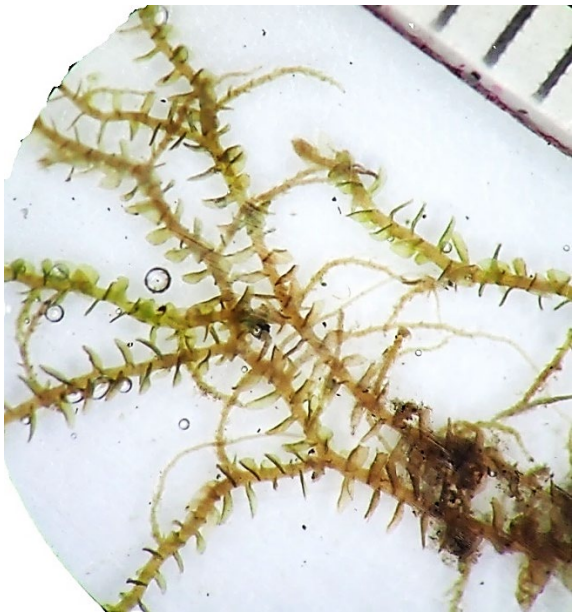


Plants small, slightly over 1 mm wide, sub-erect or creeping, forming ragged and dense mats, pale green to yellow-green or light brown when fresh, dark brown when dry. Stems wiry, stout, with large epidermal cells (hyalodermis-like). Flagelliform branches are abundant, mainly of the *Acromastigum*-type, less commonly of the *Bazzania*-type, lateral branching is terminal (*Frullania*-type). Leaves are 0.5-0.57 mm long, ovate triangular, pointed at the apex, acute or occasionally obtuse, entire, some curving up at the tips, slightly convex, with slightly reflexed margins, alternate, transversely inserted, squarrose (widely spreading from the stems). Underleaves are equal to leaves in shape, entire, and are only slightly smaller than the leaves or equal in size. Leaf and underleaf cells are uniform, isodiametric, 20-25 µm in diameter, with thick walls and very prominent nodulose trigones. Dioicous. Antheridia produced in short ventral branches, protected by brown bracts. Females not observed by us.

This species superficially resembles the common (but distantly related) *Herbertus gracilis* but differs from it in the entire leaves and underleaves. Both *Herbertus* and *Acromastigum integrifolium* have large underleaves that make the plants clearly 3-ranked.

Pale colored plants in dense mats, with abundant microphyllous branches. Kaua‘i, Faccenda 3500a (BISH). Photo by Kevin Faccenda, with permission.

Acromastigum integrifolium. Field picture showing the pale-colored plants with flagelliform branches. Note the squarrose, widely spreading leaves and underleaves, with pointed apices that curve upwards. Here growing amongst the much larger purplish-black liverwort *Pleurozia conchifolia* and the moss *Leucobryum*. ‘Eke Bog, West Maui. Photo by Zach Pezzillo, with permission.



Plants are about 1 mm wide. Leaves widely spreading, squarrose. Underleaves are large. Note abundant flagelliform branches. Scale in mm. Kauaʻi, Faccenda 3500a (BISH). Photographed by E.J. Judziewicz.

Acromastigum integrifolium. Plants have abundant ventral flagelliform branches and some lateral ones. Leaves are squarrose. Note the short, globose antheridial branch on the right. Scale in mm. Faccenda 3500a, Kauaʻi (BISH). Photo by A.V. Freire.

Ventral flagelliform branches are *Acromastigum*-type, where the branch takes the place of part of the underleaf. The larger branch is terminal and of the *Frullania*-type. Faccenda 3500a, Kaua‘i (BISH). Photo by A.V. Freire.

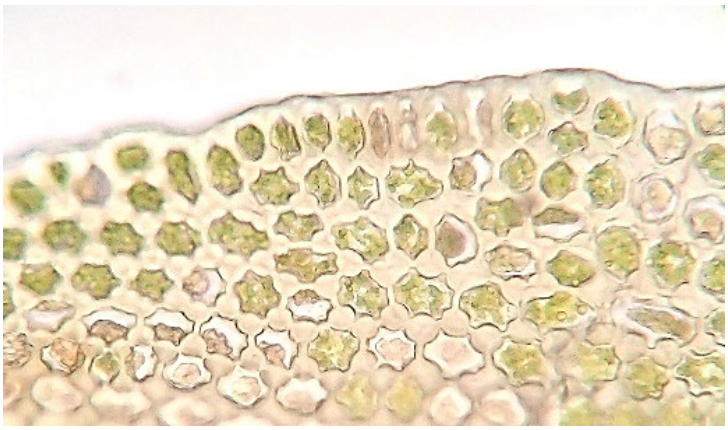
Antheridial branches are short and compressed, with brown bracts subtending the antheridia. Note the atypical underleaves associated with ventral branches (arrows). Faccenda 3500a, Kaua‘i (BISH). Photo by A.V. Freire.

Acromastigum integrifolium. Stem cross sections show the ring of large epidermal cells (cortex) with thick walls, and the smaller cells of the medulla, also with thick walls. Faccenda 3500a, Kaua‘i (BISH). Photo by A.V. Freire.

Leaves are entire and acute. Note the slight concavity along the leaf main axis and the slightly reflexed margins. Faccenda 3500a, Kauaʻi, (BISH). Photo by A.V. Freire.

Leaves are ovate-triangular, pointed, and the cells are mostly uniform in size, with bulging trigones. Faccenda 3500a, Kauaʻi, (BISH). Photos by A.V. Freire.

Acromastigum integrifolium. Underleaves are equal in shape to the leaves but can be slightly smaller. Faccenda 3500a, Kauaʻi, (BISH). Photos by A.V. Freire.



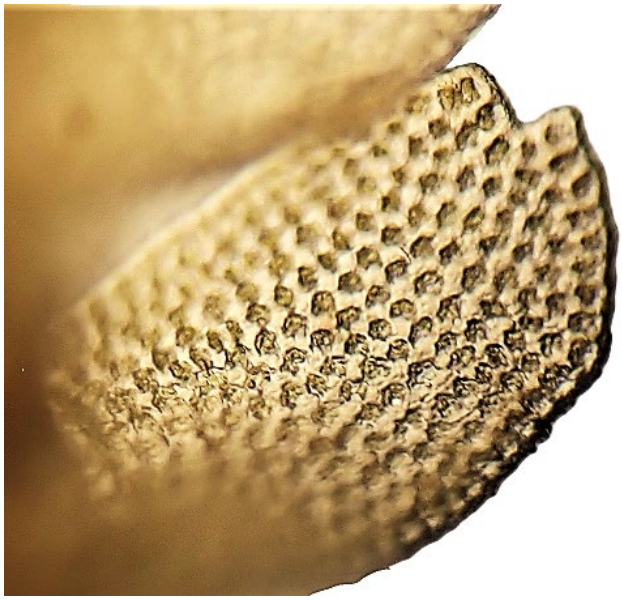
Acromastigum integrifolium. Cells have thick walls and large nodulose trigones; a border of rectangular cells is present but is not well defined. Faccenda 3500a, Kauaʻi, (BISH). Photograph by A.V. Freire.

2. *Acromastigum* cf. *cavifolium* R.M. Schust.?

We found an *Acromastigum* population on Lānaʻi with a different leaf orientation and seemingly different morphology. Plants have rounded, spoon-shaped concave leaves with obtuse rounded apices, although acute apices are present sometimes. Leaf margins are mainly entire, but some shallowly bifid leaves may be intermixed. The leaves are transversely inserted, appearing succubous* (see below), semi-erect, and oblique spreading at 45˚ angles. Leaf cells have thick cell walls with bulging nodulose trigones. Underleaves are obtuse, smaller than the leaves, and also spread at 45˚ angles. This species superficially resembles *A. cavifolium* (Engel & Glenny, 2008: 395) an Aoteoroa/New Zealand species. Unlike it, shallowly bifid leaves and acute -tipped leaves may be present. Perhaps this could just be a variant of *A. integrifolium*? This collection needs more attention. We could only study it superficially. The specimen is deposited at BISH.

*The genus *Acromastigum* is characterized by transverse or incubous leaf insertion, but Schuster (2000: 293) reports slightly succubous transitioning to clearly incubous plants under his description for the genus.

Plants with obliquely spreading leaves. Leaves rounded and obtuse. Underleaves spreading, smaller than leaves. *Acromastigum*-type ventral branches are present. Freire & Judziewicz 22-388, Lānaʻi (BISH).



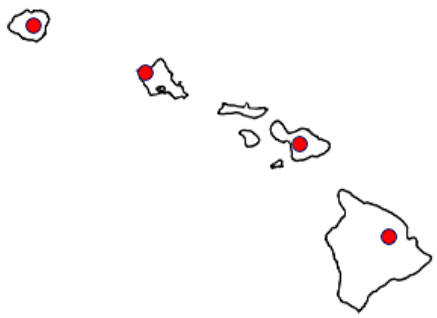
Leaves are overlapping, spreading at 45˚, and are semi-erect. They are rounded, obtuse, and some may be very shallowly bifid (see detail on right). Note the hyalodermis-like clear region on either side of flagelliform branch. Freire & Judziewicz 22-388, Lānaʻi (BISH).

Acromastigum cf. *cavifolium*. Some leaves can be acute. Freire & Judziewicz 22-388, Lānaʻi (BISH).

Anastrepta (Lindb.) Schiffn. (Anastrophyllaceae)

One species in Hawai‘i and worldwide.

Anastrepta orcadensis (Hook.) Schiffn. **Indigenous.** A cold-temperate species known from northern Eurasia and northern North America. In Hawai‘i it is rare, found in montane bogs and forests on Kaua‘i (Mt. Wai‘ale‘ale; Miller 1963: 510), O‘ahu (Pu‘u Ka‘ala), Maui (Waikamoi Preserve, Haleakalā), and Hawai‘i (Hakalau Forest N.W.R.), from 4,000-6,760 ft. Terrestrial, on soil or rock. This species is recognized by its bifid leaves that bear clusters of red gemmae at the lobe tips.

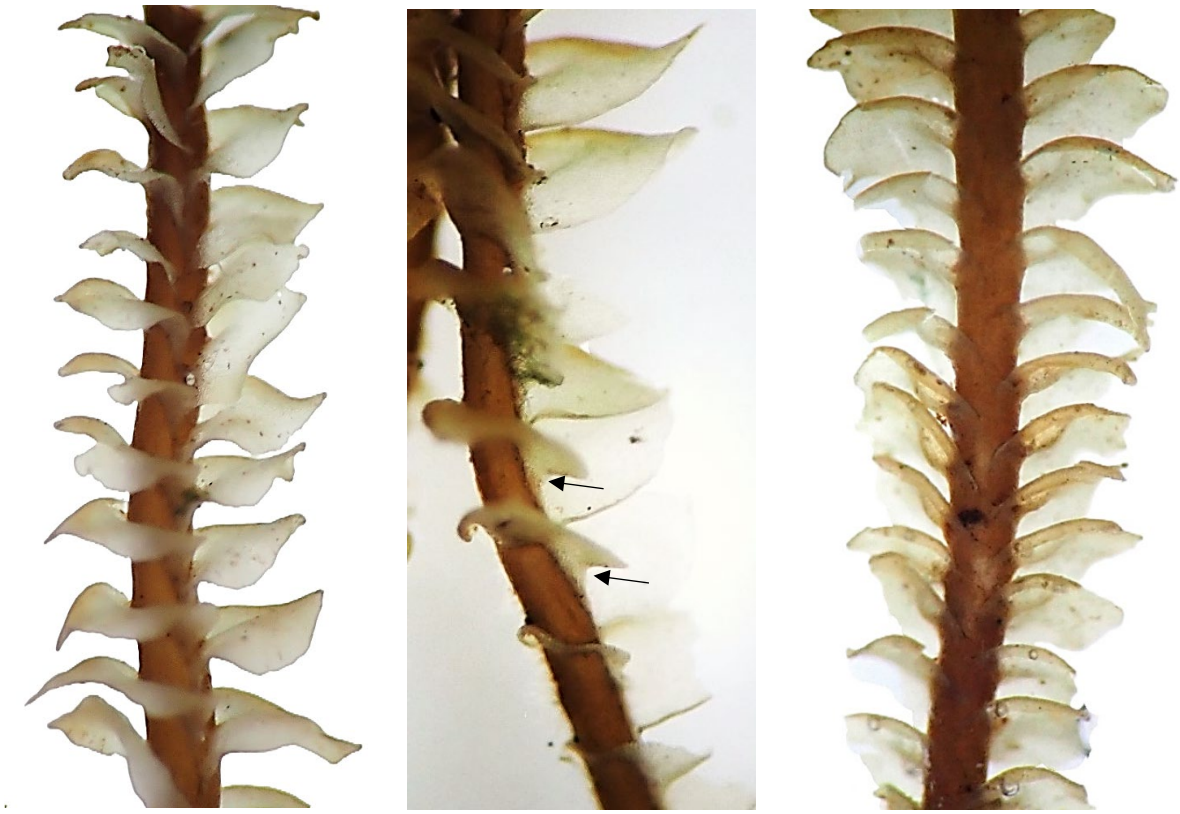


Plants are pale to dark green, 2 to several cm. long, around 2 mm broad, erect to sub-erect, with strong, brown or green stems, often with a nodding apex. Branching is terminal and lateral. Rhizoids, when present, are abundant and hyaline, along the stem ventral side. Leaves are alternate, ovate, shallowly bifid, concave in the basal half and convex on the upper half, with recurved apices and margins. Occasionally a small tooth is present near the base of one of the margins. The upper leaf margin is strongly recurved. Leaf cells are isodiametric, squarish to slightly elongated, with small to medium triangular trigones at least in some cells. A border of rectangular, thick-walled cells is present but not always clearly defined. Leaves spread at 45˚-90 ˚ angles, succubous, and the line of insertion is slightly curved on the ventral side but long-decurrent dorsally almost or to the stem midline. Underleaves absent. Reddish brown gemmae are produced at the tips of the leaf lobes. These are (1)2 celled, angular or ellipsoidal, some with small protuberances that may represent early germination (?).

Anastrepta orcadensis. Plants growing on forest soil, Pu‘u Ka‘ala, O‘ahu. May 17, 2022. Photo by E.J. Judziewicz.

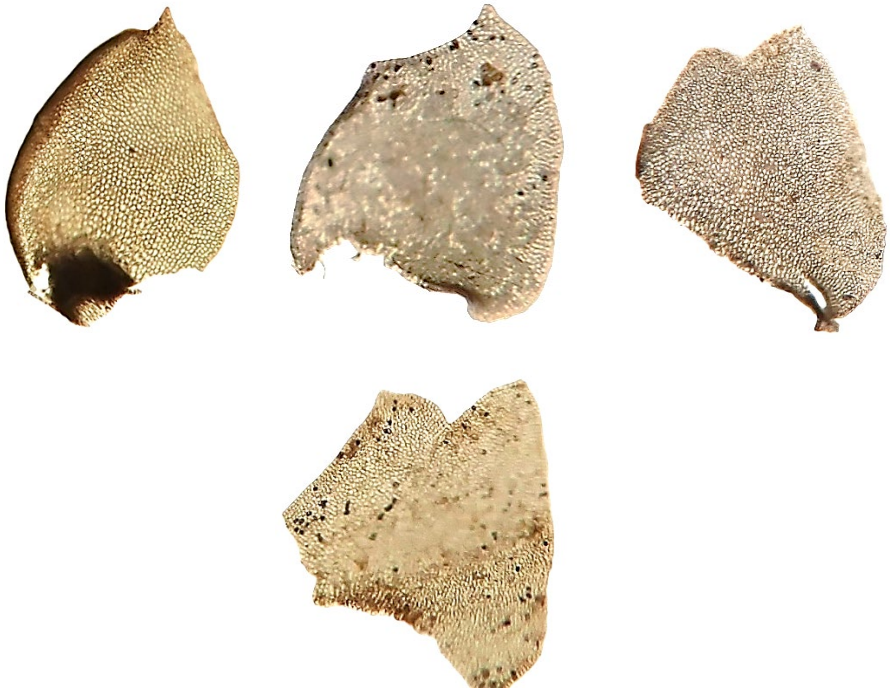
Plants are 2 to several cm long, about 2 mm broad, with stout brown stems and spreading leaves. Scale in mm. Oppenheimer 52109 (BISH). Photo by A.V. Freire.

Anastrepta orcadensis. Plants with terminal and lateral branching. Note the clusters of gemmae at leaf apices. Left: Dorsal side showing long leaf insertion, almost to stem midline. Right: Ventral side. Note the reflexed leaf margins. Waikamoi, Maui, Oppenheimer 52109 (BISH). Photo by A.V. Freire.

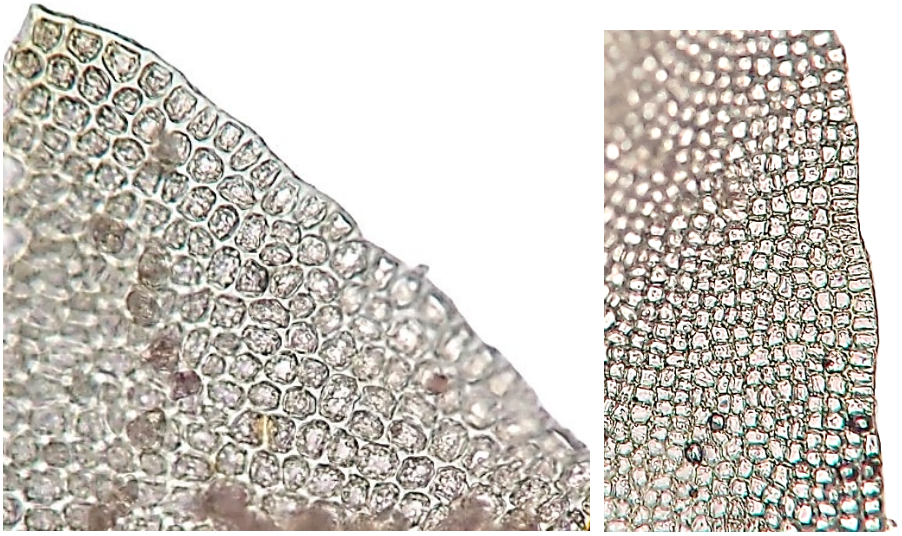


Plants with stout brown stems. Left: dorsal view with long and decurrent leaf insertion. Center: Detail of leaves, concave close to the base and convex towards the apex. Note the leaf dorsal decurrency (arrows). Right: Ventral view with slightly curved insertion. Note the reflexed upper leaf margins. Waikamoi, Maui, Oppenheimer 52109 (BISH). Photo by A.V. Freire.

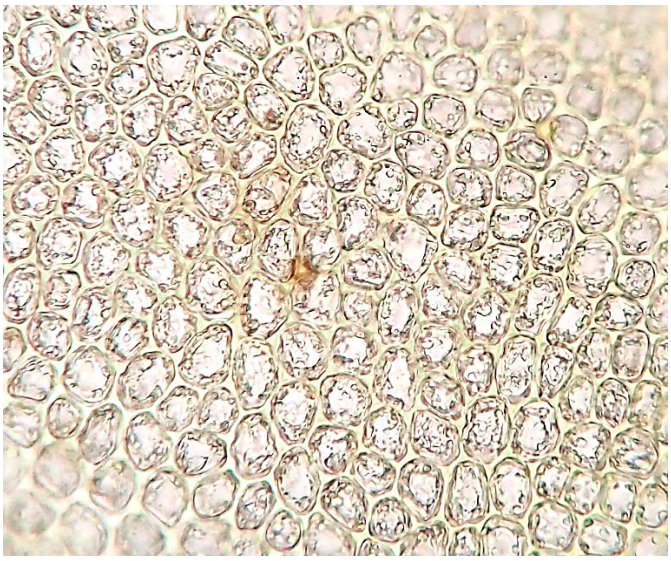
Anastrepta orcadensis. Rhizoids short and hyaline to lightly-colored, along ventral surface midline where epidermis may be colored rusty brown. Pu‘u Ka‘ala, O‘ahu, Thomas et al. (including Freire & Judziewicz) 361 (BISH). Photo by A.V. Freire.



Upper: Young leaf showing the ovate shape and shallow sinus with small lobes (one bending). Note the reflexed margin to the left (upper margin, ventral side of plant). Waikamoi, Maui, Oppenheimer 52109 (BISH). The others represent a sampler of leaf apices with different depths; beware of leaves that are incomplete at the base, Thomas 361 et al. (BISH). Photos by A.V. Freire.

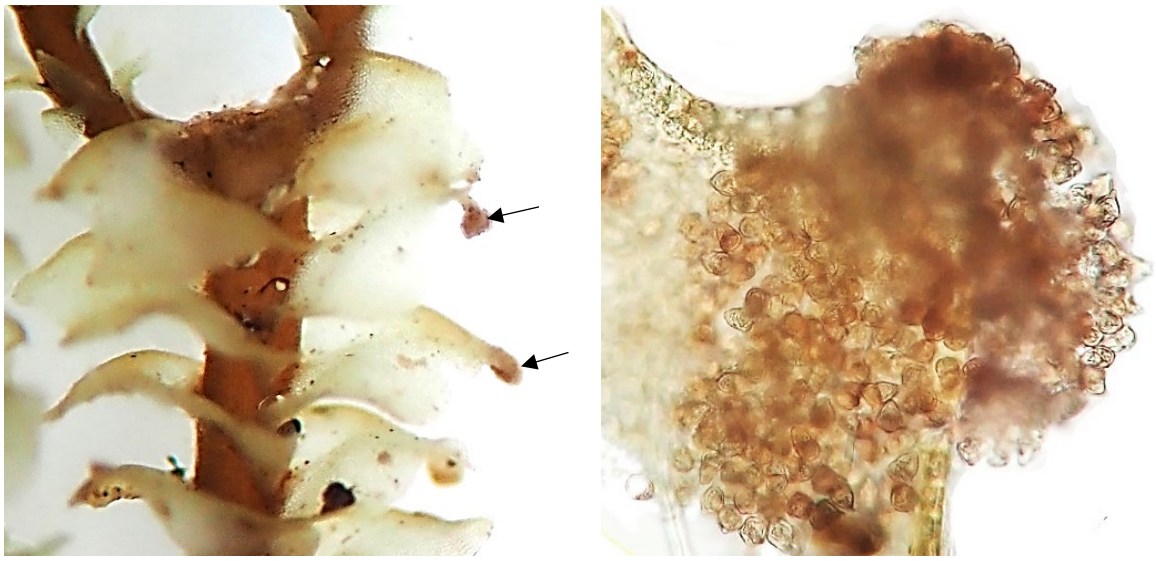


Anastrepta orcadensis. Leaves have a border of rectangular cells, these not always clearly defined. Left: Oppenheimer 52109, Waikamoi, Maui (BISH). Right: Puʻu Kaʻala, Oʻahu, Thomas 361 et al. (BISH). Photos by A.V. Freire.

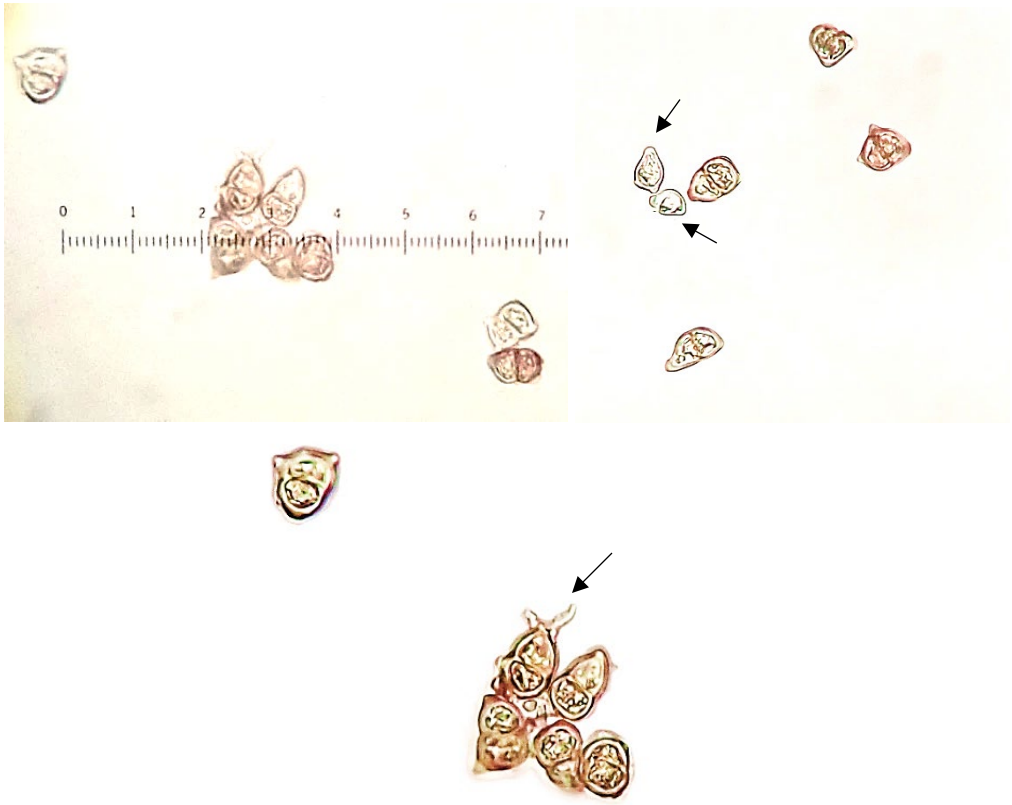


Leaf cells vary from isodiametric to elongate. Trigones are sometimes present. Thomas et al. 361 (BISH). Photo by A.V. Freire.

Anastrepta orcadensis. Leaves with broad insertion and abundant red apical gemmae. Note the shallowly bifid leaves. Thomas et al. 361, Puʻu Kaʻala, Oʻahu). Photo by Miles K. Thomas, with permission.



Left: Leaves bearing clusters of red gemmae at lobe tips (arrows). Right: Leaf lobe tip with cluster or red, angular gemmae. Oppenheimer 52109 (BISH). Photos by A.V. Freire.



Anastrepta orcadensis produces angular, usually 2-celled gemmae with protuberances. Upper left: Each scale subunit = 2.5 µm. Upper right: Some gemmae can be single-celled (arrows). Below: Protuberances may represent germination points (early rhizoids? fungal associates?) (arrow). Waikamoi, Maui, Oppenheimer 52109 (BISH). Photos by A.V. Freire.

Anastrepta cf. *orcadensis*

This population from Puʻu Kaʻala, Oʻahu, has a more slender appearance, the stems are not brown and the gemmae are yellow rather than red or brown. The leaves are flatter and not reflexed on the upper margin. Gemmae and leaf cells need to be studied under a microscope. We interpret it as a variant of *A. orcadensis*.

Anastrepta orcadensis? Top: Population of slender plants. Photo by E.J. Judziewicz. Bottom: Gemmae are produced at leaf lobe tips as yellow (rather than red) clusters. Note the flatter and more fragile- looking leaves. Thomas et al. 361, Puʻu Kaʻala, Oʻahu (BISH). Photo by Miles K. Thomas, with permission.

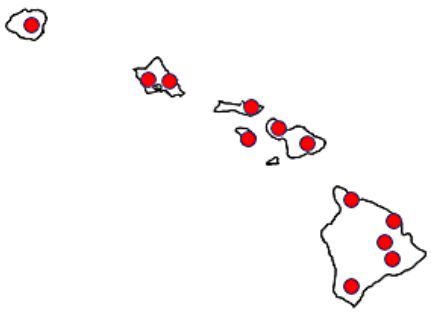
Anastrophyllum (Spruce) Steph. (Anastrophyllaceae)

At least three but perhaps up to five species in Hawai‘i; 19 species worldwide.

Anastrophyllum is recognized by its dark color, its stout stems, leaves with pointed, acute lobes (but sometimes they can be rounded), by its very thick leaf cell walls, and the large perianths usually with a hyaline, fringed mouth. The line of leaf insertion is curved ventrally but straight and perpendicular to the stem, slightly oblique on the dorsus. Plants are succubous and lack underleaves. Gemmae can be produced but are rarely observed. *Anastrophyllum* is superficially similar to *Sphenolobus minutus, Lophozia* sp. and *Marsupella emarginata; Sphenolobus minutus* has more tubular, inrolled leaves. *Lophozia* is usually green. Both *Sphenolobus* and *Lophozia* have thin-walled leaf cells with small trigones, and more abundant gemmae. *Marsupella emarginata* usually has rounded leaves, rounded-obtuse leaf lobes, and nodulose trigones that are usually not present in the very thick-walled leaf cells of *Anastrophyllum*. Of the three, *Marsupella* is the most problematic to tell apart from *Anastrophyllum* when using only vegetative characters. Like *Marsupella*, *Anastrophyllum* can have round leaves and leaf lobes. Attention to cell walls will help tell them apart; also, *Marsupella emarginata* is more fragile-looking. *Anastrophyllum* could also be confused, at first sight, with species of *Herbertus,* but the latter has prominent underleaves.

1. Plants with mostly rounded leaf lobe tips ..…….……..……...…..… ***Anastrophyllum* species 1**
1. Plants with pointed leaf lobe tips ……. **2**
   2. Plants 2-2.5 mm wide, leaves deeply bifid to at least 2/3 their length; stems usually erect..... ***A. fissum***
   2. Plants 1-1.5 mm wide, leaves bifid to at most 1/2 their length; stems procumbent or not **3**
      3. Leaves slightly concave, with symmetrical lobes ……..…….. ***A. esenbeckii***
      3. Leaves canaliculate, with asymmetrical lobes ……..…..……. ***A.* cf. *esenbeckii***

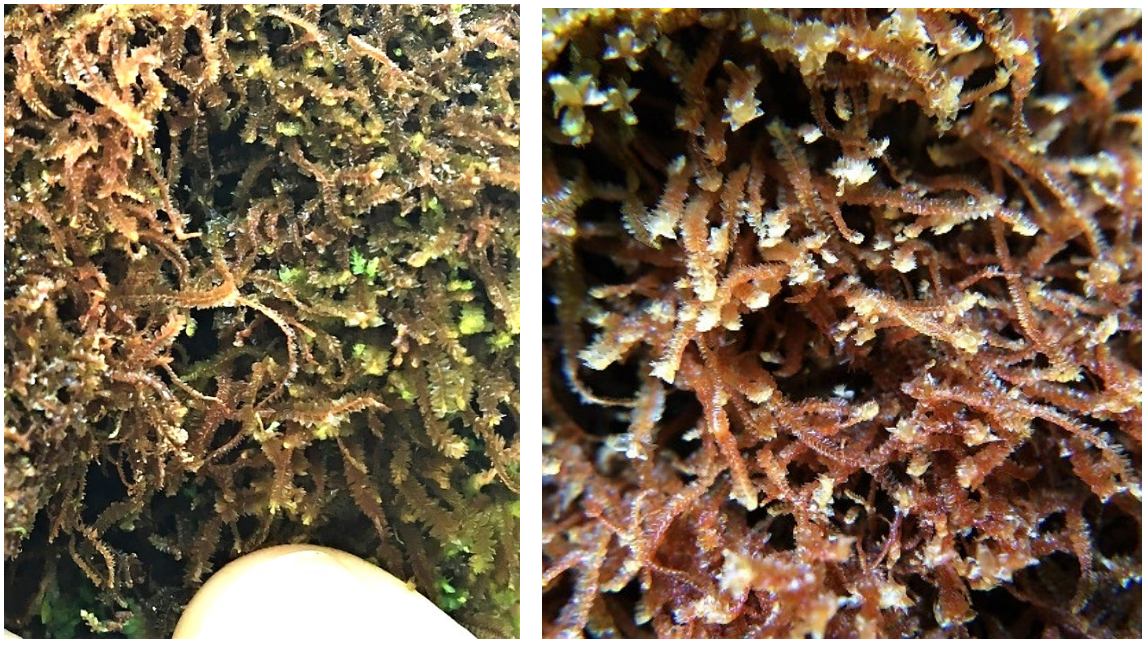
1. *Anastrophyllum esenbeckii* (Mont.) Steph. **Endemic (?).** Found on all major islands (750-5,800 ft.) in wet forests where it sometimes forms dense rusty-brown mats on tree trunks (mostly ‘ōhi‘a) and occasionally on hāpu‘u stipes, or it can grow in mixes. Found from the base of trunks to 2(5) m above ground. Plants are procumbent, loosely attached, long and narrow, around 1 mm broad, red (at least on younger leaves) to brown or in some cases blackish. Intercalary-ventral and terminal branches are present.



Flagelliform branches are often observed. Leaves are transverse-succubous, moderately decurrent; concave, with the ventral half more concave than the dorsal one; bifid, with a deep V-shaped sinus to 1/3-1/2 the leaf length; the leaf lobes are close to equal in size, the apex ending in a 1-2 celled tip. The leaf cells are thick-walled, with prominent, contiguous or nodulose trigones and large, granular oil bodies. A border of small, square leaf marginal cells is present. Perianths are large, plicate with a hyaline and fringed mouth. Gemmae may be produced at the leaf margins but are rarely observed.

Anastrophyllum esenbeckii resembles ***A. auritum*** (Lehm.) Steph., a common tropical montane or southern temperate species. However, the perianths are much broader and shorter in *A. esenbeckii*, but according to Gradstein (2021), *A. auritum* is highly variable. We cannot discard the possibility that the Hawaiian plants could be a variant of *A. auritum* but more research is needed to clarify this question.

Plants covering the lower trunk of ʻōhiʻa (*Metrosideros polymorpha*) (left). Detail of dense and loosely attached mat of procumbent plants. Hawaiʻi Volcanoes National Park, Hawaiʻi Island, Freire & Judziewicz 21-165 (HAVO).

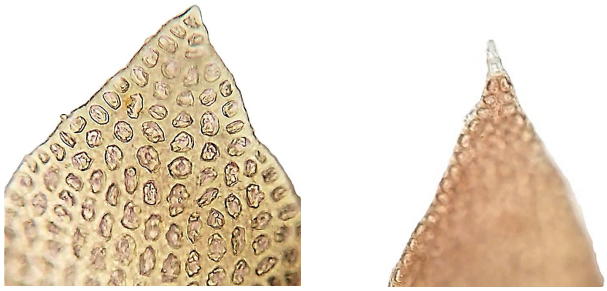


Anastrophyllum esenbeckii. The reddish-brown plants are loosely attached to their substrate, slender, elongate, projecting horizontally or hanging from tree trunks. Escape Road, Hawaiʻi Volcanoes National Park, Hawaiʻi Island Freire & Judziewicz 21-165 (HAVO).

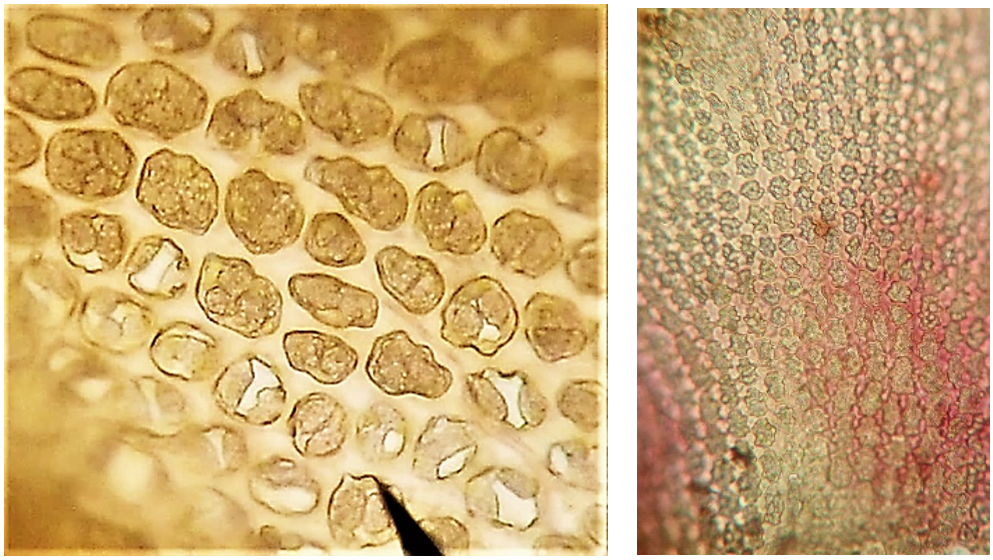
Plants are about 1 mm wide (at their widest point) and can be rather branched (scale in mm). Flagelliform branches are often present. Escape Road, Hawai‘i Volcanoes National Park, Hawai‘i Island, Freire & Judziewicz 22-962.5 (HAVO).

Anastrophyllum esenbeckii. plants are stout-looking; note branching. Left, Escape Road, Hawai‘i Volcanoes National Park, Hawai‘i Island, Freire & Judziewicz 21-165 (HAVO), dorsal view of plant; leaves are squarrose, unequally bifid, with transverse-succubous insertion. Right: Same location, Freire & Judziewicz, 21-671 (HAVO).

Leaves are concave and have pointed, more or less equal lobes with a deep "V"-shaped sinus. First two photos: Hawai'i Island, Freire & Judziewicz 22-952 (BISH). Last two photos: Maluhia Trail, Volcano Village, Hawai'i Island, Freire & Judziewicz 23-513 (BISH).



Left: Detail of leaf lobe with acute tip; note the very thick-walled cells and single-celled tip. Escape Road, Hawai'i Volcanoes National Park, Hawai'i Island, Freire & Judziewicz 21-165 (HAVO). Leaf tips can also have two cells and are sometimes hyaline. Maluhia Trail, Volcano Village, Hawai'i Island, Freire & Judziewicz 23-513 (BISH).



Anastrophyllum esenbeckii. Left: Leaf cells with large, granular oil bodies and thick walls. Freire & Judziewicz 21-165 (BISH). Right: Leaf cells can have nodulose trigones. Maluhia Trail, Volcano Village, Hawai'i Island, Freire & Judziewicz 23-513 (BISH).

Dorsal view of plants with curved, slightly decurrent and succubous insertion. Note the ventral, intercalary branches, some of which are microphyllous (arrows), and the terminal branches. Perianths are large, pleated, and tubular. Hawai‘i Island, Freire & Judziewicz 21-165 (HAVO).

Anastrophyllum esenbeckii. Plants with large and pleated perianths. O‘ahu; photo by Miles K. Thomas, with permission.

Anastrophyllum esenbeckii. Plants with plicate perianths. Left: Detail of ventral flagelliform branch (arrow). Right: Perianth with fringed, hyaline mouth. Escape Road, Hawai‘i Volcanoes National Park, Hawai‘i Island, Freire & Judziewicz 21-165 (HAVO).

Anastrophyllum* cf. *esenbeckii. A liverwort that is somewhat similar to *A. esenbeckii* grows intertwined at the base of the sedge *Rhynchospora chinensis* subspecies *spiciformis* collected from Nāmolokama, Kauaʻi. Judziewicz several plants from the herbarium specimen Flynn 3021 (BISH!). It differs from *A. esenbeckii* in having leaf lobes that are very asymmetrical, leaves more strongly concave, and "dots" of darker pigmentation are observed on the leaf cell walls.

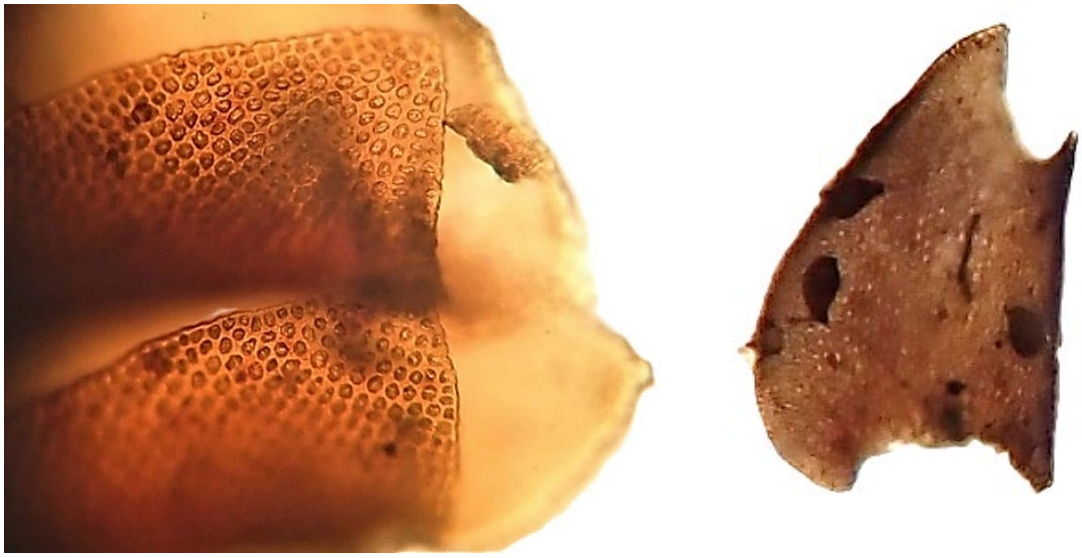
Plants are several cm long and 1.4-1.5 mm broad. Leaves are squarrose, slightly curved down (falcate), and transverse-succubous inserted. Leaves project to the stem midline on the ventral side, are canaliculate, asymmetrically bilobed, with one lobe much smaller than the other; the lobes are pointed, with a round sinus to about 1/3 the leaf length. A border of thick-walled and square cells is present on the leaves. Leaf cells are rounded, with thick nodulose trigones. Areas of darker color are observed on the cell walls (as dots), and the cells are smooth, discounting the possibility of prorulae. Perhaps the dots are the result of an uneven distribution of pigments. Perhaps this is due to differences in cell wall structure? Cells are larger and more elongated at the base of the middle of the leaf. No sexual structures were seen. An unknown epiphytic brown, bottle shaped organism, with two pores on opposite sides, grows on the leaf surfaces.

Left: Herbarium specimen of *Rhynchospora chinensis* subspecies *spiciformis*, Nāmolokama, Kauaʻi, Flynn 3021 (PTBG image online; we have not examined this collection but have examined the BISH duplicate). Right: leafy liverworts found at the base of the sedge (arrows). Photo courtesy of the National Tropical Botanical Garden.

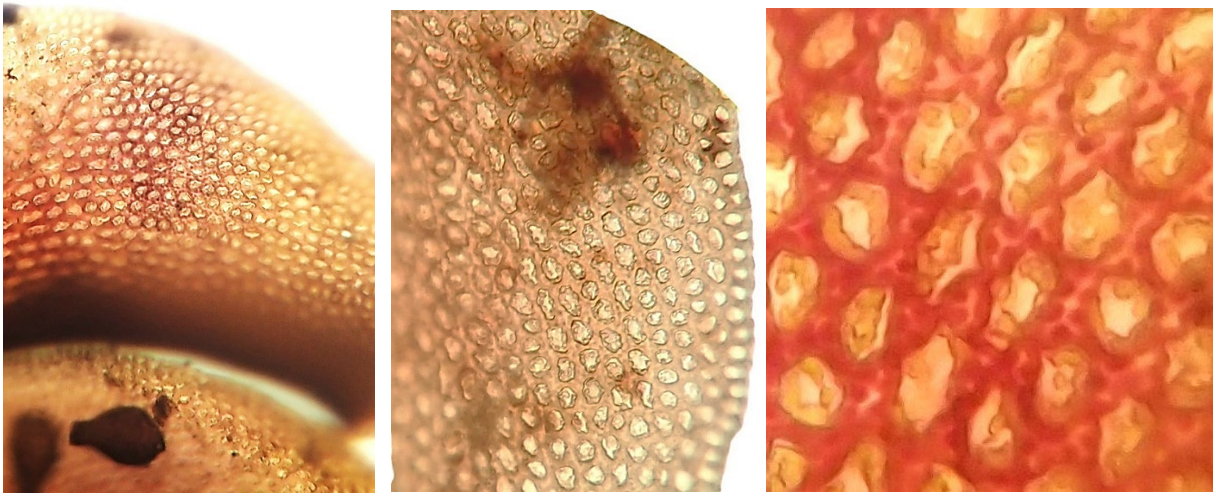
Left: Plants are long and narrow (scale in mm). Right: Intercalary branching is present. Flynn 3021 (BISH). Photos by A.V. Freire.

Anastrophyllum cf. *esenbeckii.* Ventral view of plants. Leaf insertion is curved, to the stem midline. Nāmolokama, Kauaʻi, incidental on Flynn 3021 (BISH). Photos by A.V. Freire.

Plants in dorsal view; the dorsal leaf lobe is smaller than the ventral one. Leaf insertion is almost transverse and is only slightly oblique. Flynn 3021 (BISH). Photos by A.V. Freire.



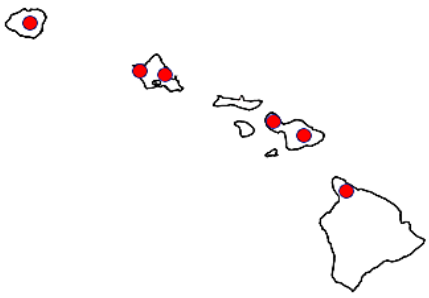
Anastrophyllum cf. *esenbeckii.* Left: Leaf lobes are pointed. Leaf cells are thick-walled and isodiametric towards the apex. Right: leaf lobes are unequal, leaf is canaliculate. Nāmolokama, Kauaʻi, incidental on Flynn 3021 (BISH). Photos by A.V. Freire.



Left and Center: Leaf cells have thick walls with confluent trigones. Note the border of small, square cells (center). Dark-colored "dots" are observed on cell walls (see detail to the right). Because cells look smooth in profile, we cannot confirm them as papillae. Incidental on Flynn 3021 (BISH), photos by A.V. Freire.

Anastrophyllum cf. *esenbeckii.* Leaves are canaliculate; stems are very thick and firm. Note the unidentified bottle-shaped organisms on the surface of the leaves. Nāmolokama, Kauaʻi, Incidental on Flynn 3021 (BISH). Photos by A.V. Freire.

2. *Anastrophyllum fissum* Steph. **Indigenous.** A striking large, reddish, deeply bifid, densely leafed species of windswept summit cloud forests (2,400-5,700 ft.) of Kauaʻi, Oʻahu, Maui, and Hawaiʻi Island (Judziewicz et al., 2025b). This is the largest species of Hawaiian liverwort with bifid leaves. The erect plants with nodding apices resemble "scarlet cobras" poised to strike. It is also reportedly present in New Caledonia (Thouvenot et al. 2011) and Tahiti, French Polynesia (Bardat et al., 2021: 77).



In the past, this species has been mistakenly identified as the similar ***A. piligerum*** (Nees) Steph. (YU), a nearly pantropical species. According to Miller (1956), the two species could be related. We agree.

Plants form dense cushions on tree trunks, rock or soil. They are succubous*, erect, dark red, large, up to 13(15) cm long and 2-2.5 mm wide, with a nodding apex. Intercalary branches are present. Flagelliform branches are observed. Leaves are imbricate, secund (towards dorsal side), deeply bifid to about ¾ the leaf length, with a long "V"-shaped sinus. Leaf bases obscure the stem's ventral midline. Leaf lobes are unequal, long triangular, acute to acuminate, and the ventral lobe is larger and canaliculate, appearing inflated. The dorsal lobe is not inflated. Lobe tips are often hyaline, conferring a frosted appearance to the plants. Leaf cells are elongated and have large confluent trigones. A border of smaller, thick-walled and square cells is present. This species is reported to be dioicous. Antheridia are produced dorsally, on reduced branches, subtended by distant leaves. Female plants bear a long perianth that can be as long as 4 mm. Perianths are narrow, tubular, pleated, with a constricted and sightly fringed mouth.

*Because the plants are erect, it is challenging to recognize the dorsal from the ventral sides. The ventral side certainly has the aspect of a dorsus. Beware!

Anastrophyllum fissum growing on rock, here with the fern *Sadleria squarrosa*. Koʻolau Range, Oʻahu. Photo by Miles K. Thomas, with permission.

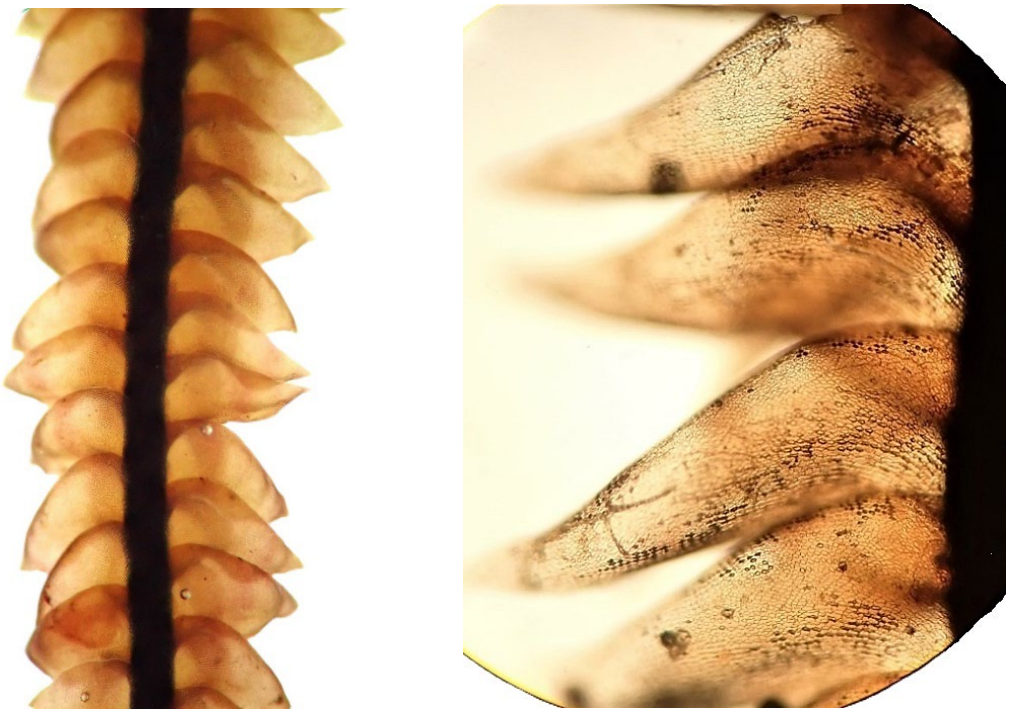
Dense cushions growing on tree trunks. Note frosted appearance due to hyaline leaf apices. Left: Poamoho, Koʻolau Range, Oʻahu, of M.K. Thomas 231 (BISH), photo by Miles K. Thomas, with permission. Right: Nāmolokama, Kauaʻi, Wood 18102 (PTBG), photo courtesy of National Tropical Botanical Garden/Ken Wood.

Anastrophyllum fissum. Plants are erect and have nodding apices bent towards their dorsal side. Nāmolokama, Kauaʻi, Wood 18102 (PTBG), photo courtesy of National Tropical Botanical Garden/Ken Wood.

Anastrophyllum fissum. Erect plants with deeply divided, secund leaves. Plants are dark red and erect, with nodding tips and very crowded, deeply bifid leaves. The hyaline leaf tips give it a “frosted” aspect. Nāmolokama, Kauaʻi, Wood 18102 (PTBG), photo courtesy of National Tropical Botanical Garden/Ken Wood.

Anastrophyllum fissum. Robust, erect plants with secund, acuminate leaves with hyaline apices. The leaves obscure the stem's ventral midline (white arrow). The plant to the left is in dorsal view (red arrow). 'Eke Bog, West Maui, 17 Mar. 2023. Photo by Zach Pezzillo, with permission.

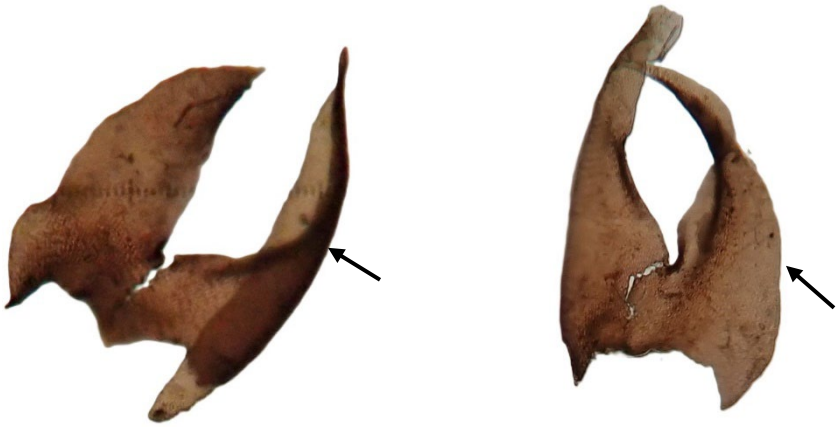
This is the largest Hawaiian bifid-leaved liverwort. Plants are large, up to 13 cm long and 2-2.5 mm broad (scale in mm). Hawai‘i Island, Kohala Mountain, el. 4,600 ft. 8 Jan. 2024, Pono Christianson s.n. (BISH). Photo by A.V. Freire.



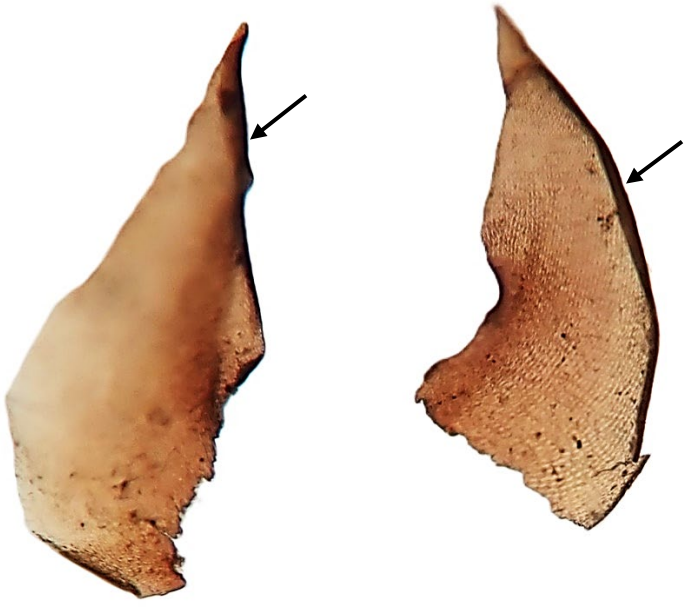
Anastrophyllum fissum. Ventral leaf lobes are canaliculate, inflated and larger than the dorsal side. They are secund, turned towards the dorsal side of the plant. Left: Hawai‘i Island, Kohala Mountain, el. 4,600 ft., 8 January 2024. Pono Christianson s.n. (BISH). Right: Pu‘u Ka‘ala, O‘ahu, M.K. Thomas et al. (including Freire & Judziewicz) 333 (BISH). Photos by A.V. Freire.

Dorsal view of plants. Plants are succubous. Left: Dorsal lobes are small and not inflated but with partially inrolled margins (arrow). Right: Intercalary ventral branch (arrow). Pono Christianson s.n. (BISH). Photos by A.V. Freire.

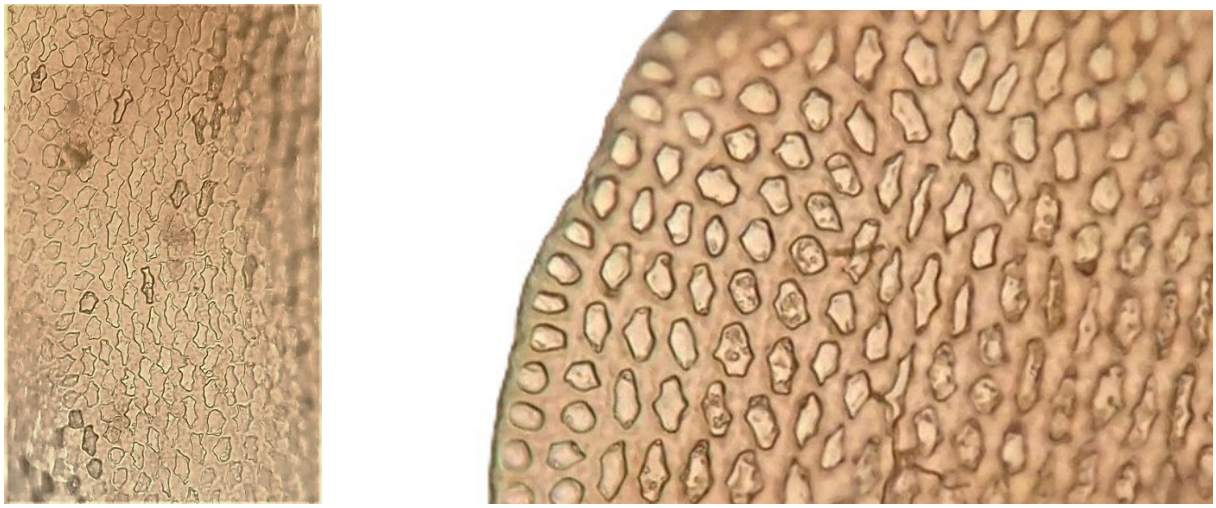
Anastrophyllum fissum. Intercalary branches are often produced. Flagelliform branches are also observed. Hawai‘i Island, Kohala Mountain, el. 4,600 ft., 8 Jan. 2024. Pono Christianson s.n. (BISH). Photos by A.V. Freire.



Leaves are deeply bifid with long, triangular lobes. Ventral lobes are canaliculate (arrows). Pono Christianson s.n. (BISH). Photos by A.V. Freire.



Anastrophyllum fissum. Leaf lobes with inrolled margins (arrows). Left: Ventral view of lobe. Right: Dorsal view of lobe. Hawai‘i Island, Kohala Mountain, el. 4,600 ft., 8 Jan. 2024. Pono Christianson s.n. (BISH). Photos by A.V. Freire.



Left: The leaf cells have large, contiguous trigones. Puʻu Kaʻala, Oʻahu, M.K. Thomas et al. (including Freire & Judziewicz) 333 (BISH). Right: Leaves have a border of thick-walled, isodiametric cells. Pono Christianson s.n. (BISH). Photos by A.V. Freire.

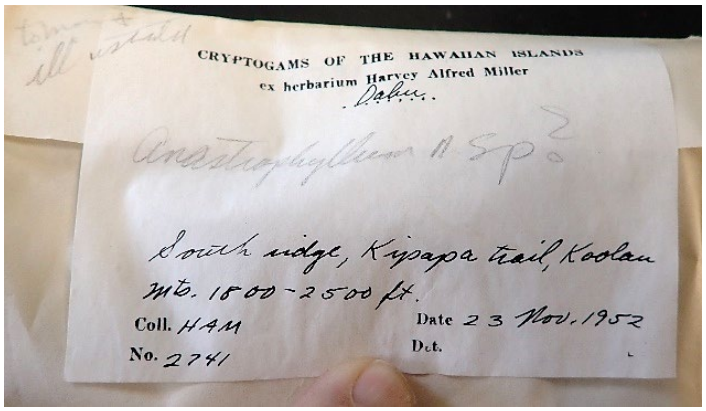
Anastrophyllum fissum. Perianths are narrow, long-tubular, pleated (left), and about 4 mm long (scale in mm), dorsally produced and with large subtending bifid bracts (right). Hawaiʻi Island, Kohala Mountain, el. 4,600 ft., 8 Jan. 2024, Pono Christianson s.n. (BISH). Photos by A.V. Freire.

The perianth's mouth is constricted and shortly fringed. Pono Christianson s.n. (BISH). Photo by A.V. Freire.

Anastrophyllum fissum. Male plant with antheridia subtended by leaves (arrows). Hawai‘i Island, Kohala Mountain, el. 4,600 ft., 8 Jan. 2024. Pono Christianson s.n. (BISH). Photos by A.V. Freire.

***Anastrophyllum* species 1.** H. A. Miller collected an *Anastrophyllum* from the South Ridge of the Kīpapa Trail, 1,800-2,500 ft., Koʻolau Range, Oʻahu, in 1952 (Miller 2741, MU). He annotated it as "*Anastrophyllum* n. sp.?" (photo of packet below). We present here the results of our brief evaluation of this specimen. The main distinctive character is the round lobe apices and rounded leaves. These could be interpreted as belonging to *Marsupella*. However, based on unpublished drawings by Miller, prominent perianths are present (but these were not observed by us). The perianths of the similar *Marsupella emarginata* are inconspicuous and remain hidden by bracts.

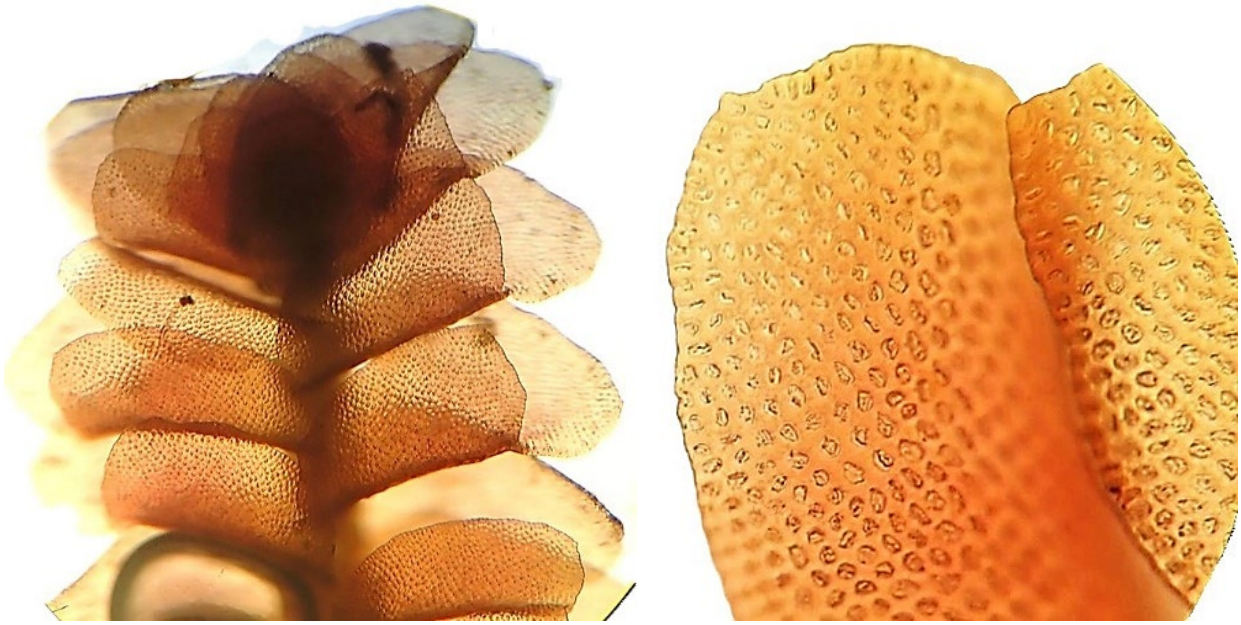
We conclude this is indeed a species of *Anastrophyllum*, a new report for Hawaiʻi, and probably a new species. Plants are reddish-brown, small, about 1.5-2 cm. long and 1 mm wide. Stems are strong, wiry, and dark. Flagelliform ventral branches are present. Leaves are rounded, flexuous, fragile-looking, spreading, and slightly folded at the midline. Leaf bases obscure the ventral stem midline. Leaf lobes are broad, rounded, with either round or obtuse and slightly pointed apices, separated by a narrow sinus usually about 1/3 the leaf length. Basal leaf cells are elongated and have prominent nodulose trigones (as in *Marsupella*). Cells become increasingly thick-walled and isodiametric towards the apex. A border of thick-walled, square cells is present but not clearly defined.



MU specimen annotated by H.A. Miller as "*Anastrophyllum* n. sp.?" (in pencil).

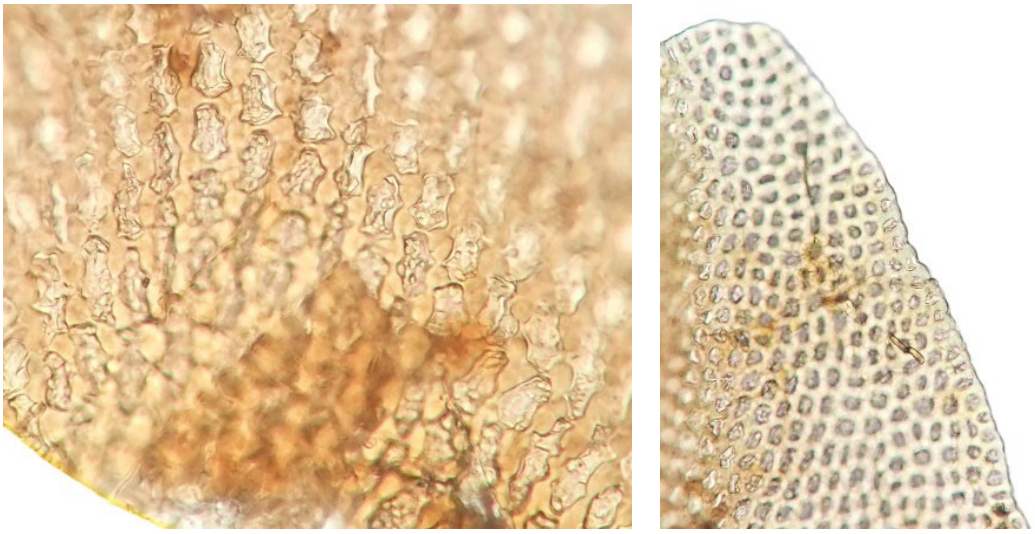
Koʻolau Range, Oʻahu (Miller 2741, MU). Plants are small, slightly over 1 mm wide (scale in mm). Photos by A.V. Freire.

Plants have a robust stem with flexuous leaves with rounded lobe apices. Left: Plant in dorsal vew. Right: Plant in ventral view. Note the ventral, flagelliform branch. Miller 2741 (MU). Photos by A.V. Freire.



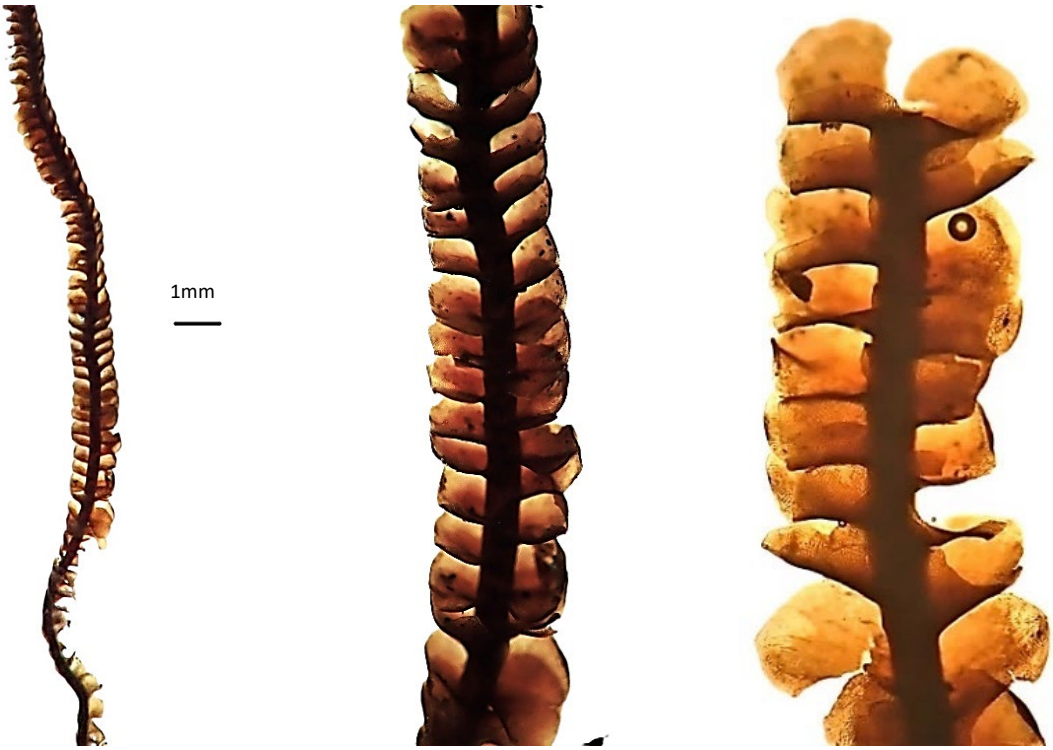
Anastrophyllum sp. 1. Left: Detail of plant in ventral view; leaves obscure the stem midline. Right: Rounded lobe with a small, obscure apiculum. Note the very thick cell walls. Koʻolau Range, Oʻahu, Miller 2741 (MU), photos by A.V. Freire.

Leaves are round, with two broad lobes and a narrow sinus. Leaf apices are rounded and obtuse or sometimes pointed. Miller 2741 (MU), photos by A.V. Freire.



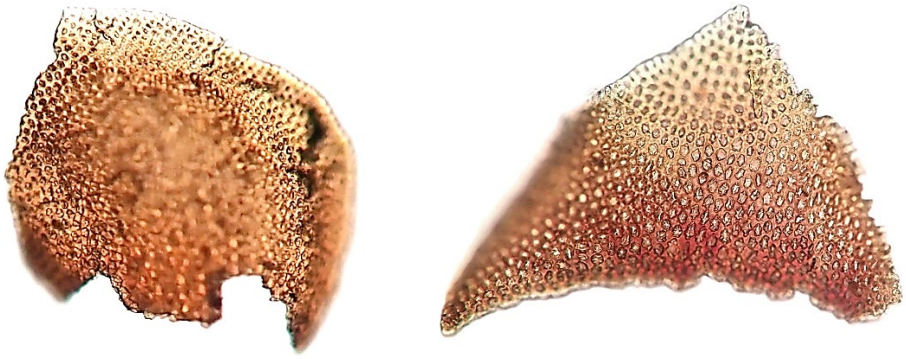
Anastrophyllum sp. 1. Left: Basal leaf cells are elongated and have prominent nodulose trigones. Right: Leaf cells become isodiametric and have thicker walls towards the apices. Note the border of small square cells not clearly differentiated from adjacent cells in this region. Koʻolau Range, Oʻahu, Miller 2741 (MU). Photos by A.V. Freire.

Problematic *Anastrophyllum* or *Marsupella* species from ‘Eke Bog, West Maui, Stemmermann 7034 (HAVO). We had very little time to study this specimen at HAVO. We identified it initially as *Marsupella emarginata* (Judziewicz & Freire, 2023: 162) because of the rounded leaves with shallow sinuses and lobes broader than long. However, the size and rigid appearance of the plants, together with the very thickened cell walls and pointed leaf lobes, suggest it may belong in the genus *Anastrophyllum*. The two genera can be difficult to distinguish without perianths. This specimen needs careful study. Perhaps perianths can be found to clarify its identity.

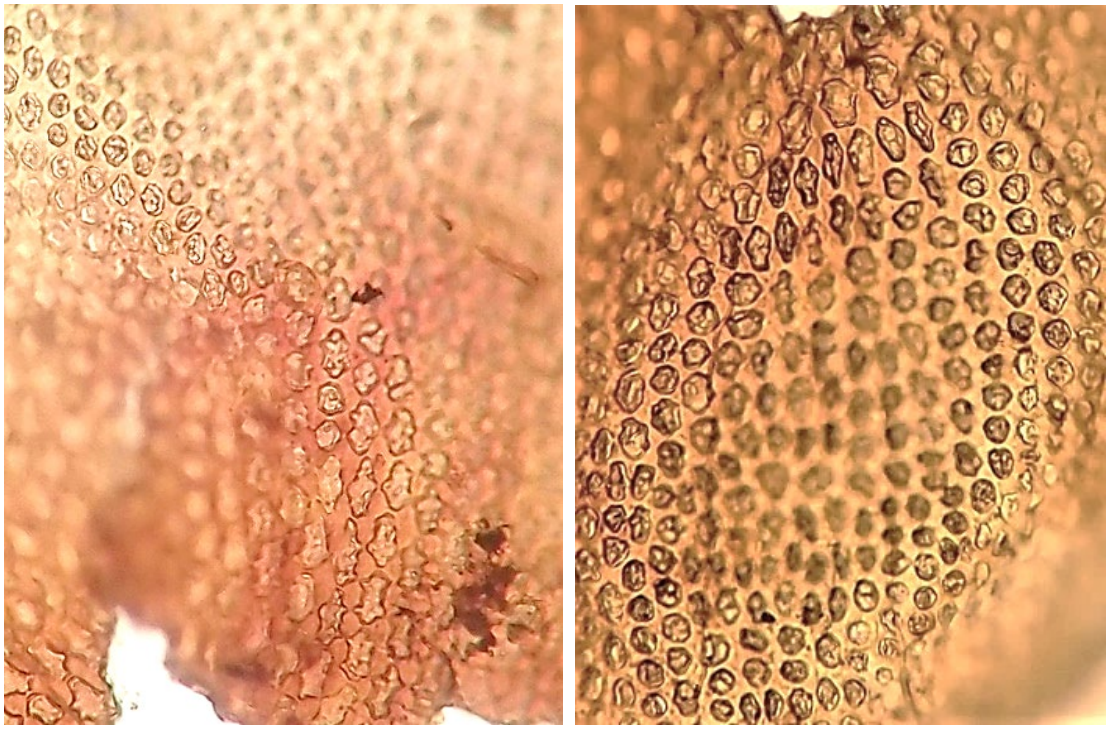


Plants are rigid looking, with spreading leaves that are somewhat canaliculate. The leaf insertion is long, transverse-succubous. Photos by A.V. Freire.

Anastrophyllum or *Marsupella* species from ‘Eke Bog, West Maui, Stemmermann 7034 (HAVO). Leaves are rounded, broader than long, bifid, with obtuse lobes and shallow sinuses. Photos by A.V. Freire.



Detail of leaf lobes showing pointed apices. Note the very thickened cell walls at the apex. Stemmermann 7034 (HAVO). Photos by A.V. Freire.

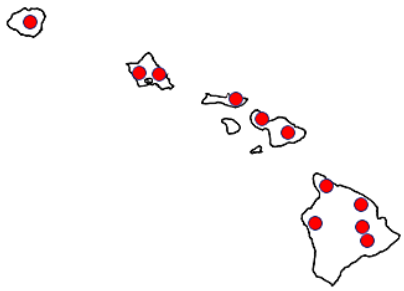


Anastrophyllum or *Marsupella* species from ‘Eke Bog, West Maui, Stemmermann 7034 (HAVO). Leaf cells have very thick walls and prominent nodulose trigones. Photos by A.V. Freire.

Asperifolia A.V. Troitsky, Bakalin & Maltseva (Calypogeiaceae)

One (or perhaps two) species in Hawai‘i; three species worldwide. This new segregate is distinct from *Calypogeia* in its partial stem hyalodermis, and leaves partially bordered by a row of horizontal cells.

Asperifolia arguta **(**Nees & Mont.) A.V. Troitsky, Bakalin & Maltseva. **Indigenous.** Treated as *Calypogeia argut*a by Staples & Imada (2006). Found on all major islands except Lāna‘i (200-4,000 ft.); see Judziewicz & Freire (2023c: 160); for Moloka‘i, Pezzillo: https://www.inaturalist.org/observations/248417045.

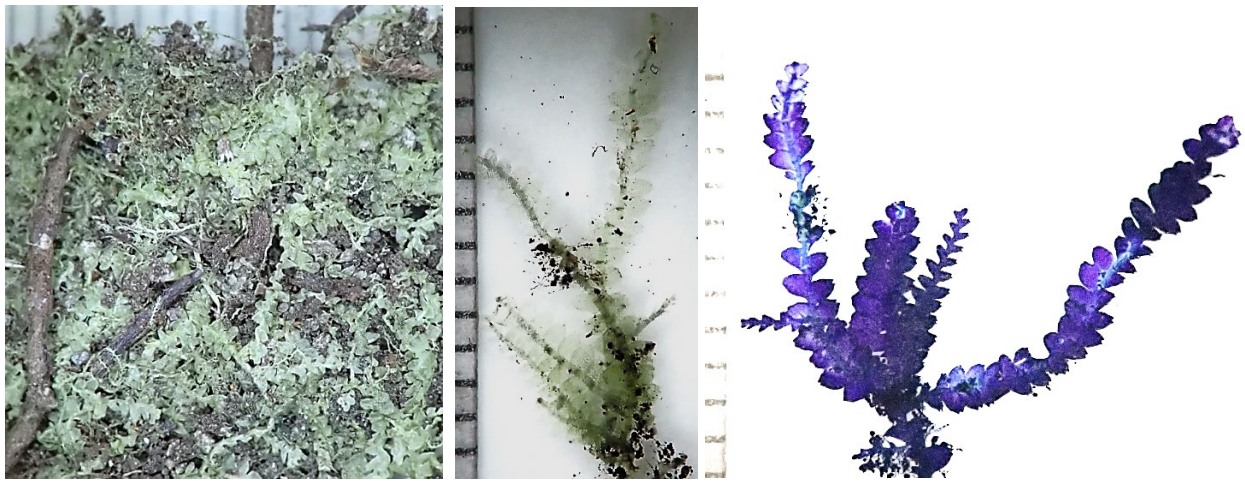


This somewhat uncommon species grows in moist, usually very shady sites, on soil or rock. Plants are pale to blue-green, up to about 2 cm long and up to 1.8 mm broad, mainly prostrate but some tips may be semi-erect. Stems are fragile, with a “partial hyalodermis” easily observed under a microscope.

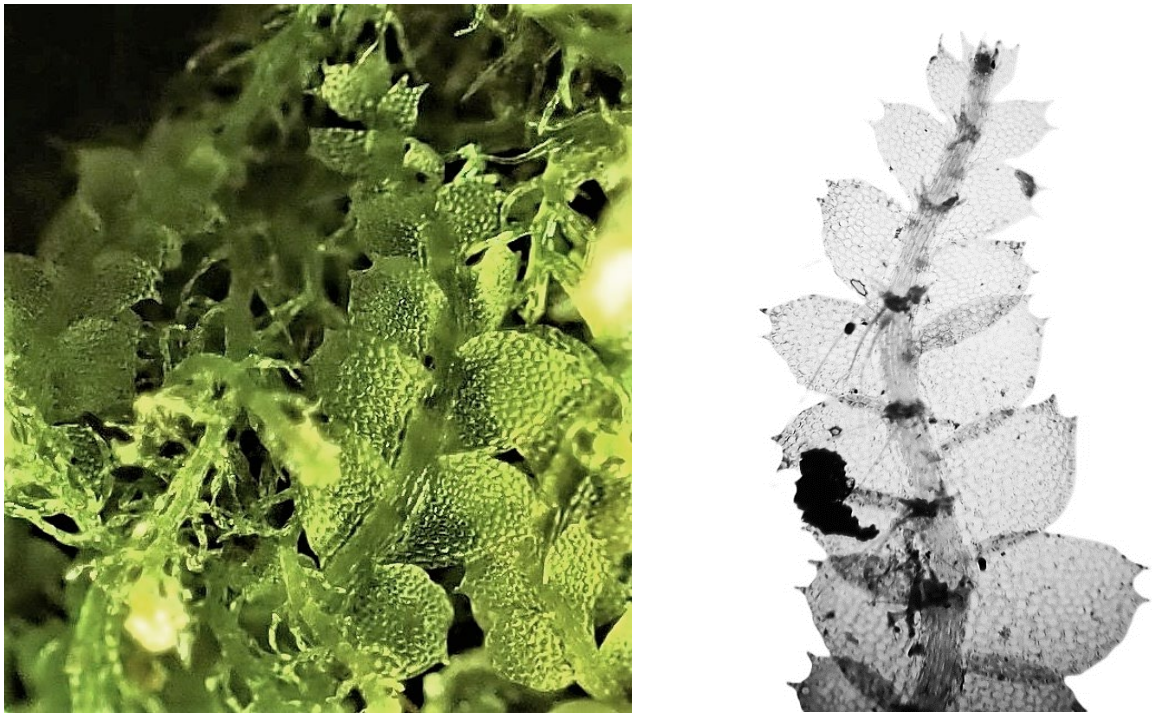
This structure is formed by two strands of large cortical cells only found on either side of the stem and is associated with leaf bases. Ventral branching is usually present at the base of plants. Rhizoids are clustered at the base of underleaves. Leaves are ovate, incubous, distant to imbricate, decurrent, about 0.7 mm long. Leaf apices are shallowly bifid, with two parallel to slightly divergent teeth (2-3 cells long) separated by a “U”-shaped sinus. Leaf cells are verrucose, bulging, large (55-87 µm long, 22-35 µm wide), thin-walled and without trigones. Leaves are partially bordered by thicker walled, rectangular cells with the long axis parallel to the leaf margin. Oil bodies are small, elliptical, and granulose, about (2)3-6(8) per cell. Underleaves are 1.5-1.8 times the stem width, patent to squarrose, deeply bifid with “elbows” at either side, or more frequently quadrifid, with a well-developed lateral tooth at either side; occasionally, an extra tooth may be observed. Clusters of gemmae may be produced at stem tips.

Bakalin et al. (2022b: 26, 34) presented molecular evidence that this species and its relatives are basal to *Calypogeia* and should be transferred to the new segregate genus *Asperifolia.* Furthermore, they presented molecular evidence that *A. arguta* is a strictly European species that does not occur in Asia (and presumably Oceania). They proposed the new species *A. indosinica* Bakalin & A.V. Troitsky to accommodate Asian collections with smaller cells and smaller underleaves. It seems to us that the Hawaiian material pertains to *A. arguta*. The plants we examined have large leaf cells and underleaf morphology in accordance with Cooke’s description (1904) of *A. arguta* (as *Calypogeia bifurca*). A more detailed study of these two species (*A. arguta* and *A. indosinica*) is needed. Previous to the Bakalin et al. papers, Sun et al. (2018: 160) gave the range of *A. arguta* (as *Calypogeia arguta*) as eastern Asia and Malesia, disjunct in Hawai‘i.

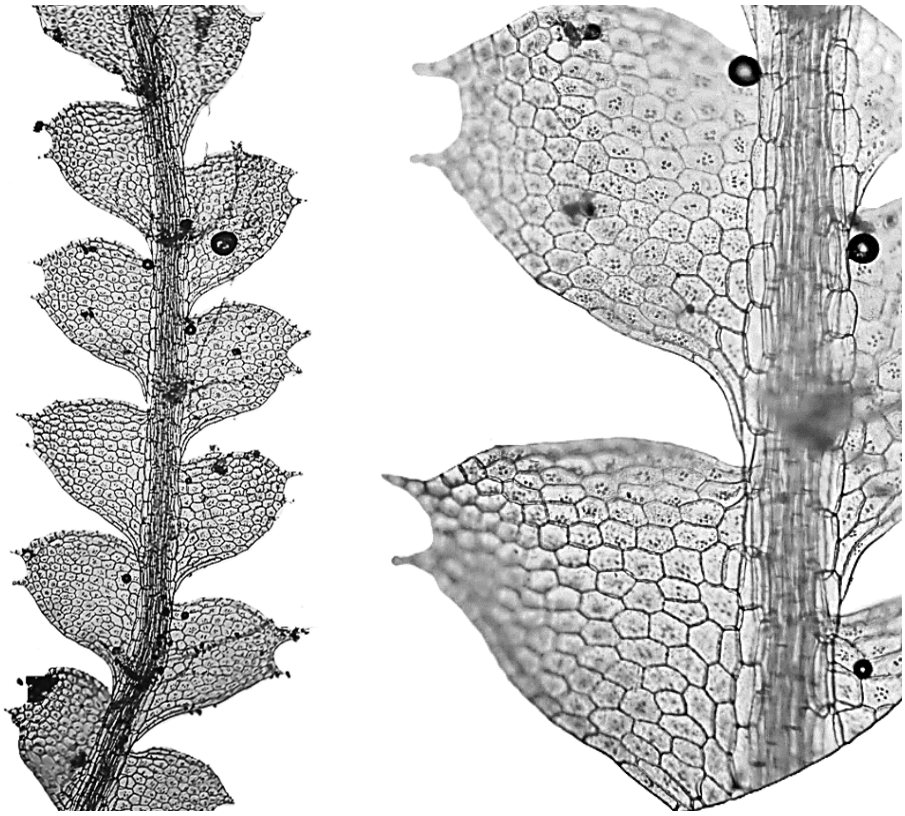
Asperifolia arguta. Left: Population on soil with prostrate habit and blue green color. Right: Detail showing the incubous insertion and raised stem tips. Volcano, Hawai‘i Island, Freire & Judziewicz 23-465 (BISH).



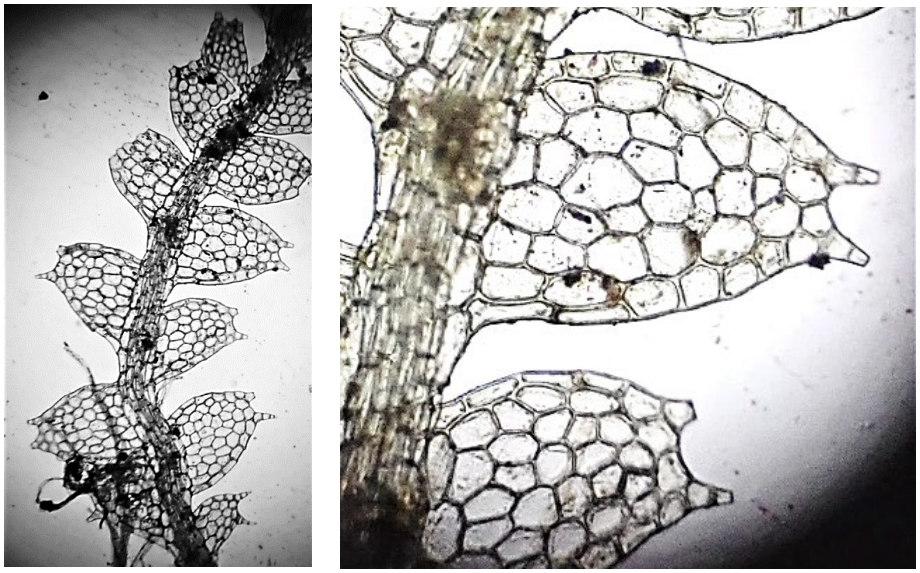
Plants are small and prostrate, fragile-looking. Right: Plant stained with toluidine blue to better show branching and size. Scales in mm. Freire & Judziewicz 23-465 (BISH).



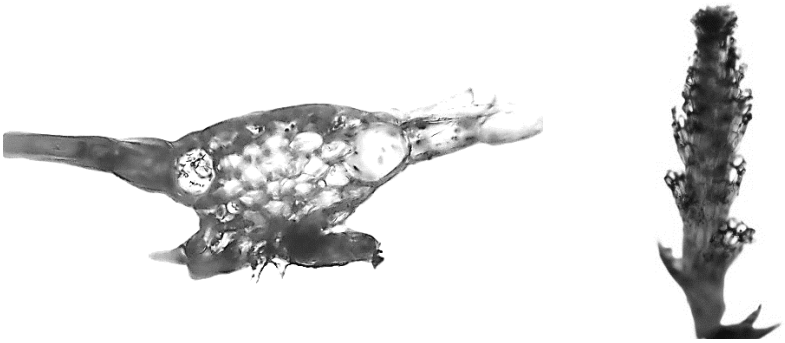
Asperifolia arguta. Here associated with *Telaranea nematodes*. Left: Leaves have incubous insertion and large, bulging cells. Freire & Judziewicz 21-92, Volcano, Hawai‘i Island. Right: Plant in ventral view showing small quadrifid underleaves and clusters of rhizoids at their bases. Volcano, Hawai‘i Island, Freire & Judziewicz 23-465 (BISH).



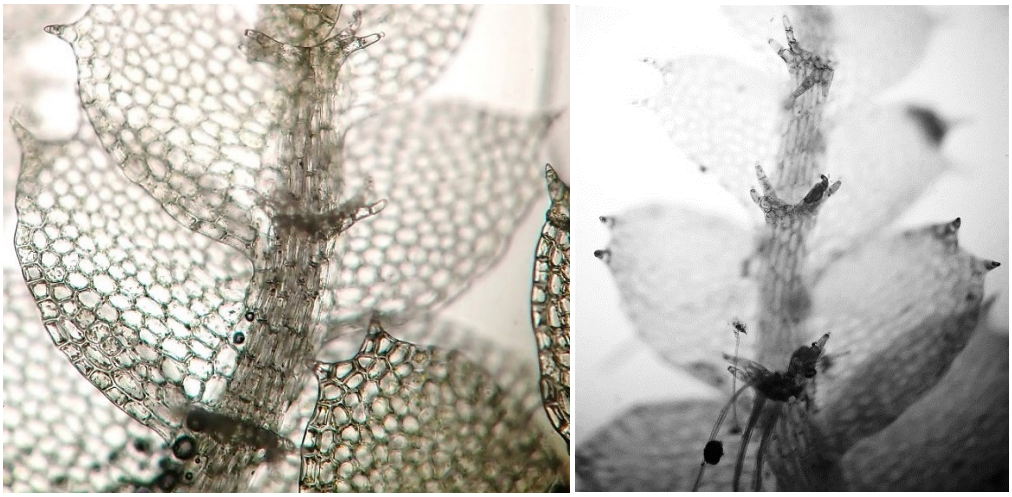
Leaves are bifid, decurrent, and partially bordered. The apical teeth are parallel to slightly divergent. Stems have two strips of large hyaline cells that form a partial hyalodermis. Note dark oil bodies and verrucae (right). Maluhia Trail, Kīlauea Lodge, Volcano, Hawai‘i Island. Freire & Judziewicz 23-430 (BISH).



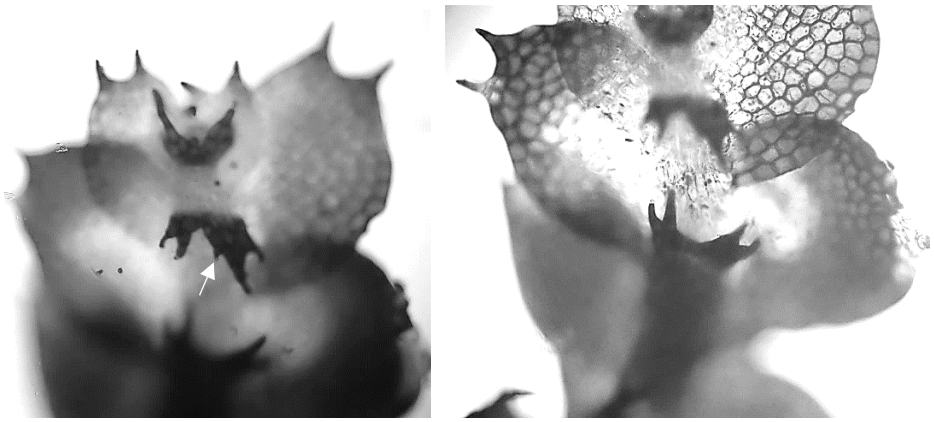
Asperifolia arguta. All characters mentioned before are present in this specimen. The leaves are decurrent, with a partial border. The apical teeth are slightly divergent, separated by a broad sinus. Stems have partial hyalodermis. Note the leaves with fewer cells when compared to the previous pictures. This is a small branch of a larger plant. Haleakalā, Maui, Higashino 10042 (HAVO). Photos by E.J. Judziewicz.



Left: Cross section of stem to show the two strands of large cortical cells associated with leaf bases. This can be interpreted as an incomplete hyalodermis. Right: Tip of gemmiferous branch. Both were stained with toluidine blue for contrast. Freire & Judziewicz 23-465 (BISH).



Underleaves are squarrose, quadrifid, with a broad sinus and very divergent apical teeth. Right: Stained with toluidine blue. Freire & Judziewicz 23-465 (BISH).



Asperifolia arguta. Left: Occasionally, underleaves may bear an extra tooth (arrow); also note the younger one above with elbows rather than lateral teeth. Right: Same plant with quadrifid underleaf. Both stained with toluidine blue. Volcano, Hawai‘i Island, Freire & Judziewicz 23-465 (BISH).

Asperifolia arguta. Leaf cells are thin-walled and verrucose. Oil bodies are small and granular. Maluhia Trail, Kīlauea Lodge, Volcano, Hawai‘i Island, Freire & Judziewicz 23-430 (BISH).

Asperifolia* aff. *arguta. This specimen from Waikamoi Preserve, Haleakalā, Maui, has the expected leaf decurrency, partial hyalodermis and bordered leaves. It differs from *A. arguta* in leaf shape; it is elliptical rather than ovate, and is broader in the middle. Leaf apices have teeth separated by narrower sinuses. The underleaves are smaller, not squarrose, and bifid with elbow(s) rather than evidently quadrifid. A more detailed study of this specimen is needed.

Asperifolia aff. *arguta.* Waikamoi Preserve Haleakalā, Maui, Freire, Judziewicz, Oppenheimer & Pezzillo 23-166, (BISH). Photos by A.V. Freire.

Bazzania Gray (Lepidoziaceae)

At least 17 species in Hawai‘i (254 worldwide); we suspect several more species are present. *Bazzania* needs much more work in Hawai‘i; Cooke’s fine treatment (1904) needs updating. Many more collections are available today compared to the limited number of specimens available in 1904, making it possible to broaden morphological concepts. Internet resources now facilitate matching specimens to pre-existing names worldwide. The kīpuka of the Saddle region between Mauna Kea and Mauna Loa appear to be a center of diversity.

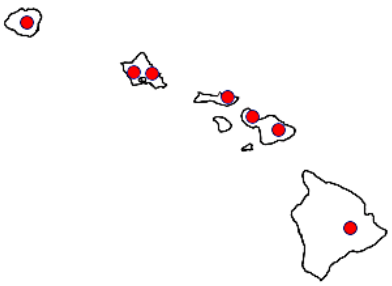
This genus is highly plastic and extremely difficult to study. Careful work is needed to comprehend the scope of morphological plasticity and to delimit species boundaries. We suspect some species may just be different morphological expressions of older names, and in need of reduction. A word of caution on endemic species is needed here, we think several may be indigenous, mostly of Asian origin, but North American and European contributions cannot be excluded. We present here a first attempt since 1904 to revisit this rich and complex genus. We pose many research questions hoping they will be addressed by future generations of botanists interested in the rich Hawaiian liverwort flora.

Bazzania is a common and easily recognized genus that is generally an epiphyte of ‘ōhi‘a and other trees but can also grow on rock and occasionally on soil. It often forms dense colonies (cushiony when moist), either appressed to their substrate, or spreading from it. The plants have bifurcate branching, and the incubous, mostly alternate leaves are often tipped with 2-3(4) small to large teeth. Underleaves are present and prominent; they are round to squarish in outline. An important diagnostic character of the genus is the presence of numerous long flagelliform (microphyllous) branches with tiny leaves, growing from the ventral (underside) surface of the stem and looking like “umbilical cords”. The growing tip of the plants is often deflexed, giving the shoots a “lobster tail” appearance. *Spruceanthus* could be superficially mistaken for this genus; however, *Bazzania* lacks leaf lobules.

Bazzania cordistipula. Habit on bark of ‘ōhi‘a (*Metrosideros polymorpha*). Volcano, Hawai‘i Island. Photos by E.J. Judziewicz.

1. Plants < 2 mm wide (usually < 1.5 mm) …… **2**
   2. Leaves distant, non-overlapping …… **3**
      3. Leaves ovate-triangular, truncate to broadly acute, with 2-3 coarse teeth; trigones absent or poorly developed …… ***B. baldwinii***
      3. Leaves narrowly lanceolate, narrowly acute, with 2 tiny teeth or entire; trigones large ... ***B. minuta***
   2. Leaves overlapping or contiguous …… **4**
      4. Leaves rounded, apices rounded, margins entire, without apical teeth ..... ***B.* sp. 1**
      4. Leaves not rounded, apices not rounded, instead truncate to acute …… **5**
         5. Leaves rectangular, slightly overlapping, or contiguous, spreading at 90˚, apices truncate with three triangular teeth …… ***B. brighamii***
         5. Leaves triangular, slightly overlapping, spreading at 45˚, apices acute, with 2 or 3 teeth …… ***B. didericiana***
1. Plants 2 mm wide or wider …… **6**
   6. Leaves entire, bidentate or with a variable number of teeth …… **7**
      7. Leaves entire, without teeth, or sporadically with one or more poorly defined teeth …… ***B. nuuanuensis***
      7. Leaves with well-defined teeth, bidentate or variously dentate, with various numbers of apical teeth on the same plant …… **8**
         8. Leaves mainly bidentate, but some with a single tooth or with no teeth …… ***B. emarginata***
         8. Leaves not mainly bidentate, with 1-4 teeth on the same plant …… **9**
            9. Leaves about as broad as long, a vittate region present …… ***B.* sp. 2**
            9. Leaves longer than broad, vittate region absent …… **10**
               10. Underleaves broader than long, more than twice wider than the stem, usually reflexed; leaf cells with large trigones …… ***B. didericiana***
               10. Underleaves not broader than long, less than twice as wide than the stem, usually appressed but sometimes reflexed; leaf cells without trigones or if present, small to large.. **11**
                  11. Leaves with sigmoidal lower margins, leaf cells with large, conspicupus trigones …… ***B.* sp. 4**
                  11. Leaves with straight lower margins, leaf cells with no trigones, or these small if present …… ***B. inaequabilis***
   6. Leaves with well-defined apical teeth, mainly tridentate, but some 4-toothed …… **12**
      12. Leaves with long-toothed laciniate apices, several of the teeth acuminate; underleaves irregularly-toothed…… ***B.* sp. 3**
      12. Leaves with short-toothed but not laciniate apices, the teeth not acuminate; underleaves entire or minutely toothed …… **13**
         13. Underleaves quadrate, usually minutely toothed; leaves clearly curved, falcate with parallel margins; trigones small or absent …… ***B. patens***
         13. Underleaves orbicular, usually entire; leaves without curved, falcate margins; trigones present Or absent …… **14**
            14. Leaves about as long as broad, with a very broad base; bases of leaves and underleaves clearly auriculate; O‘ahu …… ***B.* cf. *praerupta* or sp. 3**
            14. Leaves longer than broad; bases of leaves and underleaves not auriculate.…… **15**
               15. Underleaves overlapping; leaf cells with discrete trigones ..... ***B. cordistipula***
               15. Underleaves distant; leaf cells with small to large trigones …… ***B. sandvicensis***

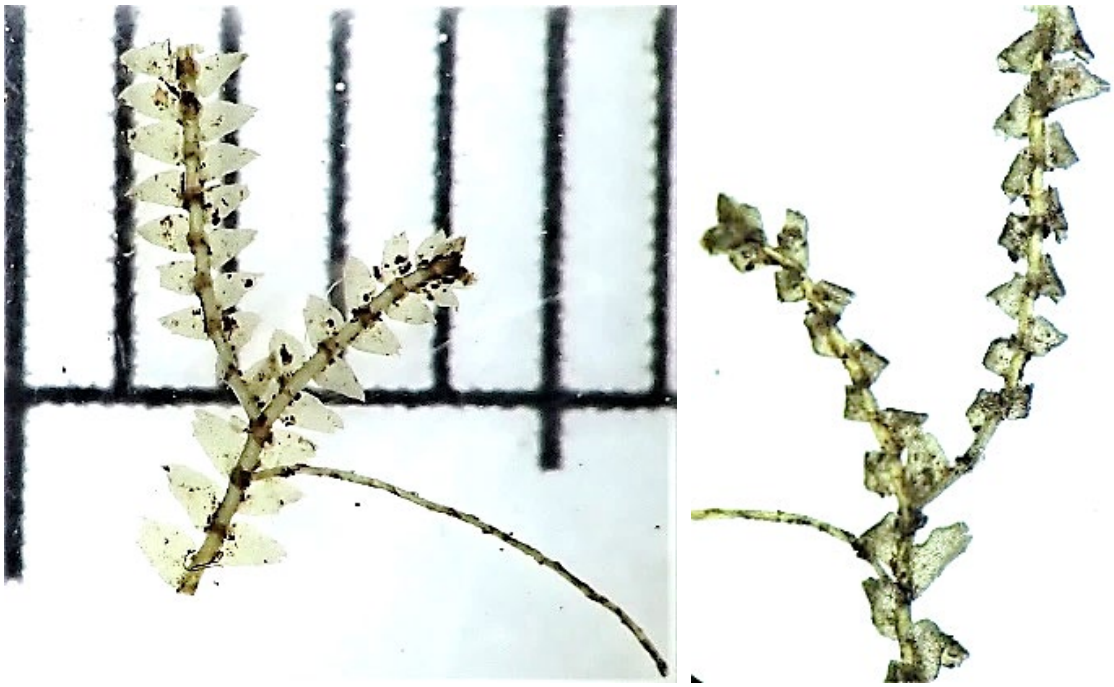
1. *Bazzania baldwinii* Austin ex A. Evans. **Endemic?** Possible affinity (Cooke, 1904): *B. triangularis* (= *B. tricrenata* (Wahlenb.) Lindb.), Eurasia. Reported for all major islands except Lānaʻi (1,500-6,150 ft.) but most specimens require confirmation. This uncommon species grows on soil, intertwined with other bryophytes. The species is recognized by its ovate-triangular and irregularly toothed leaves, usually with bi- or tridentate apices, with the upper tooth often the largest.



Plants are small, 1.1-1.6 mm wide (but Cooke (1904) and Evans (1891) described larger plants), pale to yellow-green, sparingly branched. Stems fragile. Leaf insertion is arched over the stem dorsal side. Leaves spreading, flat when wet, curled when dry, distant, ovate-triangular, usually with curved upper margins. Both upper and lower margins are entire but a lateral marginal tooth may be present on the upper margin of the basal half of the leaf. The leaf apices are usually truncate but may also be acute, often oblique, bi- or tridentate, or occasionally entire or with a single tooth. The upper tooth is usually the largest. Leaf cells are rounded, thin-walled, sometimes with small triangular trigones. A border of squarish cells with thicker walls is present. Underleaves remote, small, only slightly wider than the stem, rounded to quadrate, with a truncate apex, slightly emarginate, bilobed or erose-crenulate.

We studied the isotype (Baldwin 199) at MU. There are discrepancies between this specimen and the description and illustrations by Evans (1891) and Cooke (1904). Mainly, it lacks a larger apical leaf tooth, consistently trifid apices, and large underleaves. We identified it as *B. sandvicensis*. Likely, the type is a mix of *B. baldwinii* and *B. sandvicensis*, both terrestrial species, and the incorrect plant ended up in the MU "isotype" packet. For a lengthier discussion see entry for *B. sandvicensis*.

Bazzania baldwinii. Population on a twig. The yellow-green plants are ascending to procumbent and intermixed with other bryophytes. Waiʻaleʻale, Kauaʻi. Photos by Kevin Faccenda, with permission. https://www.inaturalist.org/observations/224591840.

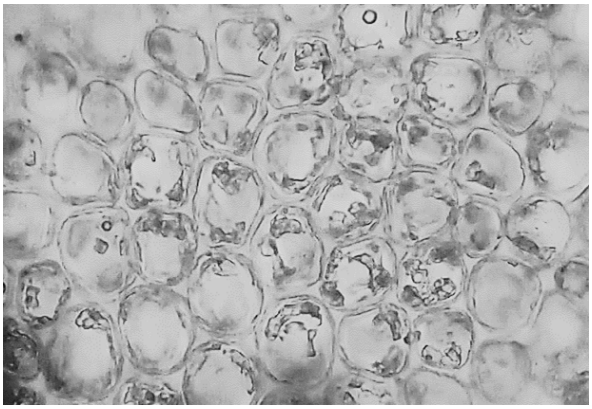


Left: Plants are small, the leaves spreading when wet; note long, whiplike, ventral flagelliform branch. Scale in mm. Right, dry plant showing curled leaves. Higashino 10176 (HAVO), photos by A.V. Freire.

Bazzania baldwinii. Left and center: Leaves are distant, ovate-triangular. Apices with (1)2-3 irregular teeth. Right: Occasionally, a lateral tooth may be observed on the basal half of the leaf (arrow). Haleakalā, Maui, Higashino 10176 (HAVO), photos by A.V. Freire.

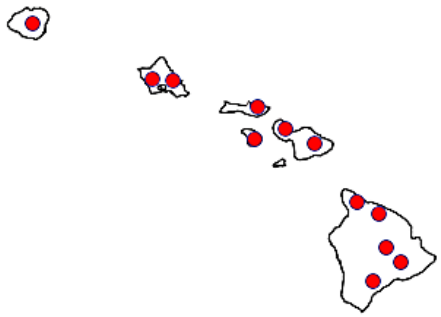
Leaves usually with a curved upper margin, mostly with oblique apices. Note the leaf border of square cells. The upper apical tooth is usually the largest. Higashino 10176 (HAVO), photos by A.V. Freire.

Underleaves are small, only slightly wider than the stem. They can be quadrate (left) to rounded (center and right) with entire to emarginate (left), lobate (center) or erose-crenulate apices (right). Higashino 10176 (HAVO), photos by A.V. Freire.



Bazzania baldwinii. Leaf cells are isodiametric, thin-walled, with small triangular trigones. Haleakalā, Maui, Higashino 10176 (HAVO), photos by A.V. Freire.

2. *Bazzania brighamii* (Austin) A. Evans. **Endemic.** Found on all major islands (1,300-6,400 ft.). It bears some resemblance to the Asian *Bazzania tridens* (Reinw., Blume & Nees) Trevis, based on the illustrations in Inoue (1974a: 24-25); but see discussion at the end of this entry. *Bazzania brighamii* and *B. inaequabilis* may be conspecific (see discussion under *B. inaequabilis*). This is a small species, commonly found in wet forests, growing on tree bark. It is easy to recognize by the squarrose, rectangular leaves tipped mainly by 3 small teeth and by the small, quadrate underleaves with a truncate, erose apex.

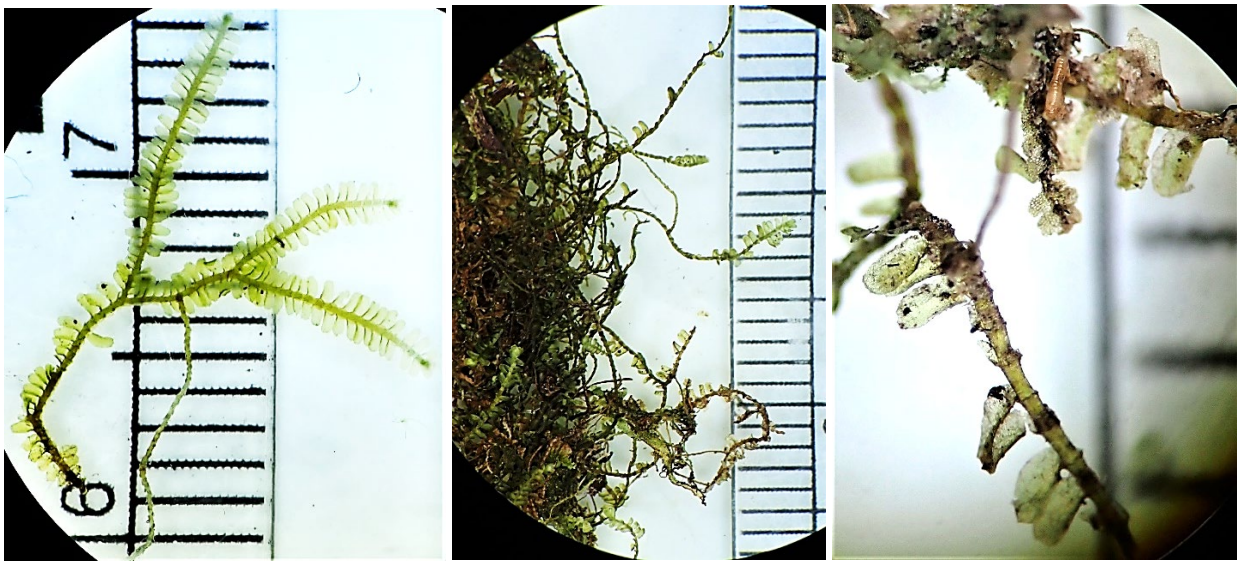


Plants are green to yellow-green, small, less than 2 mm wide, flat to slightly recurved at apex, projecting from their substrate or appressed. Stems are slender to robust. Bifurcate branching is common, flagelliform branches are frequent. Leaves are persistent or caducous, subopposite, rectangular, with nearly parallel sides, slightly falcate, slightly concave, contiguous to slightly imbricate and squarrose. Each leaf is tipped with (2)3(4) small and uniform triangular teeth. Median leaf cells have firm walls without or with very small triangular trigones. Central leaf cells from the leaf base to about ½ the leaf length are larger than adjacent cells, forming a poorly defined vittate area. Oil bodies are large, elliptical and segmented. Underleaves are distant to contiguous, small, about 1.5 times broader than the stem, squarish to slightly rounded in outline, with a truncate and erose apex, shortly fused to the leaf margins on both (or one) sides.

In his description, Cooke (1904) mentions the "antheridial spikes on the flagella" as an interesting feature for this species; we did not observe these structures.

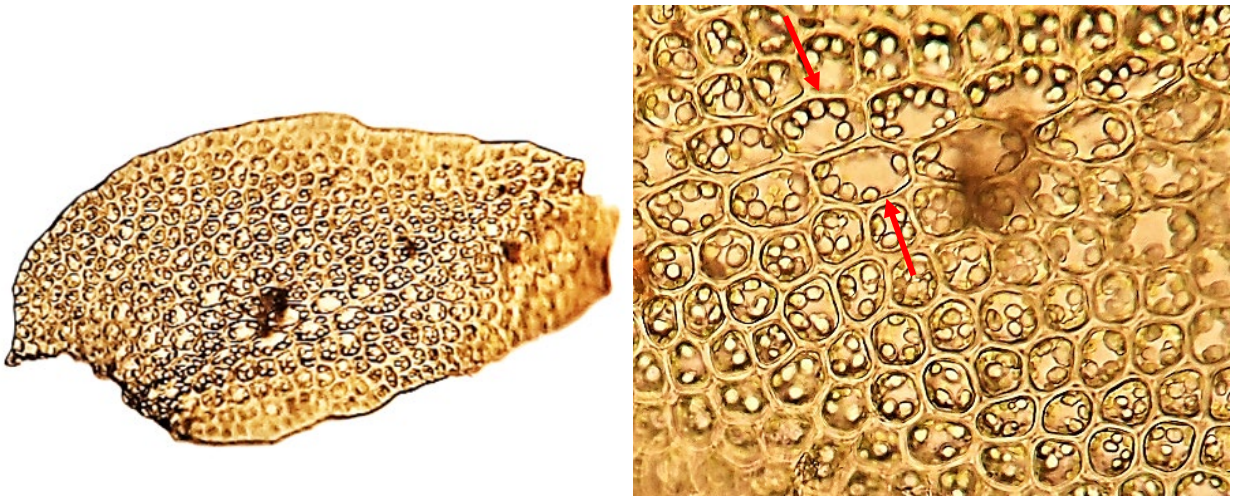
Left: Plants with flat, squarrose leaves. Volcano, Hawai‘i Island, photo by A.V. Freire. Right: Leaves rectangular, tridentate, spreading at right angles to the stem; underleaves small and quadrate. Ko‘olau Range, O‘ahu, Thomas 177 (BISH), photos by Miles K. Thomas, with permission.

Plants with parallel leaves and squarish underleaves resembling a boardwalk. Note the erose underleaf apices. Kauaʻi, Flynn 9660 (BISH). Photos by E. J. Judziewicz.



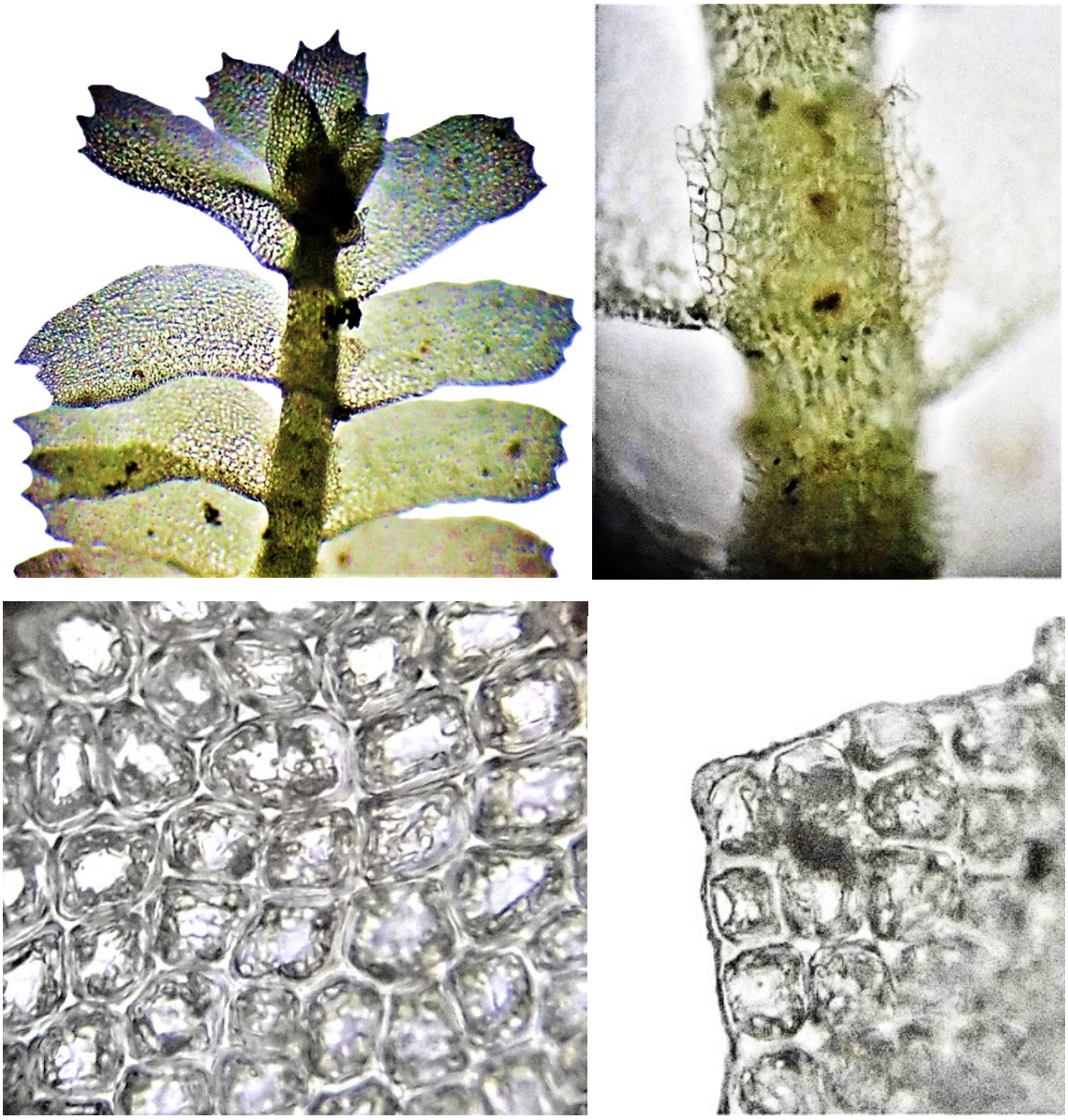
Bazzania brighamii. Left: Plants are small, less than 2 mm wide. Volcano, Hawaiʻi Island, Freire & Judziewicz 22-236 (HAVO). Center and right: Leaves are caducous. Scales in mm. Kīlauea Iki, Hawaiʻi Volcanoes National Park, Freire & Judziewicz 22-963 (HAVO).

Left: Leaves are sub-opposite; underleaves are slightly broader than the stem and shortly fused to both leaves. Right: Leaves rectangular, slightly recurved (falcate), with truncate apices bearing three short teeth. Freire & Judziewicz 22-236 (BISH).



Bazzania brighamii. Left: The central basal cells longer and broader than adjacent cells forming a poorly-defined vittate area. Right: Leaf cells are isodiametric with evenly thickened walls. Central basal cells larger and elongated forming a vittate area (arrows). Oil bodies are large, elliptical, and segmented. Volcano, Hawai‘i Island, Freire & Judziewicz 22-236 (BISH).

The following set of images is from Haleakalā, Maui, Higashino & Katahira 9978 (HAVO). This specimen was originally identified by us as *B. inaequabilis*, early in this research. We now believe it belongs to *B. brighamii.* This, we think, will be the case with many (if not all) specimens identified as the former species. Photos by A.V. Freire.

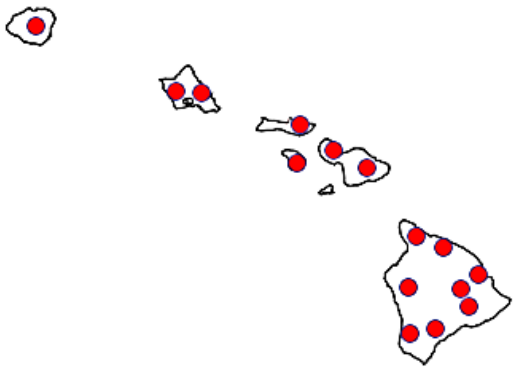


Bazzania brighamii. Top left: Leaves are rather parallel and mostly with 3 teeth. Top right: Underleaves are quadrate and erose. Bottom left: Median leaf cells are thin-walled and have small trigones. Bottom right: Apical cells are slightly thickened.

Next, we present a brief, very preliminary evaluation of ***Bazzania tridens*** (Reinw., Blume & Nees) Trevis, a possible relative of *B. brighamii*, based on the Japanese specimen, Katagiri s.n. (BISH). Note this specimen is **not** a type; the type specimen for this species needs study. As in *B. brighamii*, the specimen has squarrose, rectangular and slightly falcate leaves, with three apical teeth on a truncate apex; the underleaves are small, round and seemingly erose at their apex. However, unlike *B. brighamii*, the plants are more robust, broader and the median leaf cell walls bear more prominent trigones. At this point, due to such differences, we do not have proof that *B. brighamii* and *B. tridens* are conspecific. Is *B. brighamii* a smaller manifestation of *B. tridens* with larger trigones? Are they different enough to indicate their close relationship but not synonymy? Obviously much more study is needed. See also note under *B. patens*.

Bazzania tridens. When compared with *B. brighamii*, plants are more robust and median leaf cells bear more prominent trigones. Japan, Katagiri 491 (BISH). Photos by A.V. Freire.

3. *Bazzania cordistipula* (Mont.) Trevis. **Indigenous.** Found on all major islands (500-8,000 ft.); also found elsewhere in Oceania. This is one of the largest and commonest leafy liverworts in Hawai‘i and is likely to be noticed by even a casual observer. It forms large, sometimes shelflike cushions on the bark of ‘ōhi‘a and other tree species; it can also grow on soil or rocks. This species is recognized by its overlapping leaves tipped with three triangular teeth; its lower leaf margins that are curved upwards; its large, round and overlapping underleaves; and by its leaf cells with prominent trigones. This species is similar to and can be mistaken for *Bazzania sandvicensis*. They may be conspecific.



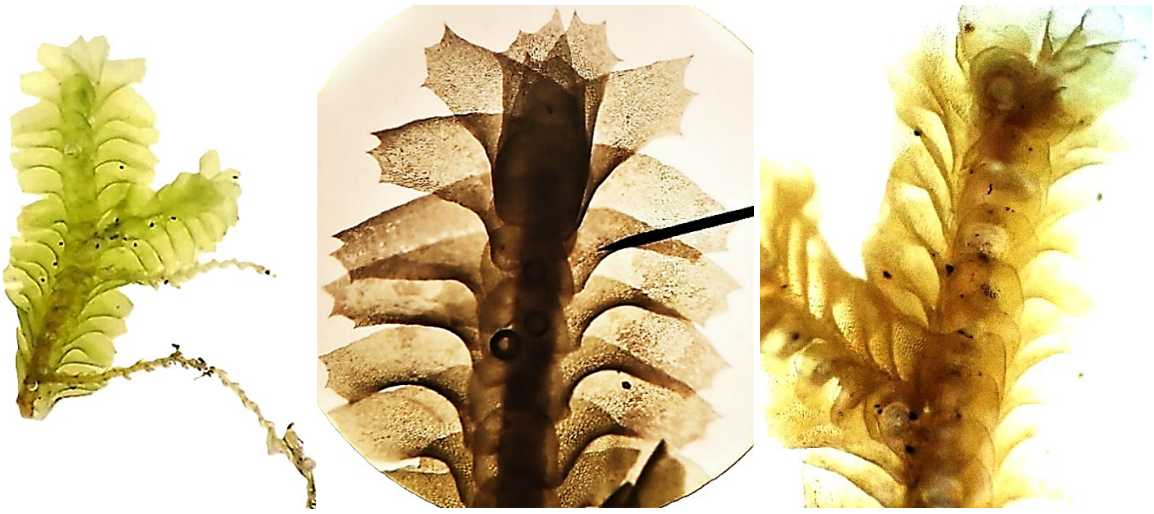
Plants are large, at least 2-2.5 mm wide, green to yellow-green or brown. Stems are stout, frequently branched, with obviously deflexed tips. Branches mainly bifurcate, ventral flagelliform branches stout and abundant. Leaves asymmetrically ovate and falcate, overlapping, truncate, each tipped with three almost uniform, short, broadly triangular teeth. Some plants do have much longer and narrower teeth. The basal half of the leaf lower margin tapers sharply to moderately from its base towards the leaf middle, so as to appear curved up, forming a “kink” or angle that may vary from 40°-90°; the upper leaf margin is slightly falcate. Apical cells are thick-walled and lack trigones; median leaf cells have prominent trigones. Oil bodies are elliptical and granulose. Underleaves are at least twice as broad as the stem, flat, appressed, round, strongly overlapping, usually with entire margins, although some may have an emarginate apex.

We see much variation in leaf shape, length of leaf apical teeth, and size of underleaves. We included some of this spectrum in our species definition (above). It is likely that we are dealing with a species complex in need of elucidation.

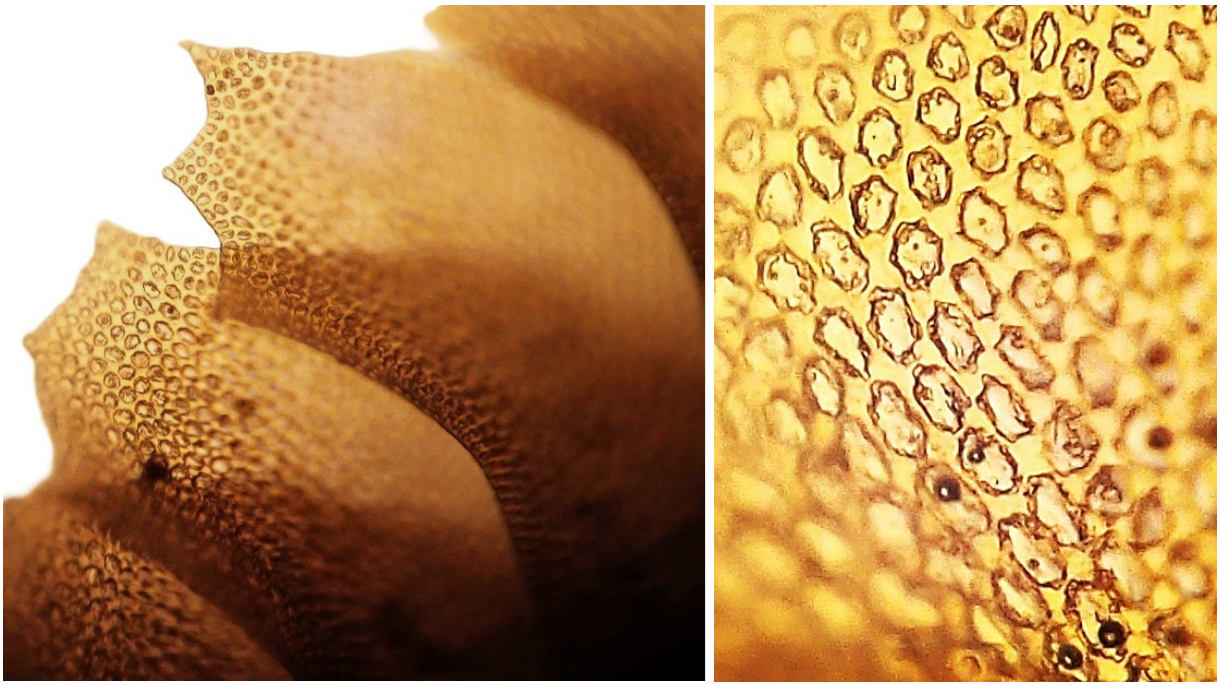
Bazzania cordistipula. On bark of ‘ōhi‘a (*Metrosideros polymorpha*), This is a very abundant, conspicuous leafy liverwort in most wet, montane Hawaiian forests. Volcano, Hawai‘i. Photo by E.J. Judziewicz.

Left: Dense cushion of *Bazzania cordistipula* growing on soil, Volcano, Hawai‘i Island. Right: Plants are large and frequently branched. Hakalau Forest N.W.R., Hawai‘i Island. Freire & Judziewicz 23-271 (BISH).

Bazzania cordistipula. Left: Plant profile showing overlapping leaves with truncate apices bearing three teeth, and more-or-less straight upper margin. The young ventral flagelliform branch resembles an umbilical cord. Right: Note the curved lower leaf margins and large, overlapping underleaves. Photos by Miles K. Thomas, O‘ahu, with permission.

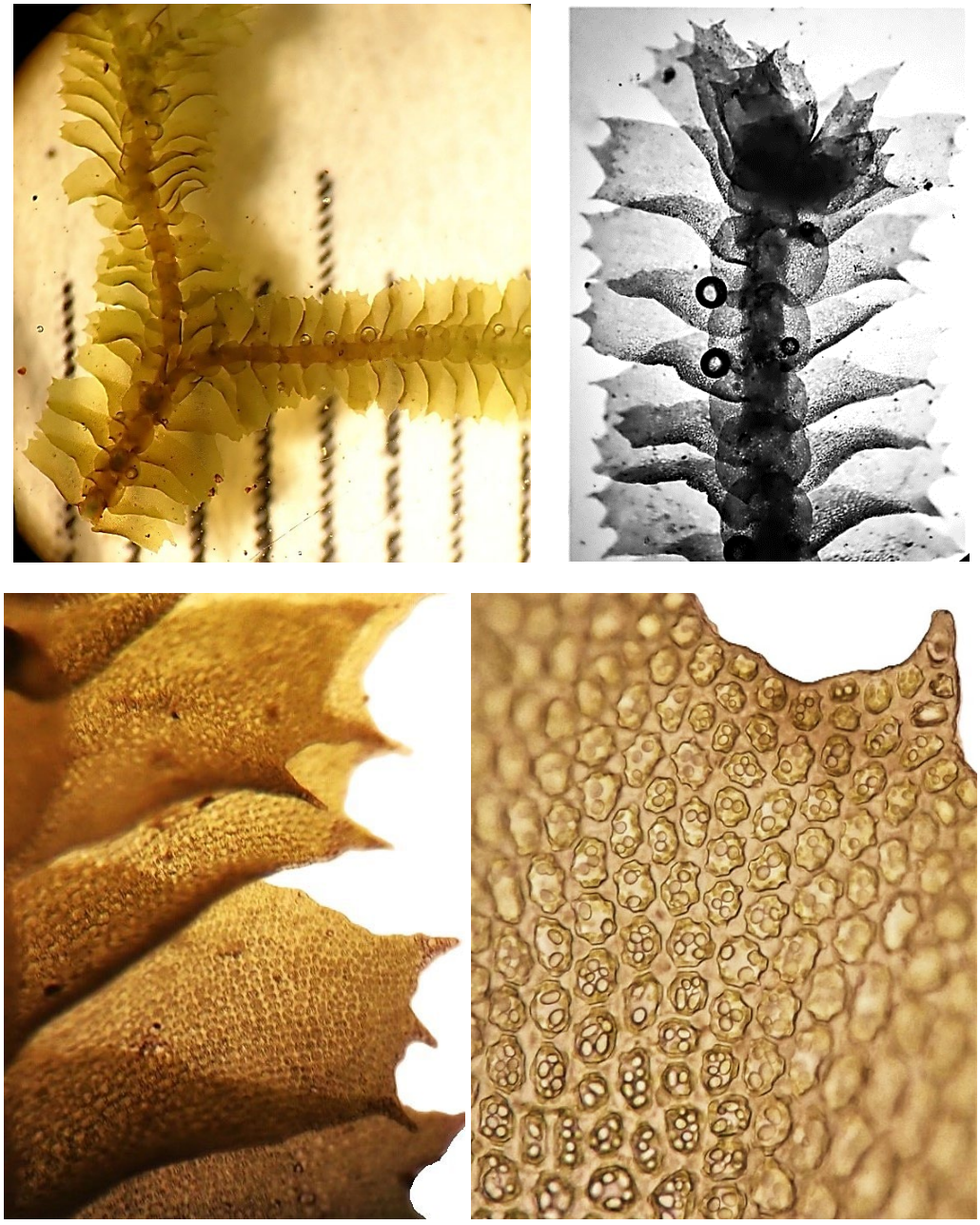


Left: Ventral view with stout flagelliform branches. Note the curved lower leaf margins. Volcano, Hawai‘i Island. Center: Upper leaf margins are only slightly curved, while lower margins are noticeably curved in their basal half (pointer). Note the short, triangular teeth. Right: Note the large, round, and strongly overlapping underleaves. Freire & Judziewicz 23-271 (BISH).



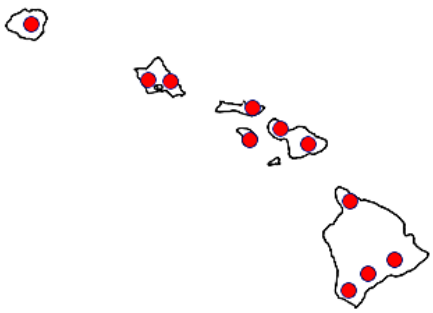
Bazzania cordistipula. Left: Leaf apices with three broad, short triangular teeth. Note the thick-walled apical cells. Right: Most leaf cells (except at the apex) have prominent trigones. Hakalau Forest N.W.R., Hawai‘i Island, Freire & Judziewicz 23-271 (BISH).

***Bazzania* cf. *cordistipula*:**
The following specimen exemplifies a variant with longer, narrower and not so uniform teeth, and with the leaf lower margins not as kinked. Perhaps part of the morphological spectrum of a *B. cordistipula* complex.



Bazzania cf. *cordistipula.* Hakalau Forest N.W.R., Hawai‘i Island. Freire & Judziewicz 23-285 (BISH).

4. *Bazzania didericiana* (Steph.) Steph. **Endemic.** Found on all major islands (2,000-6,100 ft.), but not frequent. Recognized by the variable number and irregularly-sized apical leaf teeth, with a mix of (1)2-3(4)-toothed leaves on the same plant, and by the reflexed underleaves. *B. didericiana* superficially resembles *B. cordistipula*. But the plants of the former are more slender, not as branched, and the leaves are narrower, with a variable number of apical teeth.



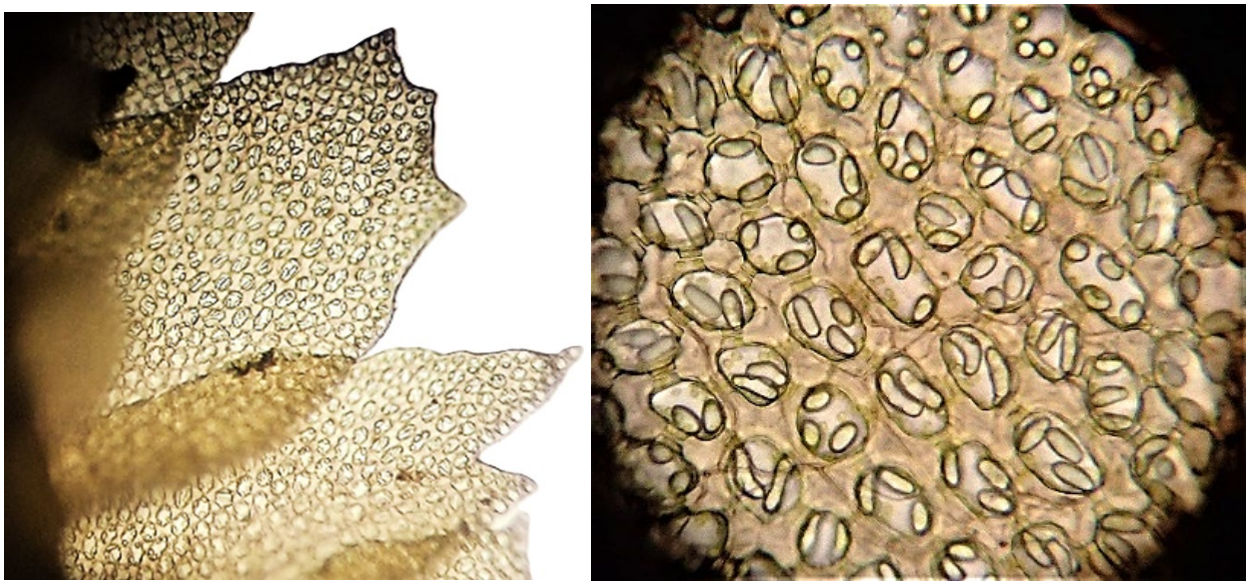
Plants are slender, 1.8-2 mm wide, yellow to pale green or brownish, loosely spreading. Branched, flagelliform branches long and abundant. Stems wiry, stout. Leaves spreading, overlapping, slightly concave, asymmetrically ovate, with falcate upper and straight lower margins, with a long dorsal insertion that extends beyond the stem midline. Leaf apices are truncate, mainly tridentate, but bearing (1)2-3(4) triangular teeth of irregular sizes and shapes on the same plant. Leaf cells have prominent trigones and large, elliptical, and segmented oil bodies. Underleaves are rectangular, laterally rounded, about twice as broad as high, distant to contiguous or slightly imbricate, about twice as broad as the stem; they are convex in their bottom half and concave above. They spread from the stem, often at wide angles; sometimes they can be squarrose. Their apices are truncate and irregular, some are slightly reflexed. Cells have prominent trigones.

Bazzania didericiana. Plants *in situ*. Populations are loosely spreading. Note their pale color, spreading leaves, and abundant, elongate, flagelliform branches. Hono o Nā Pali N.A.R., Kaua‘i, K.R. Wood 17500 (PTBG). Photo courtesy of National Tropical Botanical Garden/Ken Wood.

Left: Plants are more slender and less branched than *B. cordistipula*. Hono o Nā Pali N.A.R., Kauaʻi, K.R. Wood 17500 (PTBG). Photo courtesy of National Tropical Botanical Garden/Ken Wood. Right: Plants up to 2 mm broad. Scale in mm. Saddle area, Hawaiʻi Island, Freire & Judziewicz 22-105 (BISH).

Bazzania didericiana. Dorsal view of plants. Note the nearly transverse and long dorsal leaf insertion; the leaves extend beyond the middle of the stem, obscuring it. Freire & Judziewicz 2022-105, Saddle area, Hawaiʻi Island.

Plants in ventral view. Note the spreading leaves, wiry stems, and broad, reflexed underleaves. Left: Freire & Judziewicz 21-1056 (BISH). Right: Note the slightly imbricate underleaves. Saddle area, Hawai‘i Island, Freire & Judziewicz 22-105 (BISH).



Bazzania didericiana: Left: Bi- and tridentate leaves on the same plant. Note the large trigones in the median leaf cells. Right: Median leaf cells with prominent trigones and elongated, segmented oil bodies. Hawai‘i Island, Freire & Judziewicz 21-1056 (BISH).

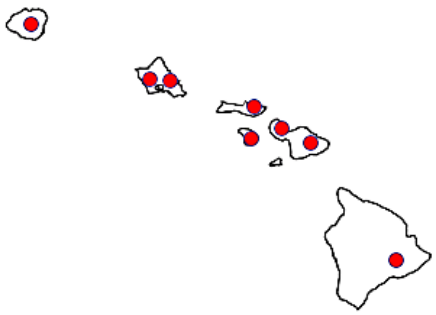
Leaves are asymmetrically ovate, with a falcate upper margin and a straight lower margin. Note the irregular teeth at the leaf apices. Freire & Judziewicz 22-105 (BISH).

Bazzania didericiana. Underleaves are rectangular, broader than high, with rounded sides. Their apices are truncate and irregular, sometimes slightly reflexed. Note the cells with prominent trigones. Freire & Judziewicz 22-105, Saddle area, Hawai‘i Island.

Ventral side of plants showing the rounded, rectangular underleaves. Left: Note the unequal number of teeth on leaf apices and the contiguous to slightly overlapping underleaves. Right: Note the spreading underleaves with truncate underleaf apices. Freire & Judziewicz 2022-105 (BISH).

Bazzania didericiana. Left: Spreading underleaves. Manukā State Wayside, Hawai‘i Island, Freire & Judziewicz 22-856 (BISH). Right: Underleaves spreading widely from the stem (arrow). Saddle area, Hawai‘i Island, Freire & Judziewicz 22-105 (BISH).

5. *Bazzania emarginata* (Steph.) C.M. Cooke. **Endemic.** Possible affinity (Cooke, 1904): *B. fallax* (Sande Lac.) Schiffn., tropical Asia. Found on all major islands (2,100-8,000 ft.), but locally common on some (Lānaʻi) while uncommon on others (Hawaiʻi). Plants are easy to recognize by their falcate, spreading, triangular and non-imbricate leaves, with two small teeth on their acute apices. It resembles *B. didericiana* but the leaves are never tridentate, are narrower and not as imbricate. Leaf apices are acute rather than truncate.



Underleaves are round rather than rectangular and are much smaller. Plants form loose tufts and are often intermixed with other liverworts. They can be up to 3 mm broad, yellow-green to brownish. Stems are fragile-looking to stout, sparingly branched, and with a few flagelliform branches. Leaves are squarrose or nearly so, distant to approximate, asymmetrically ovate, slightly falcate, with acute apices bearing (1)2 small teeth, these are usually parallel and separated by a small sinus, or apices may be pointed, without teeth. Median leaf cells have prominent trigones. Oil bodies are elongated and segmented. Underleaves are round to ligulate, only slightly broader than the stem (about 1.5 times as broad), distant to approximate, slightly to broadly spreading and usually reflexed at their margins. They have rounded to truncate and irregular crenulate apices. Perianths are ovate-cylindrical, stout, projecting from the ventral surface of the stem, in rows of two or three, originating in underleaf axes and nested by them.

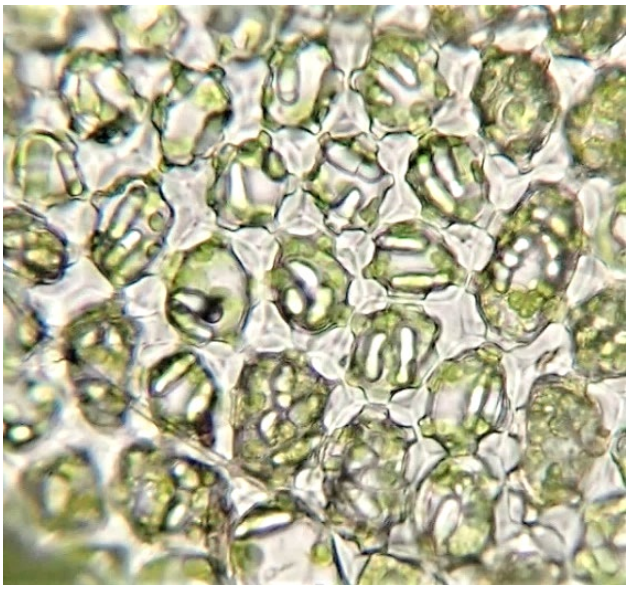
Bazzania emarginata. Left: Plants *in situ*, here with two ventral perianths. Oʻahu, Thomas et al. 382 (BISH), photo by Miles K. Thomas, with permission. Right: Plants can have stout stems. ʻEke Bog, West Maui, Photo by Zach Pezzillo, with permission.

Plants are large, about 3 mm broad. Leaves spreading, flagelliform branches present but not abundant. Note three perianths on ventral side. Scale in mm. Oʻahu, Thomas et al. 382 (BISH), photo by Miles K. Thomas, with permission.

Bazzania emarginata. Plants yellow green with bifid, slightly imbricate and falcate leaves, the underleaves here broadly spreading. Note the slightly concave leaves. Photo by Miles K. Thomas, Oʻahu, with permission.

Plants on dorsal view. Note the leaf insertion that extends to the middle of the stem dorsus. Leaves are ovate, with acute apices and (1)2 small teeth. Freire & Judziewicz 21-1004 (BISH).

Bazzania emarginata. Ventral views. Underleaves distant, small, round, with variable apices, from truncate to rounded, or irregularly crenulate. Saddle area, Hawai‘i Island, Freire & Judziewicz 2021-1004 (BISH).



Bazzania emarginata. Leaf cells are thin-walled, with prominent trigones and elongated and segmented oil bodies. Saddle area, Hawai‘i Island, Freire & Judziewicz 21-1004 (BISH).

6. ***Bazzania inaequabilis*** Steph. **Endemic(?).** This species is difficult to differentiate from *B. brighamii* (an older name) and we suspect that it is perhaps not distinct from it. Although we identified this species from all major islands except Lānaʻi (800-4,000 ft.), we now believe those specimens belong to *B. brighamii*. However, the type specimen of *B. inaequabilis* remains to be studied.

According to Cooke's (1904) discussion, the two species are closely related, and their differences are subtle. Those are mainly in size, leaf shape and leaf cell wall thickness. He describes *B. brighamii* as a smaller plant with fragile stems, the leaves with more parallel margins, and smaller leaf cells with thicker walls than *B. inaequabilis*. However, from his descriptions, we believe a more obvious difference is the tridentate leaf apex for *B. brighamii* but irregularly dentate for *B. inaequabilis*.

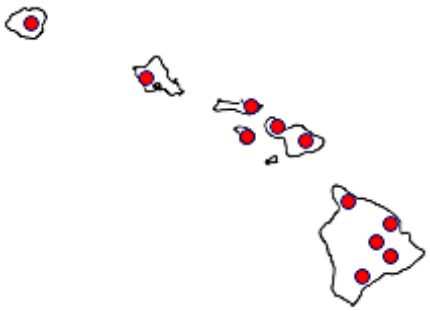
Based on our study of specimens, we see a gradation of character variation that indicates they are likely conspecific. Kevin Faccenda recently collected a specimen in Oʻahu (Faccenda 3423) that fits Cooke's concept of *B. inaequabilis*, with less parallel leaf margins and an irregular number of apical teeth. We do not have this specimen at hand for measurements and recommend a more detailed study of it. Next, we present photographs by Faccenda of his specimen 3423 as posted on iNaturalist. We are presenting them as examples of *B. brighamii* morphotype *inaequabilis*.

Plants form dense prostrate populations on a decorticate log, Oʻahu, Faccenda 3423 (BISH). Photo by K. Faccenda. https://www.inaturalist.org/observations/220210725. With permission.

Plants are prostrate and closely attached to their substrate but sometimes free and ascending. Note the squarrose, subopposite, rectangular leaves, usually imbricate but sometimes contiguous. Faccenda 3423 (BISH) (https://www.inaturalist.org/observations/220210725). With permission.

Bazzania brighamii. B. inaequabilis "morphotype". Left: Plant with squarrose, somewhat falcate, and subopposite leaves. Note the sub- parallel margins and the irregular number or apical teeth. Center: Small, quadrate underleaves with erose apices. They are shortly connate to at least one of the adjacent leaves. Right: Leaf cells are thin-walled, without trigones. Some larger cells seem to be present near the base and in the middle of the leaf. O'ahu, Faccenda 3423 (BISH) (https://www.inaturalist.org/observations/220210725).

7. *Bazzania minuta* (Austin) A. Evans. **Endemic (?).** Tiny; often growing in mixes of other liverworts. Uncommon, although found on all major islands (1,700-6,160 ft.). This species is recognized by its small size, and by its distant, lanceolate leaves. It is closest to *B. baldwinii*, but easy to differentiate from it by its minute rather than pronounced teeth (these may be completely absent in *B. minuta*), by its acute rather than truncate leaf apices and by its very prominent trigones and thick cell walls.



Pócs (1969: 82) compares the widespread tropical Asian species ***Bazzania angustistipula*** N. Kitag. to *B. minuta* and wonders whether the two species are identical; if they are, then *B. minuta* would be the correct name by priority, and this species would not be endemic to Hawai‘i. Populations are sparse, formed by few loose plants, prostrate to ascending. Plants are very small, (0.5)1-1.5 mm wide, yellowish-green, with stout stems protected by very thick 2-3 walled layers of cortical cells; medullar stem cells are also thick. Sparingly branched, with very slender flagelliform branches. Leaves are distant to approximate, spreading, flat to slightly concave, and asymmetrically lanceolate. They have acute apices and are mostly bifid, but some are entire or emarginate; very rarely a leaf may have three irregular teeth. Teeth can be divergent to parallel. The median leaf cells have very large trigones and thickened walls. Marginal cells form a border of smaller cells with thick walls. The underleaves are small, equal or only very slightly wider than the stem, rounded, distant, truncate to emarginate to slightly bifid, with small cells with thick walls.
According to Cooke (1904), leaf cells are thin-walled and have small trigones. The plants we identified as *B. minuta* have large trigones and thick cell walls but fit Cooke’s description otherwise.

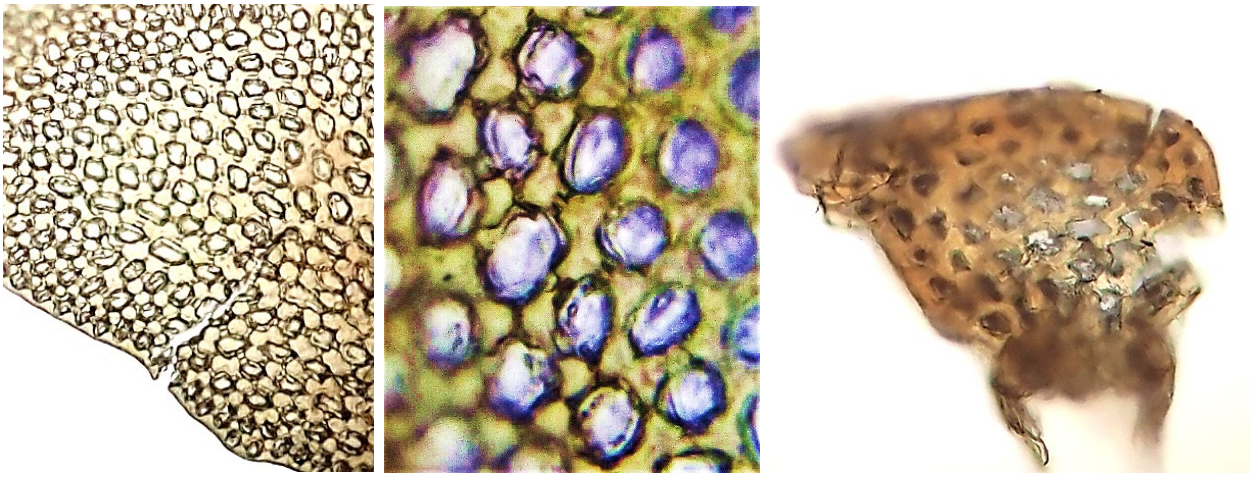
We observed gemmae-like structures on the leaf surface of some of our photographs of Oppenheimer H32342 ‘Eke Bog, Maui (BISH). Unfortunately, we do not have the specimen at hand to confirm it. We cannot exclude that these may be foreign structures. No gemmae are reported for the genus *Bazzania* so far.

Bazzania minuta. Plants form sparse populations, loosely attached to their substrate. They are seemingly unbranched. ‘Eke Bog, West Maui, Oppenheimer H32342 (BISH). Photo by A.V. Freire.

Plants have distant leaves, stout stems and are small, slightly over 1mm wide (left). Scale in mm. ‘Eke Bog, West Maui, Oppenheimer H32342 (BISH). Photos by A.V. Freire.

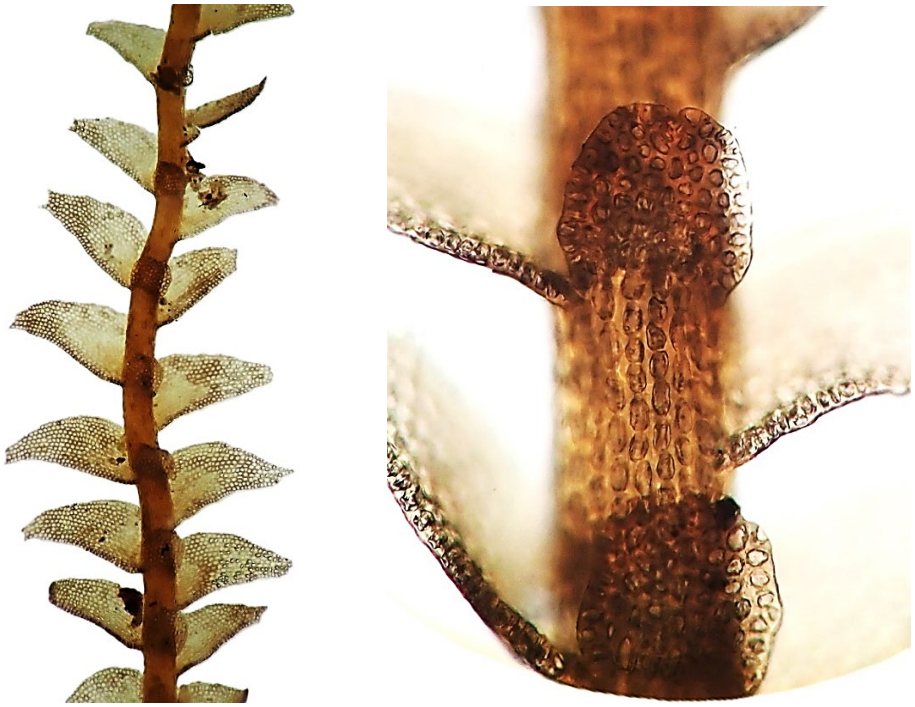
Bazzania minuta. Plants are small, usually with bifid leaves. Note the falcate upper margins and the asymmetrically lanceolate leaf shape. Note the very stout and wiry stems. Haleakalā, Maui, Stemmermann 7037 (HAVO). Photos by A.V. Freire.

Rarely a three toothed leaf may be present (arrow). Leaf surfaces appear to have gemmae (?), but this requires confirmation. ‘Eke Bog, West Maui, Oppenheimer H32342 (BISH). Some leaves may have rounded, entire apices (right), Stemmermann 7037 (HAVO). Photos by A.V. Freire.



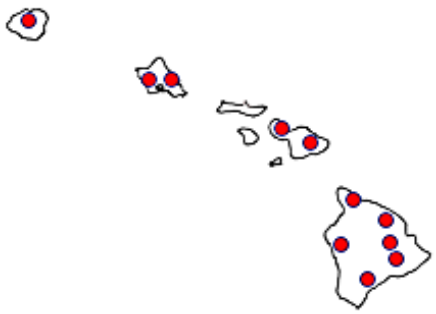
Bazzania minuta. Left and center: Leaf cells have large trigones and a border of smaller cells with very thick outer walls. Right: Stem cross section showing the very thickened cortical and medullar cell walls. Haleakalā, Maui, Stemmermann 7037 (HAVO). Photos by A.V. Freire.

Dorsal view of plant. The arched leaf insertion extends to the midline of the stem. Stemmermann 7037 (HAVO). Photos by A.V. Freire.



Bazzania minuta. Plant in ventral view. Left: Underleaves are distant, small, only slightly broader than the stem. Right: Underleaves are rounded, with entire to emarginate apices and small, thick-walled cells. Note the stem epidermal cells with thick walls. Haleakalā, Maui, Stemmermann 7037 (HAVO). Photos by A.V. Freire.

9. *Bazzania nuuanuensis* C.M. Cooke. **Endemic.** This species is known from Kauaʻi, Oʻahu, Maui, and Hawaiʻi Island (1,700-6,100 (-8,000?) ft.); on the latter island it is common in wet forests in Hawaiʻi Volcanoes National Park. Also reported from 7,000-8,000 ft. on Maui (Miller & Lamberton 4280, MU), and 7,800 ft. on Mauna Loa, Hawaiʻi Island (Miller & Lamberton 5258, MU), but these collections not yet examined by us. It can be easily distinguished by its broad, blunt to rounded, entire rather than toothed leaves, although sometimes a vague tooth or two are present. It seems possible that the Oʻahu, Maui and Hawaiʻi populations may not be conspecific. This may be a species complex.

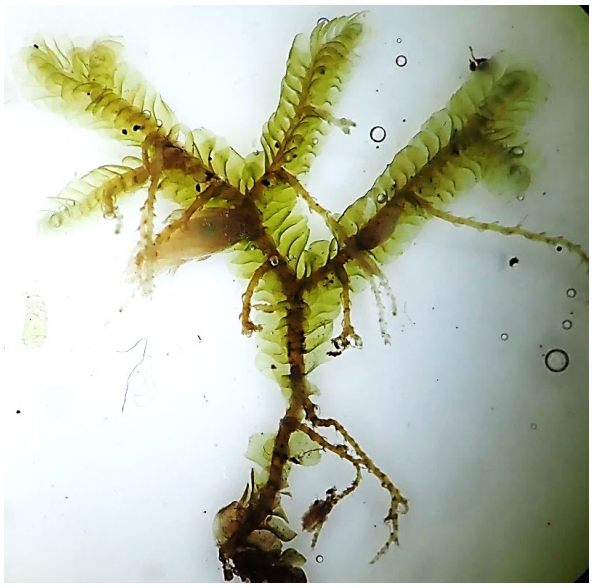


Populations form loose tufts that project slightly from their substrate. Plants are green, and slightly over 2 mm wide. Stems are stout, frequently branched and have abundant flagelliform branches that often have secondary branching and abundant rhizoids. Leaves are large, flat, squarrose, prostrate, asymmetrically ovate, slightly falcate on the upper margin, imbricate, with irregular-undulate margins and truncate to rounded apices. Sporadically, one to few irregular apical teeth may be present. Median leaf cells are elongate, with thick walls and prominent trigones; a vittate area with larger cells is present close to the base. Leaves are bordered by a layer of smaller, thick-walled quadrate cells. Leaf cell walls are finely prorulose. Underleaves are large, 2(3) times broader than the stem, overlapping, rounded, auriculate, with round to truncate apices, these irregularly undulate to emarginate. Perianths ventral, brown, ovate cylindrical, large.

Bazzania nuuanuensis. Population projecting from tree bark. Volcano, Hawaiʻi Island, Freire & Judziewicz 21-169 (BISH).

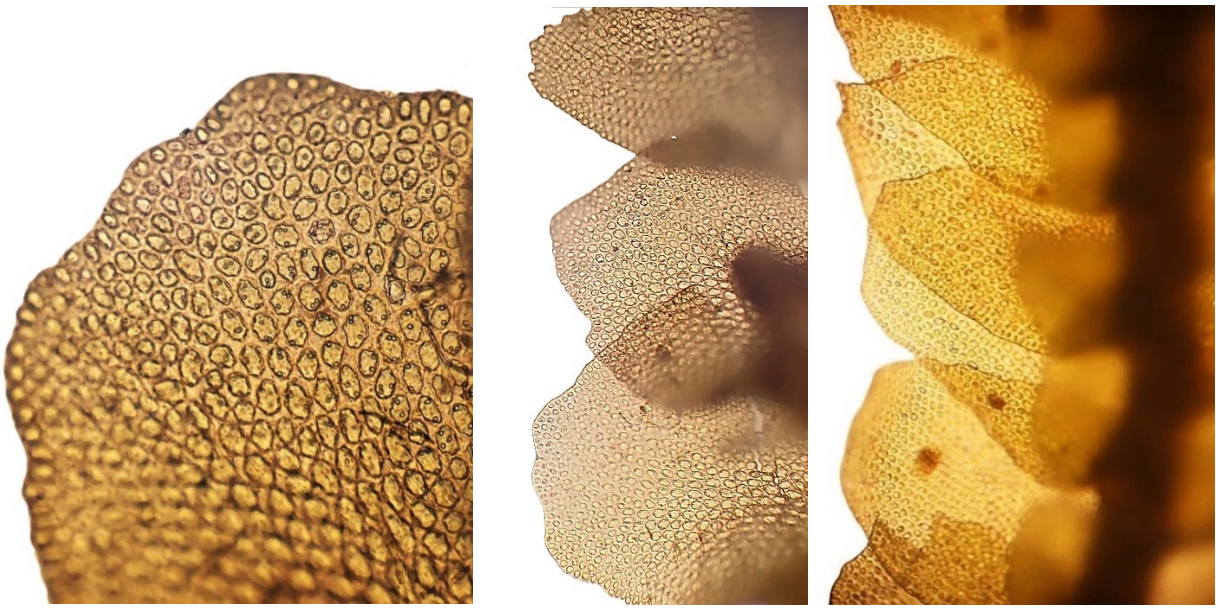
Plants flattened, with imbricate, squarrose leaves. Volcano, Hawa‘i Island, Freire & Judziewicz 20-510 (BISH).

Bazzania nuuanuensis. Plants are slightly over 2 mm wide, with flat and imbricate leaves. Scale in mm. Hawai‘i Island, Freire & Judziewicz 23-366 (BISH).

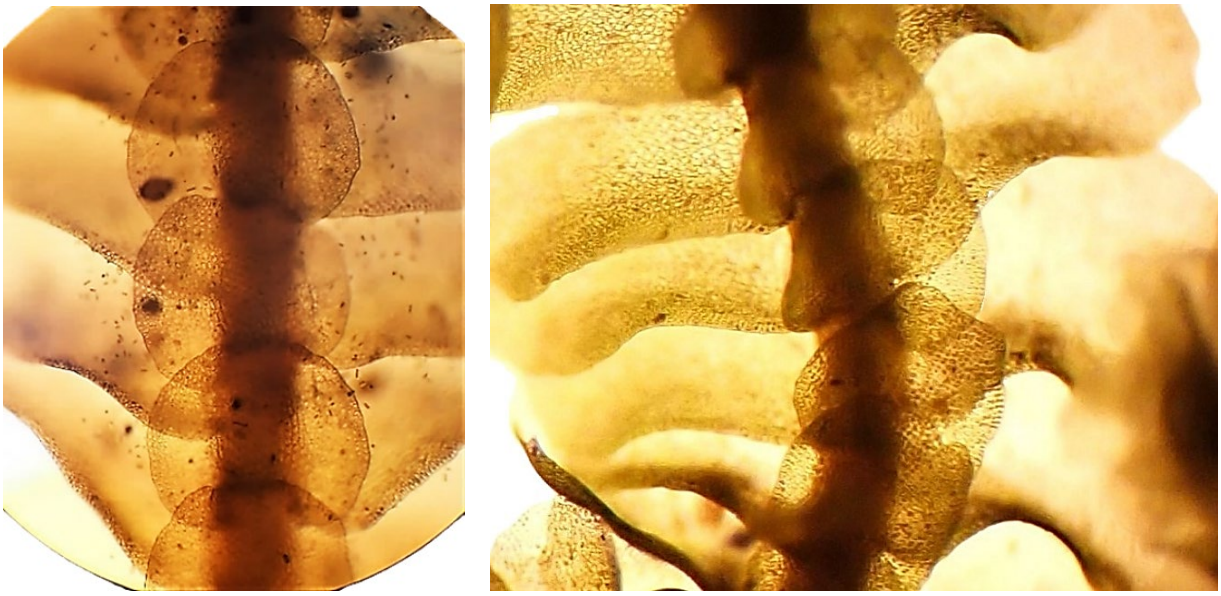


Left: Ventral side of plant with abundant flagelliform branches, some of which exhibit secondary branching. Leaves are spreading and imbricate. Note the large perianth. Hawai‘i Island, Freire & Judziewicz 22-736 (HAVO). Right: Examples of leaf apex variation within a plant. Freire & Judziewicz 23-366 (BISH).,

Bazzania nuuanuensis. Leaves are asymmetrically ovate, often with a truncate, irregularly toothed apex and a vittate area of larger cells towards the base. Upper margin is slightly falcate. Hawai‘i Island, Freire & Judziewicz 23-366 (BISH).

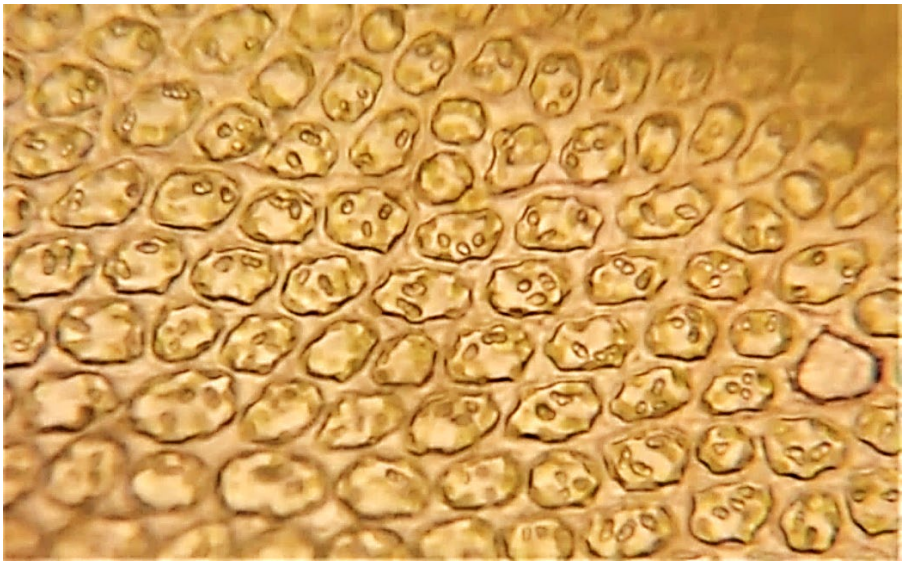


Left: Leaves are bordered by a layer of small and square cells. Center and Right: Variation of leaf apices. Left and center: Volcano, Hawai‘i Island, Freire & Judziewicz 22-557 (HAVO). Right: Occasional teeth are observed in some plants. Hakalau Forest N.W.R., Hawai‘i Island, Freire & Judziewicz 23-275 (BISH).



Bazzania nuuanuensis. Large, round, and imbricate underleaves with auriculate base. Top: Freire & Judziewicz, Volcano, Hawai‘i Island. Bottom: Hakalau Forest N.W.R., Hawai‘i Island, Freire & Judziewicz 23-280 (BISH).

Flagelliform branches sometimes have abundant rhizoids. Volcano, Hawai‘i Island, Freire & Judziewicz 22-557 (HAVO).

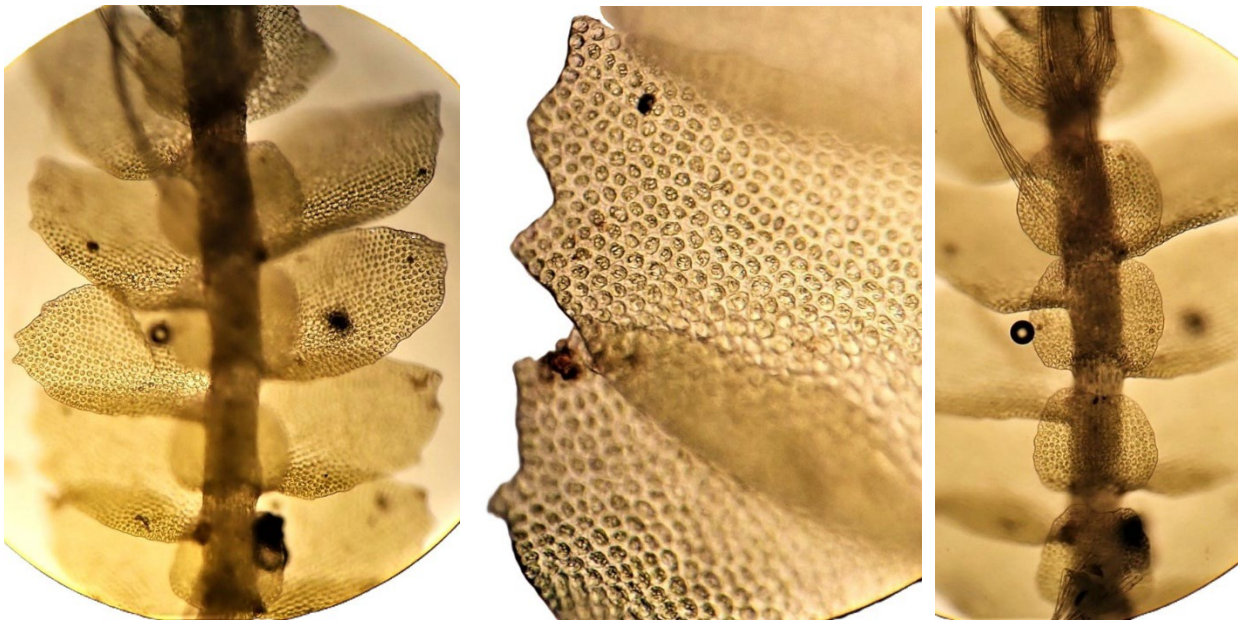


Bazzania nuuanuensis. Leaf cells with trigones and thick walls. Oil bodies elliptical, small and segmented. Hawai‘i Island, Freire & Judziewicz 23-366 (BISH).

***Bazzania* cf. *nuuanuensis*:**

The specimen below was collected Waikamoi, Preserve, Haleakalā, Maui, by Freire, Judziewicz, Oppenheimer & Pezzillo 23-161 (BISH). It resembles *B. nuuanuensis*, excepting that the leaf cells are thick-walled and do not have consistently prominent trigones. The rest of the characters seem to fit with our concept for this species. However, our study of this specimen was brief, a more detailed analysis is recommended.

Plants are about 2 mm wide. Leaves are spreading and overlapping, with truncate or some pointed apices. Scale in mm.



Bazzania cf. *nuuanuensis*. Left: Leaves either lack teeth or may be irregularly toothed, these poorly defined. Center: Leaves may have 2-3 teeth. Leaf cells are thick-walled and do not have prominent trigones. Right: Underleaves are round, over twice the stem width, truncate, and sometimes emarginate. Thick clusters of long rhizoids are found on some underleaf axils. Freire et al. 23-161 (BISH).

Bazzania* aff. *nuuanuensis, A.V. Freire & Judz. Based on Neal & Hartt 830 (BISH), "Laumaia", Hawai'i Island, "6,000-6,500 ft.", 17 August 1935. This is probably Laumai'a (now deforested), on the eastern slopes of Mauna Kea (hence the specific epithet), at about 19°46'N, 155°21.5'W, at 6,500 ft. A large, high elevation species with very crowded sinuous leaves, roughly like a sidewise S in profile; leaf apices pointed.

Plants are robust, 2-2.5 mm wide, with stout stems and at least some lateral branches, and ventral flagelliform branches. Leaves are strongly imbricated, asymmetrically ovate, with sinuous lower margins and arched upper margins that overlap, obscuring the dorsal side of the stem. Leaf apices are mainly pointed, but a few are truncate and irregularly toothed. The leaf cell walls are quite thick, and large trigones are present. Most cells are quadrate but a vittate region of large, elongated cells is present. A border of small quadrate cells with thick walls is present but not clearly defined. Underleaves are rounded, large, about 3 times the stem width, overlapping, with either emarginate or truncate-crenate apices.

Our concept is based on limited dry plant material. We think this collection is similar to *B. nuuanuensis* and likely represents an extreme of this species. The main differences are the more isodiametric leaves, the more sinuous lower leaf margins, stouter stems, and perhaps also the larger plant size. We cannot compare branching. All pictures below are from Neal & Hartt 830 (BISH), photos by A.V. Freire.

Bazzania aff. *nuuanuensis*. Plants are robust, with stout stems and imbricated leaves with sinuous lower margins. Note that a few basal leaves (left) have truncate and erose-dentate apices. Scale in mm. Hawai'i Island, Neal & Hartt 830 (BISH). Photo by A.V. Freire.

Plant in dorsal view. Leaves overlap, obscuring the stem dorsal surface. Neal & Hartt 830 (BISH); photo by A.V. Freire.

Bazzania aff. *nuuanuensis*. Leaves with sinuous lower margins and pointed apices. Note flagelliform branch (left). Hawai‘i Island, Neal & Hartt 830 (BISH). Photos by A.V. Freire.

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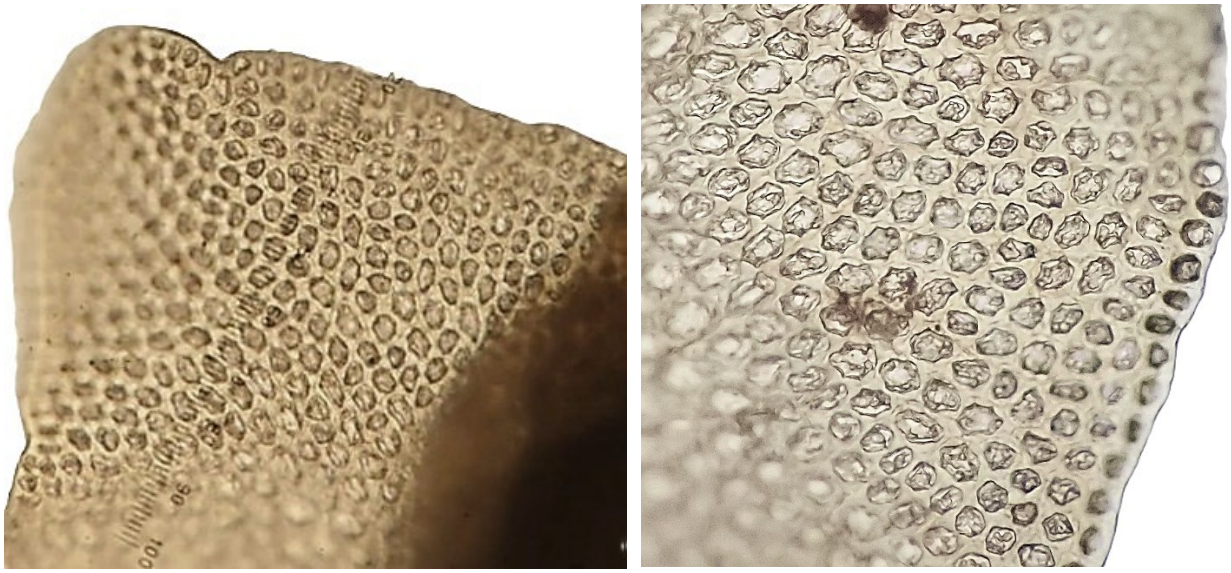
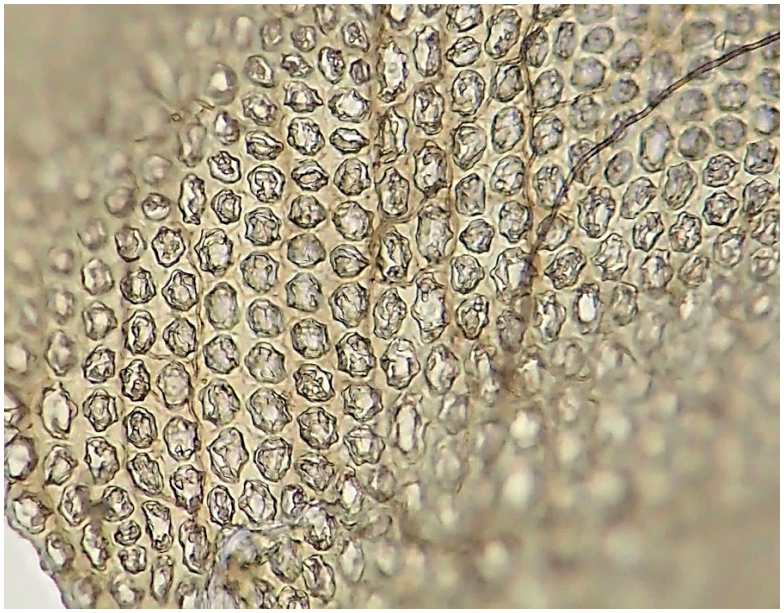
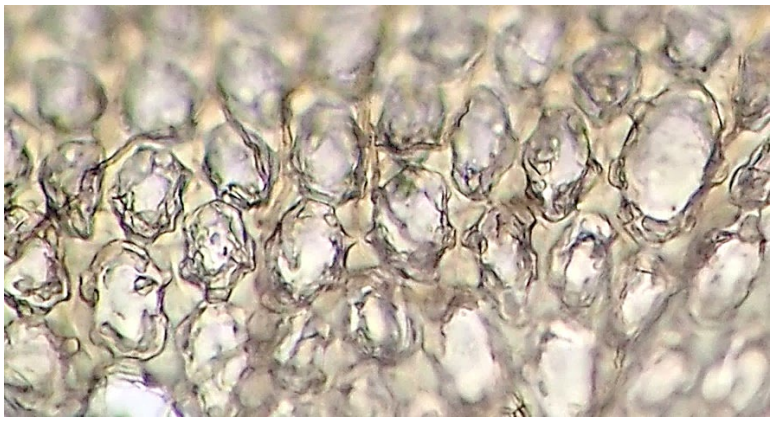
Leaves are asymmetrically ovate, with sinuous (wavy) lower margins. Note the irregular apices and vittate basal-central region. Neal & Hartt 830 (BISH), photos by A.V. Freire.



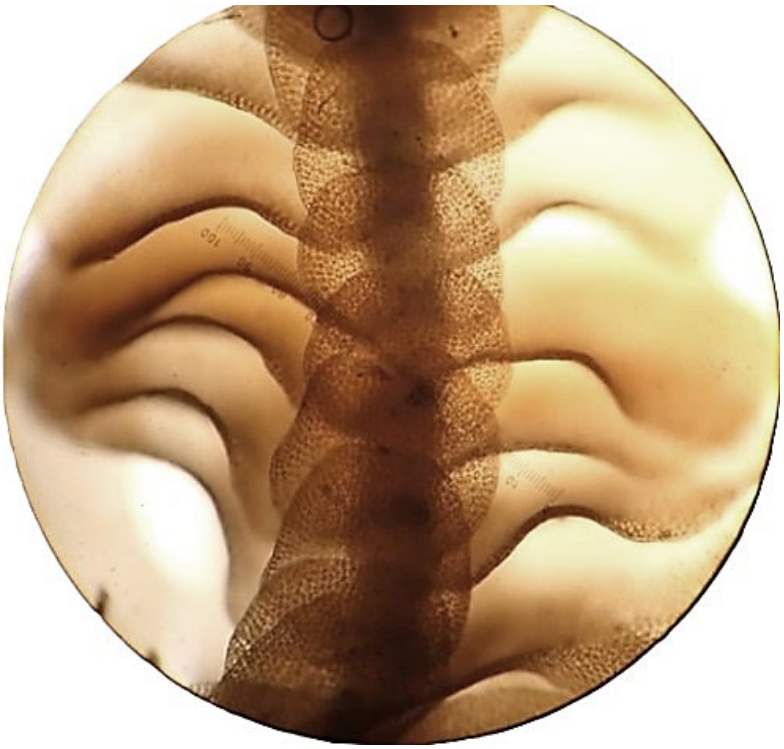
Bazzania aff. *nuuanuensis*. Apical and lateral leaf regions have quadrate to isodiametric cells with thick walls and trigones. Note the border of small quadrate cells (right). Hawai‘i Island, Neal & Hartt 830 (BISH). Photos by A.V. Freire.



Lateral isodiametric cells and central vittate region. Note prominent trigones. Neal & Hartt 830 (BISH), photo by A.V. Freire.



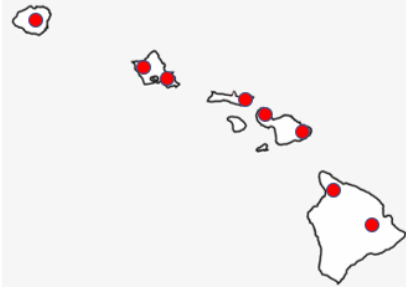
Bazzania aff. *nuuanuensis*. Detail of vittate region cells. Note the elongated cell cavities and prominent trigones. Hawai‘i Island, Neal & Hartt 830 (BISH). Photo by A.V. Freire.



Underleaves are orbicular, strongly overlapping and over three times as broad as the stem. Neal & Hartt 830 (BISH), photo by A.V. Freire.

Bazzania aff. *nuuanuensis*. Underleaves are rounded, with emarginate apices (left), but some are truncate with irregularly erose-crenate apices (right). Note threads of fungal(?) associate. Hawai‘i Island, Neal & Hartt 830 (BISH). Photo by A.V. Freire.

10. *Bazzania patens* (Mont.) Trevis. Found on Kauaʻi, Oʻahu, Maui and Hawaiʻi (1,000-4,000 ft.). **Endemic.** Possible affinity (Cooke, 1904): *Mastigobryum cubense* (= *B. pycnophylla* (Taylor) Trevis. var. *cubensis* (Steph.) Pócs), West Indies. A large, reportedly terrestrial species with arching, elongate, tridentate leaves and quadrate underleaves scarcely wider than the stem; leaf trigones are absent.



Plants are large, over 3 mm wide. Reported as prostrate. Stems stout. Leaves are seemingly caducous (but we just observed herbarium specimens that may have been damaged), contiguous to slightly imbricate, spreading, strongly falcate, with dorsal insertion shorter than the stem midline, more than three times longer than broad, with parallel margins, slightly concave, with truncate apices bearing 3(4) asymmetrical and irregular teeth. Leaf cells are quadrate, usually with evenly thickened walls, but small trigones may be present. Some plants have an off-center vittate region in the lower half of the leaf. Underleaves are distant, slightly reflexed to squarrose, their line of insertion usually slightly oblique, small, as broad as the stem or only slightly broader, quadrate to rectangular, with irregularly toothed to laciniate or erose and truncate apices.

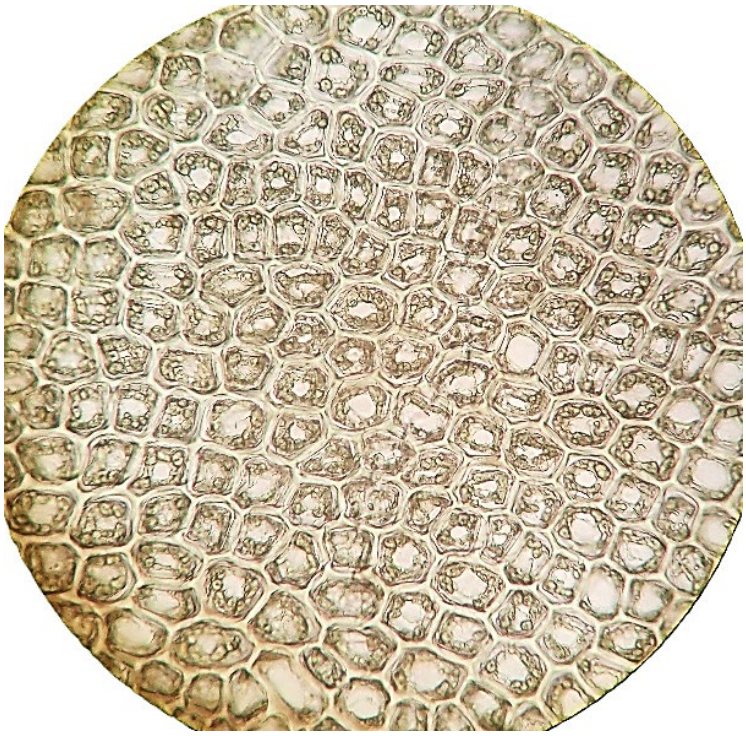
On Hawaiʻi Island (Judziewicz et al., 2025b) it is only known from Miller & Lamberton 5207 (BISH, MU), 5219 (MU), and 5221 (MU). They were all collected in 1953 from the Stainback Highway, 12 miles below Kūlani; that would be about at the junction with Kūlani Road, at an elevation of 1,700 ft. We searched the location for it unsuccessfully in 2022. The forest is rather degraded in the area, as in many unmanaged Hawaiian forests. Likely, its terrestrial habitat is threatened by feral ungulates. Miller & Lamberton 3610 (MU) from Molokaʻi, requires confirmation.

Bazzania tridens, an Asian species (Inoue, 1974a: 24-25; Khotimperwati et al., 2018) with wider, more imbricate leaves was identified from Oʻahu (from Puʻu Kaʻala and Mānoa Falls) by Z. Iwatsuki (1544a and 2108, BISH); however, we consider these collections to be *B. patens*. See also notes under *B. brighamii*.

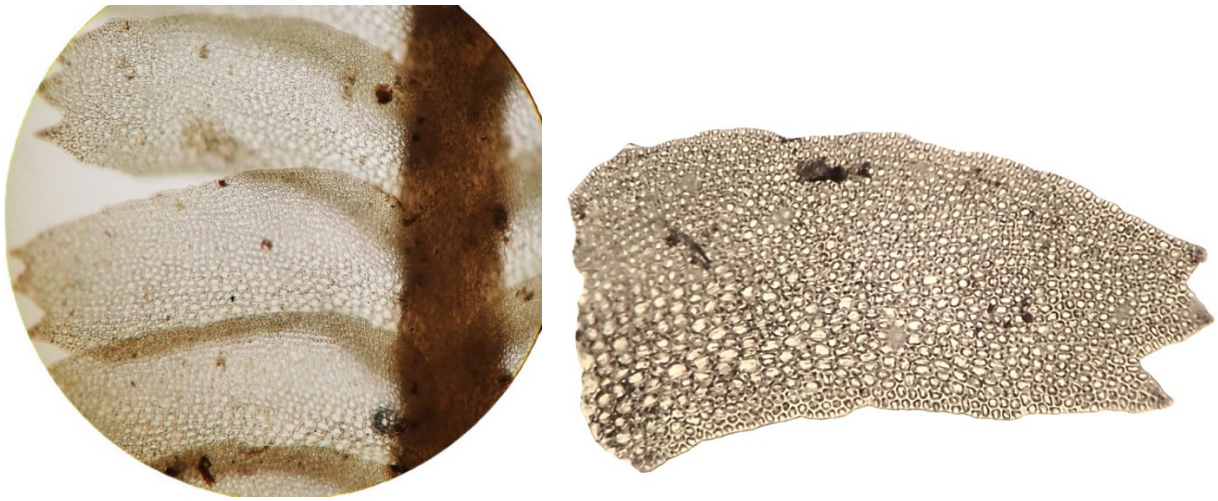
Bazzania patens. Scales in mm. Plants are large. Note bare stem section seeming to indicate that leaves may be caducous. Left: Cooke s.n., Sept. 1898, Kilohana, Kauaʻi (BISH). Right: Oʻahu, Fosberg 12312 (BISH). Photos by A.V. Freire.

Leaves are strongly arching, boomerang-like, contiguous to slightly imbricate, with parallel lateral margins; usually with three apical teeth on truncate apices. Note the lack of prominent trigones. Left: Kilohana, Kaua‘i, Cooke s.n., Sept. 1898 (BISH). Right: Miller & Lamberton 5207 (MU). Photos by A.V. Freire.

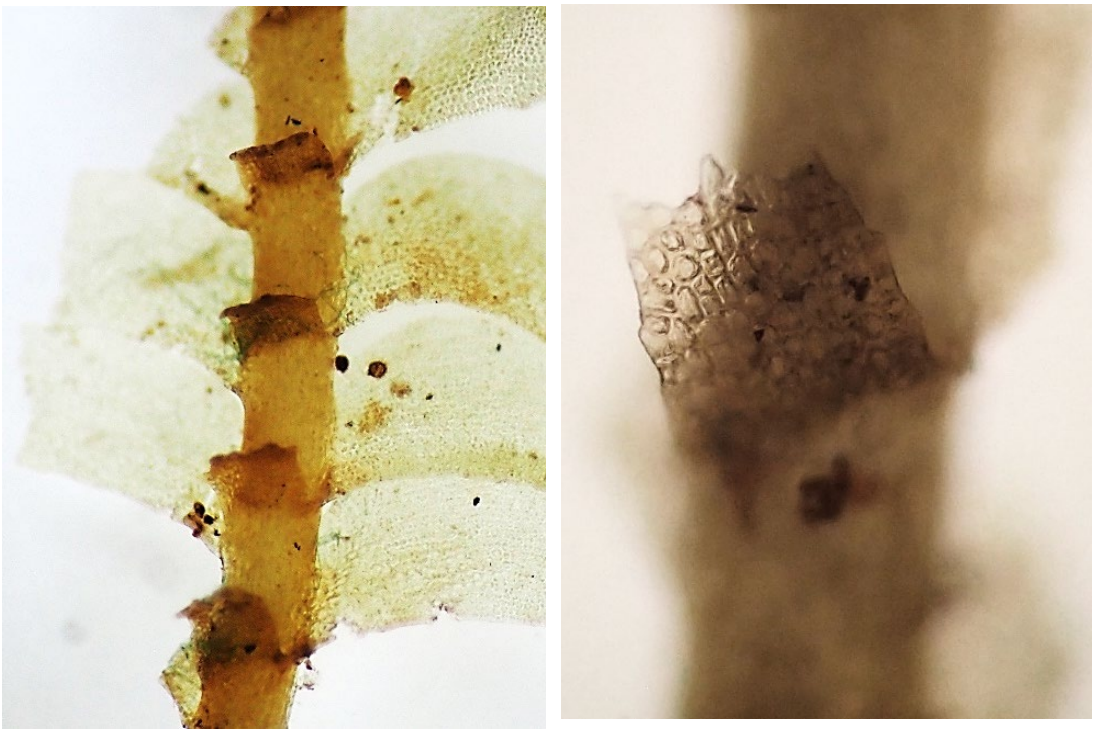
Bazzania patens. Leaf apices showing irregular teeth. Picture to the left exemplifies the less frequently observed 4-toothed leaf. Note the small trigones in the last picture. East of Kūlani Prison, Hawai‘i Island, Miller & Lamberton 5207 (MU). Photos by A.V. Freire.



Median leaf cells have moderately and evenly thickened walls, usually without trigones. East of Kūlani Prison, Hawai‘i Island, Miller & Lamberton 5207 (MU). Photo by A.V. Freire.



Bazzania patens. Left: Plant, dorsal view. Note the slightly imbricate leaves. Right: Leaf showing the different sizes of cells; smaller above and in the lower marginal region, larger in the basal bottom half of the leaf, forming a vittate region. O‘ahu, Fosberg 12312 (BISH). Photos by A.V. Freire.

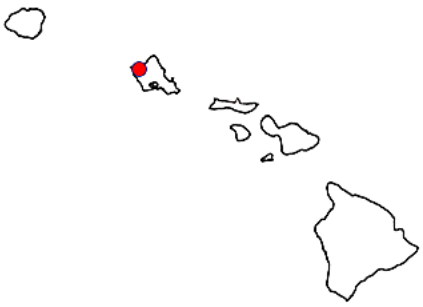


Plant in ventral view. Underleaves are small, quadrate and reflexed. Note the truncate, dentate to laciniate apices. East of Kūlani Prison, Hawai‘i Island, Miller & Lamberton 5207 (MU). Photos by A.V. Freire.

Bazzania patens. Plant with antheridial branches on the ventral side (arrows). Saddle area, Hawai‘i Island. Freire and Judziewicz 23-376 (BISH). Photos by A.V. Freire.

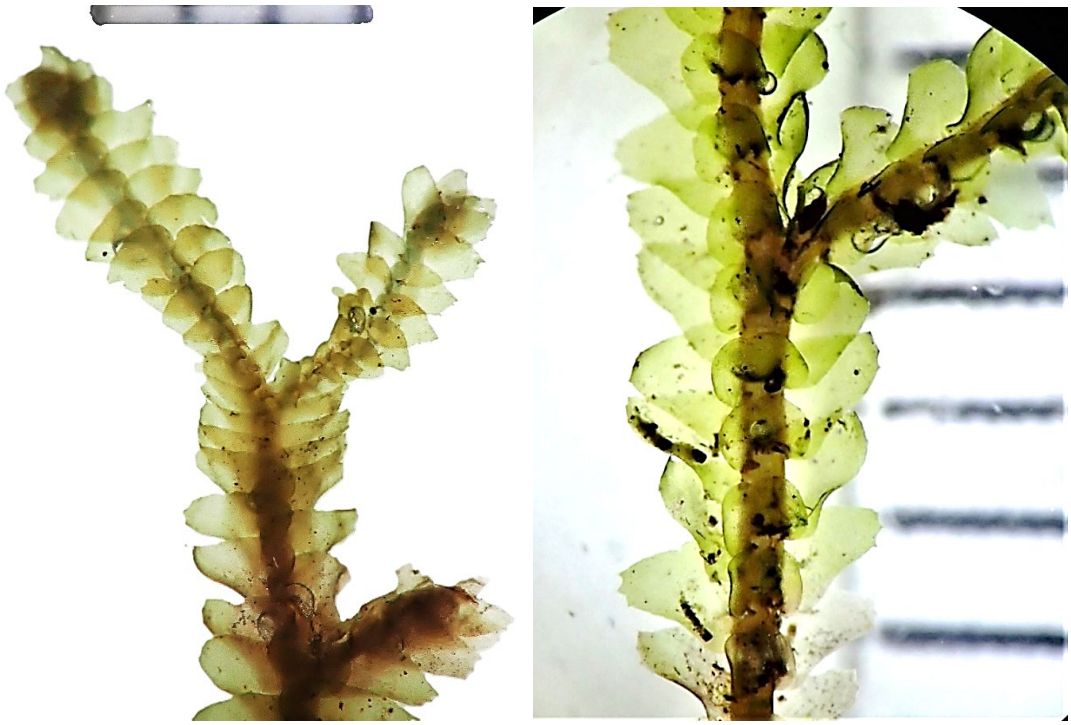
Bazzania patens. Alakaʻi Preserve, Kauaʻi, 3,900 ft., Faccenda 3919 (BISH), photo by K. Faccenda (https://www.inaturalist.org/observations/254800669), with permission.

11. *Bazzania* cf. *praerupta* (Reinw., Blume & Nees) Trevis. Indigenous. This entry is based on a specimen collected on Pu‘u Ka‘ala, O‘ahu (3,950 ft.) by Thomas et al. (including Freire and Judziewicz), BISH. We initially reported it as *B. hookeri* (Judziewicz & Freire, 2023: 166) because of its conspicuously auriculate underleaves, and its tridentate leaves. In the same report, we commented on the very broad leaf bases and leaves that are as wide as long. Based on this comment, S. R. Gradstein (pers. comm.) suggested this is likely *B. praerupta*, a variable paleotropical species, sometimes confused with *B. hookeri* (with leaves at least 1.5 times longer than wide)



(pers. comm., 2023). We agree that this specimen more closely resembles *B. praerupta* but with some differences that are discussed at the end of this treatment. We see a strong resemblance between this species and our *Bazzania* species 2. The main difference is in the non-auriculate or only slightly auriculate underleaves in species 2. *Bazzania praerupta* is included in Staples & Imada (2006) as occurring on five islands, based on Miller (1983). Other authors (Long & Grolle, 1990; Mizutani & Chang, 1986: 431 and Khotimperwati et al., 2018) also report this species for Hawai‘i but do not cite any vouchers. The Hawaiian specimen (Thomas et al. 524a) consists of large plants, about 2.5 mm wide, green, frequently branched, with stout stems and flagelliform branches. Leaves are ovate-triangular, imbricate, overlapping, spreading, concave, with very broad bases, as broad as the leaf is long, or less than 1.5 times as long as broad. Dorsal leaf insertion crosses beyond the midline of the stem. Leaf apices are truncate, with (1-2)3(4) variably shaped and sized teeth; leaf cells are quadrate, with small trigones in the middle, but larger trigones towards the mid-base section. Oil bodies are elliptical and segmented. Underleaves are distant to imbricate, about twice as broad as the stem, rounded, clearly auriculate at their base, and truncate, emarginate, to erose at the apex. All pictures below from Thomas et al. (including Freire & Judziewicz) 524a, 9 Nov. 2022, Pu‘u Ka‘ala, O‘ahu.

Plants are large with stout stems and stout flagelliform branches. Leaves are spreading and imbricate, underleaves are round and distant to imbricate. Scales in mm. Photos by A.V. Freire.



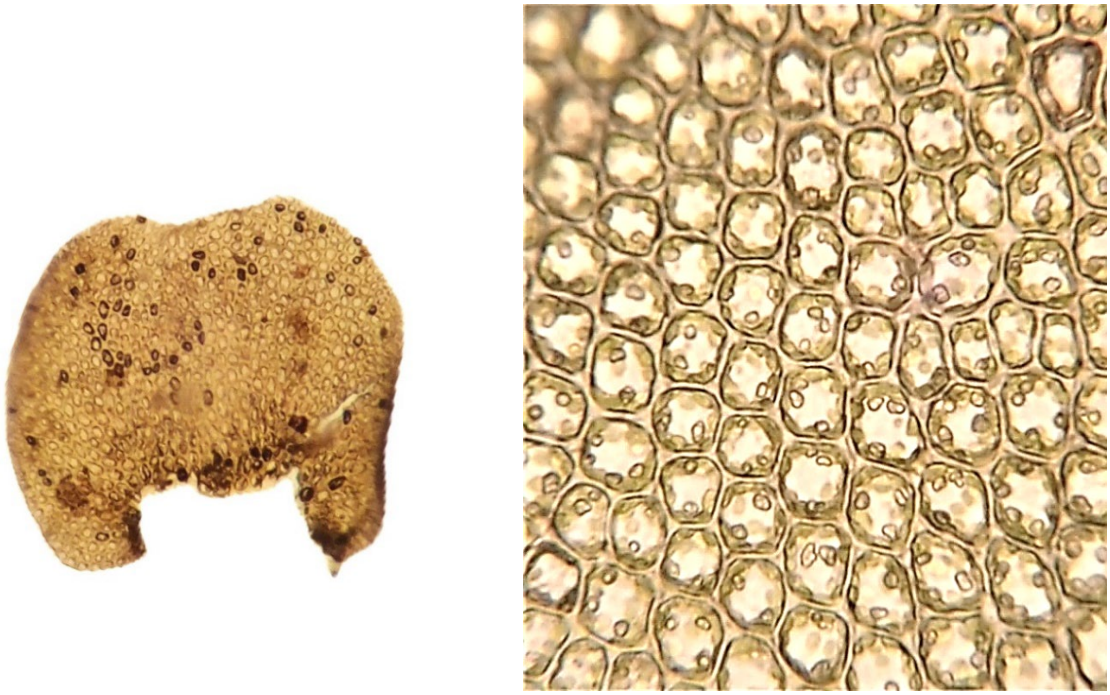
Left: Plant, dorsal view. Leaves have a long dorsal insertion. Right: Plant, ventral view. Note auriculate and rounded underleaves. Thomas et al. 524a (BISH). Photos by A.V. Freire.

Bazzania cf. *praerupta.* Ventral side of plants showing the overlapping to distant underleaves, clearly auriculate at their base. Pu‘u Ka‘ala, O‘ahu, Thomas et al. 524a (BISH). Photos by A.V. Freire.

Leaves are imbricate, broad at their base, with truncate apices, usually with 3 teeth, and variable in size and shape. Note the lower left leaf with 4 teeth (arrow). Thomas et al. 524a (BISH). Photo by A.V. Freire.

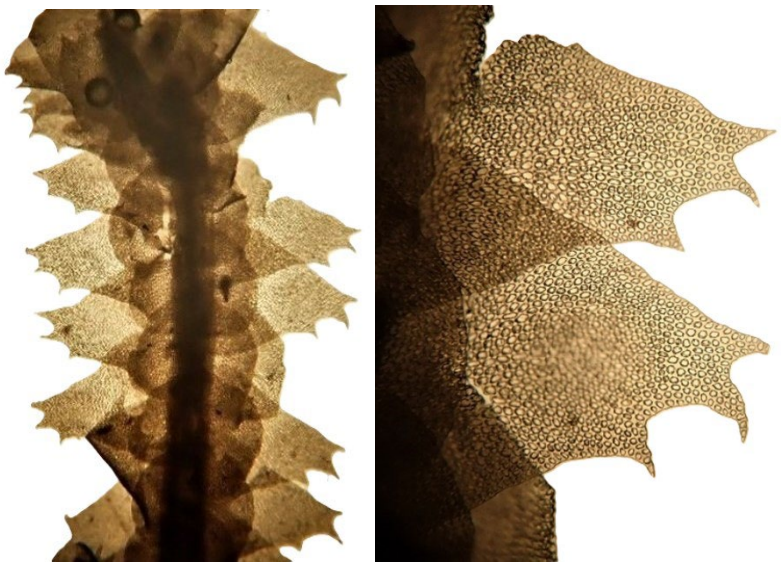
Bazzania cf. *praerupta.* Examples of leaves with broad bases and variable size and shape of teeth. Note the poorly-developed vittate region with larger trigones. Puʻu Kaʻala, Oʻahu, Thomas et al. 524a (BISH). Photo by A.V. Freire.

Examples of leaves with variable apices. Thomas et al. 524a (BISH). Photos by A.V. Freire.

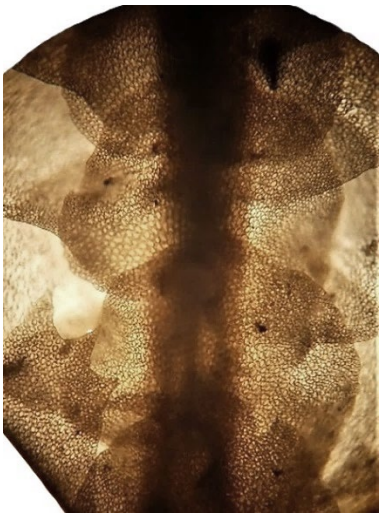


Bazzania cf. *praerupta*. Left: Example of rounded, auriculate and truncate underleaf. Right: Middle leaf cells are quadrate, with slightly thickened walls and small trigones. Note the elliptical and segmented oil bodies. Pu‘u Ka‘ala, O‘ahu, Thomas et al. 524a (BISH). Photos by A.V. Freire.

We did not study the type of *B. praerupta*, but did examine a specimen collected and identified by Hiroshi Inoue s.n. from Malaysia (BISH) for comparison. This specimen has triangular leaves with a very broad base, nearly as broad as the leaf is long; leaf teeth are asymmetrical and positioned along the lower margin of the leaf, and the teeth are rather long, unequal, and clawlike; the underleaves are large, over 3 times as broad as the stem, orbicular, and clearly auriculate. See pictures below from Malaysia, Inoue s.n. (BISH).



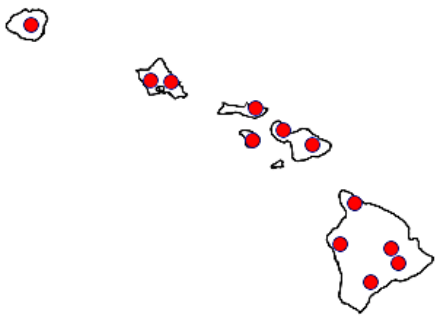
Leaf bases are very broad, note the oblique apices with large clawlike teeth. Photos by A.V. Freire.



Bazzania praerupta. Underleaves are round, auriculate, over four times as broad as the stem. Photos by A.V. Freire.

When comparing the Hawaiian collection with the Inoue specimen, we can see similarities in the leaf shape with broad bases and proportions (about as long as wide), also in the auriculate and rounded underleaves. However, we can see differences in the leaf apices (truncate versus oblique) and size of teeth; also, underleaves are much larger in the Inoue specimen. Since *B. praerupta* is a variable species, perhaps the Hawaiian specimen fits within this species and represents a different morphological expression of it…or perhaps it is a new species closely related to *B. praerupta* (?). More work is needed.

12. *Bazzania sandvicensis* (Steph.) Steph. **Endemic (?).** Rare. Reported for all major islands (1,500-6,000 ft). We suspect that most are based on misidentifications of *B. cordistipula* with which *B. sandvicensis* is very easily confused, and we think it likely that the two species are conspecific. Cooke (1904), reports that *B. sandvicensis* differs from *B. cordistipula* in its less dichotomous branching; its narrower and barely overlapping leaves; its smaller and non-overlapping underleaves; and in the thicker leaf cell walls with smaller trigones.



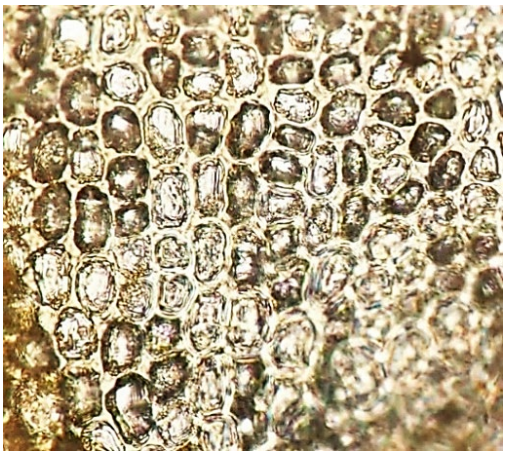
We have observed considerable variations in size of plants and leaves, as well as in leaf and underleaf imbrication within and among populations for several species in the genus *Bazzania*. Based on this, we consider the branching and cell wall architecture the most meaningful differences between the two species. However, we have studied leaves with and without bulging trigones on the same plant in specimens we identified as *B. sandvicensis*. Branching may change with habitat conditions (*B. sandvicensis* is seemingly terrestrial).

Likely, this species is a terrestrial expression of *B. cordistipula*. The orderly arrangement of leaf cells in rows, with thickened walls and small trigones in at least some leaves on each plant, is a good way to recognize this morphotype.

We encountered only a few populations in the field. We collected it on soil and rock walls and have seen herbarium specimens collected on humus or soil. We think this may be the reason this morphotype is difficult to find. As mentioned in our introduction, ungulates (pigs, also red deer on Maui Nui) are extremely detrimental to terrestrial liverworts in Hawai‘i.

Plants are green, slightly over 2 cm long and 2 mm wide or a bit wider. The leaves are ovate-triangular, slightly decurrent on the lower (ventral) margin, and tridentate with triangular teeth. Leaf cells are squarish, thick-walled, in orderly rows; small trigones are present, and they are larger and more conspicuous towards the leaf base. Plants may have some leaves with bulging trigones as in *B. cordistipula*. Underleaves are round, contiguous to slightly imbricate, about 2-2.5 times the stem width.

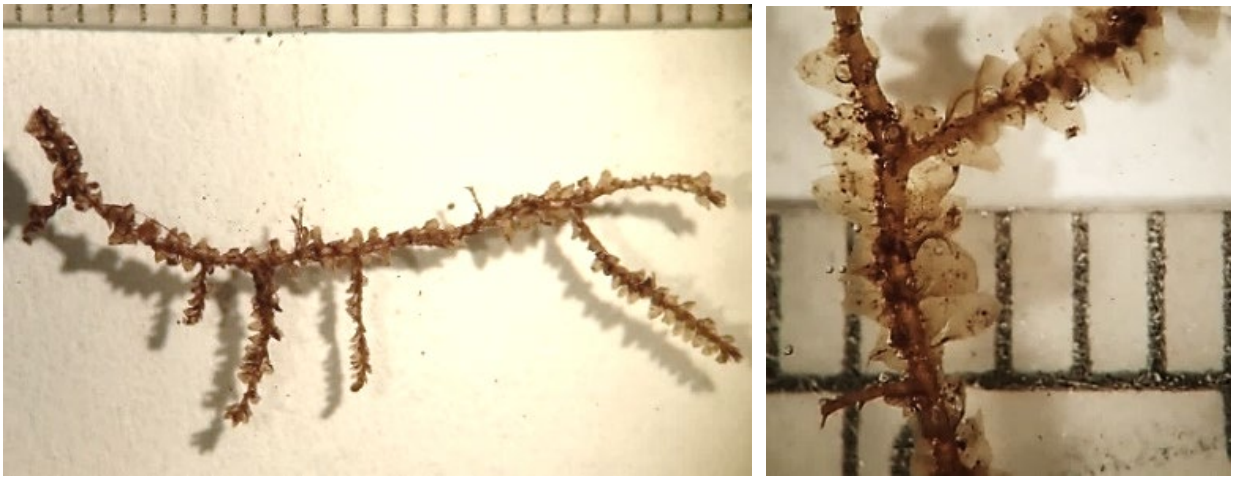
Left: Plants resemble *B. cordistipula* but are smaller, and dichotomous branching is uncommon. Right: Underleaves distant to slightly imbricate, the leaves with three teeth. Alaka‘i region, Kaua‘i, Ma 14-5915 (PTBG). Photos by A.V. Freire.



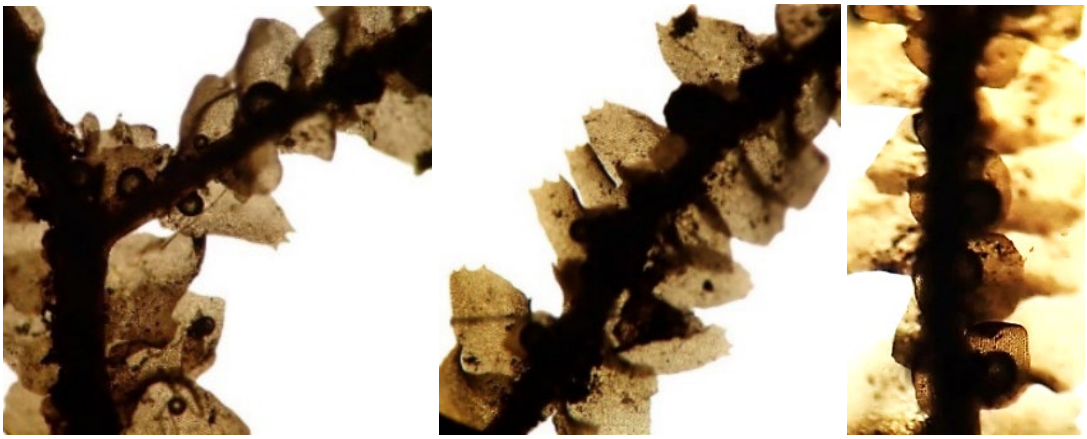
Median leaf cells thick-walled with trigones small or absent. Alakaʻi region, Kauaʻi, Ma 14-5915 (PTBG). Photo by A.V. Freire.

The "isotype" of *B. baldwinii* (Baldwin 199) at MU is not that species but is instead a good example of *B. sandvicensis* (or *B. cordistipula*). Likely, the type is a mixture of *B. baldwinii* and *B. sandvicensis*, both terrestrial species, and the incorrect plant was separated as the MU "isotype". We present it here to illustrate the lateral branching, the less imbricated underleaves, and the squarish leaf cells with thick walls lacking bulging trigones.

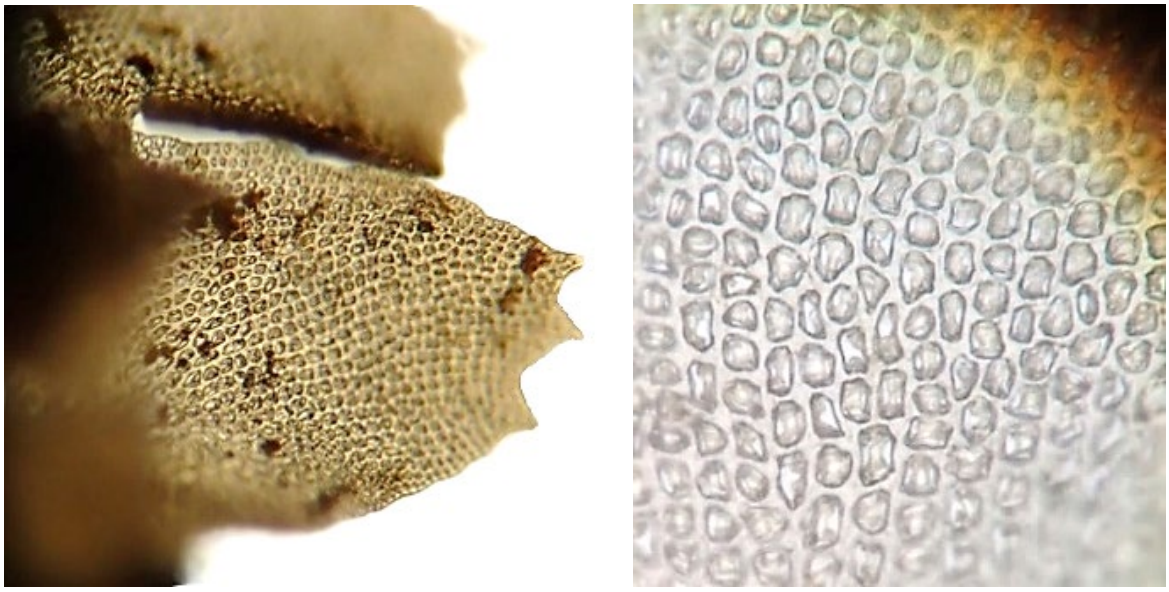
Pictures below are from West Maui, Baldwin 199 (MU). *Bazzania baldwinii* isotype, but identified as *B. sandvicensis* by Freire and Judziewicz. Photos by A.V. Freire.



Bazzania sandvicensis (according to Freire and Judziewicz). Left: Plant with lateral branching. Right: Plants are medium-sized and over 2 mm wide. Scales in mm.

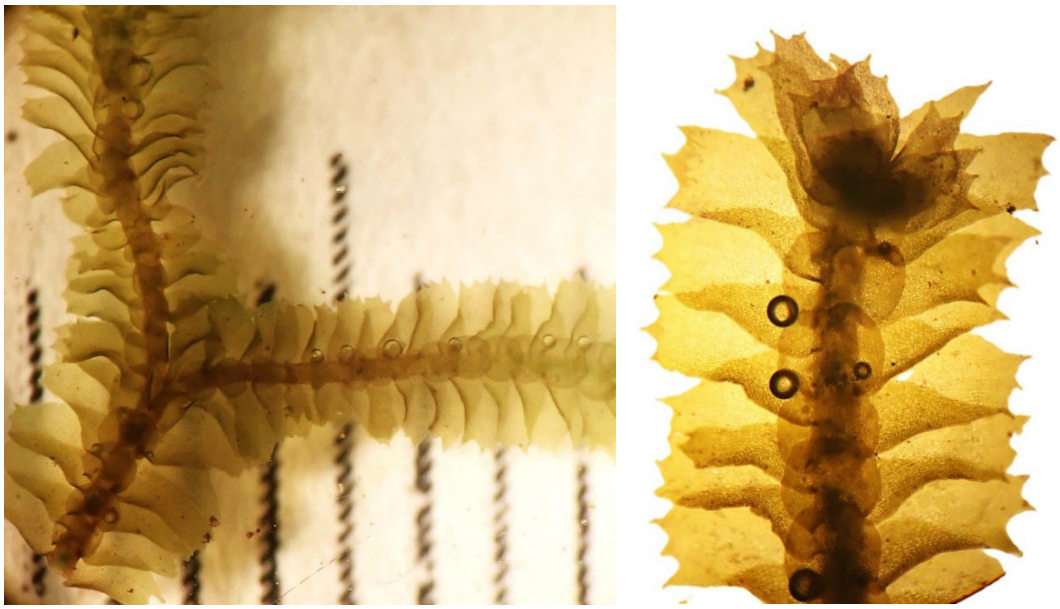


Leaves are slightly imbricate, ovate-triangular with truncate leaf apices, and are uniformly three-toothed on intact leaves. Right: Underleaves are contiguous to slightly imbricate. They are round and slightly over twice as broad as the stem. Baldwin 199 (MU). Photos by A.V. Freire.



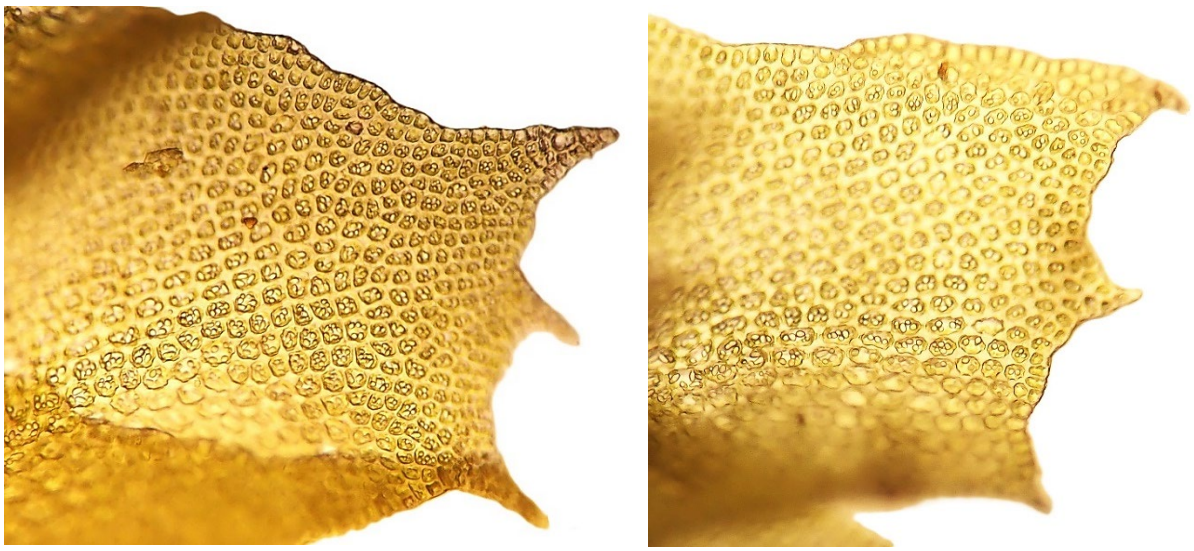
Bazzania sandvicensis. Left: Detail of leaf apex showing uniform teeth and rather orderly, parallel rows of thick-walled cells (we think these are characteristic of *B. sandvicensis*). Right: Detail of cells with thick walls and few trigones. West Maui, Baldwin 199 (MU). Photos by A.V. Freire.

Next, we present a problematic specimen already included in this notebook under *B. cordistipula*. This specimen was collected by Freire & Judziewicz 23-285 (BISH) on rock walls in the Hakalau Forest National Wildlife Refuge, Nāuhi Gulch. We consider it as intermediate between Cooke's concepts of *B. cordistipula* and *B. sandvicensis*, supporting their conspecificity. Plants do have some dichotomous branching and resemble *B. cordistipula*, but leaves are less imbricated, less curved on the lower margin, underleaves are distant to overlapping, and the apical teeth vary from short and triangular to long and narrow; but perhaps, more meaningfully, in the same plant, some leaves have quadrate cells with thick walls and small trigones forming neat rows as in *B. sandvicensis*, while others do have the bulging trigones of *B. cordistipula*. The plants were on a rock wall, resembling a more arboreal environment. All pictures below are from this specimen and photographed by A.V. Freire.

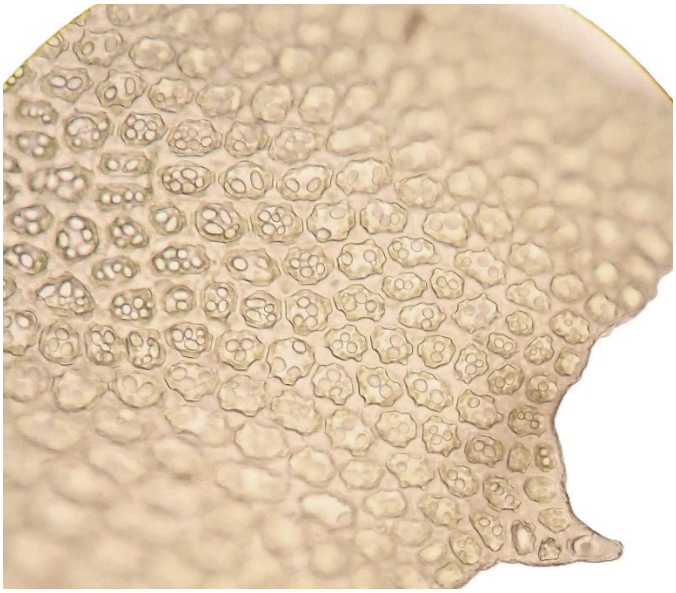


Plants are about 2.5 mm broad. Leaves and underleaves are overlapping but less than in *B. cordistipula*. Leaf apices are truncate with three variable teeth. Freire & Judziewicz 23-285 (BISH).

Bazzania sandvicensis. Although some dichotomous branching is observed, mainly it exhibits lateral, intercalary branching. Note the distant underleaves. Hakalau Forest National Wildlife Refuge, Hawai‘i Island, Freire & Judziewicz 23-285 (BISH).



Leaves from the same plant showing variation in apical teeth size and cell wall architecture. Left: Typical cell arrangement and architecture of *B. sandvicensis*. Right: Leaf cells with more bulging trigones (see below). Freire & Judziewicz 23-285 (BISH).

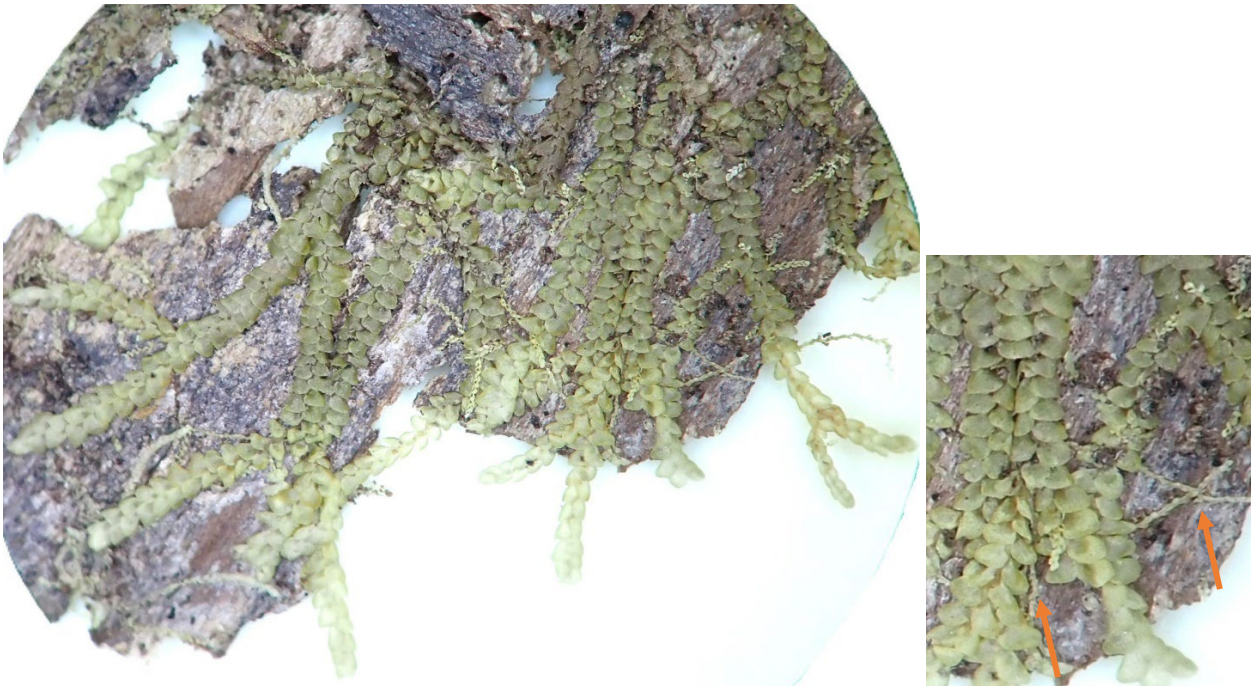


Bazzania sandvicensis. Detail of leaf with bulging trigones as in typical *B. cordistipula*. Hakalau Forest National Wildlife Refuge, Hawai‘i Island, Freire & Judziewicz 23-285 (BISH).

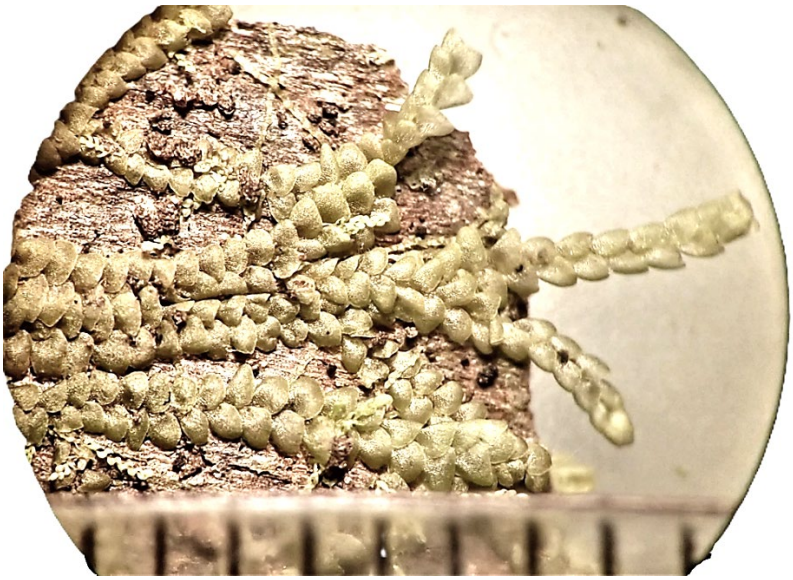
13. *Bazzania* species 1. Found as a bark epiphyte, only in a *Metrosideros polymorpha–Cibotium glaucum* forest in Volcano Village, Hawai‘i Island, elev. 3,700 ft. (Freire & Judziewicz 23-431). Distinctive in its small size (1.3-1.5 mm wide), pale color, and round leaves (the roundest of any Hawaiian species of *Bazzania*) with a vittate, trigonous base. The round underleaves are slightly emarginate apically. At first glance, in dorsal view, this species resembles a member of the Lejeuneaceae.

Plants are small, up to 1.5 mm wide, pale to whitish green, closely appressed to their substrate. Stems fragile, bifurcate, otherwise infrequently branched, with few ventral flagelliform branches that often protrude from the sides of the plants, and are also appressed and closely attached to their substrate. Leaves round-ovate, imbricate, concave, spreading when wet but curled towards the ventral side (“cupped”) when dry. Leaf apices rounded to pointed, entire. Leaves with a border of small thick-walled cells, cells around the central base and median region are small, quadrate, thick-walled and with few trigones; middle leaf and central basal cells are larger, oblong, thin-walled and with prominent cordate trigones, thus forming a vittate region. Oil bodies are small, elliptical and segmented. Underleaves distant, rounded, slightly broader than long, truncate, usually emarginate.

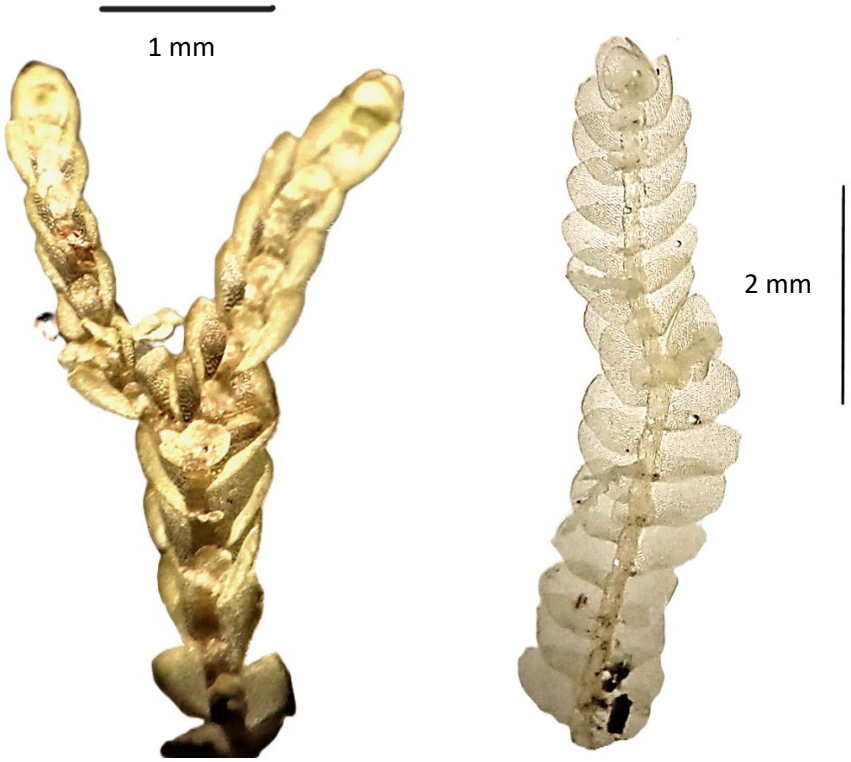
All pictures below from Maluhia Trail, Volcano, Hawai‘i Island Freire & Judziewicz 23-431 (BISH).



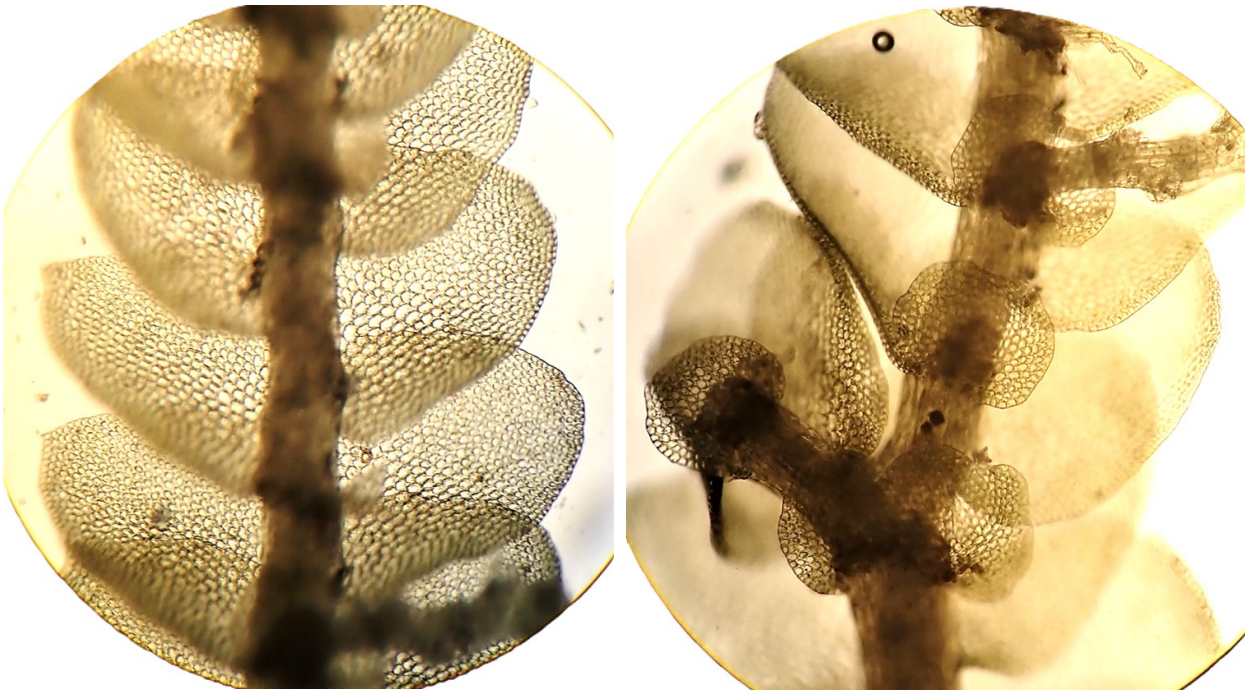
Bazzania species 1. Plants grow closely appressed to bark. Note the flagelliform branches protruding from sides of plants, seemingly helping to attach them to their substrate (arrows).



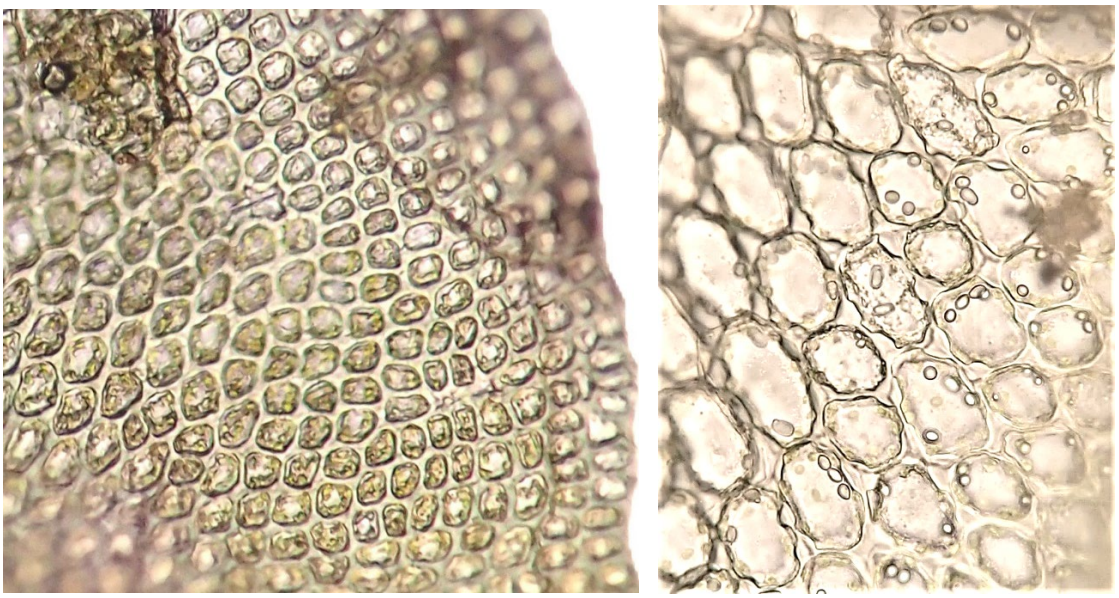
Plants are small, closely appressed to their substrate, and superficially resemble a member of the Lejeuneaceae. Scale in mm. Freire & Judziewicz 23-431 (BISH).



Bazzania species 1. Leaves "cupped" when dry (left) but spreading when wet. Leaves are ovate, with round apices, and imbricate (right). Note few small flagelliform branches (right). Maluhia Trail, Volcano, Hawai'i Island Freire & Judziewicz 23-431 (BISH).



Left: Leaves are rounded and imbricate, with a border of small thickened cells. Right: Underleaves are round, distant, emarginate. Freire & Judziewicz 23-431 (BISH).



Bazzania species 1. Left: Cells are small and quadrate with thick walls towards the leaf margins. Right: Middle leaf cells are thin-walled with cordate trigones and few intermediate thickenings. Oil bodies are small, elliptical and segmented. Maluhia Trail, Volcano, Hawai‘i Island Freire & Judziewicz 23-431 (BISH).

14. *Bazzania* species 2. We found this striking species growing colonially on a moist shaded rock face in an old growth kīpuka (at 5,000 ft.) on the Saddle between Mauna Kea and Mauna Loa, Hawai‘i Island. Populations form dense tufts. The prolific branching helps hold the large plants erect. They superficially resemble a cushion of moss. This species is closest to *B. praerupta.* They share the broad leaf bases and leaves as broad as long or less than 1.5 times longer than broad. However, the apical teeth are smaller in species 2, and the underleaves are not conspicuously auriculate. Because of these differences and our limited understanding of *B. praerupta*, we are maintaining it as a separate entry.

Plants erect, forming dense tufts, about 2 mm wide or slightly wider, and several centimeters long. Stems are stout, firm, densely branched, with abundant lateral branches, some are flagelliform at their tips; numerous ventral flagelliform branches are also produced. Leaves are imbricate, spreading, with a broad base only slightly longer than wide (less than 1.5 times as long as wide), broadly and asymmetrically ovate, with a sigmoidal lower margin; apices are truncate, with 3-4 (or occasionally more) teeth, these are usually small; some are irregular in size, and some can be “splayed” laterally. The cells near the leaf apices and on the sides of the leaf are quadrate, thick-walled, and lack distinct trigones; cells in the middle of the leaf, from the base to about ¾ of its length, have bulging trigones and are larger and elongate, forming a vittate region. Leaves are bordered by small, thick-walled, quadrate cells. Underleaves are round, contiguous to imbricate, and about 2.5 times broader than the stem; with irregular apices, some with one or a couple of teeth, emarginate or slightly erose. Perianths are produced sequentially in underleaf axils, forming rows.

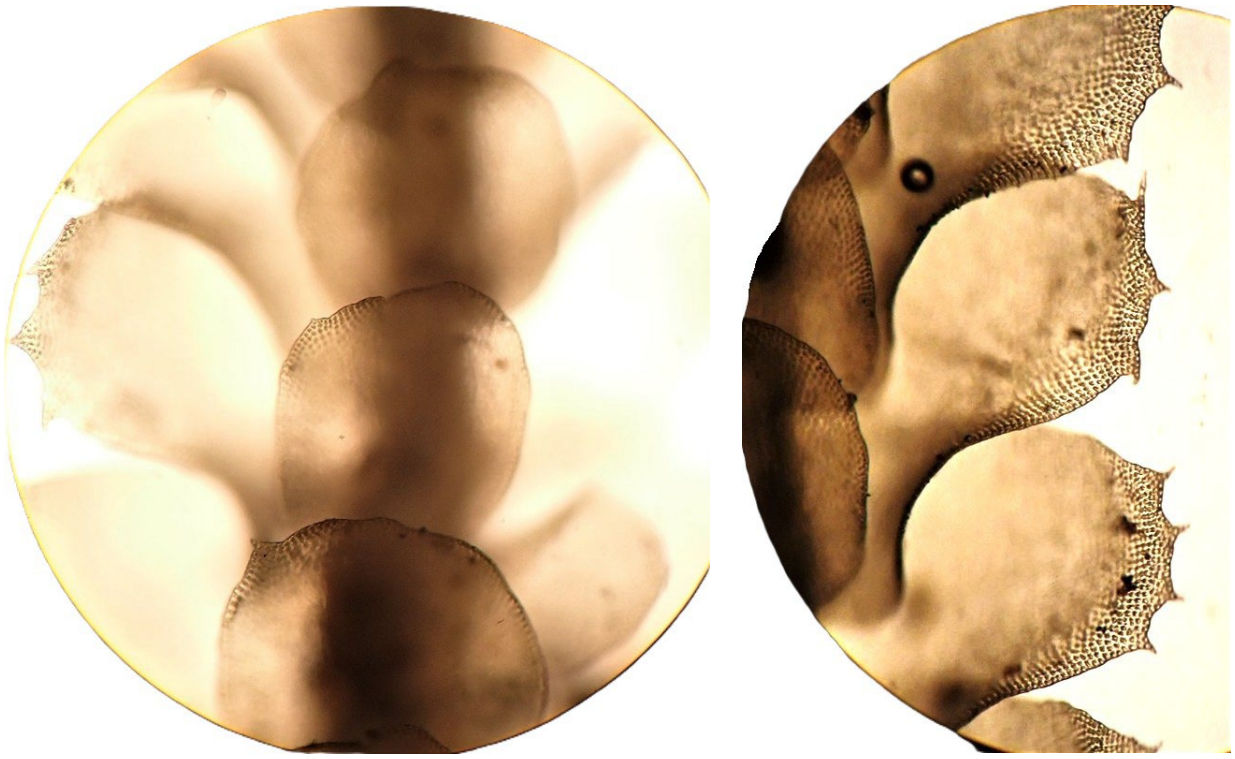
Pictures below are from Hawai‘i Island, Freire & Judziewicz 21-782 (BISH).

Bazzania species 2. Population growing on rock, consisting of erect plants forming dense mosslike clusters.

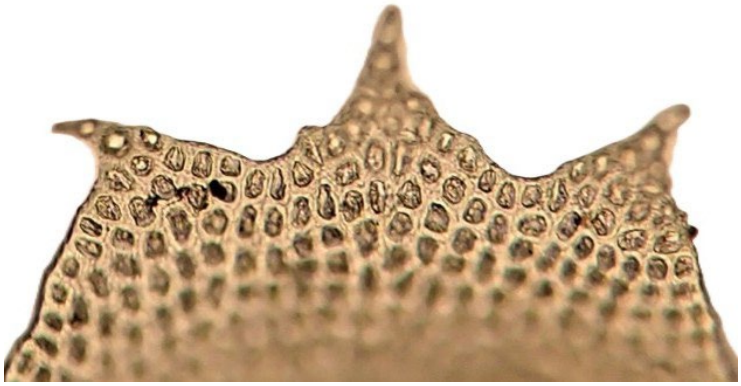
Detail of erect plants with abundant intercalary branching that facilitates keeping them vertically positioned. Also note the well-developed flagelliform branches. Freire & Judziewicz 21-782 (BISH).

Bazzania species 2. Plants are about 2 mm wide, with asymmetrically ovate leaves with a sigmoidal lower margin and truncate apices with short teeth. Note the round, contiguous to imbricate underleaves. Hawai‘i Island, Freire & Judziewicz 21-782 (BISH). Scale in mm.

Intercalary branch with a microphyllous tip. Freire & Judziewicz 21-782 (BISH).

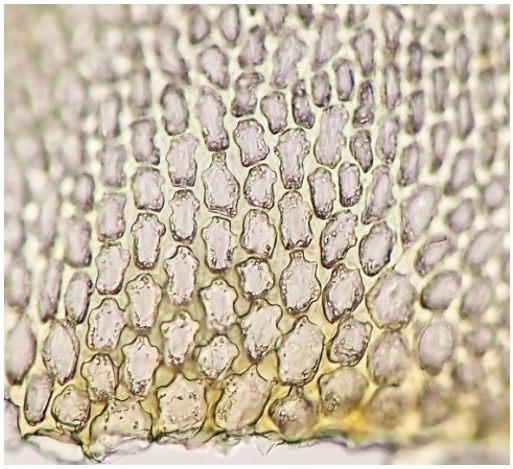


Bazzania species 2. Left: Overlapping round underleaves. Note the irregular apices, sometimes with a tooth (bottom). Right: Round ovate leaves with sigmoidal lower margin and 3-4-dentate apices. Hawai‘i Island, Freire & Judziewicz 21-782 (BISH).



Leaf apex showing the “splayed” lateral teeth and the thick-walled apical cells with no conspicuous trigones. Freire & Judziewicz 21-782 (BISH).

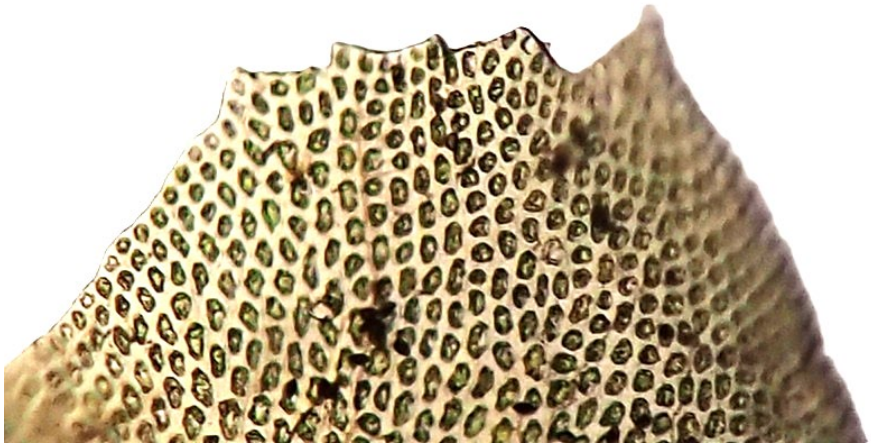
Leaf sampler showing different tooth sizes and positions. Also note the vittate region at the leaf base. Leaves are nearly as broad as long. Freire & Judziewicz 21-782 (BISH).



Bazzania species 2. Vittate region has larger, elongated cells and prominent trigones. Hawai‘i Island, Freire & Judziewicz 21-782 (BISH).

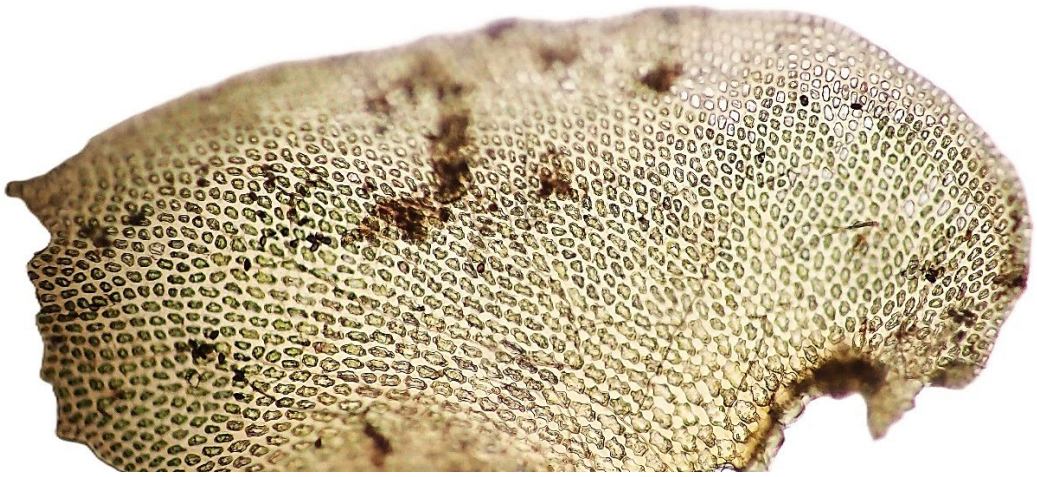
The following photos are from Hawai‘i Island, Freire & Judziewicz 23-376 (BISH). The specimen was collected about two miles from the previous specimen (Hawai‘i Island, Freire & Judziewicz 21-782. In this collection, plants are smaller and have more irregularly-sized teeth that can be more numerous (up to 5), often with one larger tooth. The plants are otherwise similar; perhaps they are part of the range of variation within this species.

Hawaiian kīpuka are small, forested areas, surrounded by extensive and inhospitable lava fields. The kīpuka are thus effectively isolated from each other, and considerable inter-population morphological variation is sometimes evident.

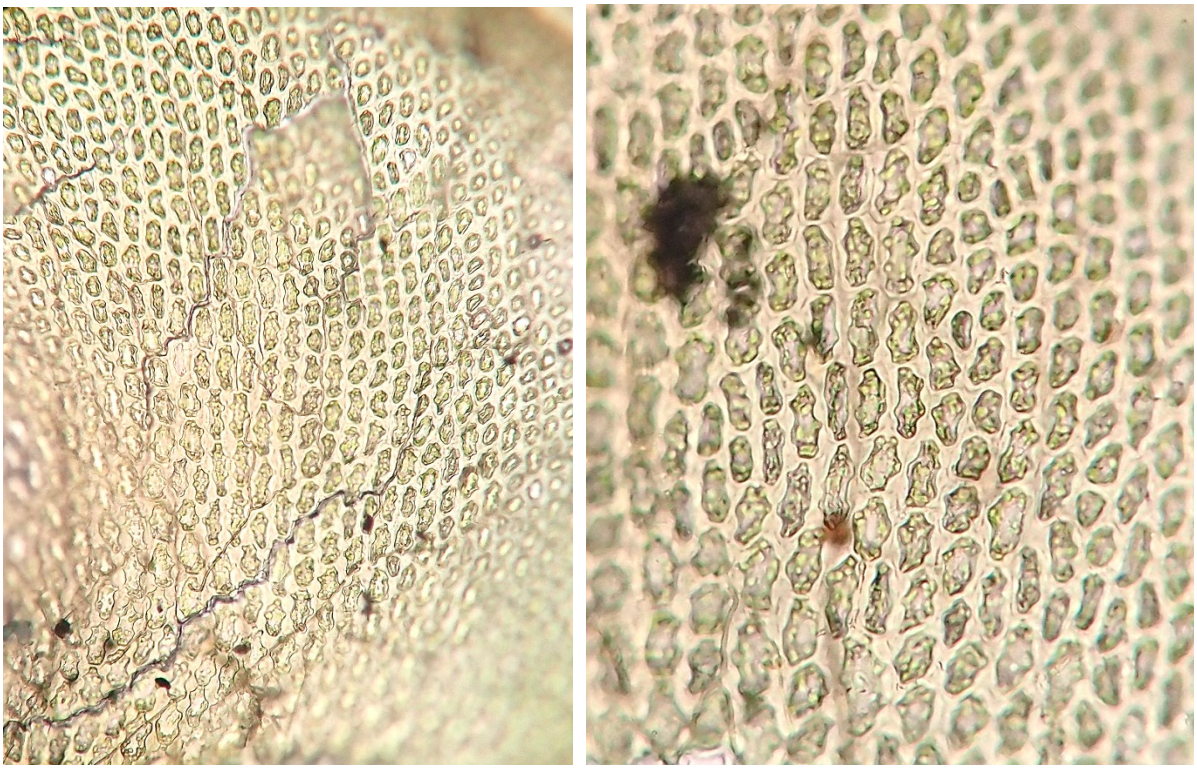


Leaf apex with 5 irregular teeth, with 4 of them barely visible. Freire & Judziewicz 23-376 (BISH).

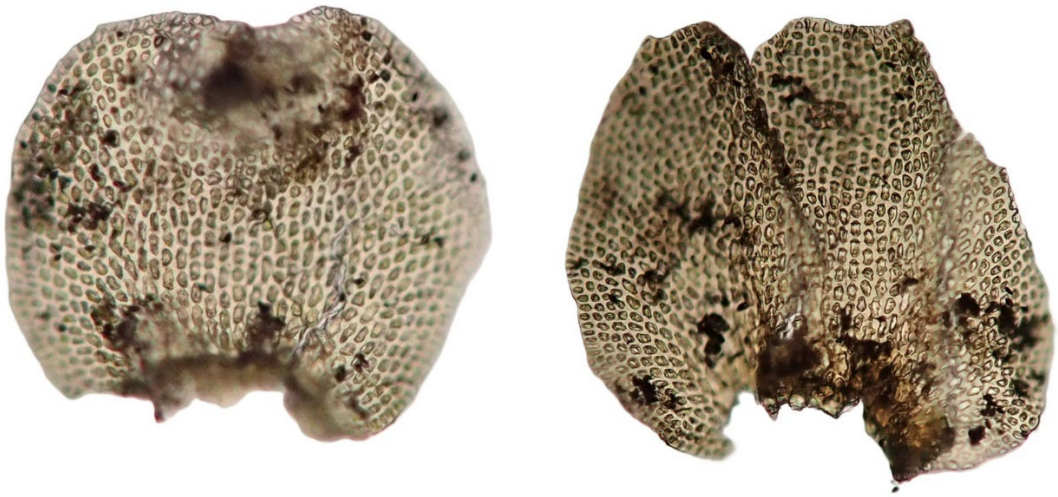
Bazzania species 2. Leaves with teeth irregular in size and number. Both are from the same plant. Note the tendency of one tooth to dominate. Hawai‘i Island, Freire & Judziewicz 23-376 (BISH).



Leaf showing the quadrate smaller cells at the sides and apical regions. The cells in the middle are larger and have prominent trigones, forming a vittate region. Freire & Judziewicz 23-376 (BISH).



Bazzania species 2. Left: Different sizes of leaf cells. They are much larger and with large trigones in the middle of the leaf. Right: Detail of vittate region, showing elongate, irregularly shaped cells with bulging trigones. Hawai‘i Island, Freire & Judziewicz 23-376 (BISH).



Underleaves are rounded, with irregular apices, from slightly (left) to moderately (right) emarginate; some can be irregularly dentate (right). Freire & Judziewicz 23-376 (BISH).

Bazzania species 2. Ventral side of plant with abundant perianths produced sequentially in the axils of the underleaves. Note the abundant flagelliform branches. Hawai‘i Island, Freire & Judziewicz 23-376 (BISH).

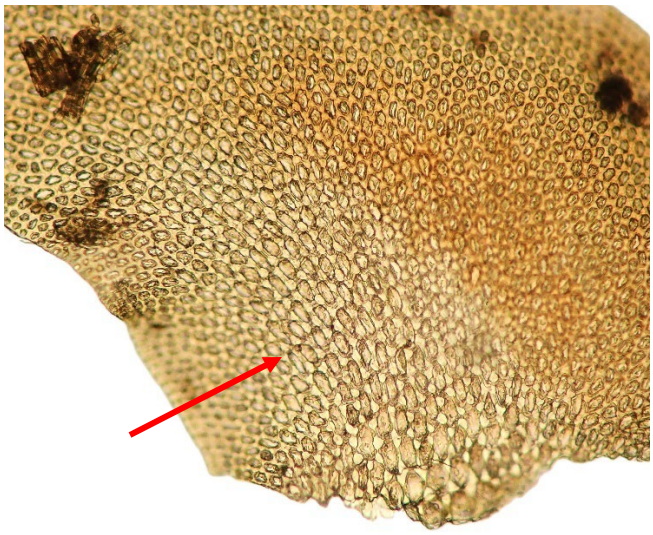
***Bazzania* cf. species 2.** This specimen consists of only one plant and a fragment; it was collected in the Saddle area of Hawai‘i Island by Freire & Judziewicz 21-816 (BISH), near the collection area of species 2. The difference between this and species 2 is the leaf shape. This specimen has longer leaves with slightly sigmoidal lower margins. The rest of the characters fit the concept of species 2. Once more, we see morphological variation between kīpuka separated by lava fields.

Plants are 3 mm wide, with overlapping sinuous, elongate leaves that bend down at their tips when mature. The leaf bases are broad, but the leaves are longer than broad. Leaf apices are irregularly toothed, with 2, 3 or 4 teeth. Leaf cells are rectangular, thick-walled, with some small triangular trigones, and some nodular and bulging ones. A vittate area at the basal midleaf consists of elongated cells with very bulging trigones. Underleaves are rounded, contiguous to slightly imbricate, slightly over twice as broad as the stem, with entire, erose, or coarsely crenate apices. A vittate region is also present.

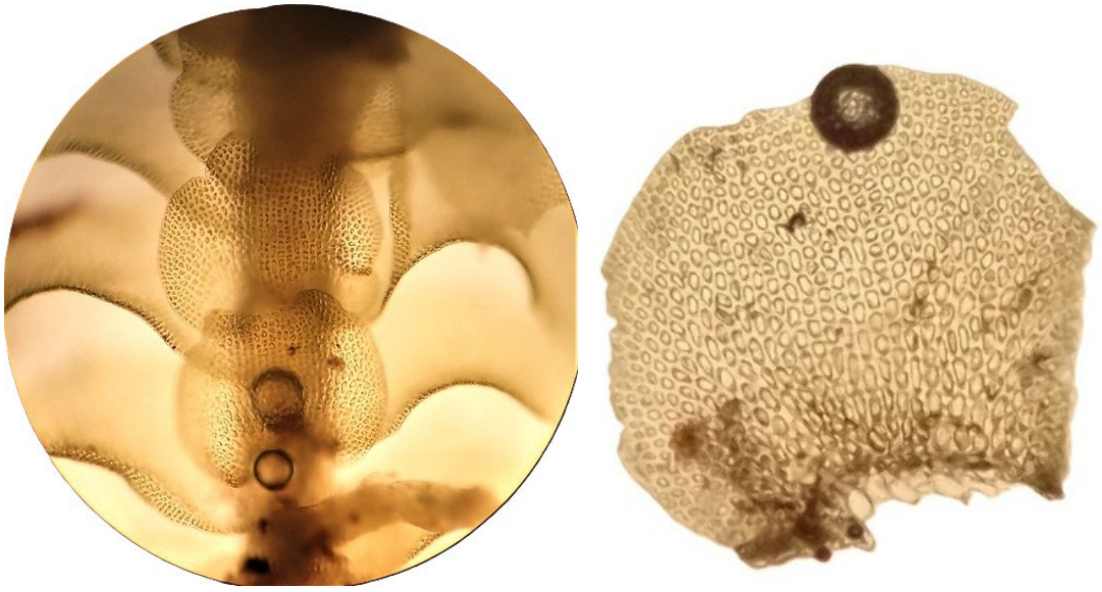
Bazzania cf. species 2. Plants are 3 mm wide, leaves are imbricate and sinuous. Leaf apices are irregularly toothed. Note the broad leaf base (right).

Leaf apices have (2)3 or 4 very irregular teeth. Freire & Judziewicz 21-816 (BISH).

Bazzania cf. species 2. Leaves have a broad base but are longer than broad (leaf is missing a small basal portion). Note the vittate area. Hawai‘i Island, Freire & Judziewicz 21-816 (BISH).

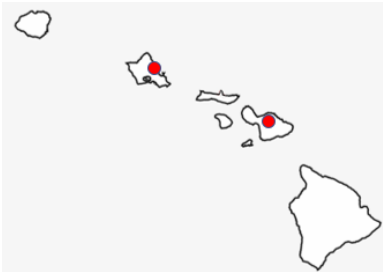


Lower median leaf cells with bulging trigones form a vittate area (arrow). Freire & Judziewicz 21-816 BISH).



Bazzania cf. species 2. Left: Underleaves are round, slightly over twice as broad as the stem, with erose, coarsely crenate, emarginate or entire apices. Right: Underleaves have a vittate area of larger cells. Hawai‘i Island, Freire & Judziewicz 21-816 (BISH).

15. *Bazzania* species 3. Found on Oʻahu (Papali Gulch, Hauʻula, Fosberg 12304, BISH), and Maui (Olinda, Miller & Lamberton 4363, MU), from 1,300-5,000 ft. Miller considered this a new, unpublished species; see discussion on next page. Plants are large and robust. The species resembles *B. cordistipula* in its tridentate leaf apices, and in having mainly overlapping, orbicular underleaves. Unlike *B. cordistipula*, the leaves have longer and more robust teeth and a much less curved leaf lower margin; median leaf cells are more isodiametric and have much smaller trigones.

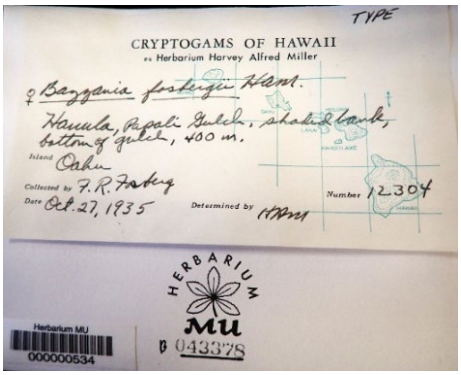


Plants are whitish-green to light brown (based on the only picture of fresh material below), robust, up to at least 5-6 cm long and over 3 mm wide; stems are stout, some with a flagelliform tip. Plants are very frequently branched, ventral flagelliform branches are numerous, long and slender ("whiplike"). Leaves are long, concave, asymetrically ovate, patent, overlapping, with a falcate upper margin and a nearly straight to only slightly incurved lower margin; upper leaf margins overlap on the dorsal side, obscuring the stem. Leaf apices are laciniate, with 3(4) long and prominent "clawlike" teeth, these are irregular in size and shape, usually broadly triangular at the base and with an acuminate tip). A few leaves may have triangular, non-acuminate, smaller teeth intermixed. Apical and lateral cells are small, quadrate, and thick-walled, without trigones. Median leaf cells are quadrate to shortly rectangular, with thin to moderately thickened walls and usually with some small to medium-sized trigones. A border of smaller quadrate cells is obvious at least in some regions of the margin. A region of larger, elongated cells with bulging trigones is present at the basal middle but is not clearly defined. Underleaves are large, three times as broad as the stem, auriculate, orbicular, contiguous to overlapping, spreading or appressed, flat or canaliculate (lateral margins rolled towards the ventral side); with variable margins and apices, some with a few irregular marginal teeth and with truncate, erose to emarginate apices, somet with 2 teeth or 2 rounded lobes. Perianths large, erect, stout, serially produced in axils of underleaves. Antheridial branches are small, globular, and much less abundant than the perianths.

Bazzania species 3. Plant *in situ*. Note the "drooping" leaves. Southern Koʻolau Range, 21.36269°N, 157.81975°W, Oʻahu, 2,100 ft., 14 June 2024. Photo by Mike Ross, with permission: (https://www.inaturalist.org/observations/223009513).

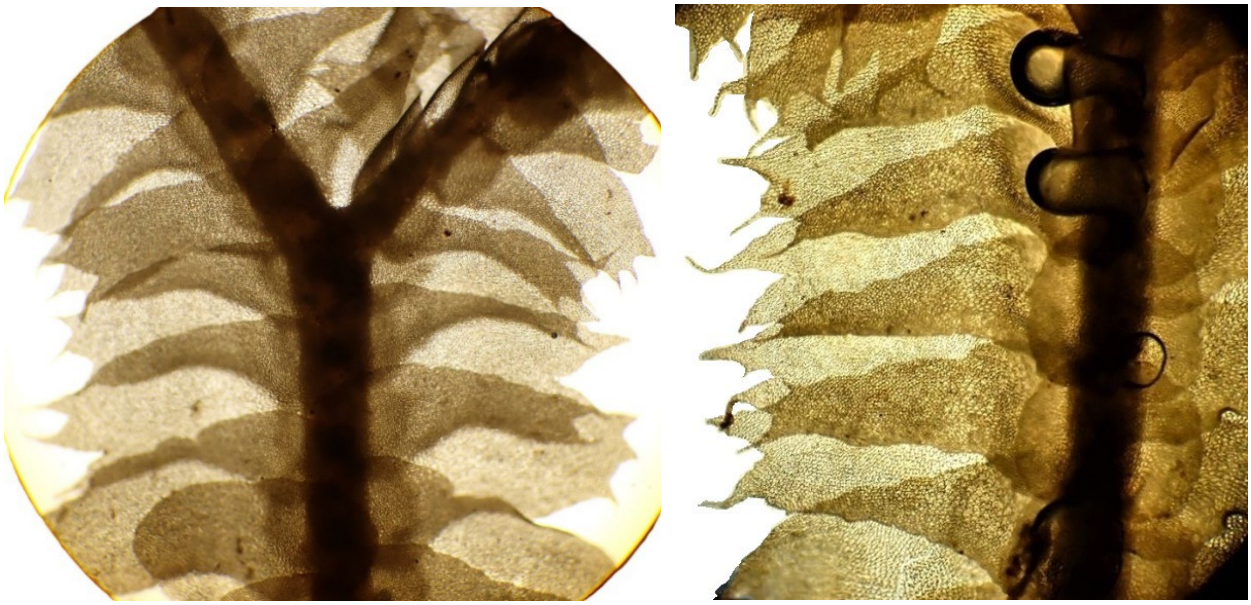
Bazzania species 3. Left: Dorsal view showing the overlapping leaves that obscure the stem dorsal surface. Right: Ventral view showing the large, overlapping underleaves. Southern Koʻolau Range, 21.36269°N, 157.81975°W, Oʻahu, 2,100 ft., 14 June 2024. Photos by Mike Ross, with permission: (https://www.inaturalist.org/observations/223009513).

Miller illustrated an unnamed new species based on Miller & Lamberton 4363, Olinda, Maui (MU). His drawings are part of an unpublished set at BISH. Although we did not have the chance to study the specimen, his drawings fit our concept of *Bazzania* sp. 3, based on our study of Fosberg 12,304, Hauʻula, Papali Gulch, Oʻahu (BISH, MU), and iNaturalist photos by Mike Ross. The underleaves are more ragged in his drawings than on the Fosberg collections, but we think they are the same species and agree it is a new one for Hawaiʻi and likely a new species of *Bazzania*. Following are our pictures and interpretations of Miller's proposed type for "*B. fosbergii*" (MU) based on Fosberg 12,304 (BISH). Photos by A. V. Freire and E. J. Judziewicz.

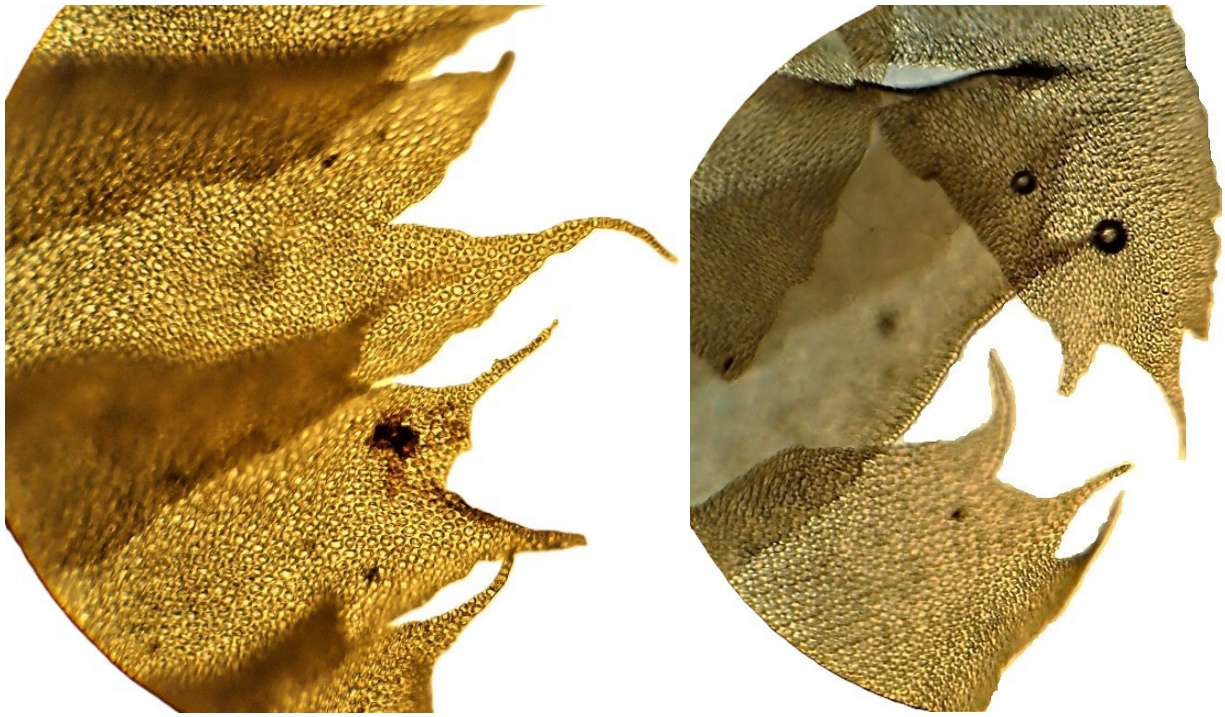


Although the name "*B. fosbergii*" remains unpublished, it seems Miller intended this specimen from MU, to be the type for the name (see upper right corner).

Plants are robust, frequently branched, with numerous long and slender ventral flagelliform branches (left). Leaves are over 1.5 mm long (center). Scales in mm. Branches may have flagelliform tips, 10 units = 1 mm. Fosberg 12,304 (MU-left and right, BISH-center). Photos by A. V. Freire and E. J. Judziewicz.

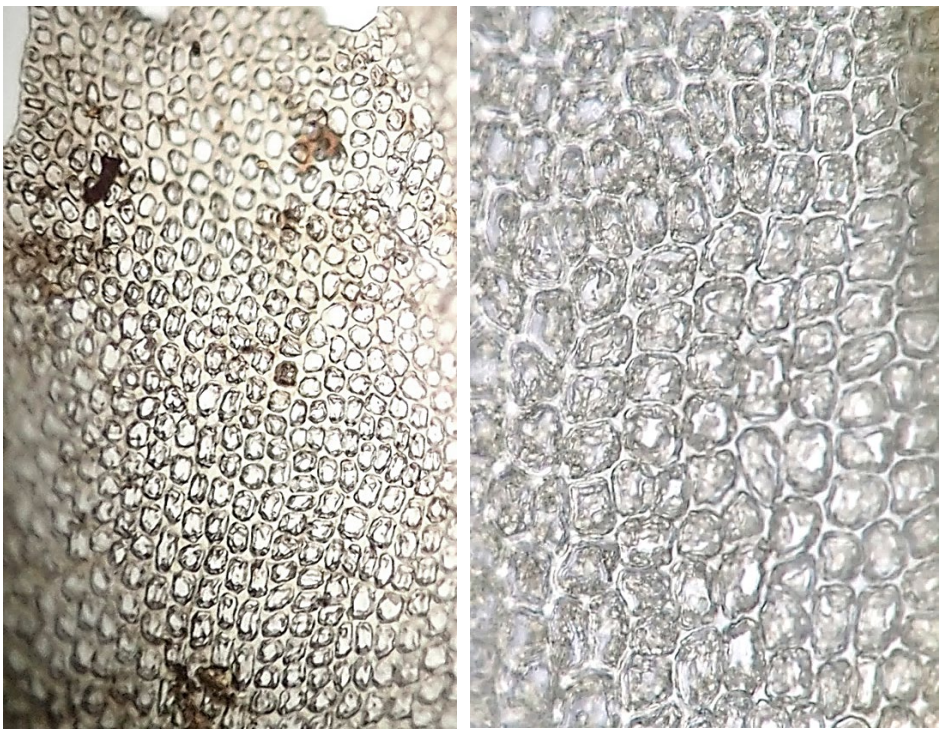


Bazzania species 3. Leaves are elongated, and mainly with coarse teeth. Note some variation between the two isotypes: The MU plant (left), has slightly curved leaf lower margins and smaller apical teeth whereas the BISH specimen has leaves with nearly straight lower margins and larger, more prominent teeth (right). O‘ahu, Fosberg 12304 (BISH and MU). Photos by A. V. Freire.

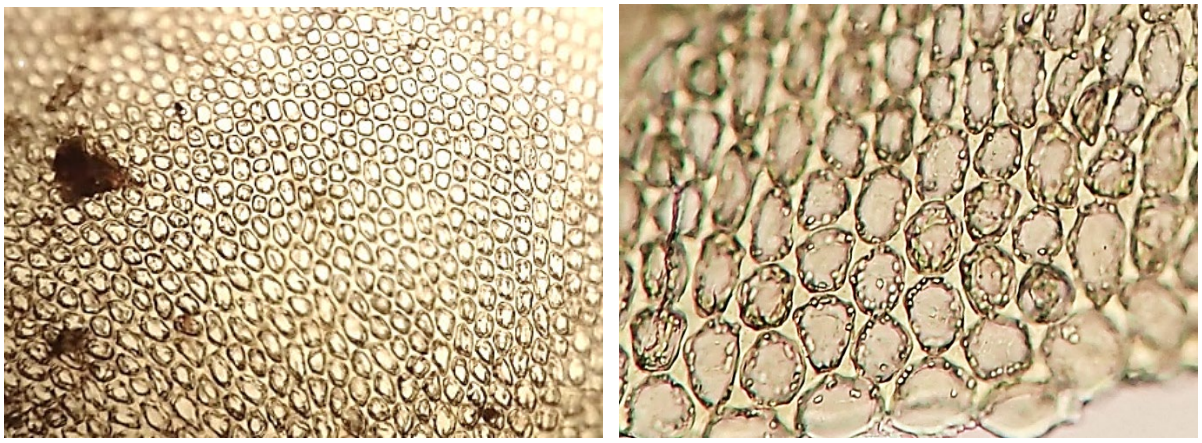


Detail of laciniate leaf apices. Apical teeth are broadly triangular, long-acuminate, and are usually irregular in size and shape. Fosberg 12304 (BISH). Photos by A. V. Freire.

Bazzania species 3. Leaves are asymmetrically ovate with a slightly falcate upper margin and slightly curved lower margin. Most leaves have 3 laciniate teeth, but some leaves may have 4 (right). Note the central and basal region of larger cells. O‘ahu, Fosberg 12304 (MU). Photos by A. V. Freire.

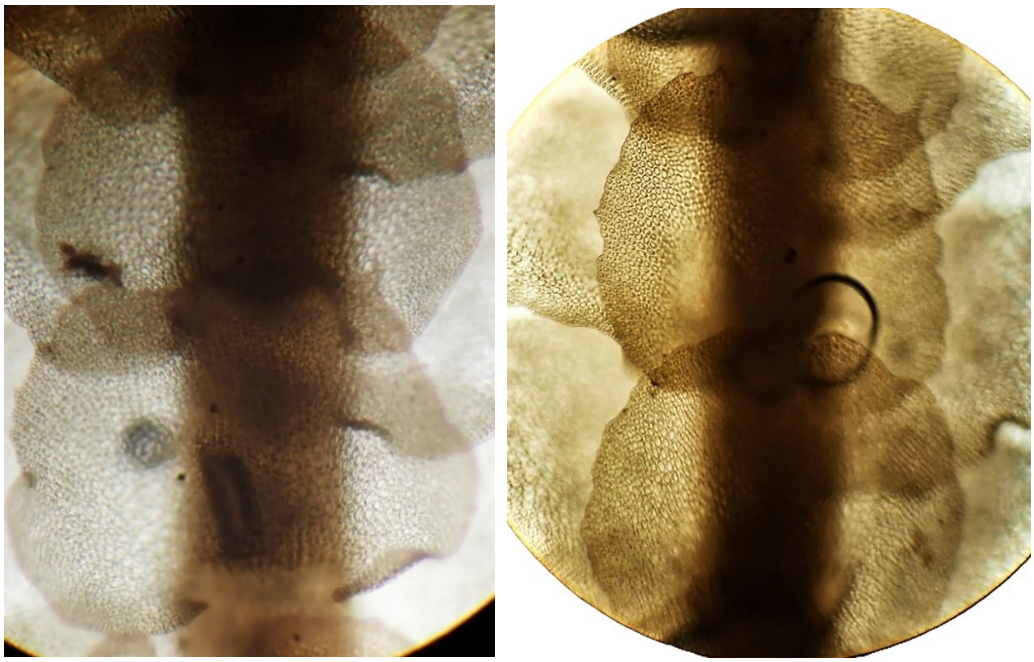


Median leaf cells are quadrate to slightly rectangular, with moderately thickened walls and small trigones; some medium-sized trigones can be present. Left: Note thick-walled apical cells (above), and the border of smaller cells (upper left). Fosberg 12304. Photos by A. V. Freire.



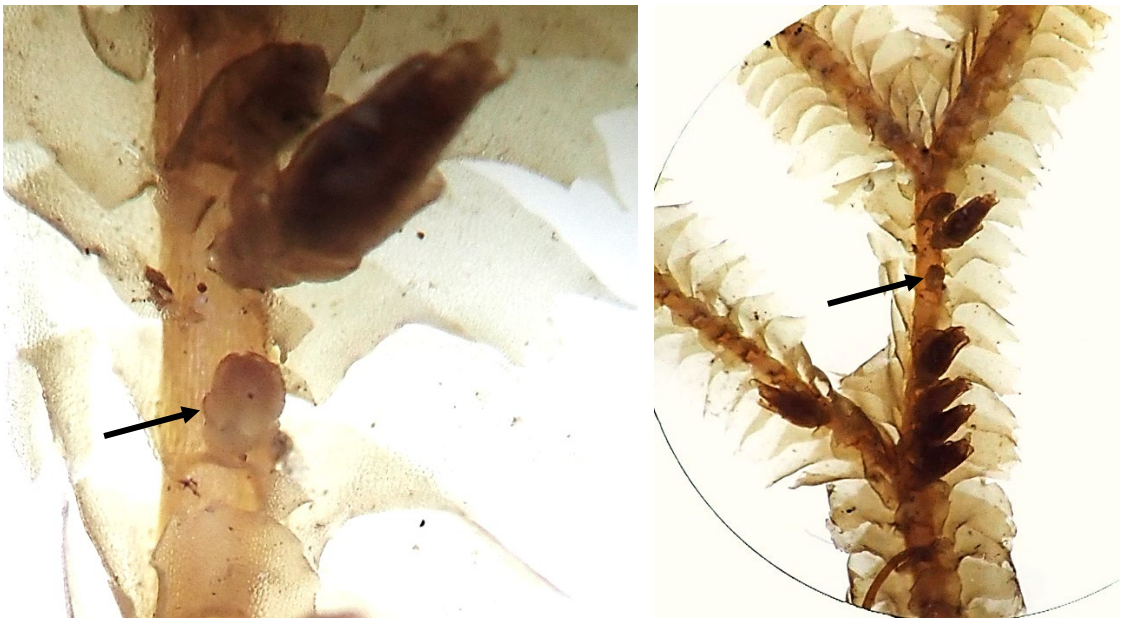
Bazzania species 3. Lateral leaf cells are quadrate and small (above in left photo). Central and basal cells are larger and have larger trigones (right). O‘ahu, Fosberg 12304 (MU, left; BISH, right), Photos by A.V. Freire.

Underleaves are orbicular and contiguous, reflexed and rolled down (left) to overlapping, appressed and flat (right). Fosberg 12304 (MU). Photos by A. V. Freire.



Bazzania species 3. Underleaves are cordate at their base (left), with a few irregular teeth of unequal sizes, with erose to irregularly crenate apices. O‘ahu, Fosberg 12,304 (Left, MU; right, BISH), Photos by A. V. Freire.

Underleaves are variable. They can be flat (1, 2) to canaliculate (3, 4). Their truncate apices have a teeth or rounded crest on either side, but can also be emarginate and sometimes denticulate (2). 1 and 3: Fosberg 12304 (MU). 2 and 4: Fosberg 12304 (BISH). Photos by A. V. Freire.



Bazzania species 3. Archegonia are serially produced in the axils of underleaves, some antheridial branches are also present (arrows). O‘ahu, Fosberg 12304 (MU). Photos by A. V. Freire.

16. *Bazzania* species 4. This is a unique species characterized by its large size, dichotomous branching, decurved leaves with sigmoidal lower margins, leaf apices with mainly 2 but sometimes with 3 short teeth, leaf cells with large and confluent trigones; and by the small, ligulate underleaves with tightly reflexed margins. It is certainly a new report for Hawai‘i, perhaps a new species for the genus, but this needs confirmation.

Sadly, we collected this and several other interesting specimens on what remains of a very rich forest on Hawai‘i Island, at the neighborhood of our Bryological Laboratory in Volcano. The forest is deplorably degraded due to grazing (the damage a couple of cows can do in a short time is considerable), ungulate infestation, and to a construction boom after the pandemic that forces new owners to clear cut their lots to be able to install unnecessary septic systems.

Plants are robust, up to 3.7 mm wide, with stout stems and frequent bifurcate branching; long whip-like flagelliform branches are abundant. Leaves are overlapping, 2-2.2 mm long, concave, decurved (towards the ventral side), asymmetrically ovate-triangular, with acute apices, bearing variable teeth, mainly bifid but with some trifid leaves intermixed on the same plant. Lower leaf margins are slightly sigmoidal; the top half of leaves are deflexed (pointing down, towards the base of plant); upper leaf margins are falcate, obscuring the stem dorsal side. Leaf cells are elliptical, thick-walled, and with very prominent and confluent trigones, but the marginal and apical cells are isodiametric and smaller. A very small band of longer and thinner cells is present in the basal center. Underleaves are contiguous to slightly imbricate, small, slightly over 0.5 mm long x 0.5 mm wide, about 1.5 as broad as the stem, ligulate, reflexed, concave at the center, and with tightly reflexed margins and truncate-erose apices.

All pictures below are from Freire & Judziewicz 23-338 (BISH), *Metrosideros polymorpha* forest, near the junction of Liona and Ala Ohia Streets, 19˚25’34” N, 155˚12’32” W, el. 3,475 ft., Volcano, Hawai‘i Island.

Bazzania species 4. Plants in ventral (left) and dorsal (right) views. Leaves decurve towards the ventral side. Note stout stems, bifurcate branching, and the whiplike ventral flagelliform branches. Scale in mm.

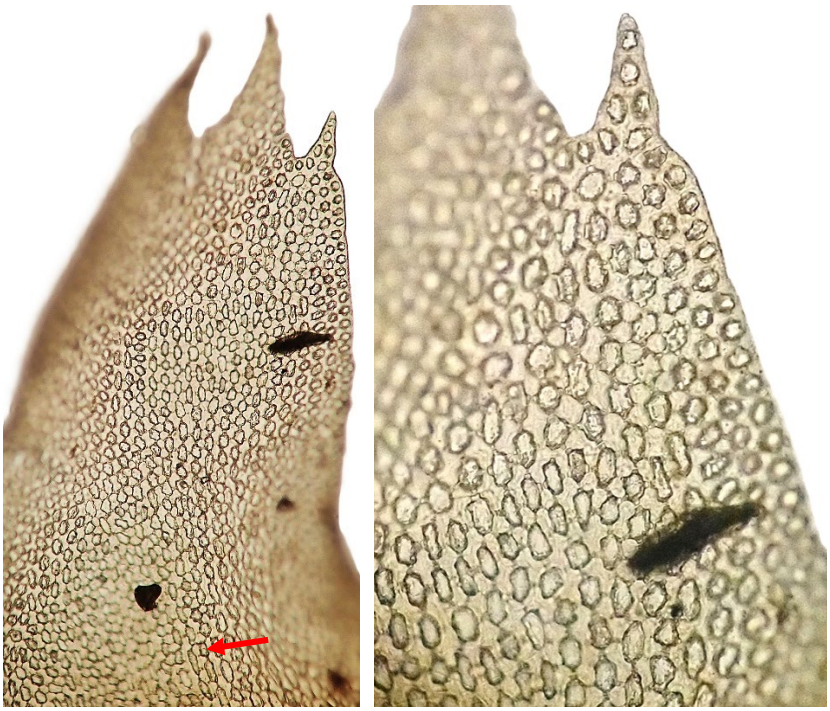
Leaves are about 1.5 mm long, sigmoidal, with the apical half deflexed (bending down). Note the apices, mainly with two divergent to parallel teeth,. Freire & Judziewicz 23-338 (BISH).

Leaf apices may have two or three teeth, variable in size and shape. Note the thick-walled cells. Freire & Judziewicz 23-338 (BISH).

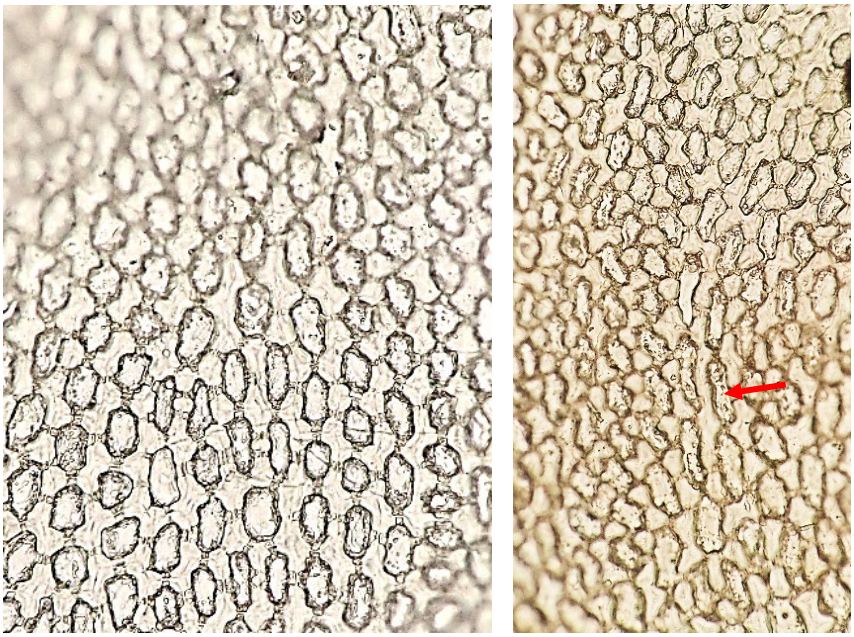
Bazzania species 4. Leaves are large (2 mm long), strongly bent, with acute tips, bearing mainly 2 but sometimes 3 teeth. These are variable in size and shape. They can be divergent or parallel. Volcano, Hawai‘i Island, Freire & Judziewicz 23-338 (BISH).

Underleaves are contiguous, ligulate, small (1.5 times broader than the stem), with erose, truncate apices and tightly reflexed margins. Freire & Judziewicz 23-338 (BISH).

Bazzania species 4. Underleaves are ligulate, with truncate-erose apices, and are slightly auriculate. Cells have confluent trigones and larger cells in the basal third of their length. Volcano, Hawai‘i Island, Freire & Judziewicz 23-338 (BISH).



Most leaf cells are elongate, but quadrate and smaller at the apex and margins. All have prominent, confluent trigones. Left: Note the narrow, vittate region (arrow), with longer cells close to the leaf base. Freire & Judziewicz 23-338 (BISH).



Bazzania species 4. Detail of confluent trigones and elliptical or elongate cells that are longer and narrower close to the base (arrow). Volcano, Hawai‘i Island, Freire & Judziewicz 23-338 (BISH).

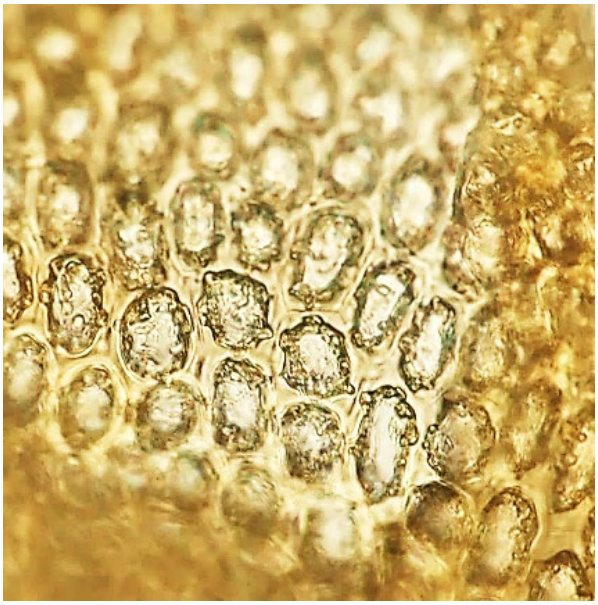
***Bazzania* species in need of more study:**

Ken Wood 14,412 (PTBG) is a robust species of *Bazzania* with robust stems and overlapping leaves and underleaves from the Makaleha Mountains, Kauaʻi. The presence of a variable number of large irregular teeth, some with acuminate tips at leaf apices, the rather parallel leaf tip margins, the very long and whip-like flagelliform branches, as well as the coarsely crenate or erose underleaf apices places it within our *Bazzania* species 3 concept. However, the width of the plant (less than 3 mm) and the very kinked leaf lower margins suggest a similarity with *B. cordistipula*. Unlike either of these species, they are not as frequently branched and have stouter stems. This specimen needs detailed study. Photos by A.V. Freire.

Plants are robust and form dense mats. They are about 2.5 mm wide and sparingly branched. Note the long, whip-like flagelliform branches (right). Left photo courtesy of National Tropical Botanical Garden/Ken Wood.

Bazzania species. Left: Leaves overlapping, spreading at right angles to the stem (squarrose). Note the kinked lower margins of the leaves. Right: Leaves with elongate, acuminate teeth. Note the rather parallel apical leaf margins. Photos by A.V. Freire & E.J. Judziewicz.

Underleaves are orbicular, large (3 times as broad as the stem), overlapping, with erose to coarsely crenate apices. Wood 14412 (PTBG). Photo by A.V. Freire & E.J. Judziewicz.



Bazzania species 4. Median leaf cells are isodiametric to rectangular, with prominent trigones. Kaua‘i, Wood 14412 (PTBG). Photo by A.V. Freire & E.J. Judziewicz.

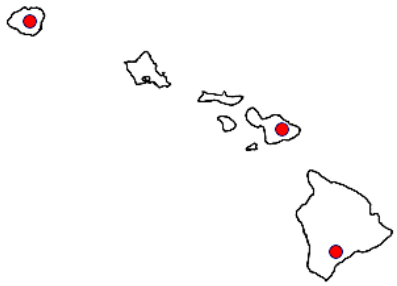
Excluded species:

***Bazzania javanica* (Sande Lac.) Schiffn.**

There are reports of the widespread Asian species *Bazzania javanica* (Sande Lac.) Schiffn. from Hawai‘i (Kitagawa, 1967: 265; Mizutani and Chang, 1986: 431; Meagher, 2015: 544), these papers indicate that *B. javanica* differs from *B. praerupta* in its narrower, less imbricate leaves and smaller underleaves. However, none of these papers cite any voucher specimens for supposed Hawaiian records, and we did not encounter any Hawaiian specimens determined as *B. javanica* at either BISH, MU, or PTBG.

Blepharostoma (Dumort.) Dumort. (Blepharostomataceae)

One species in Hawai‘i. Ten species worldwide.



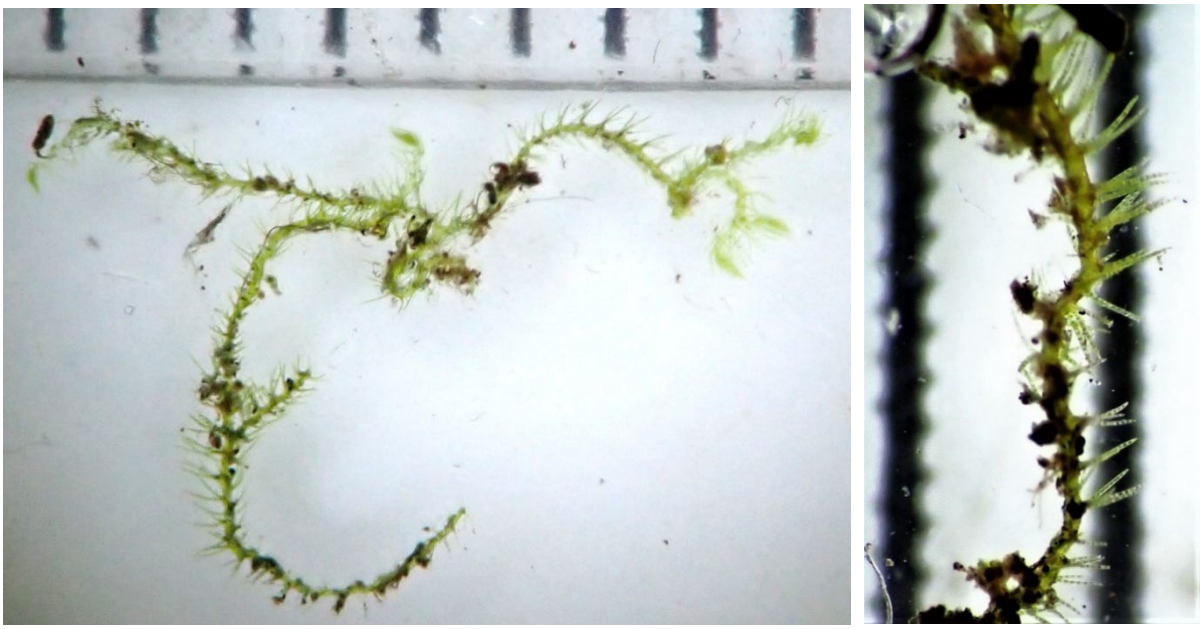
Blepharostoma trichophyllum (L.) Dumort. s.l. **Indigenous.** This tiny species is found in wet, montane forests, 3,000-6,400 ft. Present on Kaua‘i (Wood 17,993, PTBG), Maui (where it is most common) and on Hawai‘i Island. It is mainly Holarctic but also found in scattered sites throughout the tropics. In Hawai‘i it is much less common than the superficially similar genera *Kurzia* and *Telaranea*. *Blepharostoma* is larger and differs from both genera in its whitish or yellow-green rather than dark green color, and in its leaf lobes 10-13 cells long (versus 4-7 cells long in *Kurzia* and *Telaranea*). Tiny gemmae may be produced from the leaf tips. *Blepharostoma* resembles tiny conifer seedlings.

Plants are light green to yellow-green, prostrate to semi-erect, tiny, up to 0.5 mm wide. Stems are stout for the size of the plant. Leaves are divided into (2)3-4 filiform and stiff, needle-like, one-cell-thick lobes. Each lobe has a single-celled base joined to the adjacent lobe bases. Each lobe has (9)10-11(-13) rectangular cells with thick, striate walls. Median lobe cells are 2-2.2 times as long as broad and under 50 μm long. Underleaves are equal to the leaves in size but are 2-lobed.

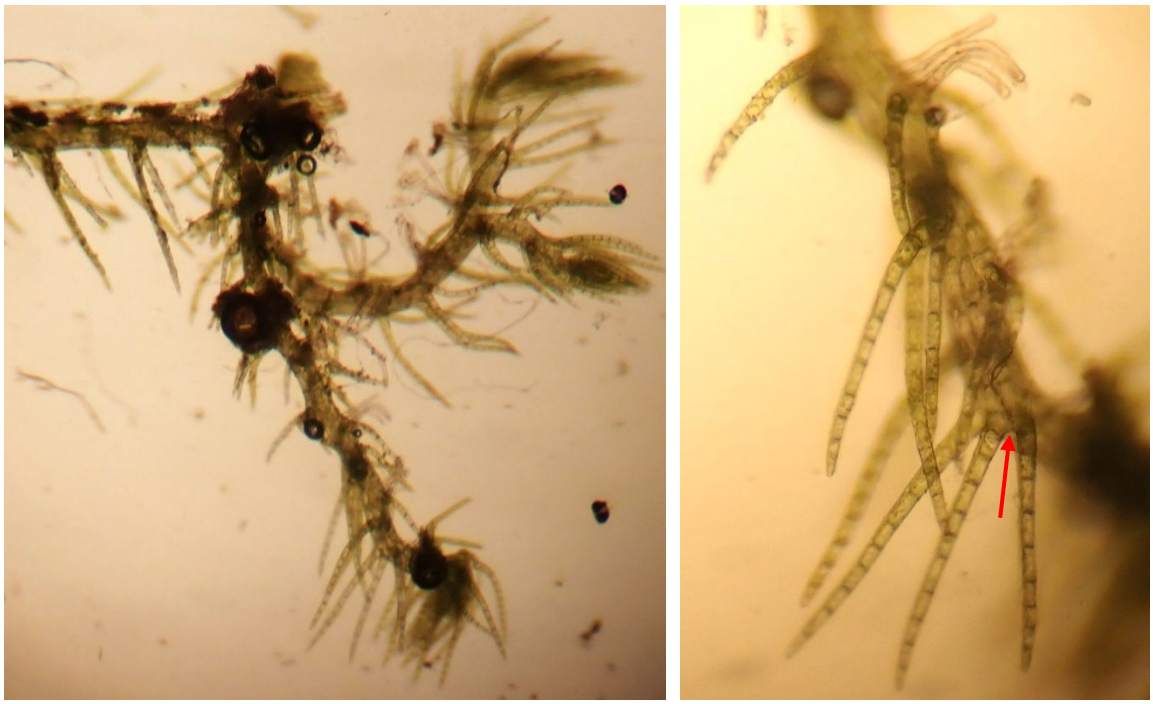
Bakalin et al. (2020b) present molecular and morphological evidence for several cryptic species in the genus, at least in eastern Asia. The morphology of the oil bodies is critical for species determination, and these have not yet been recorded for fresh Hawaiian material. The length: width ratio of the cells in the central part of the cilia is also critical for species determination (Bakalin et al., 2020b); in Hawaiian material, that ratio is clearly 2.0-2.2: 1, and not 1.5-1.8: 1 as in *Blepharostoma trichophyllum* s.s. That would appear to exclude *B. trichophyllum* from Hawai‘i and suggests affinities of Hawaiian populations with the Chinese and Russian species ***B. prima*** Vilnet & Bakalin and ***B. neglecta*** Vilnet & Bakalin, pending examination of fresh oil bodies.

Blepharostoma resembles tiny yellow-green conifer seedlings. Upper Kahuku Unit, Hawai‘i Volcanoes National Park, Freire & Judziewicz 22-737 (HAVO).

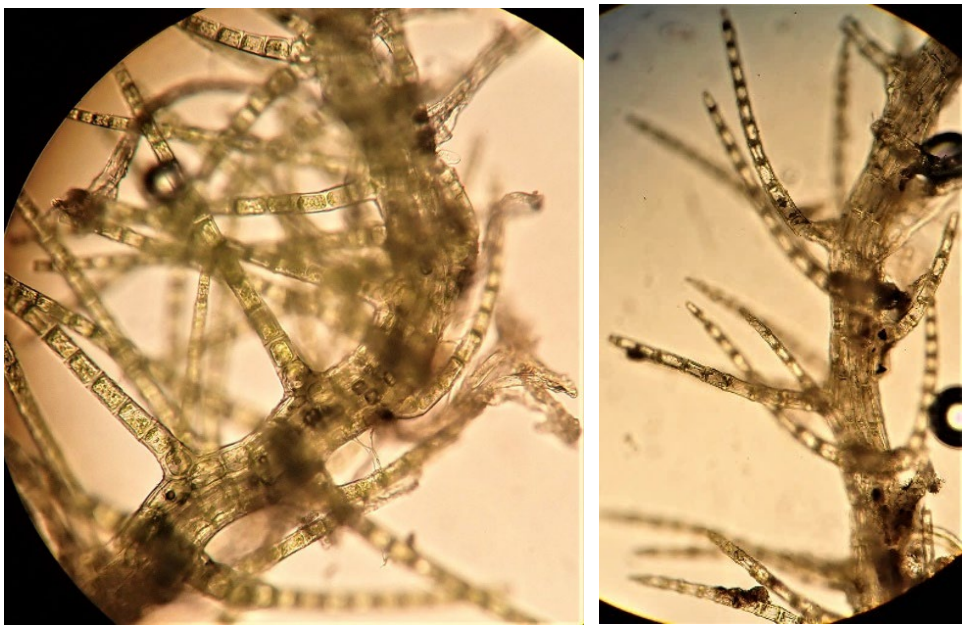
Left: As epiphyte on the hornwort *Phaeoceros carolinianus*. Right: Segment of leaf lobe; middle cells are 2.2 times longer than broad. Freire et al. 23-68 (BISH).



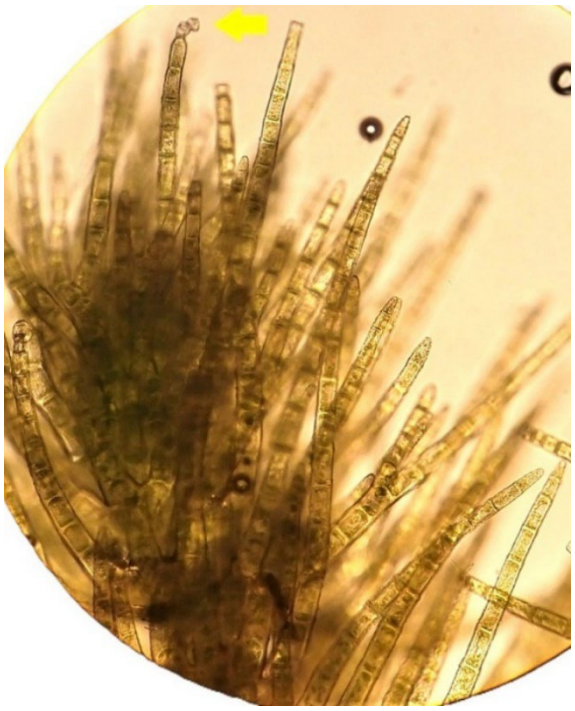
Blepharostoma trichophyllum. Plants are small, up to 0.5 mm wide. Left: Waikamoi, Haleakalā, Maui, Freire, Judziewicz, Oppenheimer & Pezzillo 23-68 (BISH). Photo by A.V. Freire. Right: Upper Kahuku Unit, Hawai‘i Volcanoes National Park, Freire & Judziewicz 22-697a (HAVO). Scales in mm.



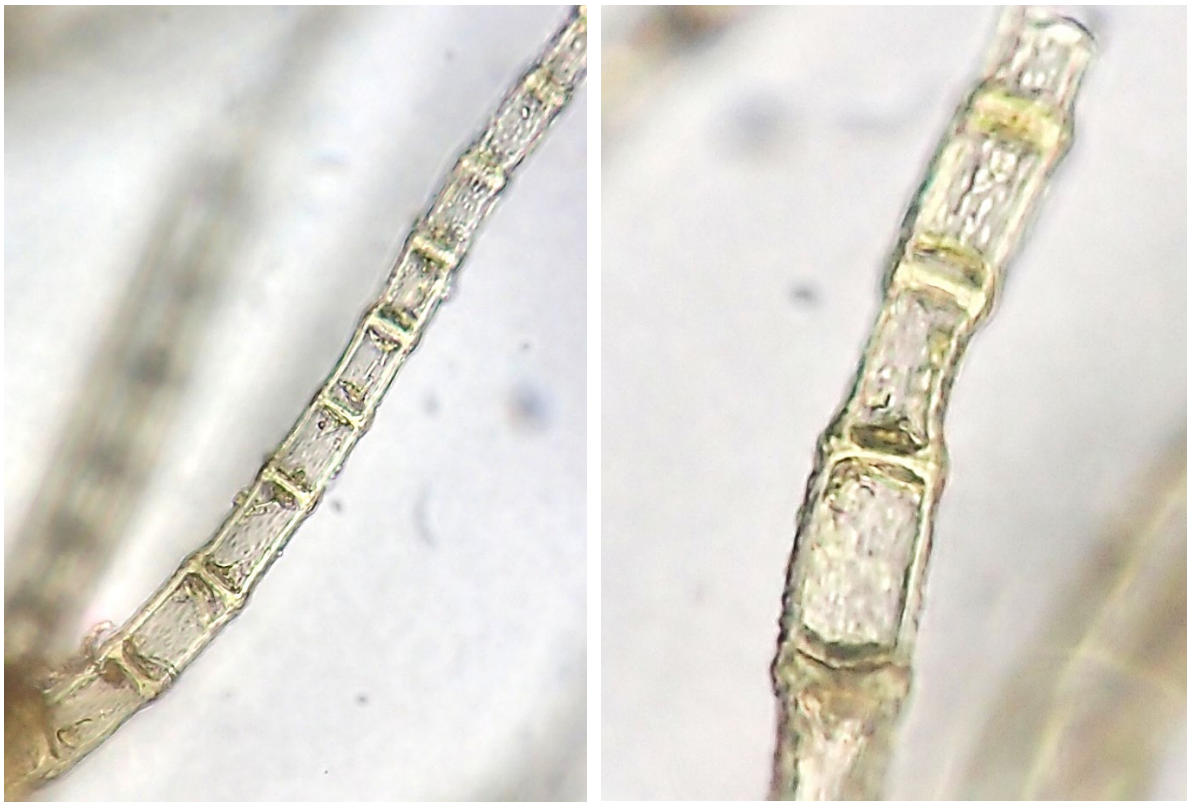
Leaf lobes (cilia) are 10-11 cells long. Lobes are joined by a single cell at their base (arrow). Note the faintly brownish-tinged rhizoids (upper right). Waikamoi, Haleakalā, Maui, Freire et al. 23-68 (BISH).



Blepharostoma trichophyllum. Leaves lobes, 10 or more cells long and one cell wide. Upper Kahuku Unit, Hawai‘i Volcanoes National Park, Freire & Judziewicz 22-697a (HAVO).



Note gemmae at leaf tips (yellow arrow), suggesting long-distance dispersal to Hawai‘i. Upper Kahuku Unit, Hawai‘i Volcanoes National Park, Freire & Judziewicz 22-697a (HAVO).



Blepharostoma trichophyllum. Leaf cell walls are thick and striate. Kīpahulu, East Maui, Pratt 1393d (HAVO). Photos by A.V. Freire and E.J. Judziewicz.

Calypogeia Raddi (Calypogeiaceae)

Four species in Hawai‘i; 59 species worldwide.

Growing on bark, soil, rock or decaying wood, often creeping several centimeters on these surfaces in elegant lines, often in deep shade and frequently associated with thalloid liverworts and hornworts. The leaf arrangement is incubous. Leaves lack lobules and their apices are rounded, cuspidate, acuminate, or minutely bifid. Their coarsely segmented oil bodies often give the young shoots a bluish cast. Underleaves are present and usually bifid but can be slightly quadrifid. Plants are monoicous, with short male and female ventral branches. Sporophytes are enclosed by a fleshy marsupium. *Calypogeia* differs from *Metacalypogeia alternifolia* and *Mnioloma fuscum* in its deeply bifid rather than entire or slightly notched underleaves (except for the rare *C. aeruginosa*, which has rounded underleaves). See Cooke (1904) and Bakalin et al. (2020a, 2022b); *C. arguta* has been transferred to the genus *Asperifolia* (Bakalin et al. 2022b).

1. Underleaves imbricate, entire to shallowly notched, five or more times as wide as the stem; plants brown or black, cylindrical; leaves not spreading, strongly cupped; rare, Kaua‘i ……..…. ***C. aeruginosa***
1. Underleaves distant to contiguous, bifid or bisbifid, up to three times as wide as the stem; plants green, Olive, or bluish-green, flat; leaves spreading, slightly if at all concave; common ….....……. **2**
   2. Underleaves with lateral “elbows” or small teeth so as to be slightly bisbifid, 3 times as broad as stem; leaves notched at apices, sometimes notches present in only a few leaves per plant ……..… ***C. tosana***
   2. Underleaves mostly bifid, without lateral “elbows” or small teeth on the main stem (but those could be present on lateral branches), less than 3 times as broad as the stem; leaves not notched at their apices (but occasional notched leaves may be present on lateral branches in *C.* cf. *confertifolia*) ……..….... **3**
      3. Plants 2.5-2.8 mm wide, underleaves 1.5-2.3 times broader than the stem, with rounded lobe tips and a border of narrow, transversely elongated cells when on main stems ….. ***C.* cf. *confertifolia?***
      3. Plants up to 2 mm wide; underleaves up to 1.5 times broader than the stem, with pointed lobe tips and lacking a border of elongated cells..…….……..…….…….…… ***C. cuspidata***

Left: *Calypogeia* species (mixed with moss *Fissidens* species), showing blue-green color of plants, Kaua‘i, Flynn 9672 (PTBG), photo by E.J. Judziewicz. Scale in mm. Right: *Calypogeia tosana,* ventral view. Note notched leaves, and prominent bisbifid underleaves; O‘ahu, photo by Miles K. Thomas, with permission.

1. *Calypogeia aeruginosa* Mitt. **Indigenous. Rare.** An eastern Asian species (Sun et al., 2018: 160) known from 4,000-12,000 ft in China, India, Taiwan, and Vietnam; disjunct on Kauaʻi, where it is rare in the bog at the summit of Mt. Waiʻaleʻale (5,100 ft.; Miller, 1963: Cranwell et al., Hawaiian Bog Survey 5100, 5237, Stockholm Herbarium, also at MU). Not seen again after these 1938 collections, and there is no material at either BISH or PTBG (Judziewicz, Faccenda & Freire, 2025: 60-61).

These striking plants have very broad holostipous (entire) underleaves and are blackish in color when dry; they could be mistaken for a holostipous Lejeuneaceae, but the leaves lack lobules. Plants are black to dark brown when dry, about 1.5 mm wide, cylindrical (vermiform), terricolous, prostrate (?); they form dense mats in wet areas. Stems are firm, rarely branched. Leaves are overlapping, orbicular, slightly broader than long, entire, concave, strongly cupped towards the ventral side of the plant, with margins inrolled ventrally, very slightly obtusely cuspidate or rounded apically. Median leaf cells are squarish to rectangular, with moderately thickened brown walls and without trigones. A border of narrow, rectangular cells is present but not always clearly defined. Underleaves are imbricate, large (about 0.7-0.8 mm wide), 4-5(-6) times the stem width, round, broader than long, conspicuously auriculate, with strongly curved insertion, and reflexed margins; some have a shallowly emarginate apex (see Miller's illustration below; we did not observe this feature).

After treating the Hawaiian specimen as *Calypogeia aeruginosa* var. *waialealeensis* H.A. Mill. & Kuwah. (Miller, 1963) and then elevating it to *C. waialealeensis* (H.A. Mill. & Kuwah.) H.A. Mill. (Miller, 1967), Miller recognized it as *C. aeruginosa* (1983). However, Bakalin et al. (2020a) question whether Hawaiian material is conspecific with Asian populations, which are recorded as occurring on open, moist cliffs and in wet sandy soil adjacent to streams. We studied the specimen collected in 1938 by Cranwell, Selling & Skottsberg 5237, on Kauaʻi, near the summit of Mt. Waiʻaleʻale (MU), and compared it with several descriptions and diagrams of *C. aeruginosa* (Mitten, 1860; Singh & Singh, 2008; Yang & Lin, 2009; Bakalin et al., 2020a). Although the plants are smaller than reported by Singh & Singh (2008) and Yang & Lin (2009), they fall within the size range according to Bakalin et al. (2020a). The leaf cell walls are thicker than reported, but there are no other differences, and we conclude that the Hawaiian specimen is *C. aeruginosa*.

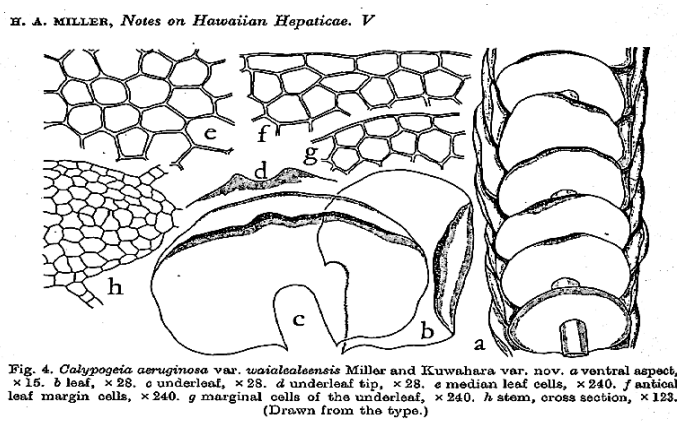
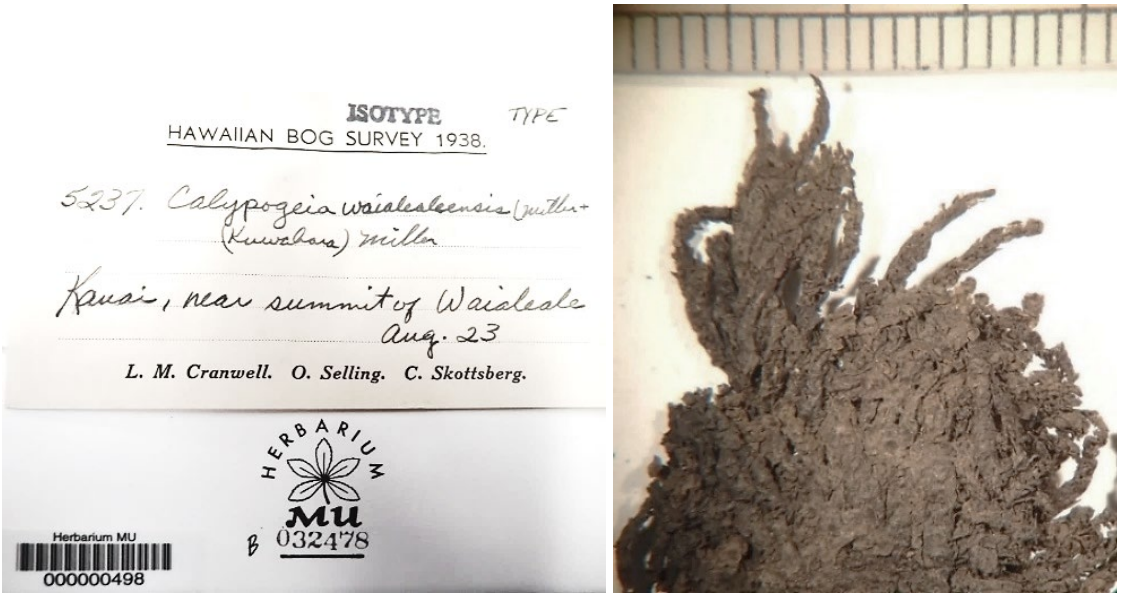


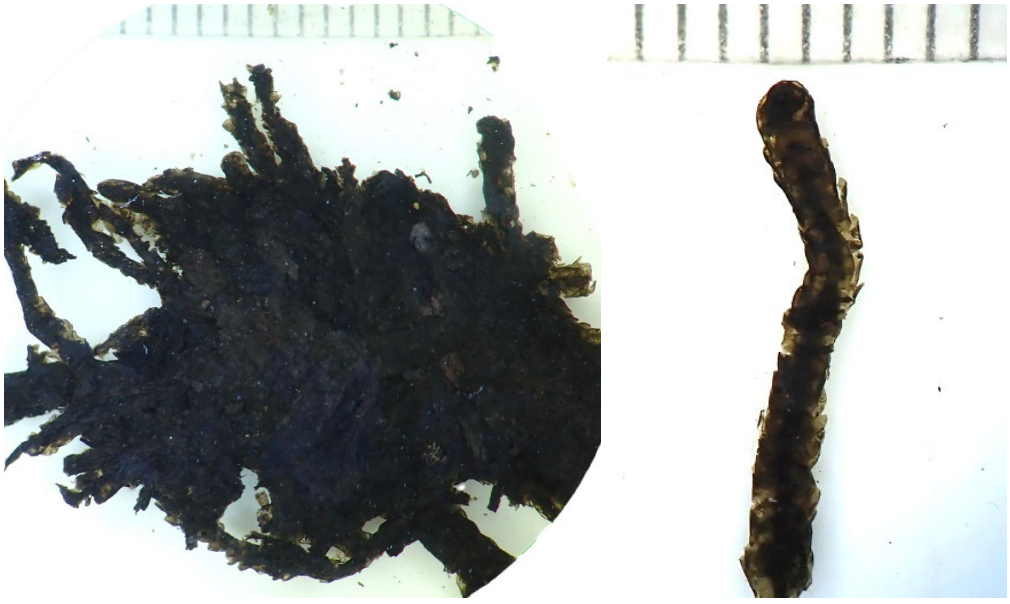
Fig. 4. *Calypogeia aeruginosa* var. *waialealeensis* Miller and Kuwahara var. nov. *a* ventral aspect, ×15. *b* leaf, ×28. *c* underleaf, ×28. *d* underleaf tip, ×28. *e* median leaf cells, ×240. *f* antical leaf margin cells, ×240. *g* marginal cells of the underleaf, ×240. *h* stem, cross section, ×123. (Drawn from the type.)

Above is Miller's (1963; Arkiv för Botanik 5(2): 489–531) figure based on Cranwell, Selling & Skottsberg 5100 and 5237, where he treated it as *Calypogeia aeruginosa* var. *waialealeensis*. Note the moderately thickened leaf cell walls (e), the border of horizontally oriented leaf cells (f), the shallowly emarginate and large underleaves, and the cupped leaves.

All pictures below are of Cranwell, Selling & Skottsberg 5237, Kauaʻi, near the summit of Mt. Waiʻaleʻale (MU), photos by A.V. Freire unless otherwise indicated.

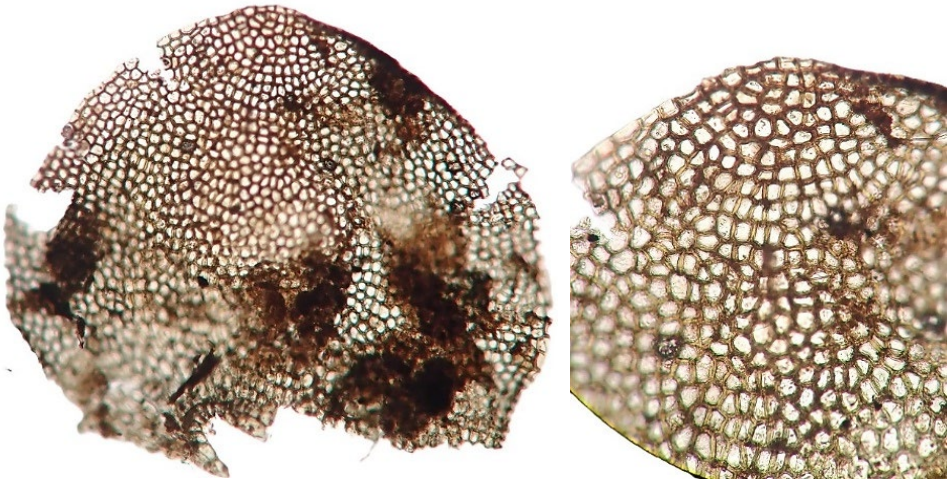


Left: We examined the type of *C. waialealeensis*, a name later reduced by Miller to *C. aeruginosa*. Right: Plants are sometimes brown when dry. They grow forming dense mats. Their aspect indicates a wet habitat. Scale in mm. Photo by E.J. Judziewicz.

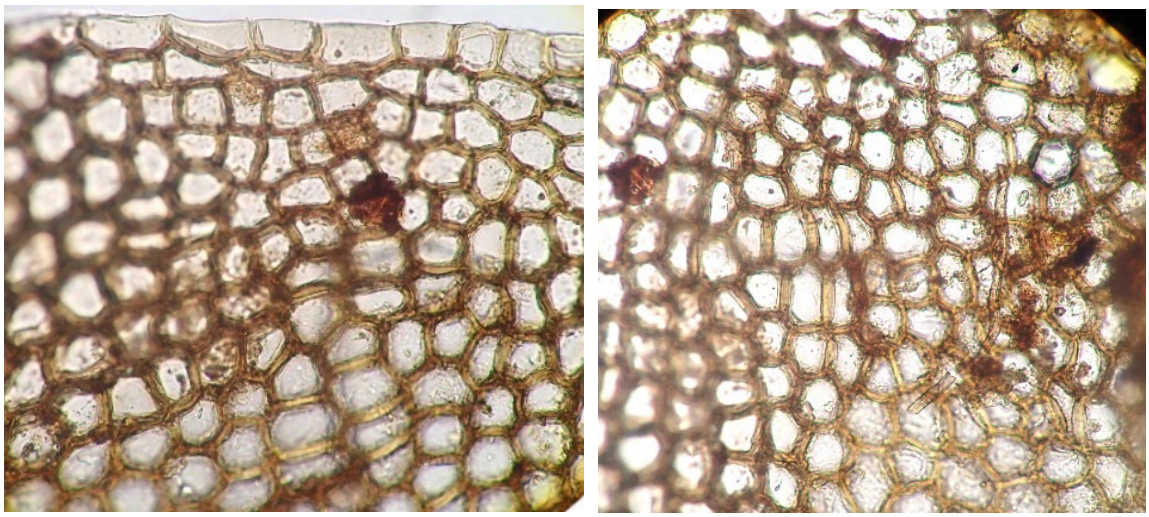


Calypogeia aeruginosa. Left: Plants can be black. Right: Plants are about 1.5 mm wide and are cylindrical (vermiform). Scales in mm. Kauaʻi, Cranwell et al. 5237 (MU). Photos by A.V. Freire.

Left: Dorsal view showing imbricate and concave leaves. Center: Underleaves are large, broader than long, and imbricate. Right: Leaves do not spread, they are cupped towards the plant's ventral side and have inrolled margins. Cranwell et al. 5237 (MU). Photos by A.V. Freire.



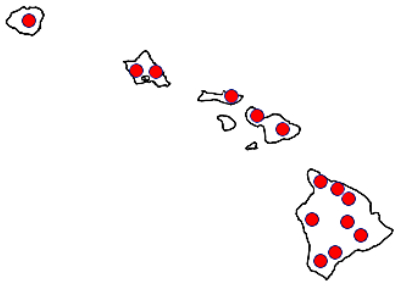
Calypogeia aeruginosa. Kaua'i, Cranwell et al. 5237 (MU). Leaves are rounded, but slightly broader than long. Right: Detail of slightly cuspidate apex. Photos by A.V. Freire.



Left: Detail of leaf border formed by horizontally elongated marginal cells with thin outer walls (above). This border is not always well defined. Right: Median leaf cells appear thick-walled. Cranwell et al. 5237 (MU). Photos by A.V. Freire.

Calypogeia aeruginosa. Left: Underleaves are auriculate and with a very arched insertion. Center: Detail of holostipous underleaf. Right: Underleaves are nearly 1 mm wide. Scale = 1 mm. Kaua‘i, Cranwell et al. 5237 (MU). Photos by A.V. Freire.

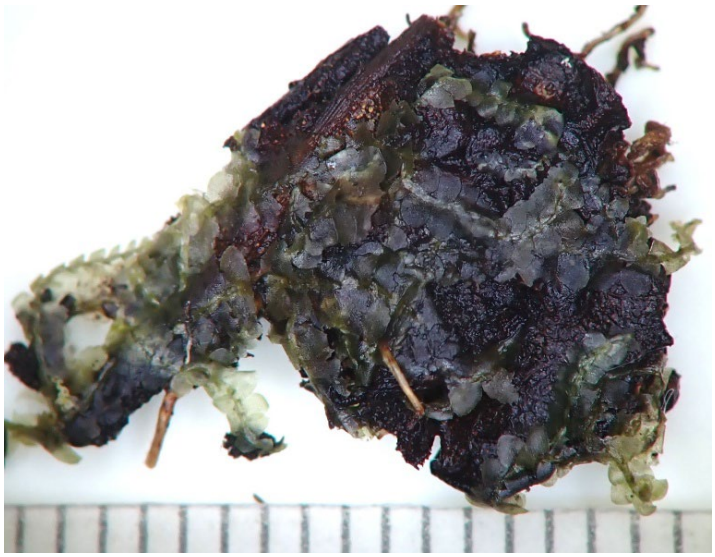
2. *Calypogeia cuspidata* (Steph.) Steph. **Indigenous.** On all major islands except Lānaʻi (2,000-7,000 ft.). Usually found on shaded soil or humus. A common and variable species also present in China and Vietnam (Bakalin et al., 2022b). It can be recognized by its leaves with pointed, rounded, or cuspidate apices; they are never notched. Underleaves are bifid, with a deep, acute sinus to beyond one-half of their length. Clusters of gemmae are produced from the stem tips.



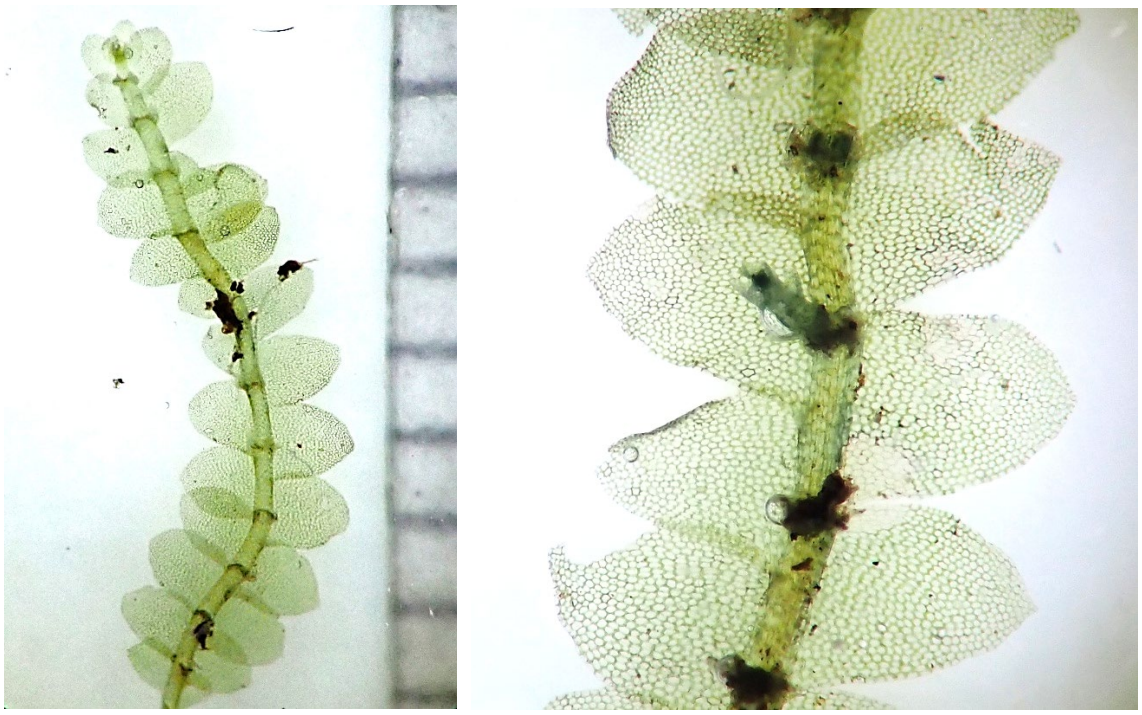
According to Miller et al. (1983) and Staples & Imada (2006), *Calypogeia confertifolia* (Steph.) and *C. hawaica* (Steph) are synonyms of *C. cuspidata*; however, see discussion under *Calypogeia* species 1. Plants grow in loose mats, they are fragile, translucent, shiny, blue-green, around 2 cm long and 2 mm wide, prostrate, but are loosely attached to their substrate. Stems are fragile and flexuous, with few intercalary branches. Leaves are contiguous to imbricate, alternate, flat to slightly concave (lengthwise), spreading, ovate, entire, with pointed, cuspidate, or rounded apices. Cells are isodiametric to elongate, with thin cell walls and a smooth surface; minute trigones may be present. Underleaves are distant, small, up to 1.5 times as broad as the stem, spreading at a (usually) broad angle, frequently squarrose, and bifid; they are divided beyond half their length, sometimes almost to their base, by a broad "V"- or "U"-shaped sinus that separates the two acute lobes.

Calypogeia cuspidata is most closely related to the Asian species *C. apiculata* (Steph.) Steph. The two species are morphologically similar; the most distinct and seemingly stable character is the smooth surface in *C. cuspidata* versus verruculose in *C. apiculata* (Bakalin et al., 2022b). The same authors separate the two species with molecular work, however, material from Hawaiʻi was not included in their analysis. More work to compare *C. cuspidata* from Hawaiʻi with *C. apiculata* is needed.

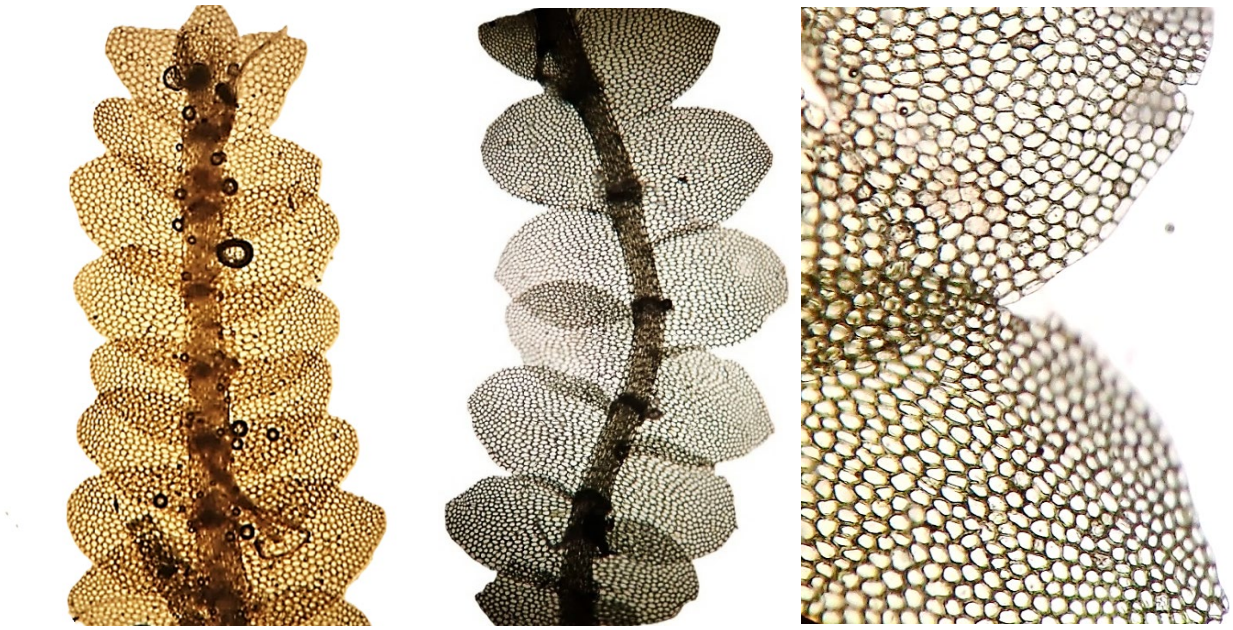
Calypogeia cuspidata. The young leaves are often bluish, especially at the plant apex (where leaves are youngest) due to the presence of azulene derivatives in the oil bodies (Bakalin, 2022b: 27). They are especially evident in young, expanding shoots. Above, Saddle area, Hawaiʻi Island, Freire & Judziewicz 21-1000 (BISH).



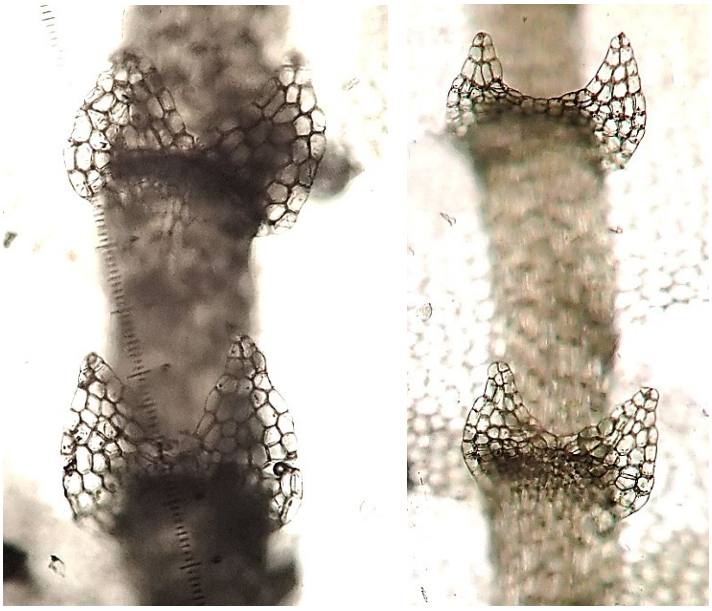
Plants are fragile, translucent and shiny. They form loose mats loosely appressed to their substrate. Freire & Judziewicz, 21-1000 (BISH).



Calypogeia cuspidata. Plants are fragile, with flexuous stems, and about 2 mm wide (left, scale in mm). They are rarely branched. Note the bluish young intercalary branch at the underleaf axis and the contiguous to slightly overlapping leaves (right). Saddle area, Hawai‘i Island, Freire & Judziewicz 21-1000 (BISH).

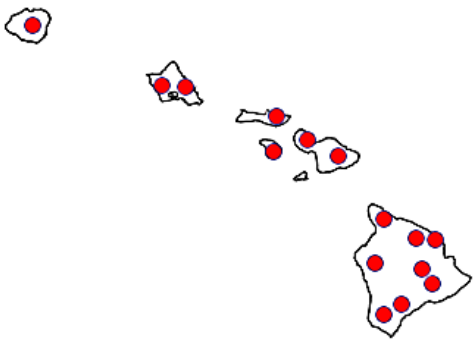


Leaves are flat, spreading, overlapping (left) to contiguous (center). Leaf apices are variable, rounded to pointed. Underleaves are often squarrose. Right: Leaves have a border of narrow cells. The thin-walled leaf cells lack or have minute trigones. Left: Volcano, Hawai‘i, Freire & Judziewicz 20-73 (HAVO). Center and right: Freire & Judziewicz 21-1000 (BISH).



Calypogeia cuspidata. Underleaves are 1.5 times as broad as the stem. They are bifid, with acute lobe tips. They have a deep and broad sinus to more than half their length. The sinus can be “V”-shaped (left) or “U”-shaped (right). They project from the stem at usually wide angles. Saddle area, Hawai‘i Island, Freire & Judziewicz 21-1000 (BISH).

3. *Calypogeia tosana* (Steph.) Steph. **Indigenous.** An eastern Asian species, disjunct in Hawai‘i (Sun et al. 2018). On all major islands (500-8,500 ft.). *C. tosana* is most closely related to the Asian species *C. yoshinagana* Steph. (Bakalin et al., 2022b). The elongate stems grow trailing in moist, deep shade. This is a common species, larger than *C. cuspidata. C. tosana* has leaf tips with shallow notches; these are intermixed with leaves without a notch, and instead with round or cuspidate to occasionally acuminate apices. Clusters of gemmae are produced from stem tips. Underleaves are bifid to about ½ of their length, with lateral elbows or teeth that make them somewhat bisbifid.



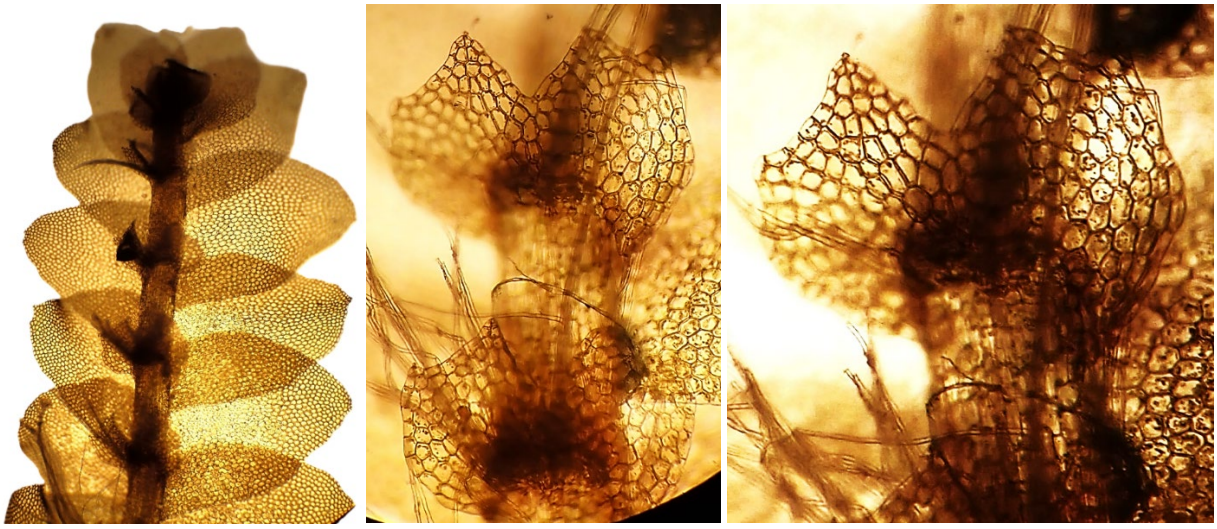
Plants are blue-green, appressed and creeping; the stems are fleshy, up to 5-6 (or occasionally more) cm long, with few intercalary branches, and are (2-)2.5-3 mm wide. Leaves are flat, ovate, imbricate, usually pointed and notched at the apex, with two tiny teeth, these just (1)2-3 cells long. Some plants may lack notched leaves and instead have apiculate, rounded or truncate apices. Mixes of notched and un-notched leaves are sometimes found on the same plant. Leaf cells are thin-walled and lack trigones; oil bodies are coarsely segmented (botryoidal), with a violet color. Underleaves are distant, broader than long, 2(-3) times the stem width, with two large lobes separated by a “V”-shaped sinus up to the middle (occasionally deeper). A small lateral protuberance or small tooth is present on the lateral margins of the lobes making the underleaves bis-bifid or nearly so. Gemmae are produced at the tips of stems. Leaves of irregular size and number of teeth (up to 5) may be present on gemmiferous branches.

Calypogeia tosana. Populations grow on shaded pockets of soil or rock; plants trail loosely. Nāhuku, Hawai‘i Volcanoes National Park, Hawai‘i Island, Freire & Judziewicz 21-195 (HAVO).

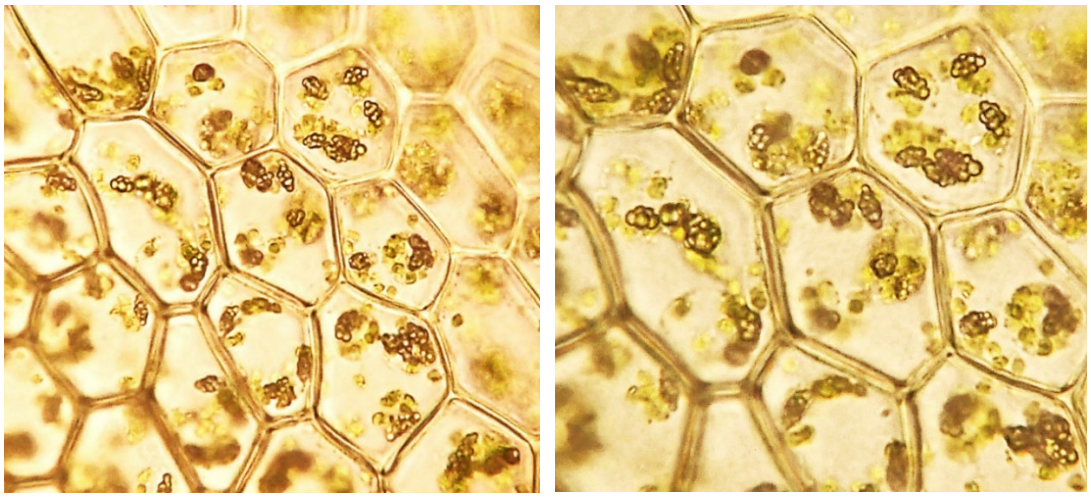
Long, prostrate and trailing blue-green plants. Nāhuku, Hawai‘i Volcanoes National Park, Hawai‘i Island, Freire & Judziewicz 21-195 (HAVO).

Calypogeia tosana. Plants are usually large and robust. Note that they produce occasional small intercalary branches. Kahuku Unit, Hawai‘i Volcanoes National Park, Hawai‘i Island, Freire & Judziewicz 22-877 (HAVO).

Leaves are mostly shallowly bifid, but some can be apiculate, rounded, or truncate at the apex. Left: Lānaʻi, Freire & Judziewicz 22-286a (BISH). Right: Freire & Judziewicz 22-877 (HAVO).

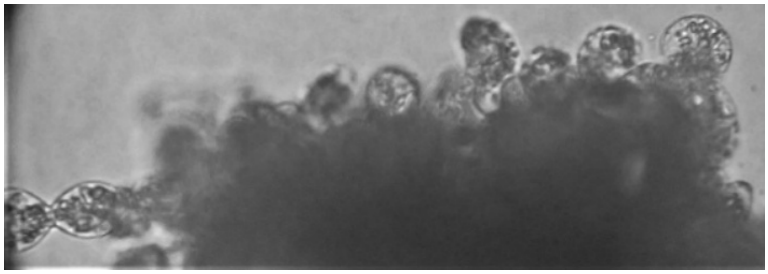


Calypogeia tosana. Left: The underleaves are about 3 times broader than the stem, and distant. Note the variability of leaf apices. Center and right: Underleaves with "V"-shaped sinuses to about 1/2 the underleaf length. Note lateral "elbows" or small protuberances or teeth that give the underleaf a bisbifid appearance. Kahuku Unit, Hawaiʻi Volcanoes National Park, Hawaiʻi Island, Freire & Judziewicz 22-877 (HAVO).



Median leaf cells with thin walls and no trigones; the oil bodies are small and botryoidal (like a cluster of grapes). Kahuku Unit, Hawai‘i Volcanoes National Park, Hawai‘i Island, Freire & Judziewicz 22-877 (HAVO).

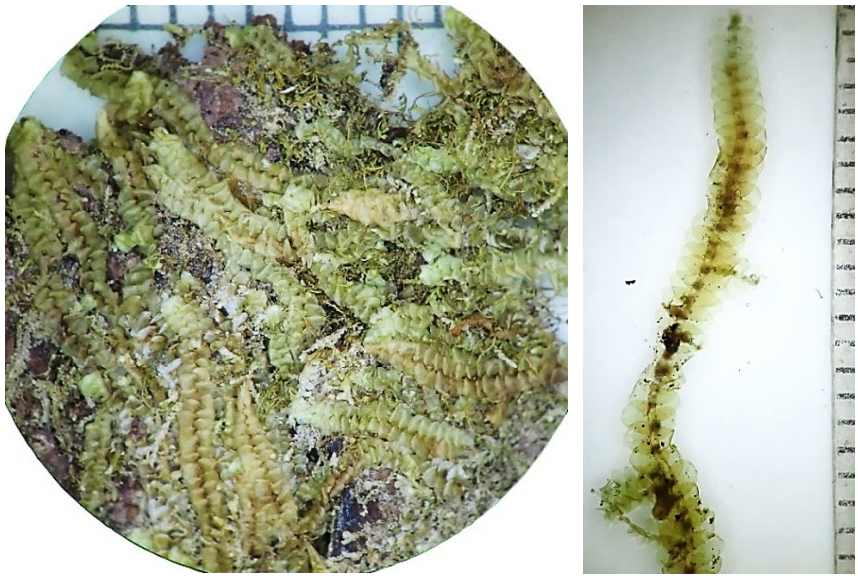
Gemmiferous shoots with apical clusters of elliptical gemmae. Note the irregular number and shape of teeth (where gemmae are produced). Freire et al. 23-68 (BISH).



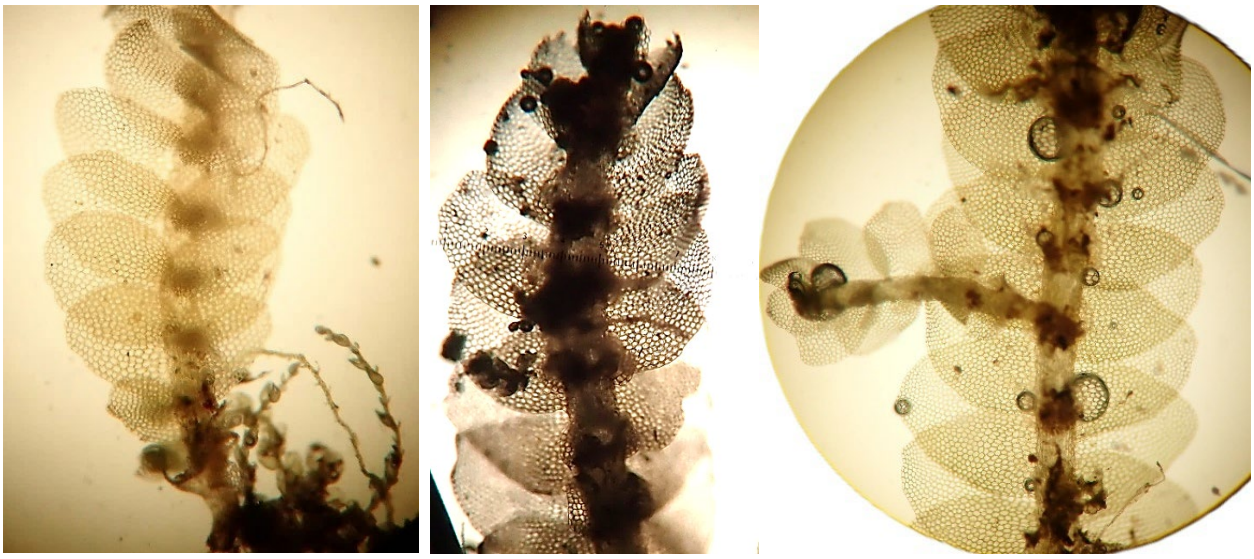
Calypogeia tosana. Detail of gemmae. Waikamoi Preserve, Haleakalā, Maui; Freire, Judziewicz, Oppenheimer & Pezzillo 23-68 (BISH).

4. *Calypogeia* cf. *confertifolia* Steph. **Endemic.** The following specimen was collected by A.V. Freire & E.J. Judziewicz 23-467, Volcano, Hawai‘i Island (BISH). We initially identified it as *C. cuspidata* because of the small bifid underleaves and the leaf apices without a notch. After careful study, we conclude that the general appearance of the plants is different from the former species. They are more robust, not as fragile or translucent. On a single plant, apices are truncate, rounded, acute, apiculate and some leaves on lateral branches are notched. The underleaves are broader, with narrower sinuses to about ½ their length, they usually have a border of narrower cells and most have rounded lobe apices. Sometimes they can have lateral teeth or rudimentary elbows (on lateral branches). We think this is a distinct species. Could it be *C. hawaica* Steph. or *C. confertifolia* Steph.? These two species were reduced to synonymy under *C. cuspidata* by Miller et al. (1983). Bakalin et al. (2020) questioned both reductions but kept the synonyms, recommending more study.

Plants are olive to brownish-green (when dry), up to 5 cm long and 2.5-2.8 mm wide, prostrate and appressed to their substrate, and often associated with *Metalejeunea cucullata*. Stems are fleshy and flexuous, with some intercalary branching. Leaves are alternate, overlapping, flat to slightly concave (but with apices curving down), spreading, ovate, entire on the main stem but some irregularly notched on lateral branches. Leaf apices are rather variable within single plants; they can be rounded, apiculate, truncate, cuspidate, or sometimes notched (on lateral branches). Cells are isodiametric to elongate, with cells, minute trigones, and marginal quadrate cells. The plant surface is smooth. Underleaves are appressed to slightly reflexed (up to 45˚), 1.5-2.3 times as broad as the stem, always bifid (on the primary stem), with rounded to sometimes pointed apices. They are divided beyond their middle by a “V”- or “U”-shaped sinus. They may have a rather well-defined border of transversely elongated cells. Some underleaves with 3 or 4 lobes are observed on lateral branches, close to the branch origin. Morphologically, this population fits the description of *C. confertifolia* provided by Bakalin et al. (2020) based on the type specimen in Geneva. Our plants can be slightly broader, and the underleaves mostly have rounded lobe tips. A border on the underleaves is not described by Bakalin et al. but was observed by us. Also, we did see a few notched leaves and quadrifid underleaves on lateral branches. We think this is a different species – perhaps *C. confertifolia*.

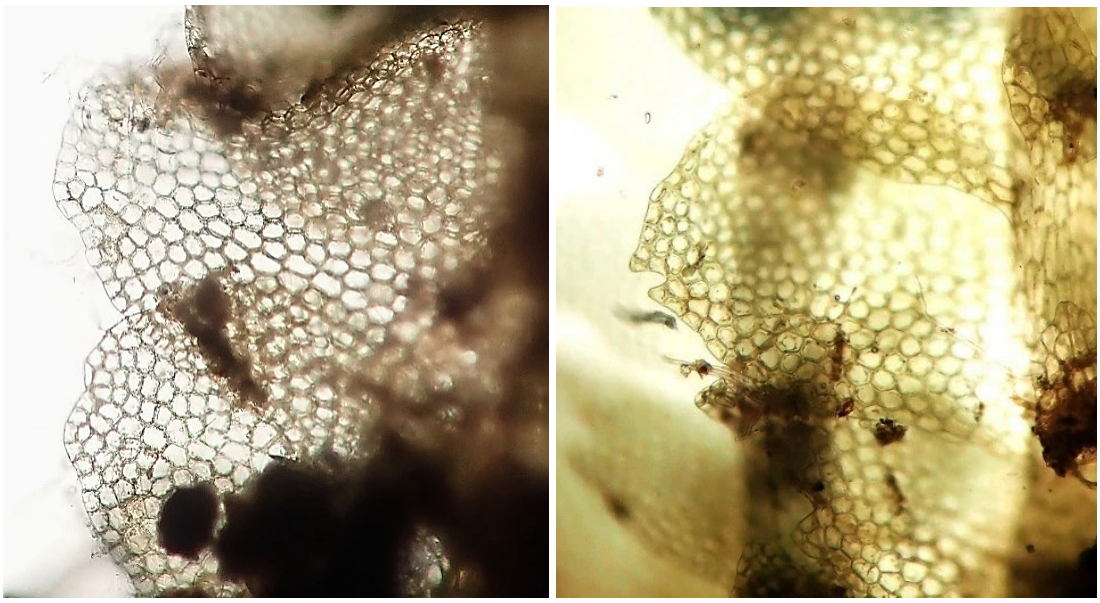


Left: Plants grow apressed to their substrate, and are associated with small leafy liverworts such as *Metalejeunea cucullata*. Right: Plants can be several centimeters long and almost 3 mm wide. Volcano, Hawai‘i Island, Freire & Judziewicz 23-467 (BISH).

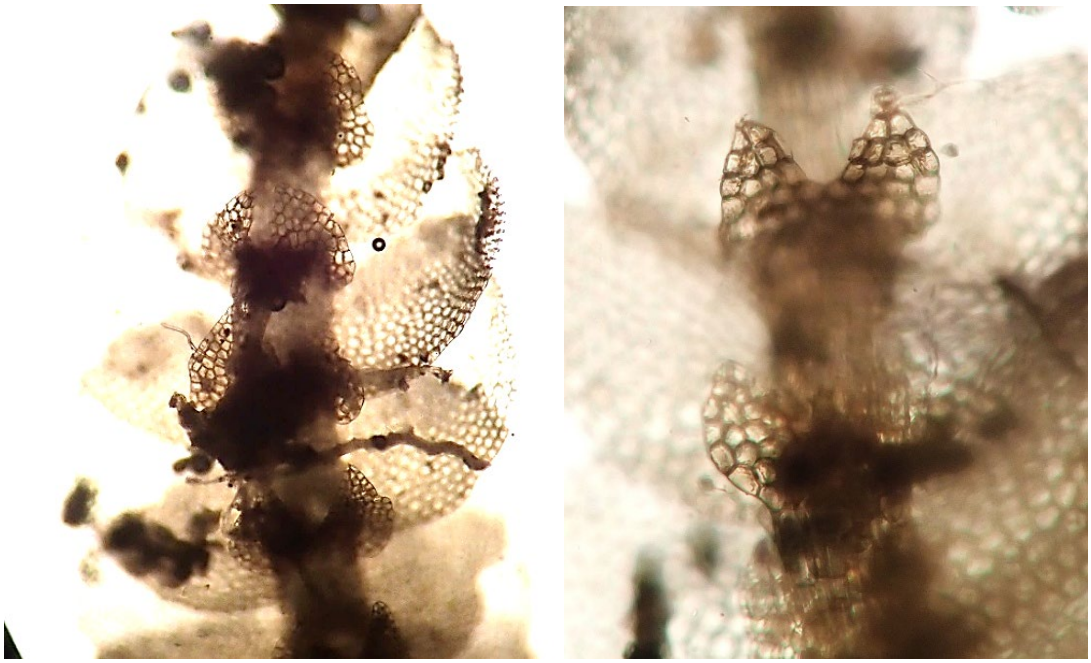


Left: Plant dorsal side showing insertion to beyond stem midline. Center: Leaves are transversely concave, with cupped apices. Right: Leaves overlap to about ½ their width. Freire & Judziewicz 23-467 (BISH).

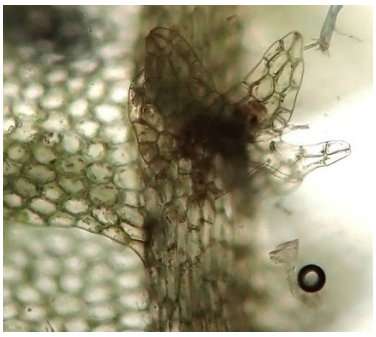
Calypogeia cf. *confertifolia*. Variation of leaf apices on primary stem. Some are rounded, truncate, cuspidate or apiculate. Volcano, Hawai‘i Island, Freire & Judziewicz 23-467 (BISH).



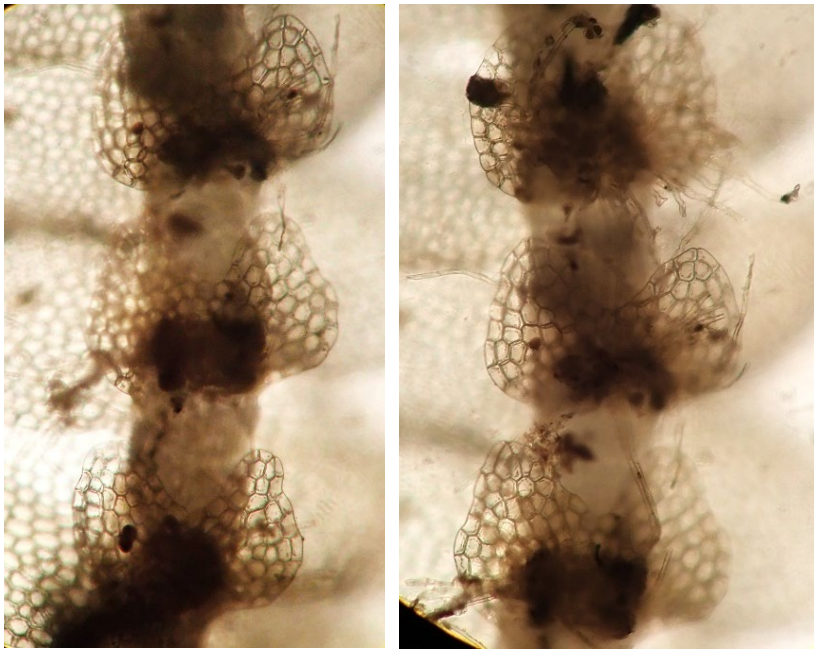
Left: Truncate apices are present. Note thin-walled leaf cells, and border of quadrate cells. Right: Occasionally, leaves on lateral branches are notched. Freire & Judziewicz 23-467 (BISH).



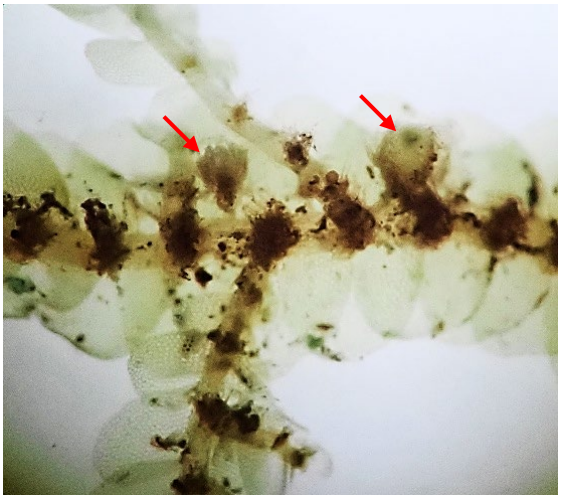
Calypogeia cf. *confertifolia*. Underleaves are deeply divided and can be up to 2.3 times broader than the stem. They project at 45° angles from the stem. Volcano, Hawai‘i Island, Freire & Judziewicz 23-467 (BISH).



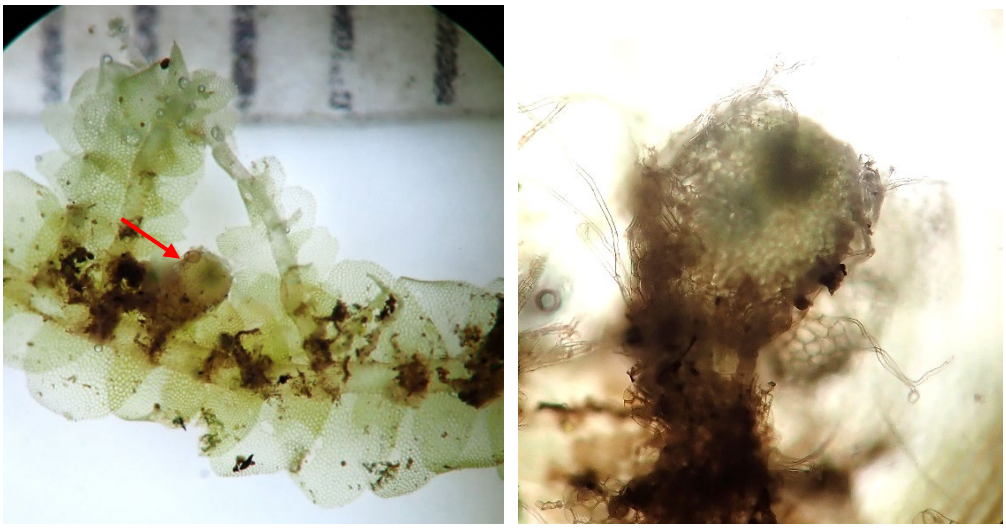
Rarely, a quadrifid underleaf is present close to the base of the lateral branches. Freire & Judziewicz 23-467 (BISH).



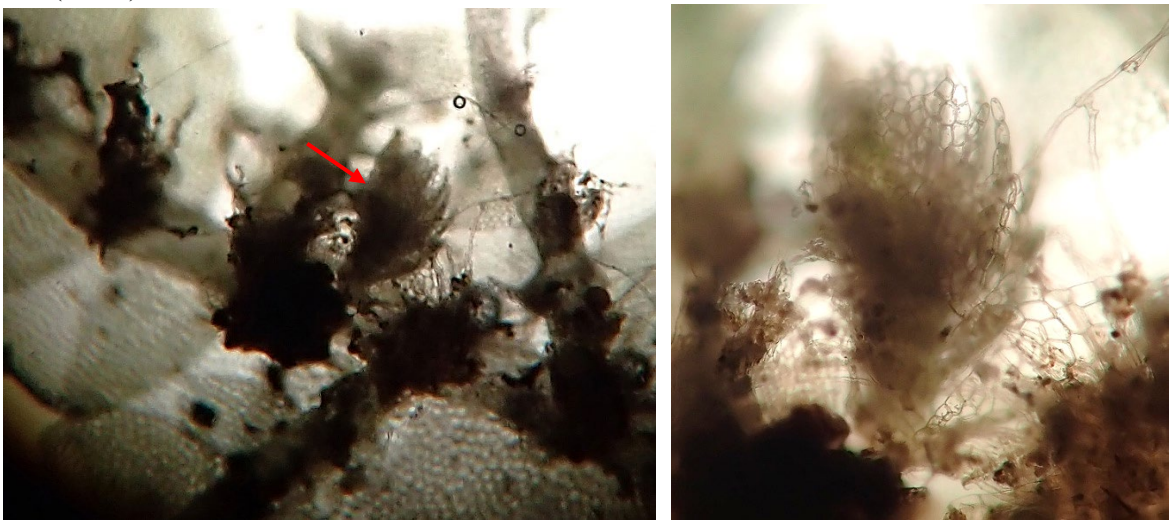
On the primary stem, the underleaves are distant to approximate, with arched insertion, slightly decurrent, with rounded lobe tips, always bifid and with a border of elongate cells. Freire & Judziewicz 23-467 (BISH).



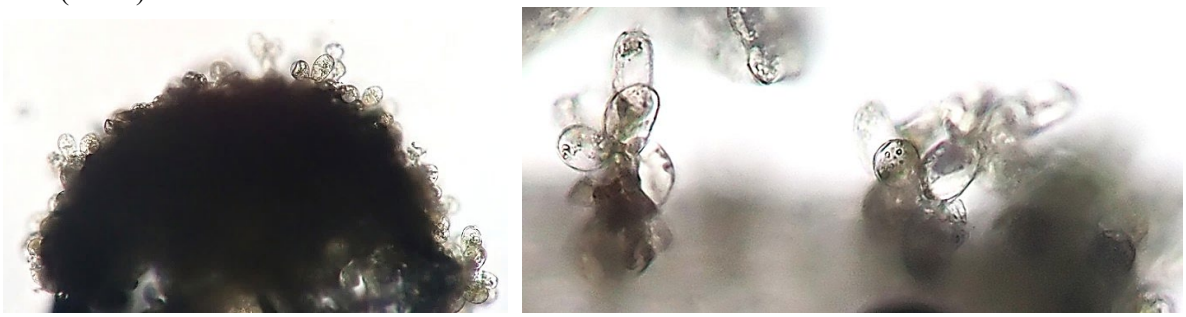
Calypogeia cf. *confertifolia*. Plants are monoicous. With short ventral male (left) and female (right) branches (arrows). Volcano, Hawai‘i Island Freire & Judziewicz 23-467 (BISH).



Plant with short ventral female branch bearing a fleshy marsupium (arrow) (scale in mm). Detail of marsupium enclosing a developing sporophyte. Note rhizoids on its surface (right). Freire & Judziewicz 23-467 (BISH).



Left: Male branches are small and ventral (left; arrow). Right: Detail of male branch. Freire & Judziewicz 23-467 (BISH).



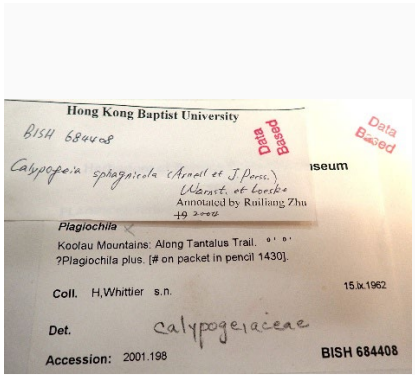
Calypogeia cf. *confertifolia*. Tip of gemmiferous branch (left), detail of elliptical gemmae (right). Volcano, Hawai‘i Island, Freire & Judziewicz 23-467 (BISH).

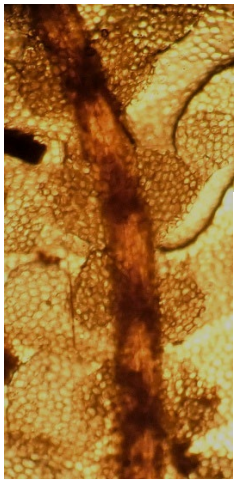
Calypogeia sphagnicola (Arnell & J. Perss.) Warnst. & Loeske was identified from the Tantalus Trail on O‘ahu (2,000 ft.) by R.-L. Zhu based on an H. Whittier collection (BISH) made in 1962. This is a boreal and austral species that is restricted to *Sphagnum* moss bogs.

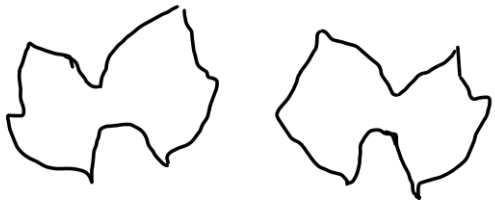
We only have a few preliminary pictures, taken by E.J. Judziewicz, of a single plant. From the limited material available, we can tell that plants are about 2.5 mm broad, have wiry stems, leaves are imbricate, spreading, ovate, apiculate, seemingly flat. Mid-leaf cells are elongate and thin-walled, without trigones. A border of small cells may be present. Underleaves are distant, broader than long, decurrent, with a curved insertion, about 3 times the stem width, appressed (?), with two broad and obtuse quadrate lobes with elbows and a broad and deep sinus, dividing the underleaves to beyond their half. A small tooth may be present only on one side of the underleaf.

Bakalin et al. (2020) mention that *C. sphagnicola* can be mistaken for *C. apiculata*, but in the latter, the underleaves are much smaller than in this specimen, only slightly broader than the stem; they do not have the “elbows” observed in our plant. Schuster (1969) and Paton (1999) describe *C. sphagnicola* as having smaller underleaves that are longer than broad and only 1.2-1.8 times broader than the stem Schuster (1969).

Because of the size and morphology of the underleaves, we think this may be *C. tosana*; also, the comparatively low elevation Tantalus Trail lacks the sphagnous habitat of this species. Tracing of underleaves below by A.V. Freire.



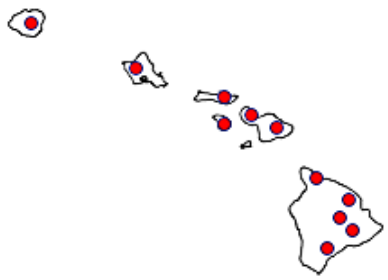




Cephalozia (Dumort.) Dumort. (Cephaloziaceae)

Two or three species in Hawai‘i (Judziewicz & Freire 2023c: 160). 36 species worldwide.

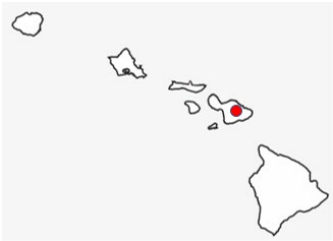
A high elevation genus of wet rocks and montane forests, often growing intertwined with other bryophytes. The delicate, translucent plants with large, thin- to slightly thick-walled cells are very attractive under a microscope. They are easily recognized by their fragile appearance, presence of a hyalodermis, and by their bifid, transverse and concave leaves. Formerly treated as *Metahygrobiella* (Staples & Imada, 2006); see Váňa et al. (2013d). The map on the right shows all collections of all species of *Cephalozia*.



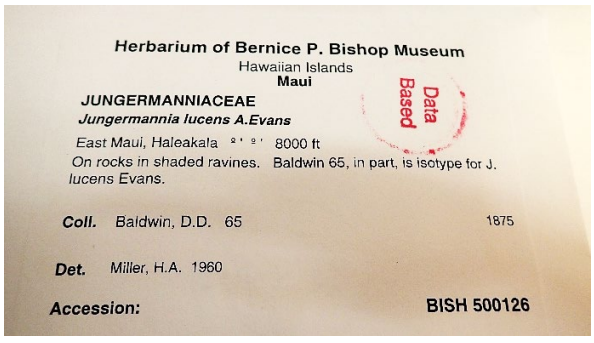
Cephalozia resembles *Fuscocephaloziopsis*, but the leaves are transversely inserted, and the lower margin of each leaf is not decurrent along the stem. Plants are fragile looking, with elongate stems and small and imbricate to distant leaves. This genus needs a thorough revision. There may be other species (here tentatively identified by us as *C. lucens*).

1. Leaves bifid to less than ½ their length, sinus round, leaves concave ……..…. ***C. lucens***
1. Leaves bifid to at least ½ their length, sinus triangular, leaves canaliculate or flat ……..……...…… **2**
   2. Leaves bifid to ½ their length, leaf lobes narrowly lanceolate, with accuminate tips, leaves strongly canaliculate, imbricate to contiguous or uncommonly distant ..……...…… ***C. maxima***
   2. Leaves bifid to more than ½ their length, leaf lobes broadly triangular, with acute tips, leaves weakly canaliculate or flat, always distant ……..…..….. ***C.* aff. *otaruensis***

1. *Cephalozia lucens* (A. Evans) Steph. **Endemic.** Treated as *Metahygrobiella lucens* by Staples & Imada (2006). East Maui (Kīpahulu and Pu‘u Ni‘ani‘au). The concave leaves are divided to less than ½ their length into two triangular lobes and have a broad sinus. We did not collect this species but present our brief study of an isotype collected on Haleakalā, Maui by Baldwin 65 (BISH). It resembles the cosmopolitan *Cephalozia bicuspidata* (L.) Dumort.



Plants are fragile, up to 2-2.5 cm long and 1.2 mm wide. Loosely threading on rock, also likely on soil(?), forming dense mats. Stems are brown and robust; a hyalodermis is not obvious but no stem sections were made. Leaves are distant to contiguous, transversely inserted and spreading, bifid, with broad triangular lobes ending in an acute tip and separated by a broad sinus to less than ½ the leaf length. Leaves are concave so as to appear slightly inflated or pouched. Leaf cells are reported to average 55 µm long by 35 µm wide by Evans (1891); the cell walls are moderately thick. Below: Isotype with long threading plants in dense mats, Maui, Baldwin 65 (BISH). Photos by E.J. Judziewicz.

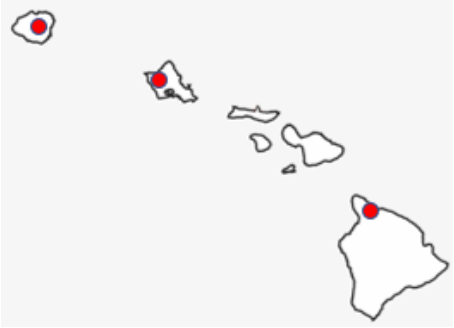

Herbarium of Bernice P. Bishop Museum
Hawaiian Islands
Maui
JUNGERMANNIACEAE
Jungermannia lucens A.Evans
Data Based
East Maui, Haleakala ° ' ° ' 8000 ft
On rocks in shaded ravines. Baldwin 65, in part, is isotype for J. lucens Evans.
Coll. Baldwin, D.D. 65 1875
Det. Miller, H.A. 1960
Accession: BISH 500126

Plants are small, with concave leaves that appear inflated (scale in mm). Baldwin 65 (BISH). Photo by E.J. Judziewicz.

The leaves are concave, bifid, divided to about 1/3 their length, with broad triangular and acute lobes separated by a broad sinus. Baldwin 65 (BISH). Photos by E. J. Judziewicz.

Cephalozia lucens. Cells are pellucid, giving the plant a delicate appearance. Walls moderately thickened. Haleakalā, Maui, Baldwin 65 (BISH). Photo by E. J. Judziewicz.

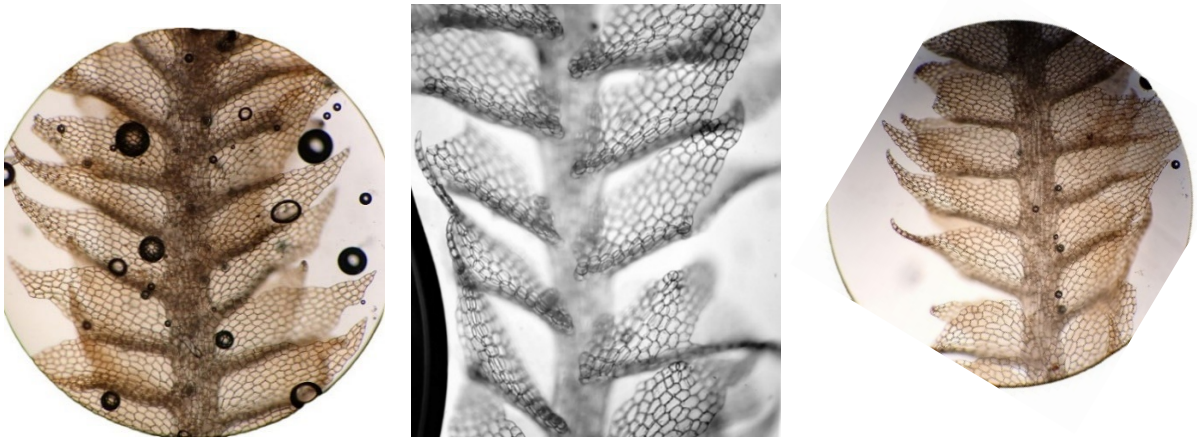
2. *Cephalozia maxima* Steph. Kauaʻi, Lānaʻi, Maui. **Endemic.** Treated as *Metahygrobiella maxima* by Staples & Imada (2006). Elevation 2,250-3,000 ft. Plants with crowded leaves. Leaves are concave and divided to ½ their length into two lanceolate lobes, separated by a broad sinus. This species appears to be most closely related to the Himalayan *Cephalozia albula* Steph. (Kitagawa, 1972: 454). We see intermediate forms between *C. lucens* and *C. maxima* and wonder if they are conspecific.



Plants fragile, transluscent, some with red or brownish tints (but only observed dry), around 1-1.5 cm long (reported 5 cm long by Stephani), up to 1.4 to 2 mm wide. Stems flexuous, with a partial hyalodermis (with a few small epidermal cells among larger ones). Intercalary branches present. Branches and some plants are top heavy, with leaves larger and more crowded towards the middle and tip. Leaves transverse, broadly inserted to the stem midline, non-decurrent, flexuous, imbricate to contiguous or sometimes distant; concave-canaliculate (concave lengthwise), so as to appear folded in half; bilobed, with two long narrow-lanceolate and robust lobes with acuminate tips, separated by a broad sinus to ½ the leaf length. Leaf cells are quadrate to rectangular, thin-walled, without trigones, large, 46-71 µm long by 31-36 µm wide (reported up to 108 µm long by Stephani), with a border of smaller and quadrate isodiametric cells. The leaf margin is irregularly crenulate on the lower half of the lamina.

Leaves crowded to distant, canaliculate, bifid, and acuminate. Note irregular leaf margin of small isodiametric cells. Scales on mm. Kōkeʻe State Park, Kauaʻi, Flynn 5083 (PTBG). Photos by A.V. Freire.

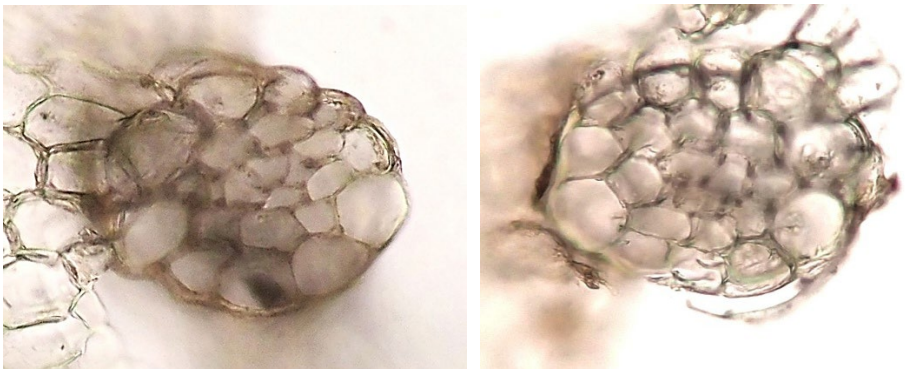
Plants have distant to imbricate leaves. Branches can be top-heavy, with longer leaves towards the middle and upper portions (center). Left: Kauaʻi, Forbes 1648k (BISH). Photo by A. V. Freire. Center and right: Kauaʻi, Flynn 5083 (PTBG), photos by A.V. Freire (center) and E. Judziewicz (right). Scales in mm.



Cephalozia maxima. Examples of plants with bifid leaves divided to ½ their length, inserted to the stem midline, not decurrent. Note the bordered leaf margins and pellucid cells. Kōkeʻe State Park, Kauaʻi, Flynn 5083 (PTBG). Photos by A.V. Freire.

Left: Young leaf. Center and right: two views of the same mature leaf. Note deep sinus and narrow-lanceolate leaf lobes with acuminate leaf apices. Also note the irregular lower margins. Flynn 5083 (PTBG). Photos by A.V. Freire.

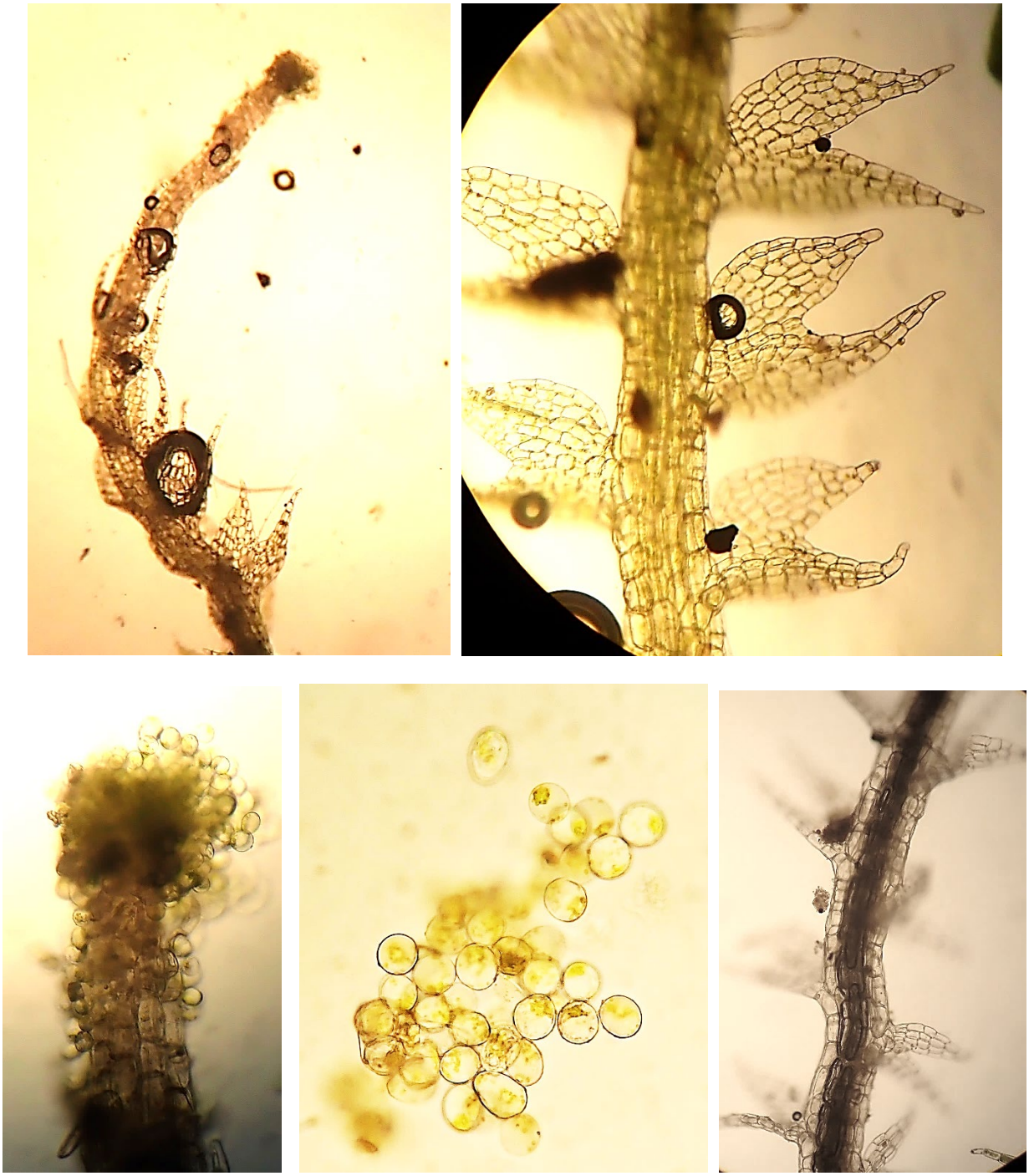
Leaf cells are rectangular to quadrate, large and thin-walled. Photographs of Flynn 5083 (PTBG). Photos by A.V. Freire.



Cephalozia maxima. Stems have an outer layer of large cells but have a few smaller cells intermixed. Kōkeʻe State Park, Kauaʻi, Flynn 5083 (PTBG). Photos by A.V. Freire.

The following specimens require detailed study.

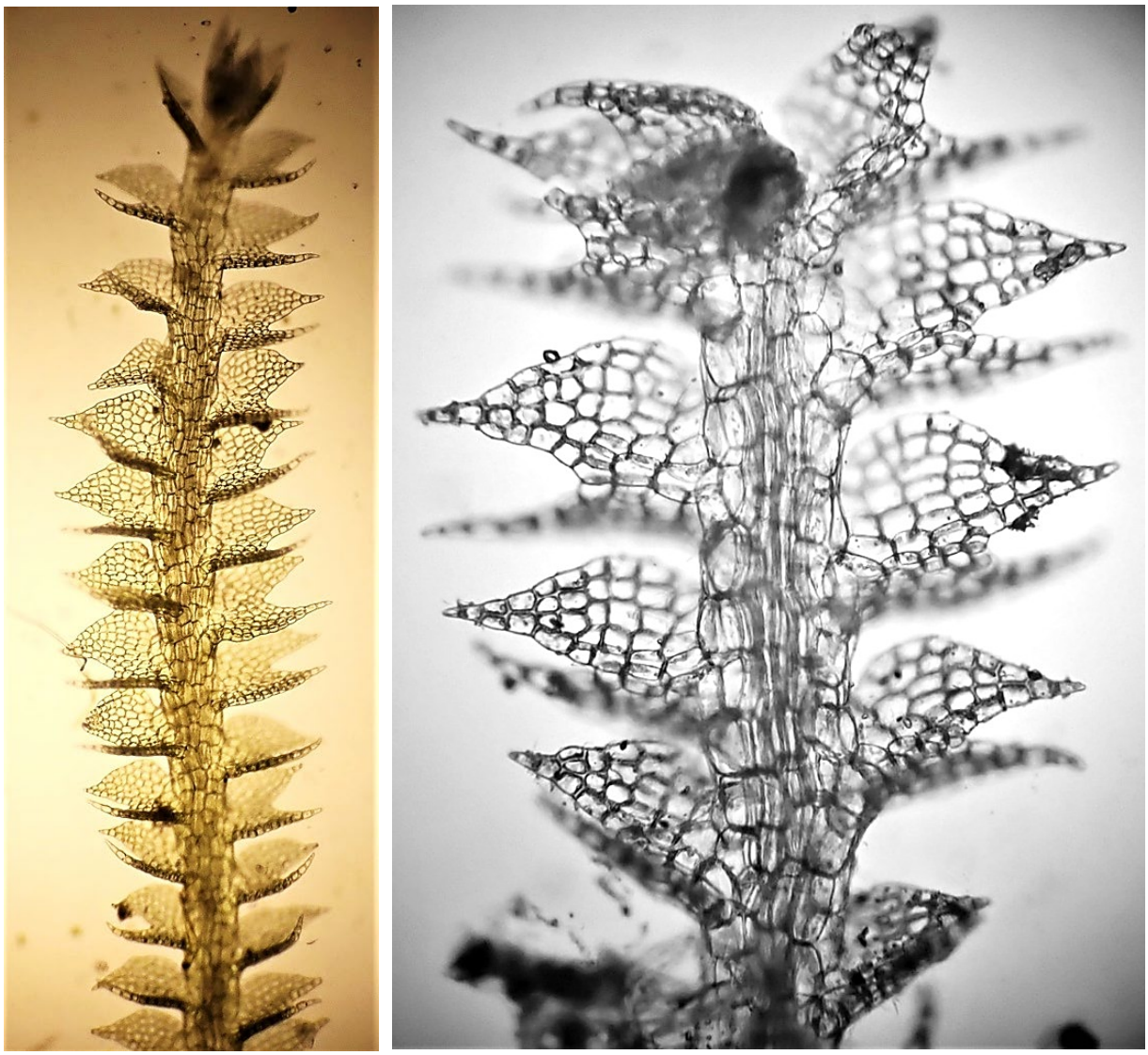
Cephalozia cf. *maxima* (?)



Cephalozia cf. *maxima*. Top row: Left, gemmiferous shoot. Bottom row: Left and center, gemmae; right: hyalodermis on young portion of shoot. ‘Eke, Kohala Mountain, Hawai‘i Island, Freire & Judziewicz 23-595 (BISH).

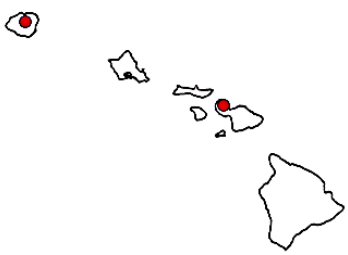
***Cephalozia* aff. *maxima* (?)**

The following specimen has less concave and smaller leaves but they are divided to half their length as in *C. maxima*. Leaf lobes are not as narrow and we do not see a border. Leaf cell walls are thicker and apparently smaller. It is possible this is a different species.



Cephalozia aff. *maxima*. Note hyalodermis (right). Pu‘u Ka‘ala, O‘ahu, M.K. Thomas et al. (including Freire & Judziewicz) 479 (BISH). Photos by A.V. Freire.

3. *Cephalozia* aff. *otaruensis* Steph. **Indigenous.** Kauaʻi, Kawaikini Summit (5,200 ft.), Wood 18891 (PTBG); Kauaʻi, Alakaʻi swamp, epiphyte on *Melicope*, Martin & Karen Hutten 20146; and West Maui, Puʻu Kukui, summit bogs, 5,500 ft., Pezzillo 1076b (BISH). No other Hawaiian material resembles these collections. Recognized by its green color, small size, frequent branching; by its fragile, fleshy stems, and by its prominent, widely spreading, and deeply bifid leaves. An Asian species that may also occur in North America (Oregon).

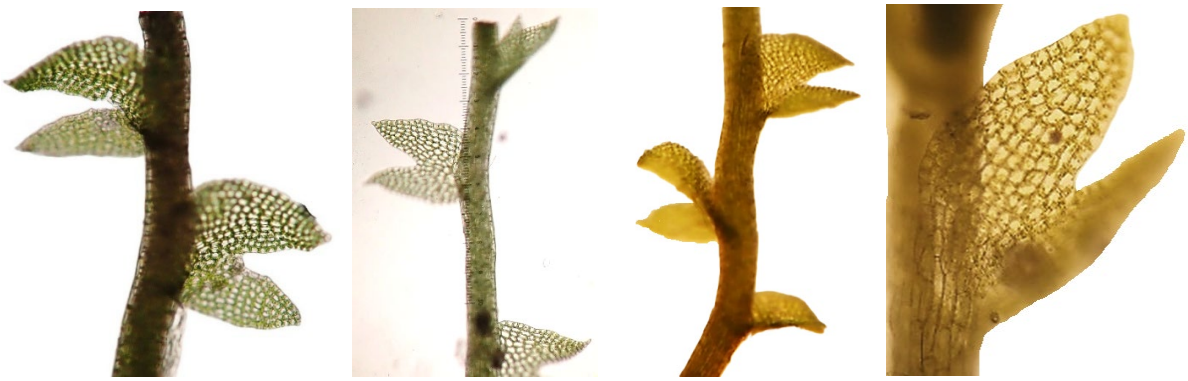


Plants are bright green, delicate, loosely attached to their substrate, prostrate to ascending, at least 6 mm long and 0.6-1 mm wide. Stems are fragile, flexuous, fleshy, and profusely branched, with branches much smaller than the main stems. Leaves are distant, transverse succubous, flexuous, spreading at 45-90˚, slightly folded in their middle, round, ovate to quadrate; bifid, divided to over ½ their length by a narrow or broad triangular sinus that separates two large, triangular, parallel to divergent lobes; these are 10-15 cells high and 7-11 cells wide at their base. Leaf cells are elongate-rectangular to quadrate, thin-walled, and lack trigones. There is a region of clearly inflated cells on the upper leaf surface just below the sinus. Leaves are bordered by rectangular cells.

The prominent leaves and flexuous, fragile stems indicate that it is a member of *Cephalozia* rather than *Cephaloziella*. However, a hyalodermis is not as clearly defined in cross sections as would be expected. The specimen resembles *C. otaruensis* as suggested by Martin Hutten (pers. comm.); we agree with this affinity. A recent collection by the Huttens (20,146) shows main stems considerably larger than the branches (see picture below). This specimen needs study to compare with Pezzillo 1076b and Wood 18891 (used for this treatment). If they are the same, then our measurements need to be revised as it is likely they are based only on smaller branches. Also, a cross section of these larger stems may show a more clearly defined hyalodermis. This taxon has also been recognized as a subspecies of the cosmopolitan *C. bicuspidata* (L.) Dumort., as subsp. (Steph.) Hatt. *otaruensis*, and also as a synonym of the Asian *C. hamatiloba* Steph. (Stotler & Crandall-Stotler, 2017; Brinda & Atwood, 2025).

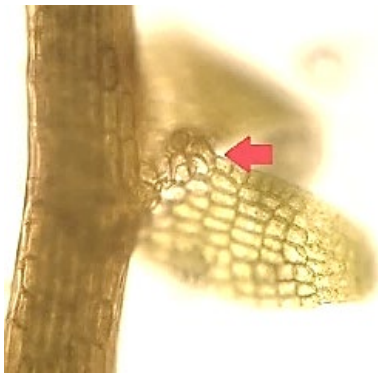
This recently collected specimen appears to follow our concept of *C. otaruensis*, but needs microscopic study for corroboration. Note more robust stems (arrow to the right), intermixed with smaller branches. Kauaʻi, Alakaʻi swamp, on the bark of *Melicope* sp., M. Hutten & K. Hutten 20146. Photo by M. Hutten and K. Hutten.

Plants are at least 6 mm long and just short of 1 mm wide, and are often branched. First photo: Scale in mm. Second photo: Scale units = 26 µm. Images 1, 2 and 3 from Pu‘u Kukui, summit bogs, 5,500 ft., West Maui, Pezzillo 1076b (BISH). Photos by A.V. Freire. Image 4: Kawaikini Summit, Kaua‘i (5,200 ft.), Wood 18891 (PTBG). Photo by E.J. Judziewicz.

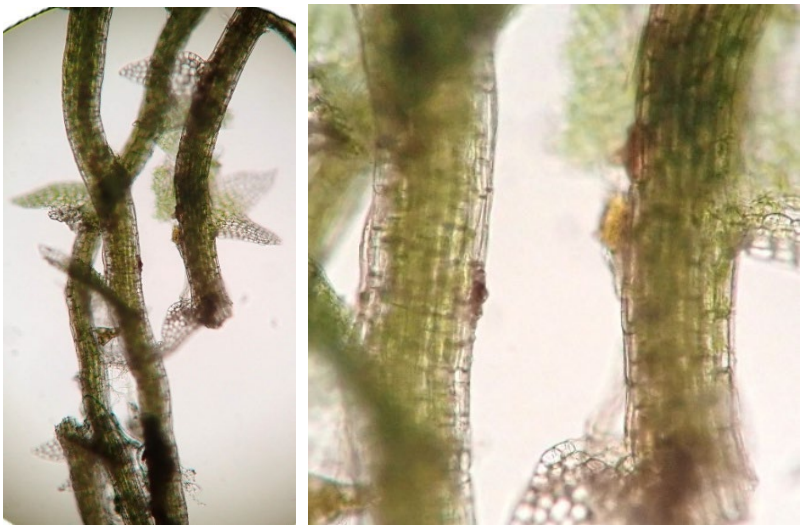


Leaves are distant, spreading at 45-90˚, flexuose, and slightly folded in the middle. They are deeply bifid, with a triangular sinus and large, triangular lobes. Pu‘u Kukui, summit bogs, 5,500 ft., West Maui, Pezzillo 1076b (BISH). Second photo: Scale units = 26 µm. Photos by A.V. Freire and E.J. Judziewicz.

Cephalozia aff. *otaruensis*. Leaf sampler. Note the deep sinus, acute lobes and shape variaiton. A leaf border of rectangular to quadrate cells is present. Left: Kaua‘i, Kawaikini Summit (5,200 ft.), Wood 18891 (PTBG). Photo by E.J. Judziewicz. Images 2-5: Pu‘u Kukui, summit bogs, 5,500 ft., West Maui, Pezzillo 1076b (BISH). Second photo: Scale units = 5.1 µm. Photos by A.V. Freire.



Red arrow points to a distinctive region of inflated cells on upper surface of leaf, just below the sinus. Pu‘u Kukui, summit bogs, 5,500 ft., West Maui, Pezzillo 1076b (BISH). Photo by E.J. Judziewicz.



Cephalozia aff. *otaruensis*. Above: Stems have a translucent peripheral area that resembles a hyalodermis. Below: Stem sections revealed an outer, single layer of large cells with thickened walls but they are of similar size to the inner cells. Pu‘u Kukui, summit bogs, 5,500 ft., West Maui, Pezzillo 1076b (BISH). Photos by A.V. Freire. Scale in lower right photo: 2.5 µm per unit.

Cephaloziella (Spruce) Schiffn. (Cephaloziellaceae)

At least 6 species in Hawai‘i (92 species worldwide). Bakalin et al. (2024: 11) present molecular evidence that *Cephaloziella kiaeri* and *C. microphylla* (the latter related to our “species 1”) should be transferred to *Cylindrocolea*. *Cephaloziella* and *Cylindrocolea* are similar; both are tiny plants with bifid leaves. Unlike *Cylindrocolea*, in *Cephaloziella* the leaves are transversely inserted, are not constricted at the base, and the leaf cells are usually thick-walled. *Cephalozia* and *Cephaloziella* differ in that *Cephalozia* has larger leaf cells and a hyalodermis, the latter absent in *Cephaloziella*.

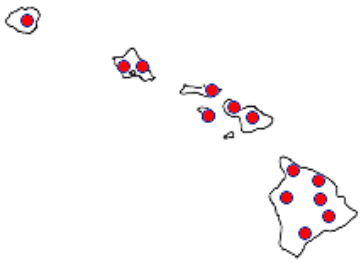
1. Leaves horizontally or longitudinally (parallel to the stem’s main axis) inserted, constricted at the base, leaf cells thin-walled ……..... ***Cylindrocolea***
1. Leaves succubous or transversely inserted, not constricted at the base, leaf cells usually thick-walled but sometimes thin-walled ...…….....…….…… **2**
   2. Hyalodermis absent; leaf cells less than 20 µm long, thin- or thick-walled; oil bodies present; leaves small and inconspicuous, up to 2.5(3) times longer than the stem diameter ……...……. ***Cephaloziella***
   2. Hyalodermis present; leaf cells more than 25 µm long, thin-walled; oil bodies absent; leaves conspicuous, over three times longer than the stem diameter (except *C.* aff. *otaruensis*) ... ***Cephalozia***

Members of the genus *Cephaloziella* are minute, creeping plants (less than 1 mm wide, or more often less than 0.5 mm wide), often growing on soil or rock, but occasionally on bark. Leaves are tiny, bilobed with a “V”-shaped sinus, transverse-oblique with a long insertion, almost to the stem midline. Several species 1-2-celled gemmae. This is a difficult genus that requires much more study in Hawai‘i, where we suspect more species are present.

1. Leaves pinnately toothed, with several teeth 1-3 cells long ...…..…… ***C.* sp. 1 (aff. *C. microphylla*)**
1. Leaves entire, serrulate, crenate or with a 1-celled tooth, but never pinnately toothed ……..…… **2**
   2. Plants reddish; leaves crowded, spreading less than 45º; leaf cells thick-walled ……. ***C. kilohanensis***
   2. Plants green; leaves distant, spreading at 45-90º; leaf cells thin- or thick-walled ….……... **3**
      3. Underleaves present
         4. Leaves oblique-transversely inserted, no (or sparse) gemmae produced at shoot tips .. ***C. heteroica***
         4. Leaves oblique-horizontally inserted, abundant gemmae produced at shoot tips .. ***C.* aff. *heteroica***
      3. Underleaves lacking …….. **5**
         5. Leaf length at least 1.5 times the stem width, leaf lobes clearly divergent ……..…….. ***C.* sp. 2**
         5. Leaf length about the same as the stem width, leaf lobes parallel to slightly divergent ……... **6**
            6. Leaf margins serrulate ……..…….. ***C.* sp. 3**
            6. Leaf margins entire or irregular but not serrulate ……..…… ***C. kiaeri***

Cephaloziella species often grow mixed together. It is easy to mistake one from another due to their tiny size. In some cases, the fragments separated from a collection are not the same species but are instead community associates. A word of caution is needed: When preparing duplicates it is necessary to very carefully confirm the identity of the plants to be separated. We encountered misidentified plants when studying fragments of isotypes.

1. *Cephaloziella heteroica* (C.M. Cooke) Douin. **Endemic(?).**
A member of subgenus *Cephaloziella* (Söderström et al., 2016). This is the commonest and most widespread species of *Cephaloziella* in Hawai‘i and is found on all major islands (1,200-6,600 ft.). Possible affinity (Cooke, 1904): *C. hebridensis* Steph., Vanuatu. A CINC herbarium annotation (by M.A. Fulford?) suggests that this species is conspecific with the Holarctic species *C. stellulifera* (Taylor ex Carrington & Pearson) Croz. (see discussion below).



This tiny species grows in pockets of soil among rocks in the Ka‘ū Desert and along the Mauna Loa Road on Hawai‘i Island, where it is locally common, often with *Isopaches bicrenatus*; it can also be found in wetter, forested areas throughout Hawai‘i.

Plants are dark green, tiny, 4-6 mm long, slightly over 0.3 mm broad, loosely attached to their substrate, forming small, loose mats. Stems are robust and wiry, turning black when dry, sparingly branched. Leaves are small, transversely inserted, distant, spreading mainly at 45º, somewhat quadrate, with irregularly crenate margins, slightly concave, and deeply bifid; the leaf lobes are parallel to divergent, separated by a broad “V”-shaped sinus (45º or wider) to slightly over ½ the leaf length; each lobe is triangular, (5)6-8(9) cells broad at the base, 6-8(9) cells long, the apices mainly acute but rounded in some leaves, and usually tipped by 1-2 single-rowed, smaller, hyaline cells that lend a “frosty” aspect to the dry plants. Leaf cells are quadrate to rectangular, sometimes round-quadrate, firm-walled, usually without trigones or with tiny triangular ones. Minute, variably bifid underleaves are often present, but these are sometimes rather underdeveloped, asymmetrical, or absent on the same plant. Archegonia are clustered at the apex of short, tufted branches with crowded serrulate bracts above. Perianths are elongate, close to 1.3 mm long at maturity, and narrowly tubular and plicate, with a hyaline upper portion and an irregular, truncate mouth. Perianth bracts are short and serrulate. Androecia were not observed. Spores are small, purple, deeply pitted, and with thick ridges. One- to two-celled gemmae are often produced at shoot tips or sometimes at leaf margins.

We identified this species based on the presence of variably shaped and sized underleaves, a feature not described or observed in other species from Hawai‘i. Our description has some discrepancies with Cooke’s protologue. The leaves we observed are not squarrose but instead spread at 45˚, and gynoecia develop on short lateral branches (much as described and illustrated for *C. kilohanensis*), rather than from main stems. However, Cooke (1904) mentions that gynoecia and androecia are variable, and that perianths can be born on postical branches.

We briefly studied fragments of an isotype, Cooke s.n., 1898, Kaua‘i (BISH). The plants have small leaves, about as long as the stem diameter, rather than twice as long as described in the protologue and observed by us on various collections. Some leaf lobes have rounded rather than acute lobe tips, and leaf cells seem thicker walled (pictures on next page). No underleaves were observed. These fragments do not agree with the protologue and figures of *C. heteroica* and we suspect that they might belong to *C. kiaeri*.

PLATE XV.

Heteroicous: plants green, loosely cæspitose: stems subsimple or branching from the postical aspect, prostrate at the base, apex ascending, circular in section, about 6 cells in diameter, internal and cortical cells similar, with slightly thickened walls, the latter in about 15 longitudinal rows; rhizoids colorless, scattered on the ventral surface: leaves distant, transversely inserted, squarrose, somewhat concave, subquadrate, bifid more than one-half, lobes spreading, ovate, acute, entire, separated by an obtuse sinus, about 7 cells long, 4 or 5 cells broad: leaf-cells with uniformly thickened walls, cell-cavities sometimes rounded, trigones minute or lacking: underleaves very small, about 4 cells broad at base, variable in form, lanceolate-ovate to broadly quadrate, apices acute, obtuse or bifid, with unequal, acuminate to obtuse, spreading to connivent lobes; cells of the underleaves small, with uniformly thickened walls: ♀ inflorescence usually borne on the main stem, with a sterile or floriferous innovation, sometimes on a short postical branch; bracts in 2 or 3 pairs; innermost bracts broadly ovate to broadly quadrate, bifid (one-fourth to one-third), lobes triangular, acute, denticulate; innermost bracteole suborbicular, connate on both sides, bifid, lobes triangular, acute, denticulate; bracts of second row broadly ovate, bifid (about one-third), lobes triangular-ovate, acute, spreading, slightly denticulate; bracteole of second row connate on both sides, ovate, bifid (about one-third), sometimes quadrified, lobes ovate, acute, slightly denticulate: perianth broadly fusiform, terete below, bluntly three-keeled above, mouth slightly contracted, irregularly lobed, lobes denticulate; innovations lateral or postical, arising just below the second bracteole or from the axil of a bract: androecium borne just below the female flower or intercalary on a vegetative branch; ♂ bracts in 3 to 10 pairs, imbricated, suberect, slightly concave, about twice the size of the leaves of the vegetative branches, bifid (about one-half), lobes broadly ovate-triangular, acute, widely spreading, sinus broadly lunate; bracteoles ovate, bifid (about three-fourths), lobes subulate, parallel; antheridia borne singly.

Stems 0.08^{mm} in diameter; leaves 0.15^{mm}x0.16^{mm}; leaf-cells at margin 19μx16μ, at middle of base 20μ; innermost ♀ bracts 0.45^{mm}x0.6^{mm}; innermost bracteole 0.38^{mm}x0.4^{mm}, ♀ bracts of second row 0.45^{mm}x0.5^{mm}; bracteole of second row 0.35^{mm}x0.3^{mm}; perianth 1.25^{mm}x0.45^{mm}; ♂ bracts 0.25^{mm}x0.25^{mm}.

Kauai; Kilohana (Cooke), growing on an exposed bank.

This species varies greatly in almost every character pertaining to the male and female flowers. In rare instances the ♀ inflorescence is borne on a short postical branch with the androecium median between the ♀ bracts and the main stem. Usually the ♀ inflorescence is borne on a main branch or an innovation and sometimes as many as three or four floriferous innovations are given off in succession. The ♀ bracts and bracteoles vary greatly both in size and form. The underleaves also vary greatly.

C. heteroica is nearest to *Cephaloziella Hebridensis* Steph., from the New Hebrides Islands.[1] This species differs in its dioicous inflorescence, in its carinate leaves with acuminate lobes, in its smaller leaf-cells, and in the entire mouth of its perianth.

[1] Hedwigia, xxxii, 316, 1893.

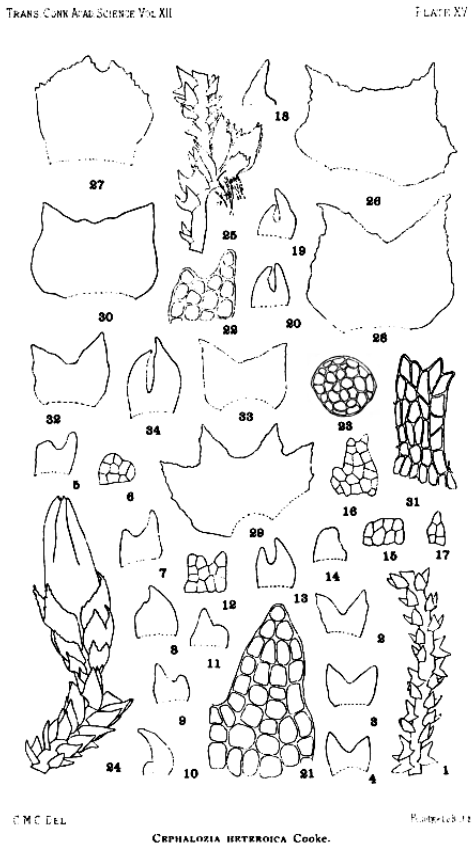
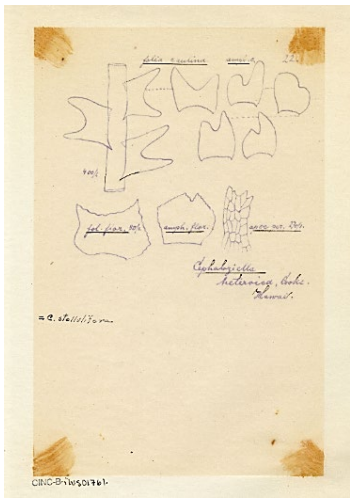


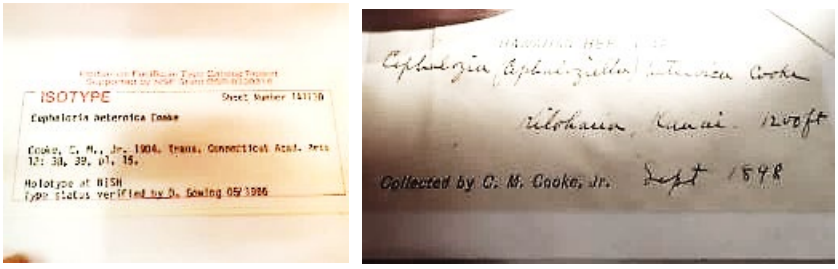
PLATE XV.

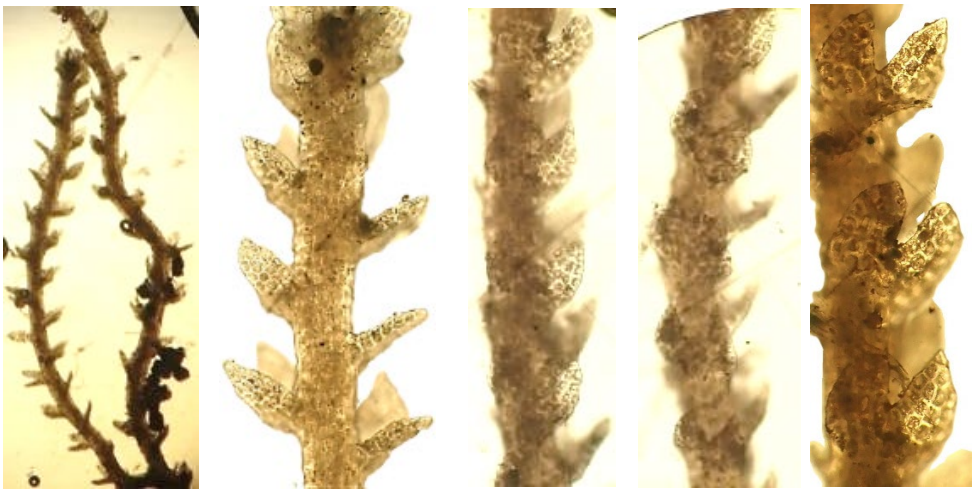
Cephalozia heteroica Cooke, p. 38.—Fig. 1. Part of stem, postical view, ×30.—Figs. 2–4. Leaves, ×80.—Figs. 5–16. Underleaves from a single stem, ×200.—Fig. 17. Underleaf from a second stem, ×200.—Figs. 18–20. Underleaves from a third stem, ×200.—Fig. 21. Cells of leaf, ×270.—Fig. 22. Cells of underleaf, ×270.—Fig. 23. Cross-section of stem, ×200.—Fig. 24. Perianth, postical view, ×30.—Fig. 25. Unfertilized female flower, showing innovation, ×30.—Fig. 26. Innermost bract, ×80.—Fig. 27. Innermost bracteole, ×80.—Fig. 28. Bract of second row from same flower, ×80.—Fig. 29. Innermost bract and bracteole, ×80.—Fig. 30. Bract just below innovation, ×80.—Fig. 31. Apex of perianth, ×270.—Figs. 32, 33. Male bracts, ×80.—Fig. 34. Male bracteole, ×200. All drawings from the type-specimens, collected by the writer at Kilohana, Kauai.

Cephaloziella heteroica. Protologue and illustrations with captions (Cooke, C.M. 1904). The Hawaiian Hepaticae of the tribe Trigonantheae. Transactions of the Connecticut Academy of Arts and Sciences 12: 1-44).



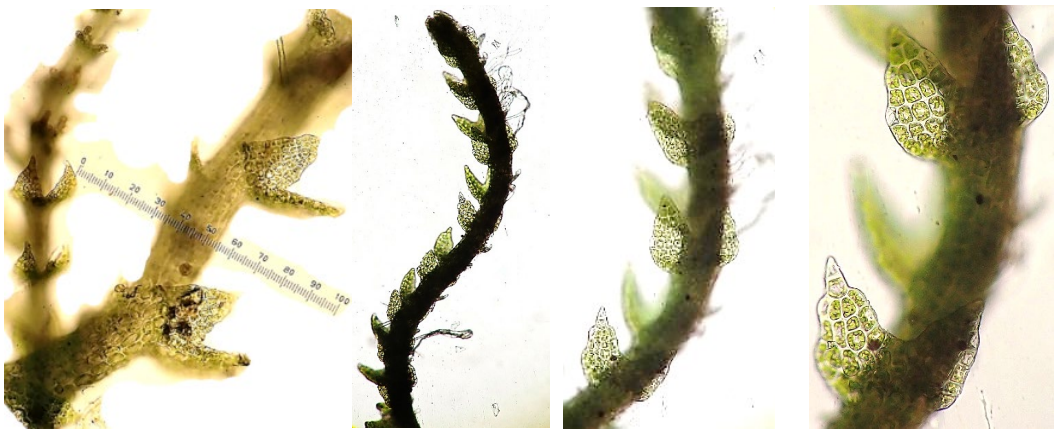
This illustration of unknown authorship (perhaps by F. Stephani?) shows four different underleaves (upper right), some with asymmetrical lobes. The annotation (by M.H. Fulford?) below the drawings indicates this species is conspecific with *C. stellulifera* (Taylor ex Carrington & Pearson) Croz. Margaret H. Fulford Herbarium, University of Cincinnati (CINC) (2025).
Occurrence dataset https://doi.org/10.15468/xkca3p accessed via GBIF.org on 2 Mar. 2025.
https://www.gbif.org/occurrence/4421544351



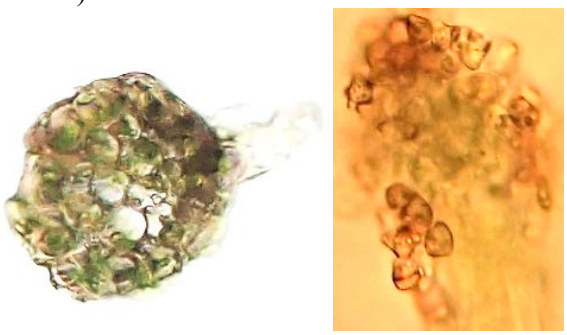


Cephaloziella heteroica. Isotype: Cooke s.n., Kauaʻi, Sept. 1898 (BISH). Leaf lobes are 4-5 cells broad at their base and (4)5-6 cells long, and some are rounded at their apex. Photos by E.J. Judziewicz.

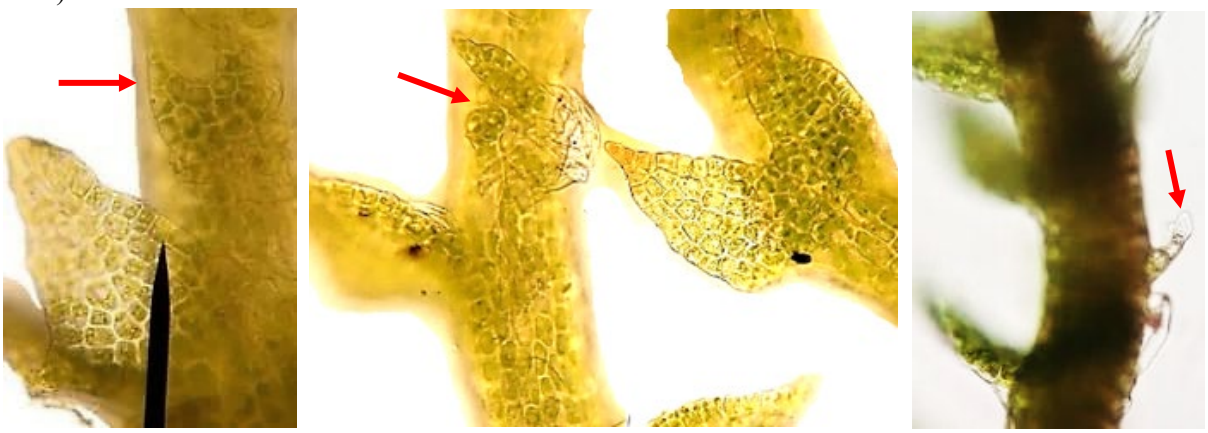
Cephaloziella heteroica. Above: Dark green population forming a dense mat. Plants are tiny, about 0.3 mm wide. Note the long perianths and tufted archegonial branches. Below: Dry specimen with blackened stems and leaves that resemble green scales, some as if tipped by frost. Note the crowded archegonial branches (arrows). Freire & Judziewicz 22-632 (HAVO).



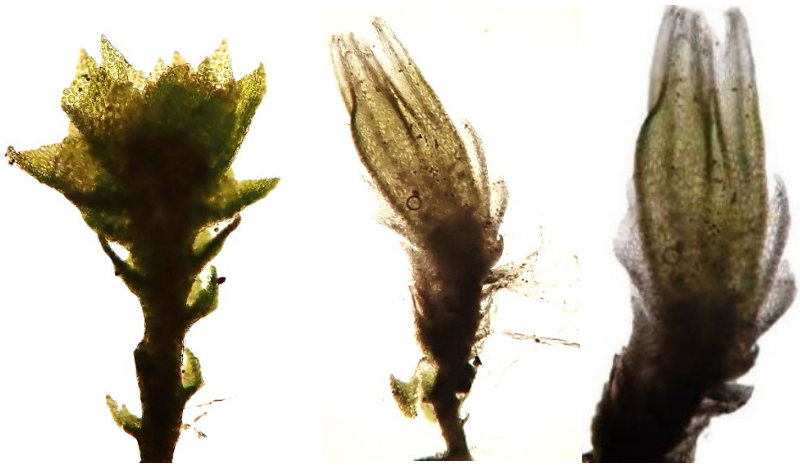
Plants have spreading bifid leaves with a deep broad sinus and robust stems. Leaf cells have slightly thickened walls with some small trigones. Left: Kīlauea, Hawai‘i Island, Freire & Judziewicz 2021-1087b (HAVO). Scale units = 5.1 µm. Three right photos: Upper Kahuku Unit, Hawai‘i Volcanoes National Park, Freire & Judziewicz 22-632 (HAVO).



Left: Stem cross section showing the lack of a hyalodermis, Upper Kahuku Unit, Hawai‘i Volcanoes National Park, Freire & Judziewicz 22-632 (HAVO). Right: Reddish (ellipsoidal, 1-2-celled) gemmae at stem apex, Waikamoi Preserve, Haleakalā, Maui, Freire, Judziewicz, Oppenheimer & Pezzillo 23-100 (BISH).

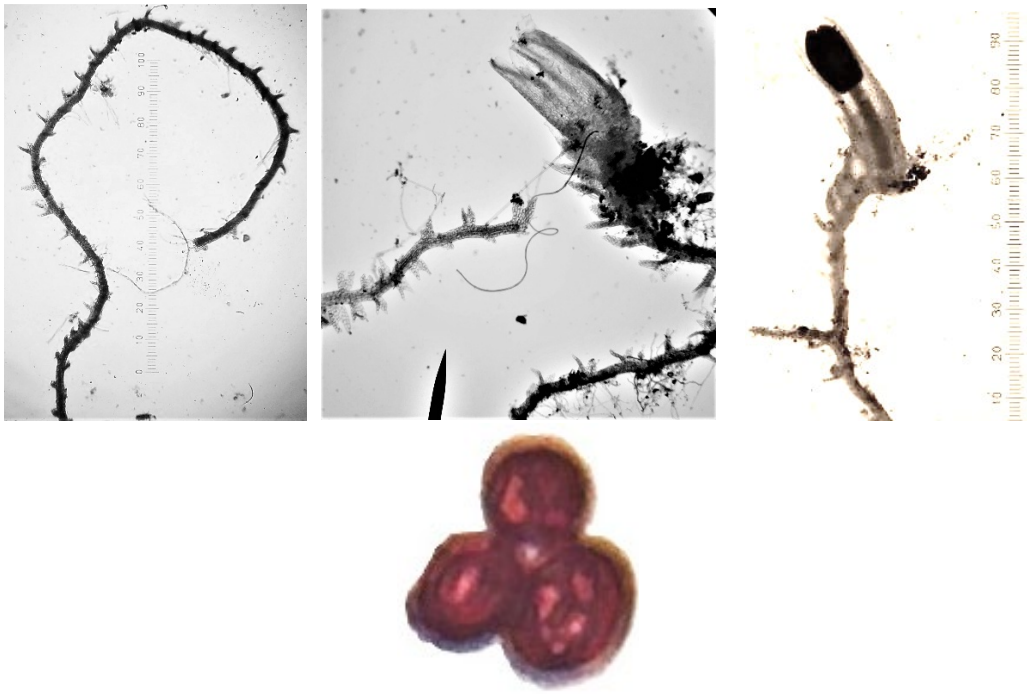


Cephaloziella heteroica. Left and center: Underleaves variable; some are tiny and bifid (left, arrow); others are asymmetrical (center, arrow). Mauna Loa Road, 6,000 ft., Hawai‘i Volcanoes National Park, Hawai‘i Island, Freire & Judziewicz 20-959 (HAVO). Right: Underleaves can be highly reduced and underdeveloped. Note the bulging apical cell on both underleaf lobes (arrow), perhaps functioning as a slime papillae. Upper Kahuku Unit, Hawai‘i Volcanoes National Park, Freire & Judziewicz 22-632 (HAVO).



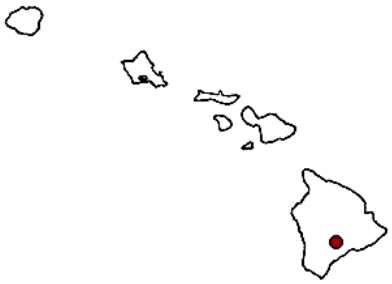
Left: Short gynoecial branch. Note the crowded and serrulate bracts. Middle: Perianths are produced on lateral branches. Right: Perianths are pleated, keeled, narrow, and tubular, with a hyaline and truncate mouth. Note the short and serrulate bracts. Upper Kahuku Unit, Hawai‘i Volcanoes National Park, Freire & Judziewicz 22-632 (HAVO).

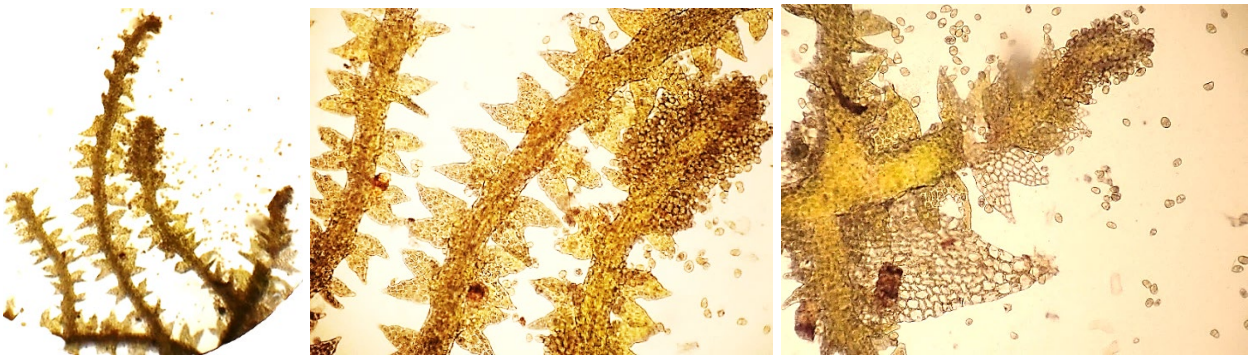
The following specimen was collected by us at Tree Molds, Hawai‘i Volcanoes National Park, Hawai‘i Island, Freire & Judziewicz 21-401 (HAVO). It was fertile, with mature sporophytes. Spores are small (but we do not have their dimensions). The leaf size and morphology agrees with *C. heteroica*. This specimen should be revisited to photograph and document elaters and spore size.



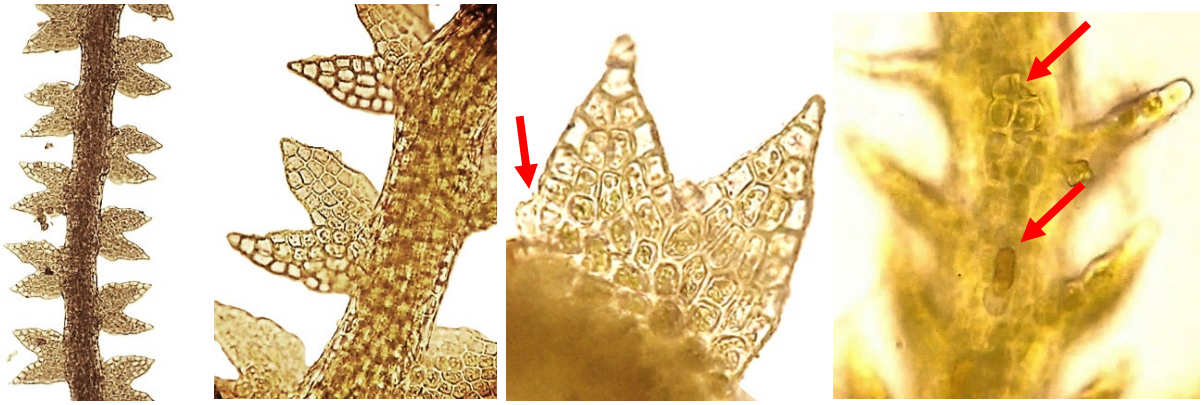
Cephaloziella heteroica. Top three photos: Plants with perianths and sporophyte (right: scale units = 26 µm). Bottom: Spores are minute, purple, and have deep areolae and thick ridges. Hawai‘i Volcanoes National Park, Hawai‘i Island, Freire & Judziewicz 21-401 (HAVO).

1a. *Cephaloziella* aff. *heteroica* (?). A tiny, rare plant found at high altitude (over 6,000 feet) rain forest in the Kahuku Unit of Hawai‘i Volcanoes National Park. Plants are very small (250 µm wide), green, and profusely branched. The stems are robust and firm. Leaves are obliquely to nearly horizontally inserted, bilobed, with a broad “V”-shaped sinus to ½ or slightly over their length. Lobes are broad at the base and acute; with an occasional tooth or with 1-2 protruding marginal cells forming small projecting “elbows”. A margin of hyaline cells is sometimes observed. Small rudimentary underleaves are sometimes present but very reduced. Bicellular or unicellular gemmae are abundantly produced.



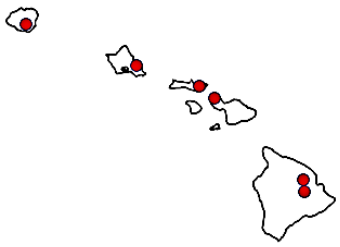


Stems are frequently branched. Plants produce abundant 1-2-celled elliptical gemmae (10-16 µm long) at stem apices. Center: Robust stems with abundant gemmae, these produced mainly at the stem tips. Right: Gemmae can be unicellular but are usually 2-celled (note: the large leaf at bottom left corner does not belong to this plant; it has trigones). Freire & Judziewicz 21-655 (HAVO).



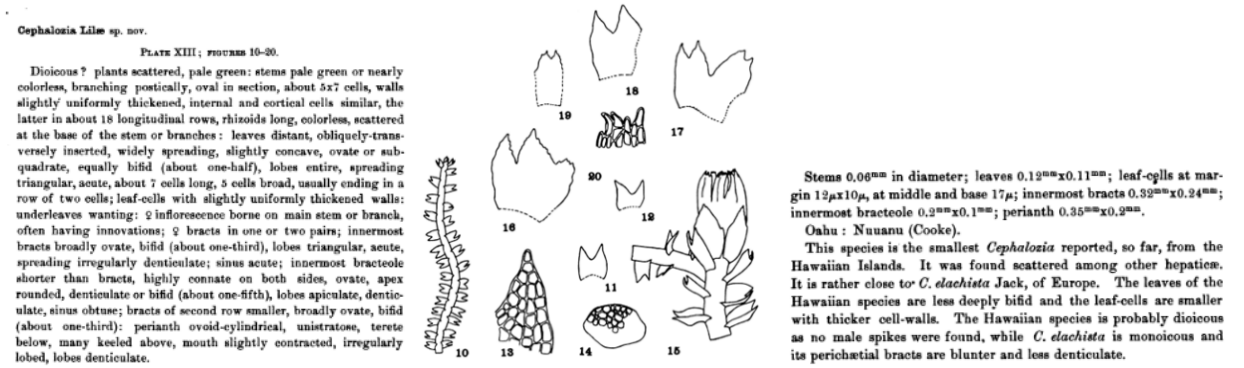
Left and second images: Leaves oblique-horizontal; bifid to ½ or slightly more, lobes divergent, the sinus “V”-shaped. Note the slightly constricted leaf base. Third image: Leaf borders sometimes irregular with a hint of “elbows” (arrow). Leaf cells rectangular, with slightly thickened walls. Right: Hint of underleaves (arrows; upper 4-celled, lower a single cell). Kahuku Unit of Hawai‘i Volcanoes National Park, Freire & Judziewicz 21-655 (HAVO).

2. *Cephaloziella kiaeri* (Austin) Pearson. **Indigenous.** Treated as *Cylindrocolea kiaeri* by Váňa et al. (2013b); as *Cephaloziella lilae* in Staples & Imada (2006); and more recently as *Cephaloziella kiaeri* by Lee & S.R. Gradstein (2021: 52) and Judziewicz & Freire (2023c: 161). Almost pantropical. Possible affinity (Cooke, 1904): *C. elachista* (Jack) Schiffn., Eurasia and North America. Confirmed for Kauaʻi, Molokaʻi, Maui and Hawaiʻi Island; also reported from Oʻahu (Cooke, 1904).



The plants are tiny, 3-6 mm long, about 0.25 mm wide; the bifid leaves have short, parallel, and acute lobes; cells are thick-walled and lack trigones. Clusters of bicellular gemmae are frequently observed. Monoicous*. Plants are light green, sometimes with red pigmentation; they form dense mats of procumbent stems, attached to their substrate only at their base. Stems are stout, rarely branched. Leaves are tiny, distant, spreading at about 90˚, oblique-transversely inserted, slightly concave, quadrate, bifid, with a triangular sinus to about 1/3 their length. Leaf lobes are triangular, 5-6 cells wide at their base by 5-7 cells long, with acute tips. Leaf cells are quadrate, small (10-15 µm long), thick-walled, and lack trigones. Abundant bicellular gemmae 13-17 µm long are present. Perianths are produced on short lateral branches, protected by bracts with entire but irregular margins. We only observed immature perianths, but according to Cooke (1904) they are broad, terete, pleated, and have a broad and truncate mouth. Antheridia are produced on conspicuous lateral branches with about 6 pairs of concave, imbricate bracts. Váňa & Piippo (1989) observed that plants are weakly conduplicate (with rudimentary water sacs), a feature captured in Miller's unpublished illustration for *C. lilae* (a synonym); however, we have not observed this feature.

*In his description, Cooke questions if the plant is dioicous (see below); we did find a plant bearing both male and female organs, therefore showing it to be monoicous.



Cephalozia Lilæ sp. nov.

PLATE XIII; FIGURES 10–20.

Dioicous? plants scattered, pale green: stems pale green or nearly colorless, branching postically, oval in section, about 5x7 cells, walls slightly uniformly thickened, internal and cortical cells similar, the latter in about 18 longitudinal rows, rhizoids long, colorless, scattered at the base of the stem or branches: leaves distant, obliquely-transversely inserted, widely spreading, slightly concave, ovate or subquadrate, equally bifid (about one-half), lobes entire, spreading triangular, acute, about 7 cells long, 5 cells broad, usually ending in a row of two cells; leaf-cells with slightly uniformly thickened walls: underleaves wanting: ♀ inflorescence borne on main stem or branch, often having innovations; ♀ bracts in one or two pairs; innermost bracts broadly ovate, bifid (about one-third), lobes triangular, acute, spreading irregularly denticulate; sinus acute; innermost bracteole shorter than bracts, highly connate on both sides, ovate, apex rounded, denticulate or bifid (about one-fifth), lobes apiculate, denticulate, sinus obtuse; bracts of second row smaller, broadly ovate, bifid (about one-third): perianth ovoid-cylindrical, unistratose, terete below, many keeled above, mouth slightly contracted, irregularly lobed, lobes denticulate.

Stems 0.06mm in diameter; leaves 0.12mmx0.11mm; leaf-cells at margin 12µx10µ, at middle and base 17µ; innermost bracts 0.32mmx0.24mm; innermost bracteole 0.2mmx0.1mm; perianth 0.35mmx0.2mm.

Oahu: Nuuanu (Cooke).

This species is the smallest *Cephalozia* reported, so far, from the Hawaiian Islands. It was found scattered among other hepaticæ. It is rather close to *C. elachista* Jack, of Europe. The leaves of the Hawaiian species are less deeply bifid and the leaf-cells are smaller with thicker cell-walls. The Hawaiian species is probably dioicous as no male spikes were found, while *C. elachista* is monoicous and its perichætial bracts are blunter and less denticulate.

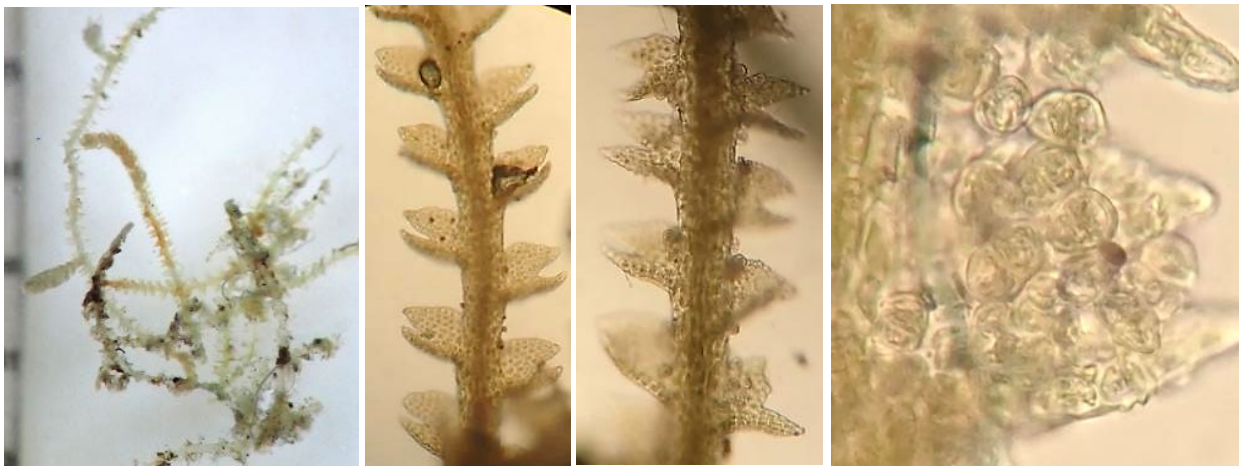
Cephalozia lilae C.M. Cooke, from Plate XIII (Cooke, C.M., 1904). The Hawaiian Hepaticae of the tribe Trigonantheae. Transactions of the Connecticut Academy of Arts and Sciences 12: 1-44).

The description and figure arecongruent with our concept of *Cephaloziella kiaeri*, but not with the fragment from the supposed YU holotype (see below).

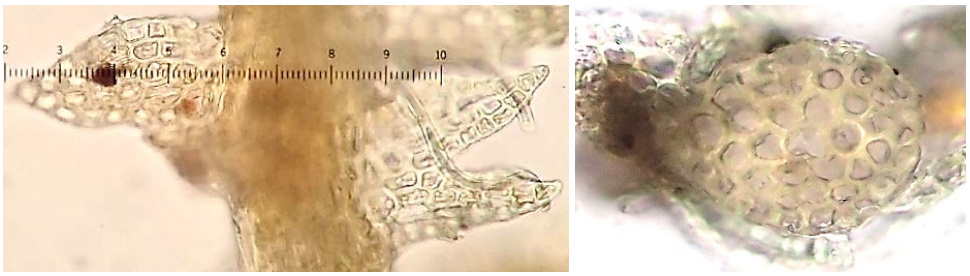
Cooke (1904) described and illustrated *Cephalozia lilae* C.M. Cooke (= *Cephaloziella kiaeri* in our conception) as having acute leaf lobes (his Plate XIII: 11-13, see above). Yet the fragments of the "isotype" we examined at MU (Nuʻuanu, Oʻahu, 16 Dec. 1902, Cooke 4, fragment of YU holotype) have rounded leaf lobes (below) unlike those in Cooke's figure or any other *Cephaloziella* we examined from Hawaiʻi, which have, at most, only a few slightly rounded lobe apices on some plants. Although we can't be certain, we suspect that there was some confusion splitting the YU holotype; and need to question whether the provenance of the material below is Hawaiian. We did not include the characters observed on the MU "isotype" in our description.

Cephaloziella lilae, fragments of the isotype at MU (from YU, perhaps a mixed collection). Plants are tiny, with stout stems and distant, spreading bifid leaves. Leaf cells have thick walls. Note the rounded leaf lobe apices. Scale on second photo in mm. Photos by E.J. Judziewicz.

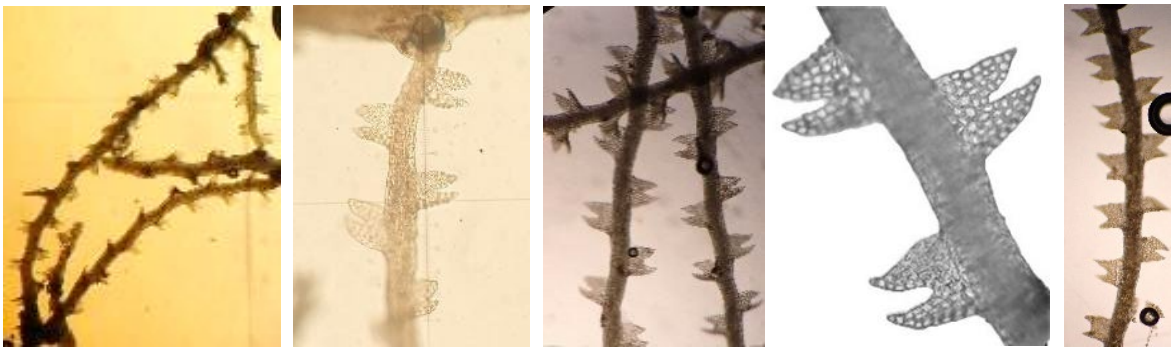
Plants are loosely attached to their substrate and form dense mats. The thickened plant tips are most likely clusters of gemmae. Upper Lumahaʻi Valley, 2,700 ft., Kauaʻi, epiphytic on *Psychotria mariniana* (Rubiaceae), Wood 17409 (PTBG). Photo courtesy of National Tropical Botanical Garden/Ken Wood.



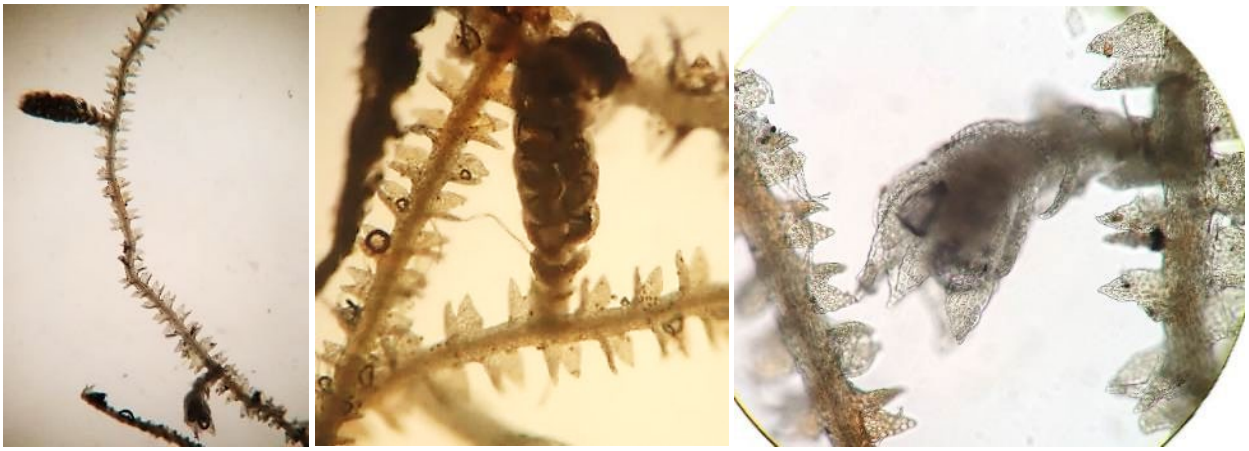
Cephaloziella kiaeri. Left: Plants are tiny. Scale in mm. Second photo: Plants have small, bifid, spreading and concave leaves, only a few with rounded lobe apices. Note the clusters of gemmae in leaf axils in the third picture and detail of the 2-celled gemmae (right). Upper Lumahaʻi Valley, 2,700 ft., Kauaʻi, Wood 17409 (PTBG). Photos by E.J. Judziewicz.



Left: Leaf cells are thick-walled. Scale subunits = 2.5 µm. Right: Stem cross section shows the lack of a hyalodermis. Stem width = 75 µm. Upper Lumahaʻi Valley, 2,700 ft., Kauaʻi, Wood 17409 (PTBG). Photos by A.V. Freire.

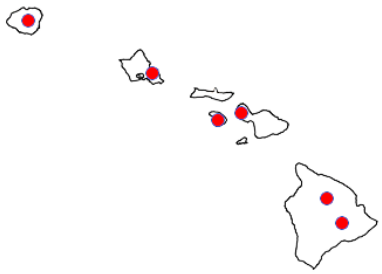


Diversity of leaf morphology. All share acute, non-divergent lobes with narrow sinuses. Two left photos: West Maui, Stemmermann 2355 (BISH). Photos 3 and 4: Molokaʻi, Oppenheimer H11514 (BISH). Far right: Kauaʻi, Wood 14400 (PTBG). Photos by E.J. Judziewicz.



Cephaloziella kiaeri. Left: Plant with antheridial (above) and gynoecial (below) branches. Center: Showing antheridial branch. Right: Gynoecial bracts are bifid, with irregular margins and thick-walled cells. Upper Lumahaʻi Valley (2,700 ft.), Kauaʻi**,** Wood 17409 (PTBG). Photos by A.V. Freire and E.J. Judziewicz.

3. *Cephaloziella kilohanensis* (C.M. Cooke) Douin. **Endemic?** A member of the subgenus *Cephaloziella* (Söderström et al., 2016). Found on all major islands except Moloka'i, from 1,200-5,100 (-13,000) feet. Possible affinity (Cooke, 1904): *C. exiliflora* (Taylor) Douin, Australia, Oceania, and Aotearoa/New Zealand (Engel & Glenny, 2008: 584). A specimen collected in 1952 (Amy Greenwell B-86, MU) at 13,000 feet near the summit of Mauna Kea, at the base of a moss clump, is the highest collection of any Hawaiian liverwort we have examined.



Plants reddish, interwoven in mats of *Kurzia hawaiica* and *Telaranea nematodes* or among mosses, in shade, 175-200 µm wide. Stems rigid, brownish, 65 µm wide, sparingly branched. Leaves imbricate to contiguous, obliquely succubous, concave, ascending, spreading at 45˚ or less, bilobed about halfway, 137 x 70 µm. Lobes 5-6 cells wide at base, 6 cells long, acute, tipped by 1-2 cells. Sinus acute to obtuse. Leaf margins entire but irregular or slightly serrulate. Cell walls thick; trigones lacking; cells at base of lobes 22-23 x 10-13 µm, quadrate to rectangular. Oil bodies elongate, apparently smooth(?). Underleaves absent (?). Rhizoids frequent but not abundant, on ventral side. Perianths terete, with a constricted mouth.

Jiří Váňa (1940-2018) examined the BISH type in 1977; his annotation questions whether this species is distinct from *C. heteroica* (see next page). The two species are similar and perhaps might be conspecific. *C. kilohanensis* is red, has crowded leaves above, more irregular leaf margins and thicker-walled cells. In our experience, color or even cell wall thickness are not reliable characters to separate Hawaiian liverwort species. Our study of the types was too brief to allow for a reduction; further study is needed, and the presence or absence of underleaves needs to be checked.

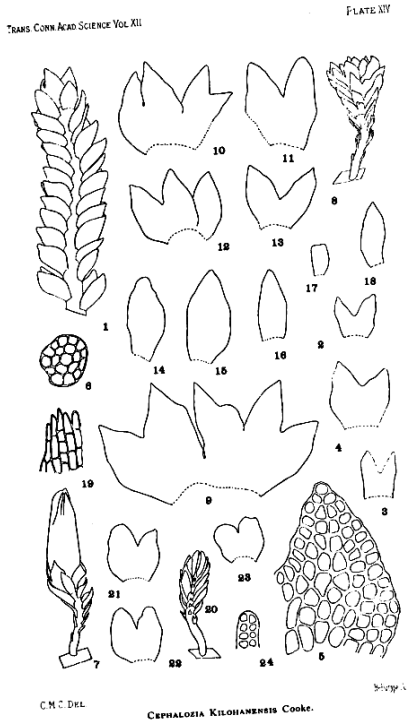


Plate XIV.

Cephalozia Kilohanensis **Cooke, p. 37.—Fig. 1. Apical part of stem, postical view, × 60.—Figs. 2, 3. Lower leaves, × 80.—Fig. 4. Upper leaf, × 80.—Fig. 5. Cells of leaf, × 270.—Fig. 6. Cross-section of stem, × 200.—Fig. 7. Perianth, × 30.—Fig. 8. Unfertilized female flower, × 30.—Fig. 9. Innermost bracts connate with bracteole, × 80.—Figs. 10, 11. Innermost bracts and bracteole, × 80.—Figs. 12, 13. Bracts and bracteole of second row, × 80.—Figs. 14–18. Consecutive bracteoles from an unfertilized female flower, × 80.—Fig. 19. Apex of perianth, × 200.—Fig. 20. Male branch, × 30.—Figs. 21–23. Male bracts, × 80.—Fig. 24. Male bracteole, × 200. All drawings from the type-specimens, collected by the writer at Kilohana, Kauai.**

Illustrations with captions taken from: Cooke, C.M,. 1904: The Hawaiian Hepaticae of the tribe Trigonantheae. Transactions of the Connecticut Academy of Arts and Sciences 12: 1-44.

Cephalozia Kilohanensis, sp. nov.

PLATE XIV.

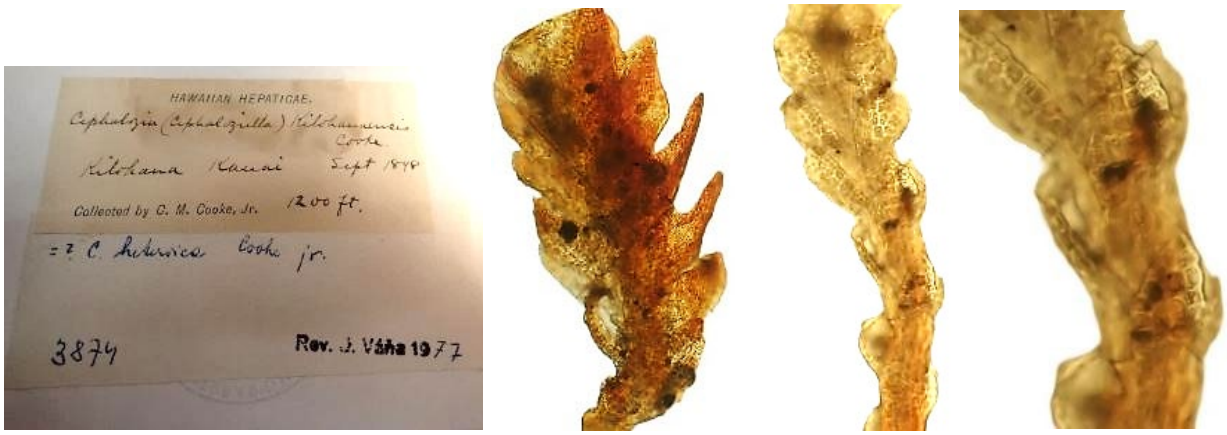
Autoicous : plants minute, cæspitose, reddish brown : stems prostrate, light brown, sparingly branched from the postical surface, about 5 cells in diameter, internal and cortical cells similar, the latter in about 12 longitudinal rows ; rhizoids numerous, scattered on the lower surface of the stem : leaves near the apex of the stem imbricated, almost transversely inserted, concave, assurgent, subquadrate, broadly ovate, bifid (about one-half), lobes entire, spreading, 6 to 10 cells long, 4 to 7 cells broad, triangular-ovate, apex acute to obtuse; sinus usually obtuse: leaf-cells with much thickened walls, trigones lacking or minute : underleaves wanting : ♀ inflorescence borne on a short postical branch ; bracts in 3 to 6 pairs ; innermost bracts similar to the leaves but from 2 to 3 times as large, broadly ovate, bifid (one-third to one-half), lobes unequal, the postical the larger, acute or obtuse, sinus separating lobes acute or obtuse, margin entire or nearly so; innermost bracteole narrowly ovate, connate on one or both sides, apex acute, obtuse or bifid, when bifid the lobes are unequal, triangular, acute; other bracts similar but smaller than innermost bracts ; other bracteoles narrowly ovate, acute or obtuse, slightly connate on one or both sides : perianth cylindrical, terete below, obtusely keeled near the apex, 1 cell thick, upper third hyaline, mouth contracted, irregularly denticulate : ♂ spike usually occupying a short postical branch ; ♂ bracts in 5 to 10 pairs, similar to leaves, closely imbricated, concave, unequally bifid, lobes ovate, obtuse, entire ; ♂ bracteoles rudimentary, minute, ligulate; cells of bracteole small subquadrate; antheridia borne singly: spores minute, round, purplish, verruculose ; elaters blunt ; bispiral.

Stems 0.08^{mm} in diameter ; leaves 0.18^{mm}x0.15^{mm} to 0.3^{mm}x0.28^{mm}; cells of stem 16μ in diameter ; leaf-cells at margin 19μx16μ, at base 24μx18μ ; innermost bracts 0.35^{mm}x0.3^{mm}, bracteole 0.35^{mm}x0.15^{mm} ; perianth 0.95^{mm}x0.4^{mm} ; ♂ bracts 0.25^{mm}x0.2^{mm}; spores 9μ ; elaters about 160μx9μ.

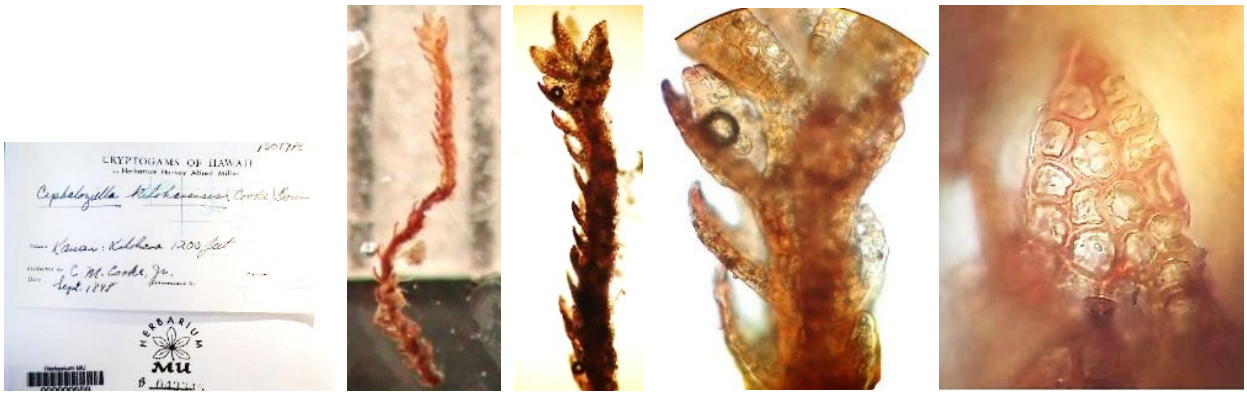
Kauai : Kilohana (Cooke), growing on the ground.

This species resembles *C. exiliflora* (Tayl.) Trevis. at first sight but differs in a large number of important characters. The Hawaiian species is autoicous while the New Zealand species is dioicous, the leaves of the former are larger, and more imbricated near the apex, the walls of the leaf-cells are slightly thicker, the ♂ and ♀ organs are not acrogenous but are borne on postical branches, and lastly the perichætial bracts are not denticulate.

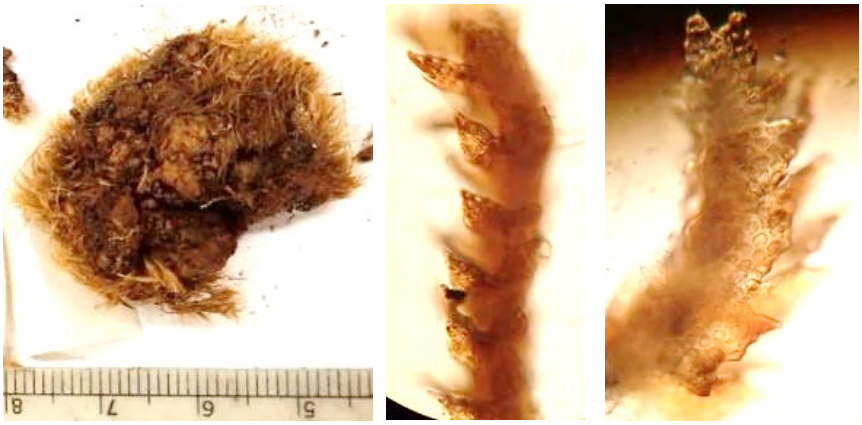
Protologue and illustrations with captions taken from: Cooke, C.M., 1904: The Hawaiian Hepaticae of the tribe Trigonantheae. Transactions of the Connecticut Academy of Arts and Sciences 12: 1-44.



Cephaloziella kilohanensis. Left: See annotation by Jiri Váňa, 1977. Second picture: Crowded leaves with thick walls and reddish pigment. Third and fourth pictures: Male branch(?) with cupped bracts. Note the distant and smaller, flatter leaves below. Cooke s.n., Kilohana, Kaua‘i (holotype or isotype, BISH). Photos by A.V. Freire.



Plants are reddish and small, with ascending leaves and thick walls. Scale in mm. Cooke s.n., Kilohana, Kaua‘i (Isotype, MU). Photos by A.V. Freire.

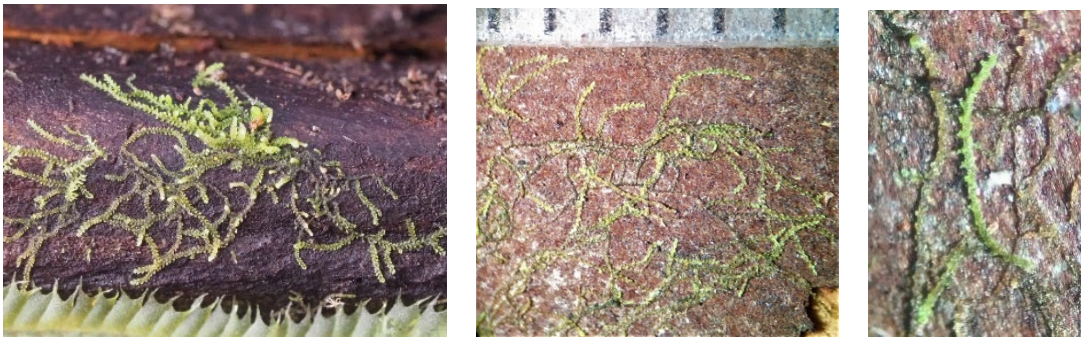


Left: Plants were found at the base of this moss clump near the summit of Mauna Kea, 13,000 ft., Hawai‘i Island, Greenwell B-86 (MU). This is the highest elevation collection of any Hawaiian liverwort. Photos by E.J. Judziewicz. Second photo: Note the similarity of leaf shape to *C. heteroica*.

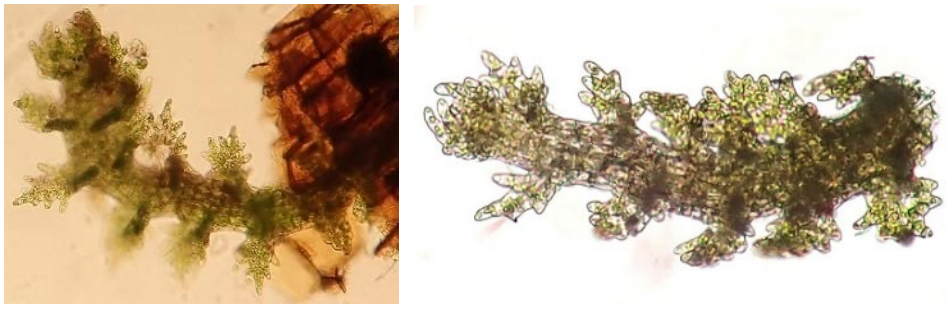
Cephaloziella kilohanensis. Left: Perianths. Right: Bifid leaves with thick walls. O‘ahu, Forbes 2539 (BISH). Photos by E.J. Judziewicz.

4. *Cephaloziella* species 1. Affinity ***C. microphylla*** (Steph.) Douin from Asia, as described and illustrated by Huang & Lin (2009) from Taiwan, and in the Bryophyte Flora of Doi Suthep-Pui National Park, Chiang Mai, Thailand (2025, online). However, it does not resemble Japanese populations as illustrated by Inoue (1976a: 40-41). This tiny species, creeping on bark, hāpuʻu stipes, and also epiphytic on hornworts (2,500-4,300 ft.), is found on Lānaʻi (Judziewicz, Freire & Bogner, 2023) and Hawaiʻi Island (Hualālai, Mauna Loa, and Kīlauea), in wet montane forests. Perhaps overlooked on other islands.

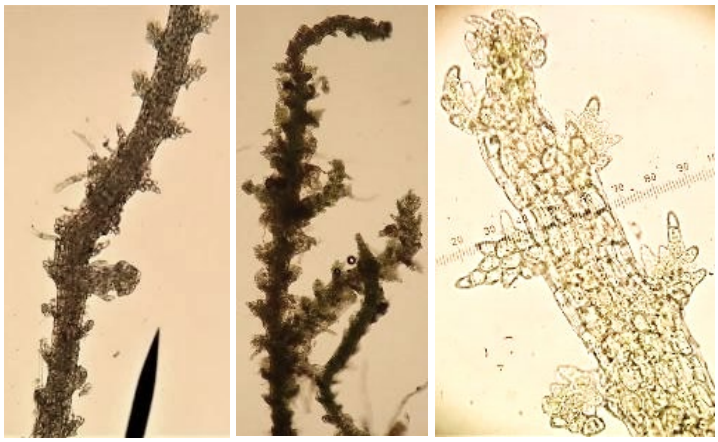
We first noted this extraordinary species in 2020 while examining collections made by Linda Pratt in the East Rift Zone of Hawaiʻi Volcanoes National Park in the 1980s. It was also recently photographed by Kevin Faccenda on Huālalai in January 2024 and by Randal Mindell along the Kūlani Road, Hawaiʻi Island: (https://www.inaturalist.org/observations/257020714) in December 2024. The stems are relatively rigid and prominent. The minute (50-60 µm long) leaves have two unequal lobes that are pinnately divided, each lobe resembling a tiny Christmas tree, one larger than the other. We have observed some populations with elliptical, 2-celled gemmae (but beware, as the plants house a wealth of algae). Antheridial branches are short, with crowded, pinnately divided, verrucose bracts. Perianths are long, terete, pleated, and have a truncate mouth.



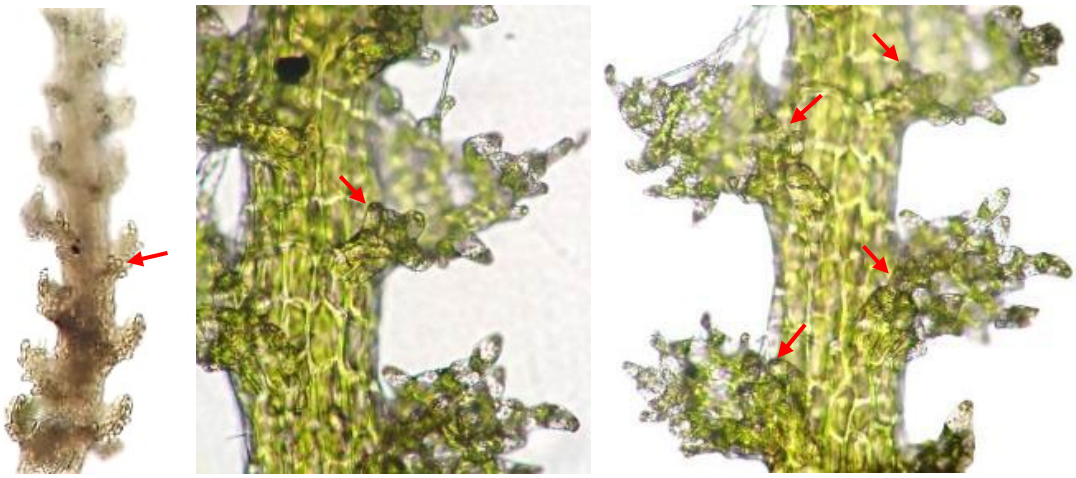
Left: Plants are closely attached to their substrate. At the bottom is the much larger *Lophocolea bicuspidata*. Hualālai, Hawaiʻi Island, 3,450 ft., photo by Kevin Faccenda, with permission (https://www.inaturalist.org/observations/196235317). Center and right: Plants are tiny, closely appressed to their substrate (a dried hāpuʻu stipe). Scale in mm. Nāhuku, Hawaiʻi Volcanoes National Park, Freire & Judziewicz 21-410 (HAVO).



Cephaloziella species 1. Leaves are lobed, with the appearance of tiny Christmas trees. Left: Puʻu Makaʻala N.A.R., Hawaiʻi Island, Freire & Judziewicz 22-215 (BISH). Right: Hawaiʻi Island, Judziewicz 17,131 (BISH). Photo by A.V. Freire.

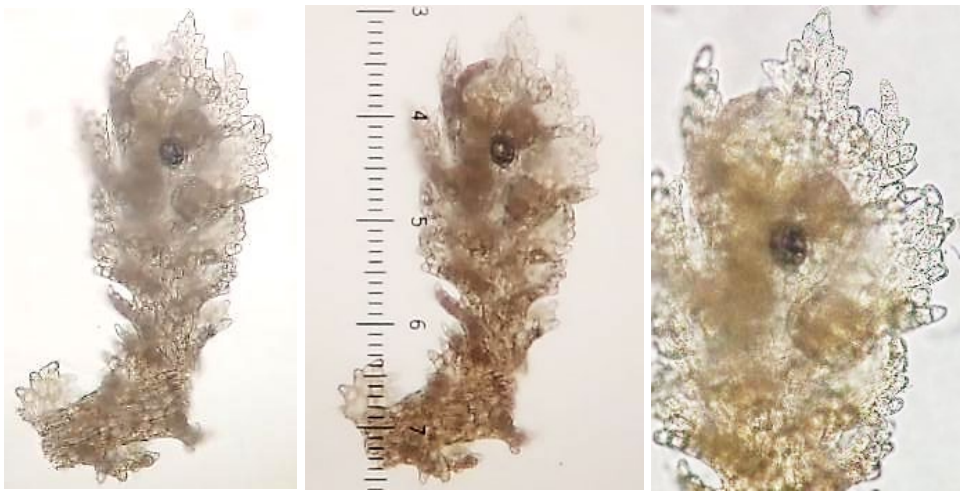


Left: Stems are thick and prominent compared to the tiny leaves. Nāhuku, Hawai‘i Volcanoes National Park, Freire & Judziewicz 21-410 (HAVO). Center: Branches are frequently observed. Pu‘u Maka‘ala N.A.R., Hawai‘i Island, Freire & Judziewicz 22-215 (BISH). Right: Scale units = 2.5 µm. Hawai‘i Island, Judziewicz 17,131 (BISH).



Leaf lobes are asymmetrical, the dorsal to be much smaller and more transversely inserted (arrows). Hawai‘i Island, Judziewicz 17,131 (BISH). Photos by A.V. Freire.

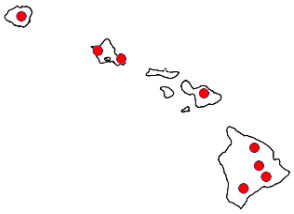
Cephaloziella species 1. Ventral leaf lobe. Note the thin-walled cells and verruculose surface. Hawai‘i Island, Judziewicz 17,131 (BISH). Photo by A.V. Freire.



Antheridial branch with crowded, toothed and verrucose bracts. Scale units = 9.7 µm. Hawai‘i Island, E.J. Judziewicz 17,131 (BISH). Photos by A.V. Freire.

Cephaloziella species 1. Perianth is pleated, long-tubular with a truncate mouth, 0.6 mm long and 0.2 mm wide. Note “growths” on the mouth – are these gemmae or algae? Hawai‘i Island, E.J. Judziewicz 17131 (BISH). Photo by A.V. Freire.

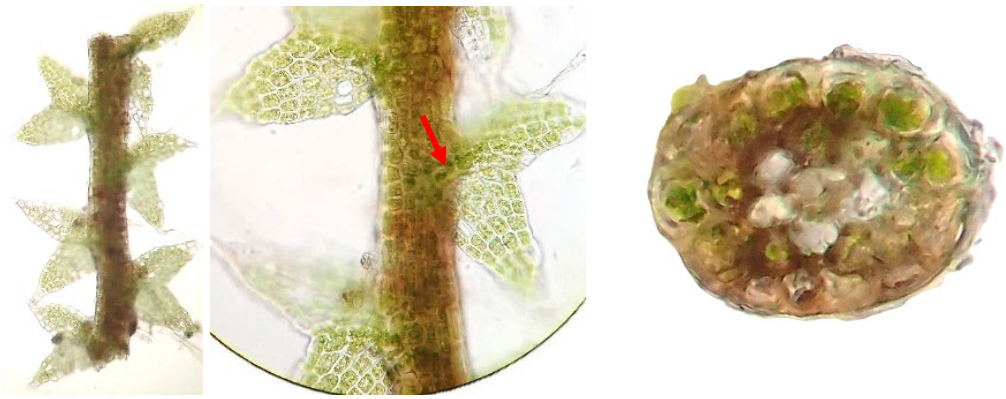
5. *Cephaloziella* species 2. Indigenous. Occasional; Kauaʻi, Oʻahu, Maui and Hawaiʻi (200-5,800 ft.). Tiny plants, with distant leaves that spread at nearly 90° angles. Leaves are deeply bifid with a broad triangular sinus and clearly divergent, narrow, triangular lobes. Underleaves are lacking.



Populations intertwined with mosses or forming small loose mats on soil. Plants green, small, about 3 mm long, 0.3(-0.35) mm wide. Stems firm and wiry, brown, turning black when dry, mainly unbranched, loosely attached. Leaves are small, spreading at almost 90°, with a long insertion line that forms a "V"- shaped fold in the middle of the blade's base; they are bifid, deeply divided to slightly over ½ of their length by a broad "V"-shaped sinus that separates two clearly divergent and narrowly triangular lobes; these are 5-6 cells wide at their base and 5-7 cells long, tipped by 1-2 hyaline cells, the apical one acute. One of the lobes often bears an "elbow" or a prominent tooth. Underleaves are absent. The leaf cells are moderately thick-walled and rectangular, mainly without trigones, but sometimes with a few scattered trigones. Archegonia are produced at the apex of main stems, protected by serrulate and crowded bracts. The perianths are terminal, terete and pleated, with serrulate bracts. They are long tubular, about three times as long as broad and with a slightly constricted mouth and hyaline above before sporophyte emergence. After sporophyte emergence they are broad, short, about twice as long as broad, and with a wide, truncate mouth. The different proportions (length/width) we interpret as two stages of maturity, with the upper portion of the perianth is ripped during sporophyte emergence. Males were not observed.

Cephaloziella species 2. Left: Plants are tiny and often intertwined with mosses. Scale in mm. Second photo: Detail of plants with perianth (bottom arrow) and terminal crowded bracts protecting archegonia (arrow above). Photos 3 and 4: Plants are small, with rigid stems and spreading leaves. Scale in mm (photo 3) and scale units = 26 µm (photo 4). Hawaiʻi Island, Freire & Judziewicz 22-829 (BISH).

Left: Leaves are distant, spreading at almost 90˚, with a broad and deep sinus. Center: Leaves may bear a prominent tooth at the base of one of the lobes. Right: Leaves have divergent lobes and are tipped by an acute, hyaline cell. Leaf cells are rectangular with moderately thickened walls. Note the “elbow” at the base of left lobe (arrow). Hawai‘i Island, Freire & Judziewicz 22-829 (BISH).



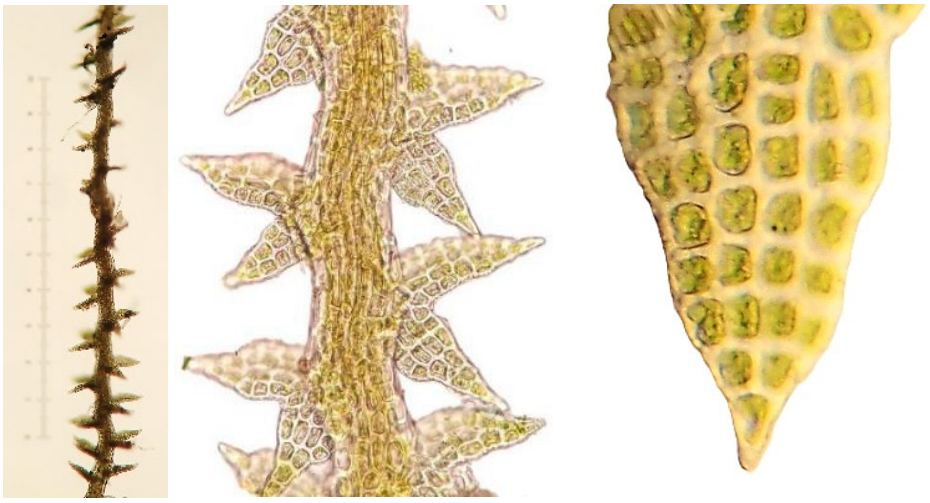
Flattened plant showing divergent leaf lobes, separated by a broad sinus. Center: Detail of “pleat” (arrow) in the leaf center, due to “V”-shaped insertion. A hyalodermis-like region is suggested in the two left photos, but is not evident in stem cross section (right photo). Hawai‘i Island, Freire & Judziewicz 22-829 (BISH).

Cephaloziella species 2. Left: Perianths are hyaline above, long-tubular, pleated, with a slightly constricted mouth before sporophyte emergence. Center and right: Perianths are broad, about twice as long as wide, with a broad and truncate mouth. Presumably the upper portion of the perianth is ripped off by the emergent sporophyte. Note the denticulate bracts (right). Hawai‘i Island, Freire & Judziewicz 22-829 (BISH).

The following pictures are of a specimen collected at a high-elevation rain forest, in the Saddle area of Hawai‘i Island. It appears to be a high-altitude variant of *Cephaloziella* species 2. The plants are slightly smaller (260 µm wide); leaves are 150 µm long, divided more deeply, to roughly 2/3 of their length; the leaf lobes are 4-5(7) cells wide and (4)5-7(9) cells long, and the leaf cells are quadrate and mostly thicker-walled and verrucose. Perianths are abundant, hyaline above, tubular, keeled, and pleated with serrulate, thick-walled bracts. They have a constricted mouth that broadens after sporophyte emergence.

All pictures below from Saddle area of Hawai‘i Island, Freire & Judziewicz 21-800 (BISH).

Left: Plants are tiny, prostrate and form small dense mats. Note the prominent hyaline perianths; scale at top in mm. Center and right: Perianths are long and terete, keeled, with a truncate mouth. Note young sporophyte in green (center). The filaments at the apex are algae. Perianth mouth is open after sporophyte emergence (right). Hawai‘i Island, Saddle area, Freire & Judziewicz 21-800 (BISH).



Cephaloziella species 2? The leaves are squarrose, divided deeply, with divergent and long-triangular lobes. Note the thick leaf cell walls (right). Saddle area, Hawai‘i Island, Freire & Judziewicz 21-800 (BISH). Left: Scale units = 9.7 µm.

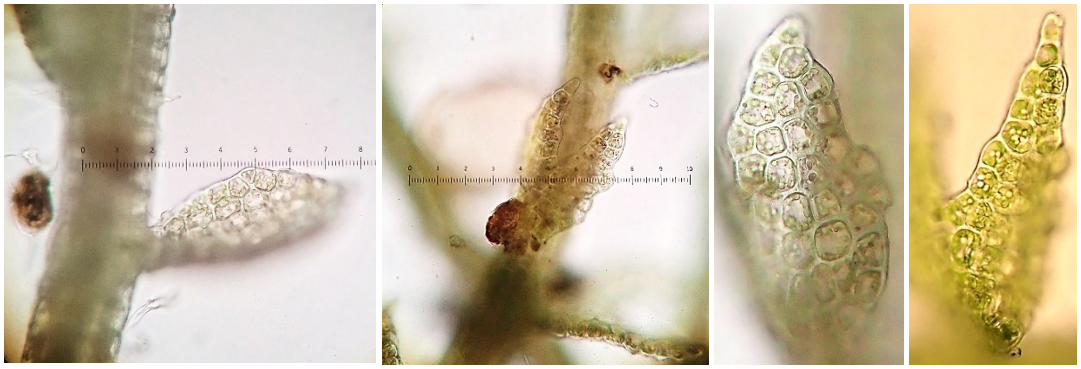
6. *Cephaloziella* species 3.

The following specimen, collected on Maui, differs from other Cephaloziellas in its serrulate leaf margins and thickened cell walls. We did not get to study this specimen in any detail and present here a brief description based on the photos shown below. The plants are tiny, with rigid stems and contiguous to distant leaves that spread at 45˚; they are rigid, ascending and almost transversely inserted (?), they are folded lengthwise in the middle. Leaves are divided by a triangular sinus to about halfway. The lobes are triangular and acute. The leaf margins are markedly serrulate. Leaf cells have thick walls. This species needs work!

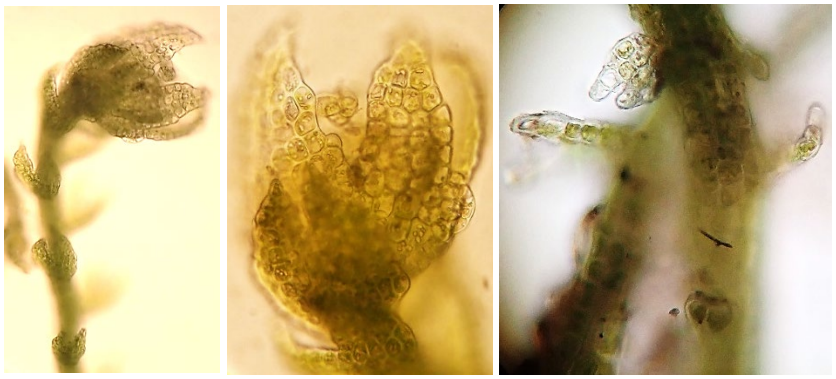
Waikamoi Preserve, Haleakalā, Maui; Freire, Judziewicz, Oppenheimer & Pezzillo 23-68 (BISH).

7. *Cephaloziella* (?) Freire & Judziewicz 23-231 (BISH). ʻĀwehi Gulch, Hakalau Forest National Wildlife Refuge. These tiny plants are a puzzle. The upper leaves are bifid, well-developed, and rounded, while the older leaves are reduced to tiny knobs or reduced laminas. Underleaves may be present. This species needs work!

Photos 1 and 2: Scales in mm. Photo 3: Scale units = 9.7 µm.



Photos 1 and 2: Scale units = 2.5 µm.



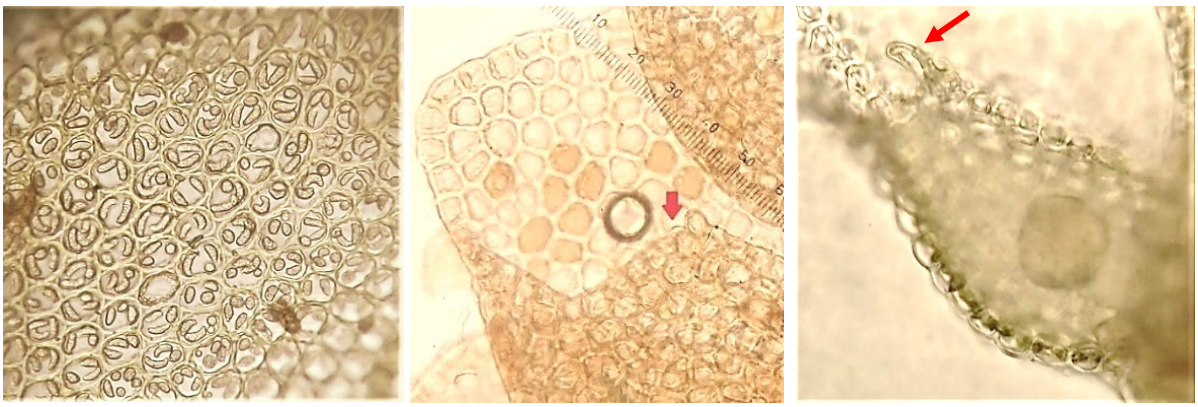
Photos 1 and 2: Apical gemmae. Photo 3: Reduced leaves.

Cheilolejeunea (Spruce) Steph. (Lejeuneaceae)

Eight species in Hawai‘i (187 species worldwide). Four species were previously reported for Hawai‘i, but there are at least 4-5 more species: An unpublished H.A. Miller species has very large underleaves and a short narrow sinus (Miller 2781, MU, not examined by us) and was collected from Hālawa Ridge (el. 1,200-2,400 ft.), Ko‘olau Range, O‘ahu. There are at least four other possible species (found at the end of this treatment).

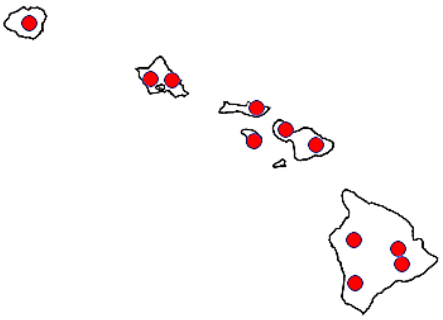
Cheilolejeunea differs from *Lejeunea* in the following character tendencies: leaf cell oil bodies few (rarely one) and large, sometimes giving the plant a slight brownish color; lobules often cylindrical, sometimes inflated, with the slime papillae distal (above) to the tooth (at lobule apex between tooth and the keel); and underleaves mostly larger and rounder.

1. Underleaves holostipous (entire); rare, Kaua‘i ..... ***C.* sp. 2**
1. Underleaves schizostipous (bifid; examine carefully, the sinus can be short and narrow) **2**
   2. Plants with a partially tinged with reddish or orangish..... **3**
      3. Lobules small, less than 1/5 the lobe length ..... ***C. hawaica***
      3. Lobules large, over ½ the lobe length (at least at stem apices) ..... ***C.* sp. 3**
   2. Plants not reddish or orangish-tinged **4**
      4. Leaf lobules with a long, single-celled, fang-like tooth **5**
         5. Lower margins of leaves clearly bent or kinked in the middle; lobule sharply pointed..... ***C. decursiva***
         5. Lower margins of leaves straight, not or barely bent or kinked in the middle; lobule tooth with a rounded tip **6**
            6. Leaf cells lacking trigones ..... ***C.* sp. 1**
            6. Leaf cells with conspicuous trigones ..... ***C. hawaica***
      4. Leaf lobules with a small single-celled tooth or with a short two-celled tooth **7**
         7. Underleaves barely notched, with a short slit-like sinus; lobe tips often overlapping (connivent) ..... ***C. stenoschiza***
         7. Underleaves clearly notched to at least 1/3, with a triangular sinus; lobes never overlapping … **8**
            8. Lobules large, at least 50% the length of the lobe ..... ***C.* sp. 4**
            8. Lobules smaller, at most 40% the length of the lobe ..... ***C. intertexta***



Characters of *Cheilolejeunea*. Left: (1)2-3 large oil bodies per cell (*C. stenoschiza*). Center: The lobule slime papillae is distal to (above) the lobule tooth (*C.* sp. 3). Right: Lobule tooth can be elongate and prominent (*C.* sp. 1). Photos by E.J. Judziewicz.

1. ***Cheilolejeunea decursiva*** (Sande Lac.) R.M. Schust. **Indigenous.** A member of subgenus *Cheilolejeunea* (Söderström et al., 2016). Found on all major islands (1,500-5,700 ft.) and in tropical Asia and Africa. This tiny, easily overlooked species can be distinguished by the kink (close to 90˚ angle) formed between the lobe's postical margin and the lobule keel; the lobule has a pungent, fanglike tooth. Leaf cell walls with small trigones. See Zhu & Lai (2005).



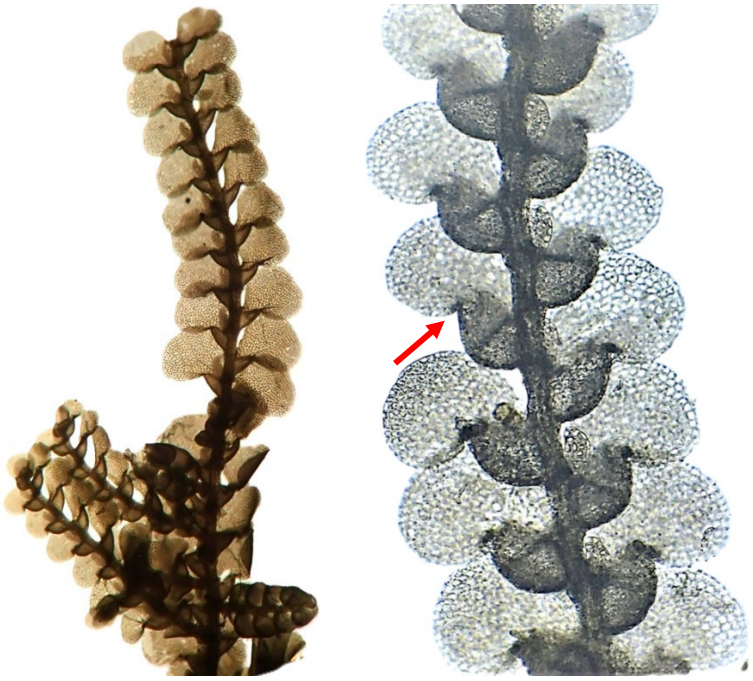
Grolle (1977) reduced the supposedly Hawaiian endemic *Trachylejeunea oahuensis* A. Evans to the broadly distributed *Cheilolejeunea decursiva*. We recognize this reduction and do not include the former in our treatment.

Plants olive-green, vermiform, small, (5)6-7 mm long, up to 0.8-0.9 mm wide, creeping. Stems often branched. Leaves obovate, spreading at 45˚ from the stem, falcate with upper lobes spreading at 90˚, imbricate to contiguous, concave, entire, rounded at the apex, overarching the stem; kinked near the middle of the lower margin, with a sharp angle (90˚ or nearly so) at the point where the lobule keel joins the keel-free portion of the lobe. Lobule ½ to slightly under 1/3 the lobe length, ovate, inflated, with the free margin usually inrolled, but sometimes flattened along the keel-free margin; with a long, single celled, pointed, fang-like apical tooth, this somewhat horizontally oriented (not standing erect). Middle leaf cells slightly elongated, marginal cells quadrate. Leaf cell walls slightly thickened, with small to large trigones. Underleaves about twice as broad as the stem, distant, oblong-obovate to oblong-orbicular, bifid, with a narrow "V"-shaped sinus that splits the upper half or third of the underleaf into two lobes. Antheridia produced on short lateral branches with two rows of concave and imbricate antheridial scales. Perianths on short lateral branches, obovate, inflated, smooth, obovate, with five smooth keels and shortly beaked.

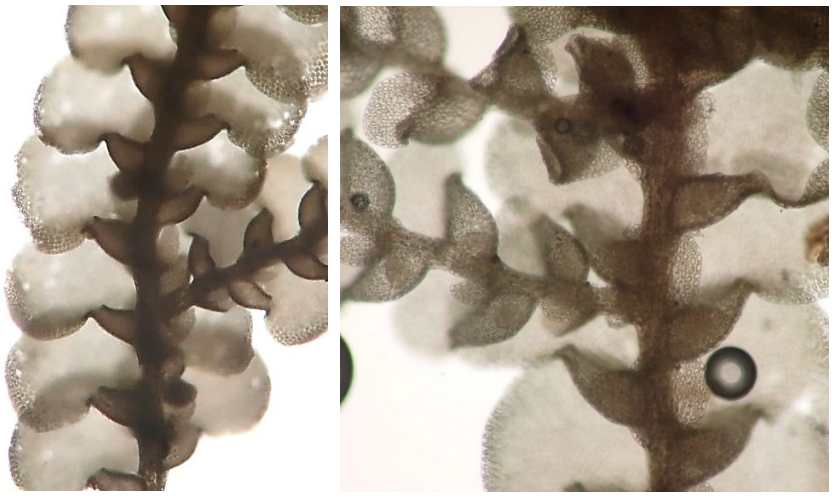
The specimen collected in the ʻŌlaʻa Trench, Hawaiʻi Volcanoes National Park by Waite s.n. (HAVO) has larger leaf lobules that are flattened along their free margin rather than inrolled. We consider this population an extreme morphological type within the species and include it in our treatment.

Cheilolejeunea decursiva. Plants are small and vermiform; they creep on bark. Left: Fresh plants are olive-green. Scale in mm. Photo by E.J. Judziewicz. Right: Dry plants are olive brown. Photo by A.V. Freire. Hawaiʻi Island, Judziewicz 17,185 (BISH).

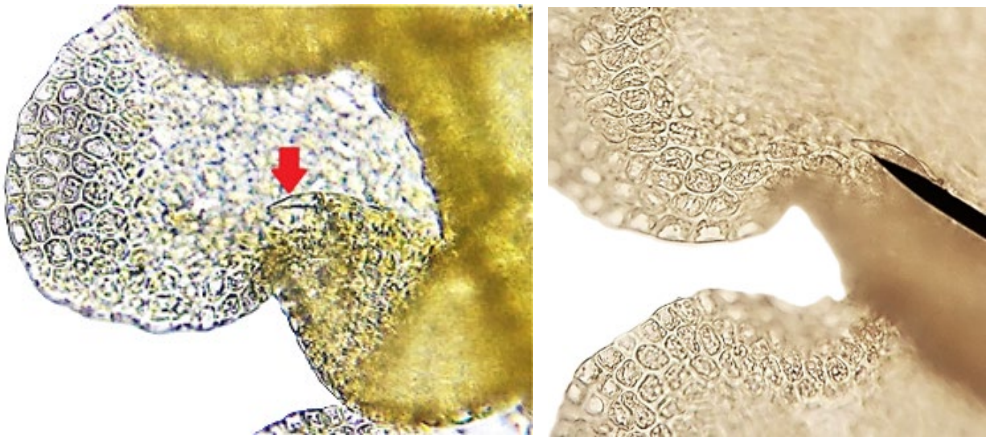
Left: Plants are slightly less than 1 mm wide. Scale in mm. Hawai‘i Island, Judziewicz 17,185 (BISH). Photo by E.J. Judziewicz. Right: Plant about 0.9 mm wide. Note male branch. Scale in mm. O‘ahu, Faccenda 3707 (BISH). Photo by A.V. Freire.



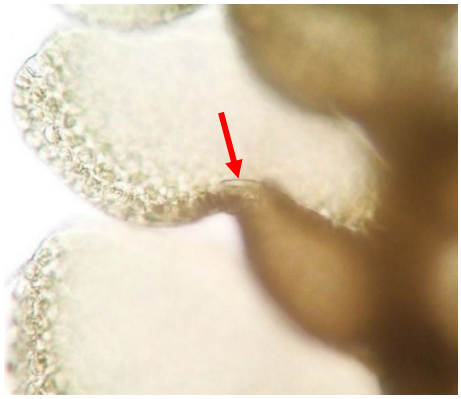
Cheilolejeunea decursiva. Left: Plant with cylindrical, partially inflated lobules, vegetative branches, and a male branch. Ko‘olau Range, O‘ahu, Faccenda 3707 (BISH). Photo by A.V. Freire. Right: Leaves strongly bent due to the sharp angle (about 90°, arrow) between the lobule keel and lower margin of lobe. Note the broader lobules on this plant. ‘Ōla‘a Trench, Hawai‘i Volcanoes National Park, Waite s.n. (HAVO). Photo by E.J. Judziewicz.



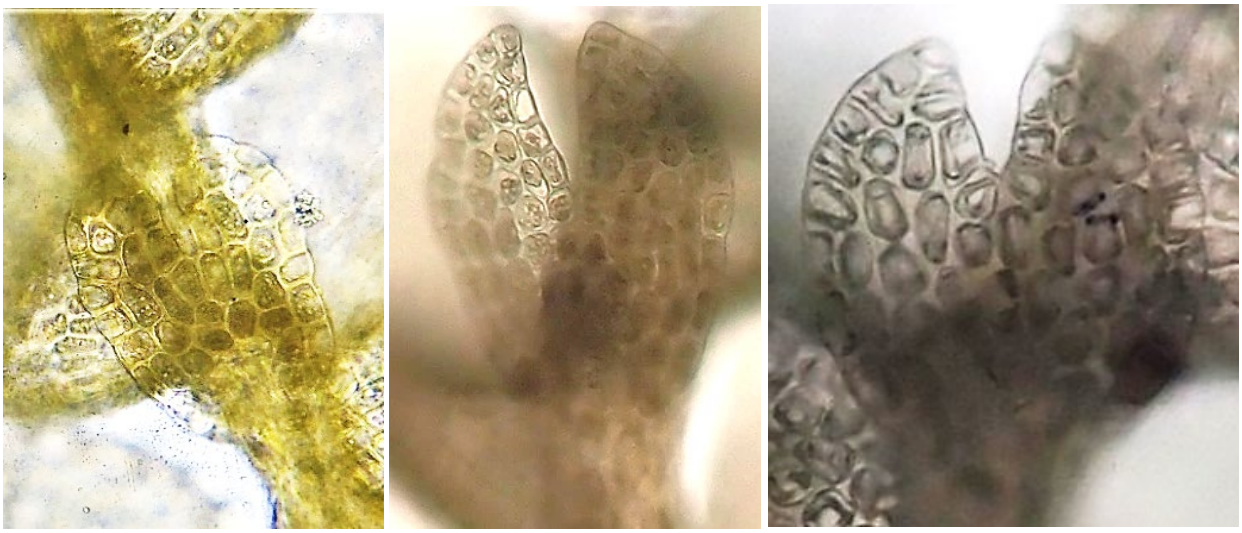
Left: Branching is of the *Lejeunea* type. Hawai‘i Island, Judziewicz 17,185 (BISH). Photo by A.V. Freire. Right: Detail of *Lejeunea*-type intercalary branching (under leaf lobe and with basal collar). Saddle area, Hawaii Island, Freire & Judziewicz 21-806 (BISH).



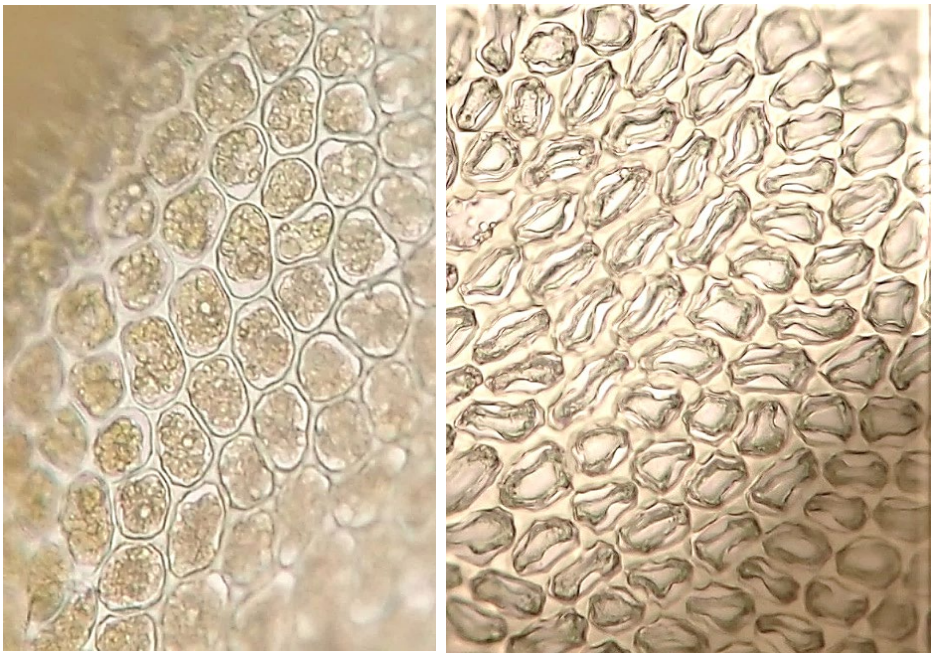
Left: Fang-like tooth (red arrow) on lobule. ‘Ōla‘a Trench, Hawai‘i Volcanoes National Park, Waite s.n. (HAVO). Right: South Kona, Hawaii Island, Pratt 3356 (HAVO). Photos by E.J. Judziewicz.



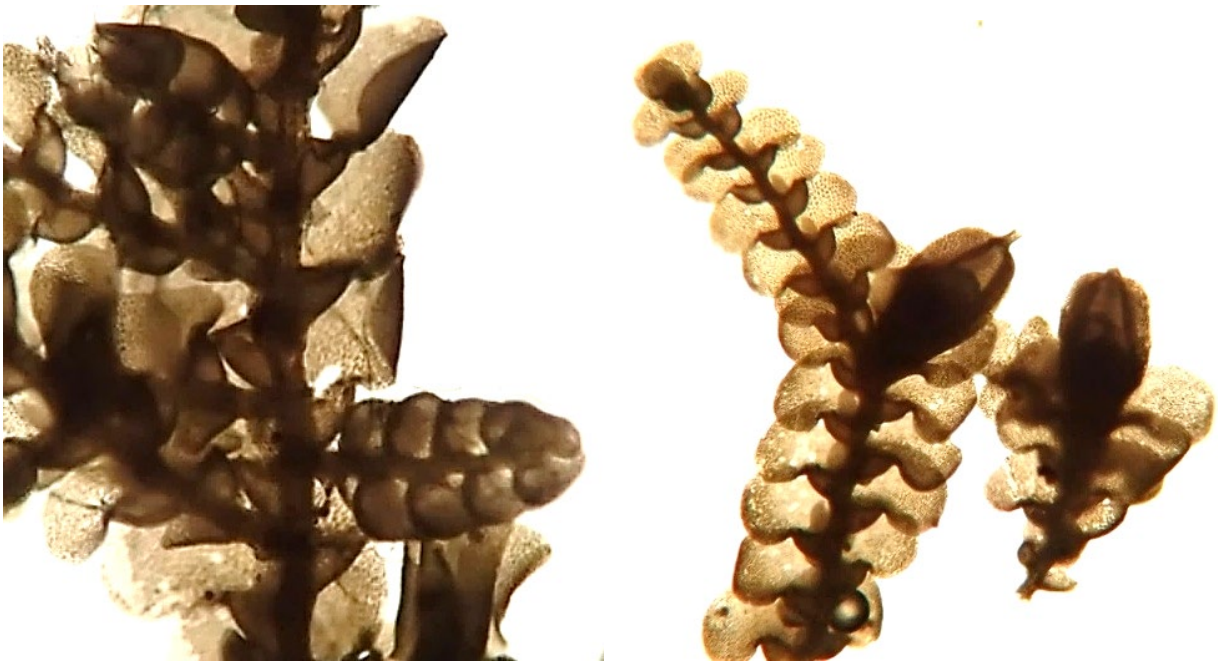
Cheilolejeunea decursiva. The distinctive lobule tooth is often nearly horizontally positioned and may be difficult to find. Special attention is needed! Hawai‘i Island, Judziewicz 17,185 (BISH). Photo by A.V. Freire.



Left and Center: Underleaves are obovate and bifid. Left: ʻŌlaʻa Trench, Hawaiʻi Volcanoes National Park, Waite s.n. (HAVO). Photo by E.J. Judziewicz. Center: Faccenda 3707 (BISH). Photo by A.V. Freire. Right: Underleaves can also be sub-orbicular to orbicular. Hawaiʻi Island, Freire & Judziewicz 21-806c (BISH).



Cheilolejeunea decursiva. Leaf cells can have small (left) to large (right) trigones. Left: Koʻolau Range, Oʻahu, Faccenda 3707 (BISH). Photo by A.V. Freire. Right: Saddle area, Hawaiʻi Island, 5,100 ft, Freire & Judziewicz 21-806c (BISH).



Left: Male branch with concave and paired antheridial bracts. Koʻolau Range, Oʻahu, Faccenda 3707 (BISH). Right: Inflated perianths with beak and keels. Hawaiʻi Island, Judziewicz 17,185 (BISH). Photos by A.V. Freire.

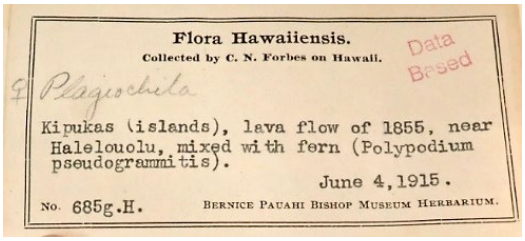
Cheilolejeunea decursiva. Perianth with 5 smooth keels. Hawaiʻi Island, Judziewicz 17,185 (BISH). Photo by A.V. Freire.

2. *Cheilolejeunea hawaica* Steph. **Indigenous or Endemic.** A member of subgenus *Cheilolejeunea* (Söderström et al., 2016). Rare. Found intermixed with other hepatics; the type was collected by Baldwin from Maui. Possible affinity (Evans, 1900): *C. aneogyna* (Spruce) A. Evans, tropical America. *C. hawaica* is recognized by its reddish pigmentation, distant underleaves, small leaf lobules, cells with large trigones, and by the presence of a vittate region. Barbara Thiers (1996), notes on the Geneva holotype that the species is "near" the Paleotropical ***C. serpentina*** (Mitt.) Mizutani:

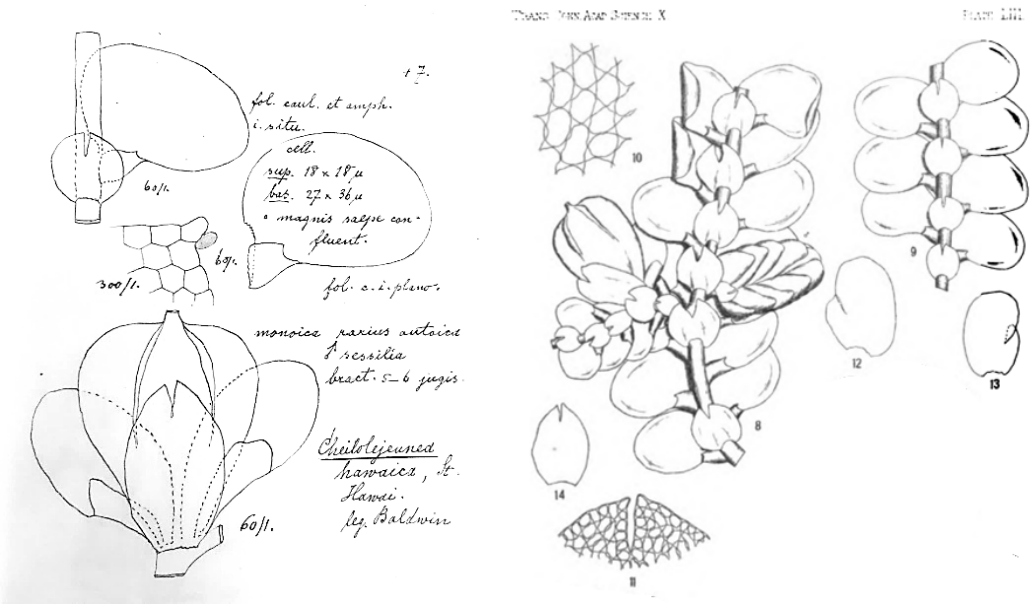
(https://www.villege.ch/musinfo/bd/cjb/chg/adetail.php?id=100563&base=img&lang=en). This latter species is regarded as a synonym of the pantropical ***C. rigidula*** by some authors (e.g., Wigginton, 2018). Plants reddish, at least 5-6 mm long and slightly over 1 mm wide. Stems firm, with thick-walled epidermal cells, sparingly branched. Leaves long-spreading at 90˚ from the stem, mostly concave but occasionally flat, contiguous to slightly imbricate, oblong, 1.5-2 times longer than broad, entire, with a rounded apex. Lobules are small, only about 1.5 times broader than the stem diameter, ovate-triangular, mostly inflated and inrolled but sometimes flattened; with a single, conspicuous, slightly hooked tooth with a rounded tip. Underleaves distant to contiguous or even slightly overlapping, flat to revolute in their lower half, slightly reflexed, orbicular to oblong (longer than broad), notched to about 1/3 to ½ their length, about 3-3.5 times the stem width. Leaf cells thick-walled and with prominent trigones, elongated, but marginal cells quadrate to rectangular; cells larger towards the base of the leaf, forming a vittate region. Male branches short and compressed, produced laterally; antheridial bracts concave. Perianths lateral, obovate, smooth, with 4 keels, flat on one surface but inflated otherwise, with a short beak.

We gleaned this species from a mixed collection of liverworts (*Bazzania emarginata, Calypogeia cuspidata, Chiastocaulon combinatum, Cryptolophocolea ciliolata, Drepanolejeunea ungulata*, and *Jubula javanica*) made in a forest on the saddle between Mauna Loa and Mauna Kea, between Halealoha and the Wailuku River [ca. 4,000 ft.?], Hawai'i Island, by Charles Forbes 685g.H in 1915 (BISH). We used these plants to exemplify the species. We also studied a collection from Keahikauō Bog, West Maui (Herbst 6610.1, BISH). This specimen has all the characters observed in *C. hawaica,* but with overlapping rather than distant underleaves, thus modifying the species concept of Evans (1900). The red pigment is only observed at the very tip (we just had few fragments to study).

Two specimens at BISH collected by Cooke in Kaua'i (numbers 10 and 110) were annotated by Miller as *C. hawaica*. We did not have the chance to study them. They need to be compared with Forbes 685g.H. Some specimens named by us as *C. hawaica* at BISH and PTBG are likely to be erroneously identified. Our concept for the species has evolved.

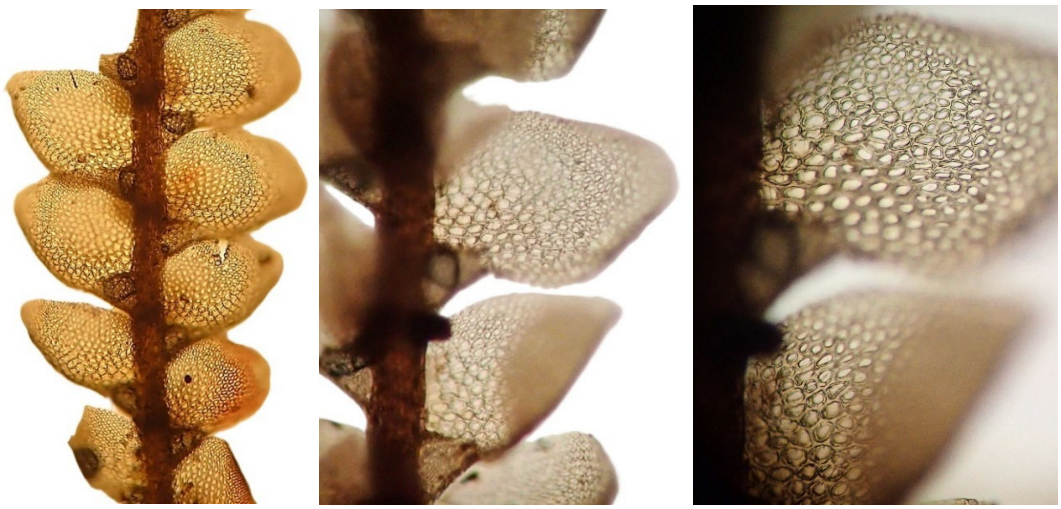


The specimen collected by Forbes 685g.H. (BISH), identified as *Plagiochila*, contains a mix of liverworts that includes the plants used by us to exemplify *C. hawaica*.



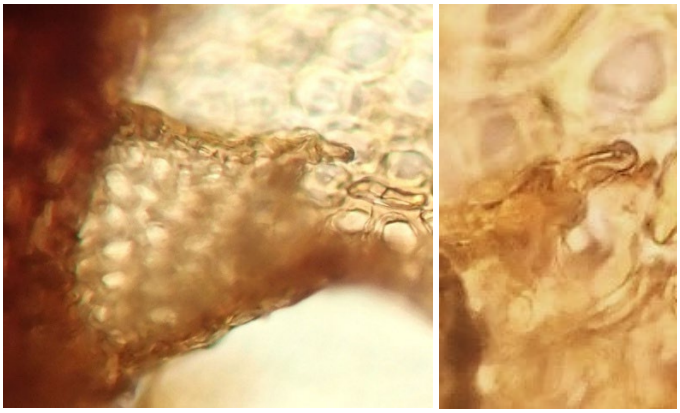
Left: Illustrations by Stephani (ca. 1920). Right: Illustrations by Evans (1900).

Cheilolejeunea hawaica. Plants small, reddish, and with distant underleaves. Note the spreading, elliptical leaves. Scales in mm. Left: Plant with male branch. Center: Concave leaves. Right: Note the small leaf lobules. Forbes 685g.H (BISH), photos by E.J. Judziewicz (left) and A.V. Freire (center and right).

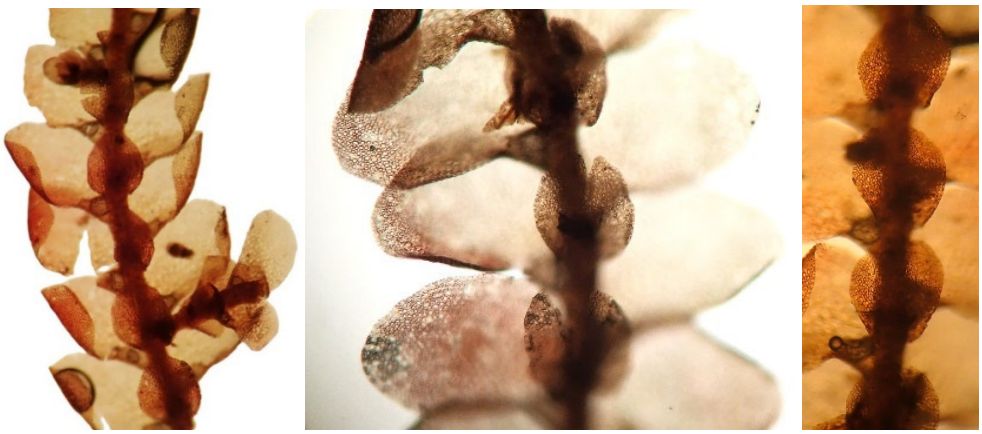


Leaves have a vittate region with larger cells that extends to almost half the blade. Forbes 685g.H (BISH). Left: Photo by E.J. Judziewicz. Center and right: Photos by A.V. Freire.

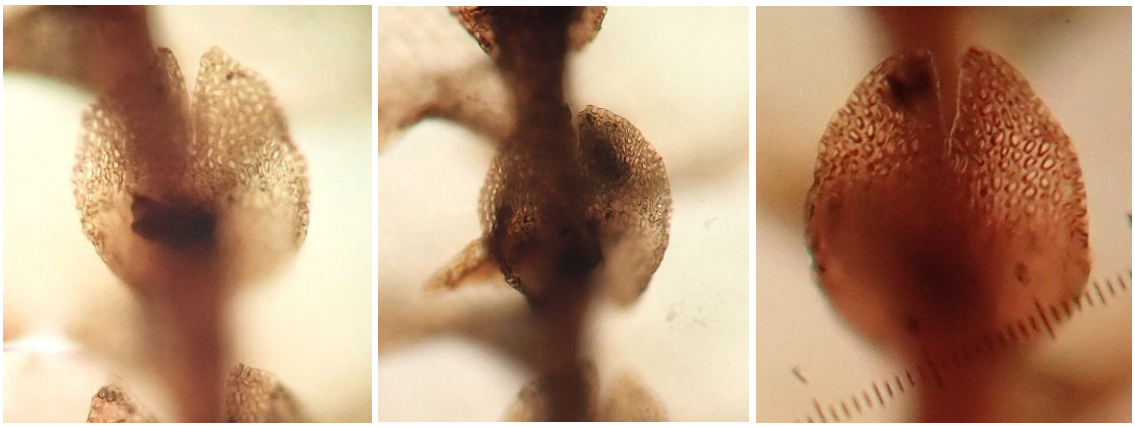
Leaf lobules are ovate-triangular, small, inrolled and have an apical tooth. Note the thick-walled stem epidermal cells (right). Forbes 685g.H (BISH). Photos by A.V. Freire.



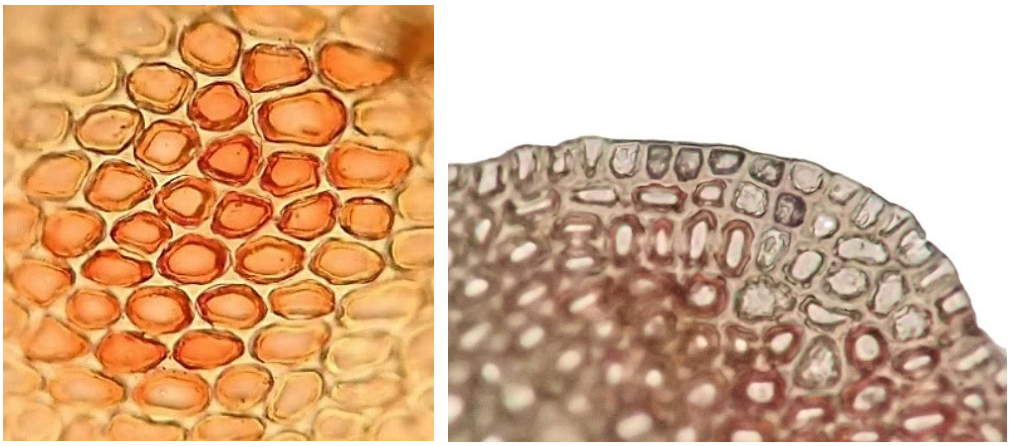
Cheilolejeunea hawaica. Left: Lobule with apical tooth. Right: Detail of tooth with rounded tip. Hawai‘i Island, Forbes 685g.H (BISH). Photos by E.J. Judziewicz.



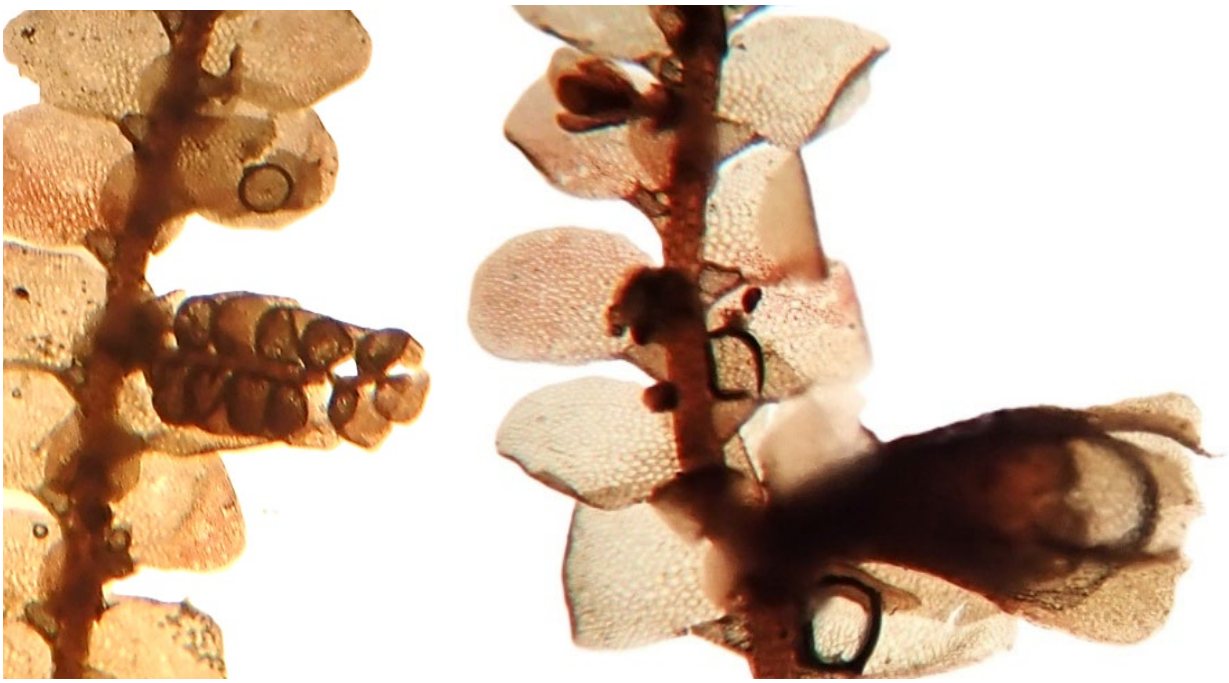
Underleaves are distant, they never overlapping. Left and center: Photos by A.V. Freire. Right: Photo by E.J. Judziewicz. Forbes 685g.H (BISH).



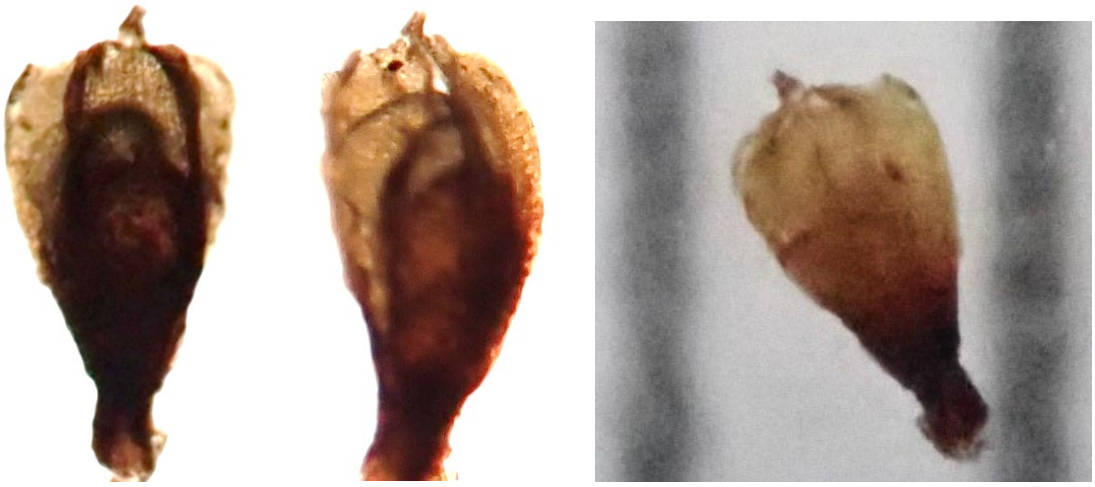
Underleaves are orbicular, about 3 times as broad as the stem, split at the apex into two pointed lobes by a narrow sinus. They have a curved insertion, their bottom half curved towards their ventral side, away from the stem. Left: Photo by E.J. Judziewicz. Center and Right: Photos by A.V. Freire. Forbes 685g.H (BISH). Scale units = 10 μm.



Cheilolejeunea hawaica. Median leaf cells have conspicuous trigones; marginal cells are quadrate to rectangular. Forbes 685g (BISH), Hawai‘i Island. Photos by E.J. Judziewicz (left) and A.V. Freire (right).

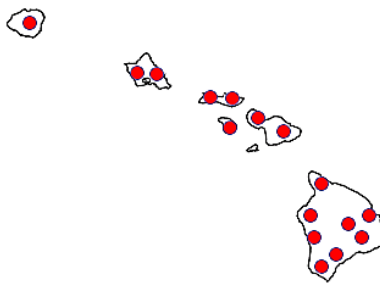


Sexual organs are produced on short lateral branches. Left: Plant with antheridial branch. Right: Plant with perianth. Photos by E.J. Judziewicz (left) and A.V. Freire (right). Forbes 685g.H (BISH).



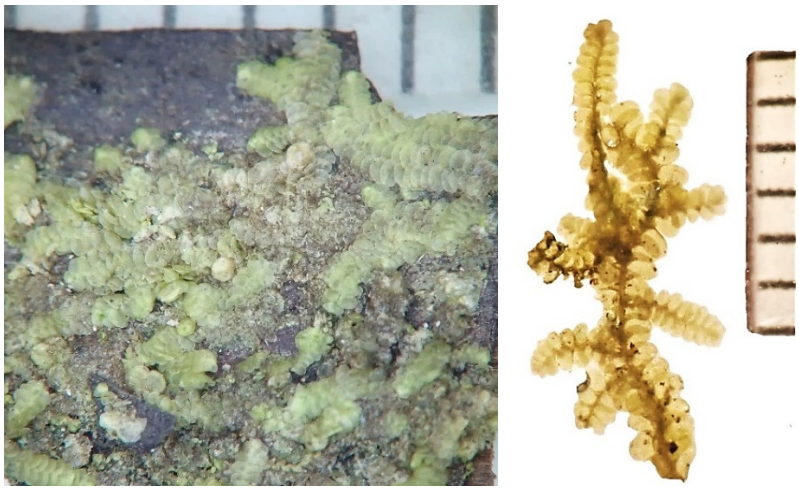
Cheilolejeunea hawaica. The perianth is beaked, keeled (left), bilateral, flattened on one surface, but bulging or inflated on the other (center). Right: Scale = 1 mm. Forbes 685g.H (BISH), Hawai‘i Island. Photos by A.V. Freire.

3. *Cheilolejeunea intertexta* (Lindenb.) Steph. **Indigenous.** A member of subgenus *Euosmolejeunea* (Spruce) Kachroo (Söderström et al., 2016). Found on all major islands (0-5,100 ft.), often at lower elevations and on exotic tree species. It is one of the only leafy liverworts recorded from dry West Moloka‘i (Miller, 3907, MU). This common pantropical species is recognized by its large, round underleaves split about ½ their length by a narrow sinus, by its imbricate oblong leaves, and by being profusely branched. It could be mistaken for the common, weedy *Lejeunea flava*; both have similar underleaves. *Cheilolejeunea intertexta*, however, has just a few large oil bodies in each leaf cell, and its leaves are generally more overlapping.

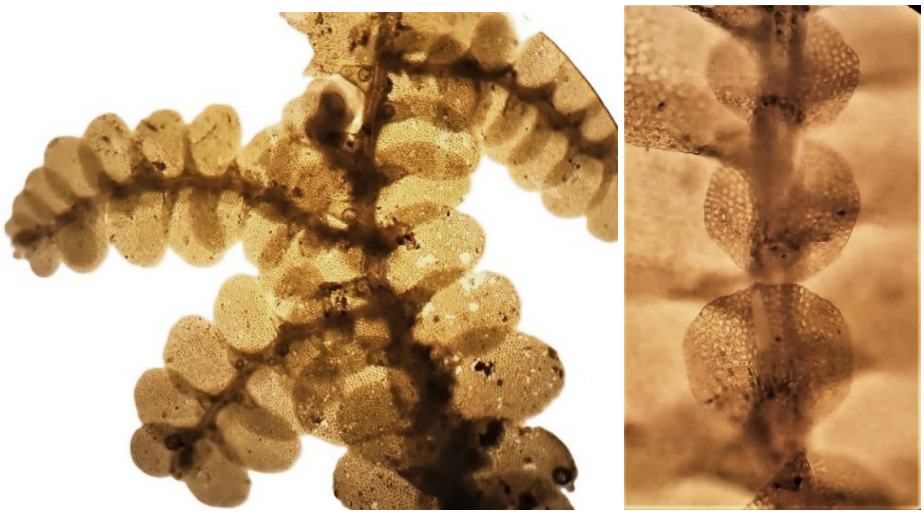


Plants light green, at least 10 mm long and up to 1.5 mm wide, creeping and closely appressed on bark, and abundantly branched. Leaves entire, slightly to strongly imbricate, spreading at 90˚ or nearly so, oblong-elliptical, slightly falcate, with truncate and rounded apices. Leaf lobules are small, about twice as long as the stem diameter, inflated, inrolled, ovate-triangular, with a truncate apex that bears a small and inconspicuous tooth. Underleaves contiguous, orbicular, 3-3.5 times as broad as the stem, with curved insertion, divided to about ½ their length by a narrow sinus, separating two slightly divergent lobes. Median leaf cells have slightly to moderately thickened walls, some with small trigones. Marginal cells are smaller and quadrate to rectangular. Oil bodies 1(2) per cell, large, elliptical, and clearly segmented. Perianths globose, obovate, beaked, keeled, and small. We did not see the papillae described by Evans (1900).

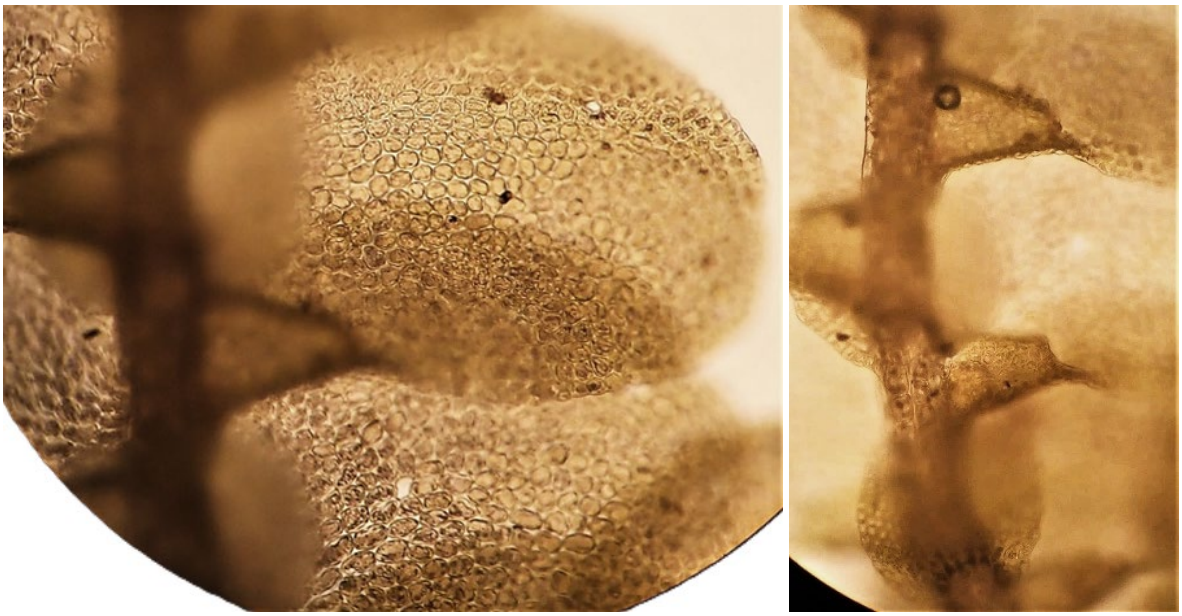
Cheilolejeunea intertexta includes Staples & Imada’s (2006) reports of *C. pyriflora* (type: Honolulu, Fleischer 85); see Miller’s determination: (https://www.villege.ch/musinfo/bd/cjb/chg/adetail.php?id=142399&base=img&lang=en) and *Hygrolejeunea pacifica* (type: Honolulu, Faurie 562, G not seen; isotype, MU!).



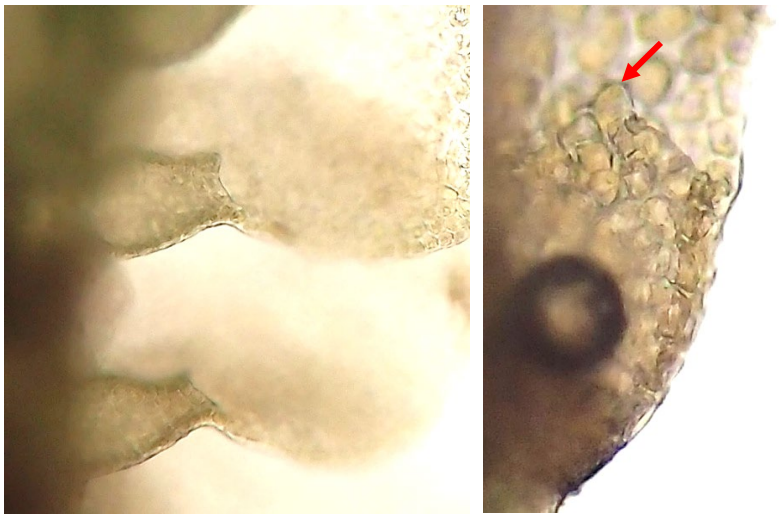
Cheilolejeunea intertexta. Left: Dried specimen. Ko‘olau Range, O‘ahu, Faccenda 3653 (BISH). Photo by A.V. Freire. Right: Plants are profusely branched. Scales in mm. Banyan Tree Drive, Hilo, Hawai‘i Island. Freire & Judziewicz 22-240 (BISH).



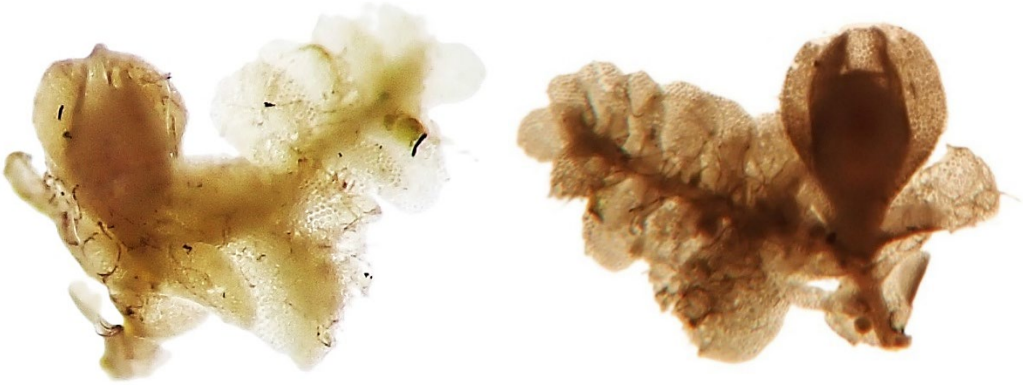
Left: Plants with broadly spreading, imbricate leaves. Right: Underleaves orbicular and large (about 3-3.5 times as broad as the stem), bifid and divided to about ½ their length by a narrow sinus. Banyan Tree Drive, Hilo, Hawai‘i Island. Freire & Judziewicz 22-240 (BISH).



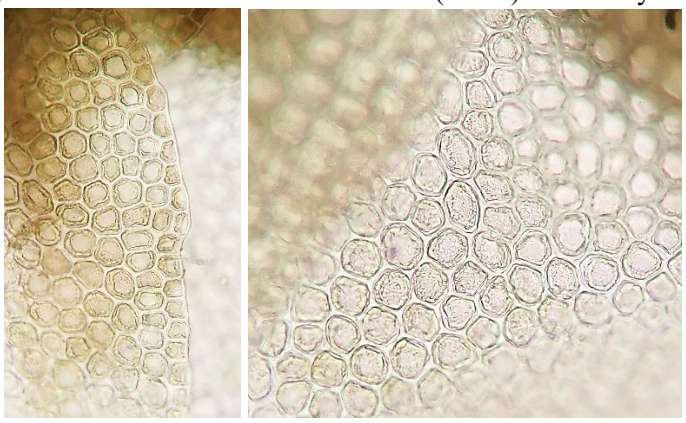
Cheilolejeunea intertexta. Left: Oblong-elliptical leaves bear small ovate-triangular lobules. Note trigones at leaf center. Right: Lobules are inflated and inrolled with truncate apices. Banyan Tree Drive, Hilo, Hawai‘i Island. Freire & Judziewicz 22-240 (BISH).



Leaf lobules have a truncate apex that bears a small tooth. Faccenda 3653 (BISH). Photos by A.V. Freire.

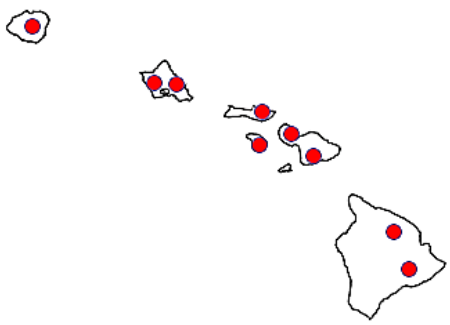


Perianths are obovate, globose and 5-keeled. Faccenda 3653 (BISH). Photos by A.V. Freire.



Cheilolejeunea intertexta. Marginal leaf cells are quadrate to rectangular, and smaller than the median cells. Median leaf cells have moderately thickened walls with trigones small or absent. Koʻolau Range, Oʻahu, Faccenda 3653 (BISH). Photos by A.V. Freire.

4. *Cheilolejeunea stenoschiza* (Ångstr.) A. Evans. **Endemic or indigenous.** A member of subgenus *Cheilolejeunea* (Söderström et al., 2016). Found on all major islands (700-5,500 ft.). Distinctive in its large, round underleaves with a short slit-like sinus, the tips of the lobes often slightly connivent. Leaf lobules large, rectangular and flat, with a broad, straight and truncate apex. Perhaps related to holostipous sp. 2 below. R.L. Zhu regarded the Geneva holotype as a synonym of the Madagascaran, Asian, Australasian, and Oceania species ***Cheilolejeunea trapezia*** (Nees) Kachroo & R. M. Schust.:



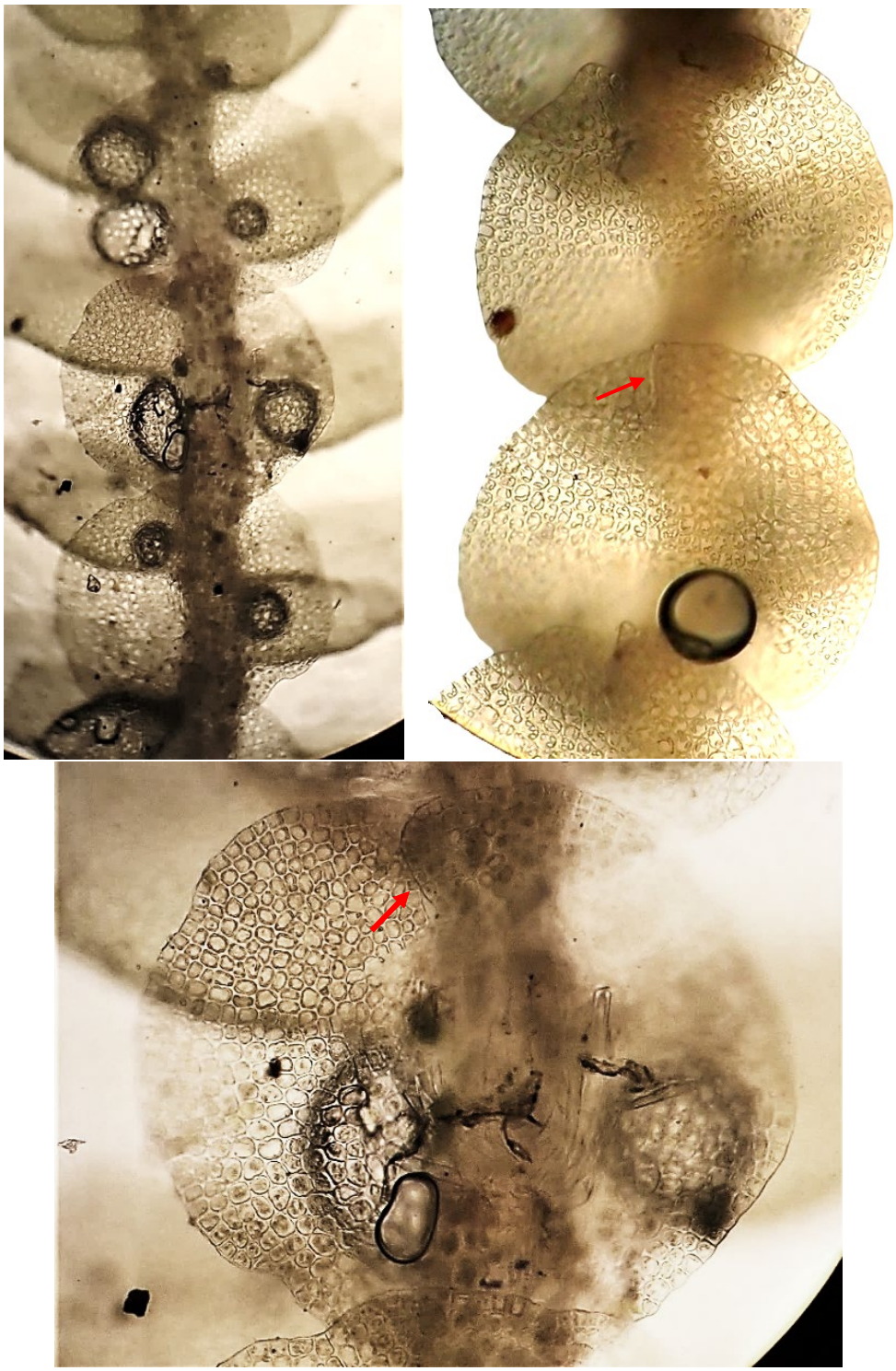
(https://www.ville-ge.ch/musinfo/bd/cjb/chg/adetail.php?id=101070&lang=en). However, the plants from Hawai‘i do not resemble illustrations of this widespread species.

Plants light to whitish green, robust, close to 2 mm broad, creeping, closely appressed to bark. Stems thin but wiry, sparingly branched. Leaves imbricate, entire, broadly spreading, oblong ovate, with rounded apices, slightly falcate, lower margin with a slight kink at the level of the lobule apex. Lobules are large, only slightly under ½ the length of the lobe, flattened to slightly inflated at the keel, rectangular; with a broadly truncate, straight apex bearing a small, erect, 1-2-celled tooth; sometimes with a bulging cell towards the middle; yet in other cases, no teeth are observed. Underleaves are orbicular, flat, contiguous to overlapping, large, about 5 times as broad as the stem; with a short, slit-like, narrow, and inconspicuous sinus (1/5 to ¼ the underleaf length), that separates two lobes that are sometimes connivent and overlapping. Cells with small trigones and with 2-3 large, segmented oil bodies.

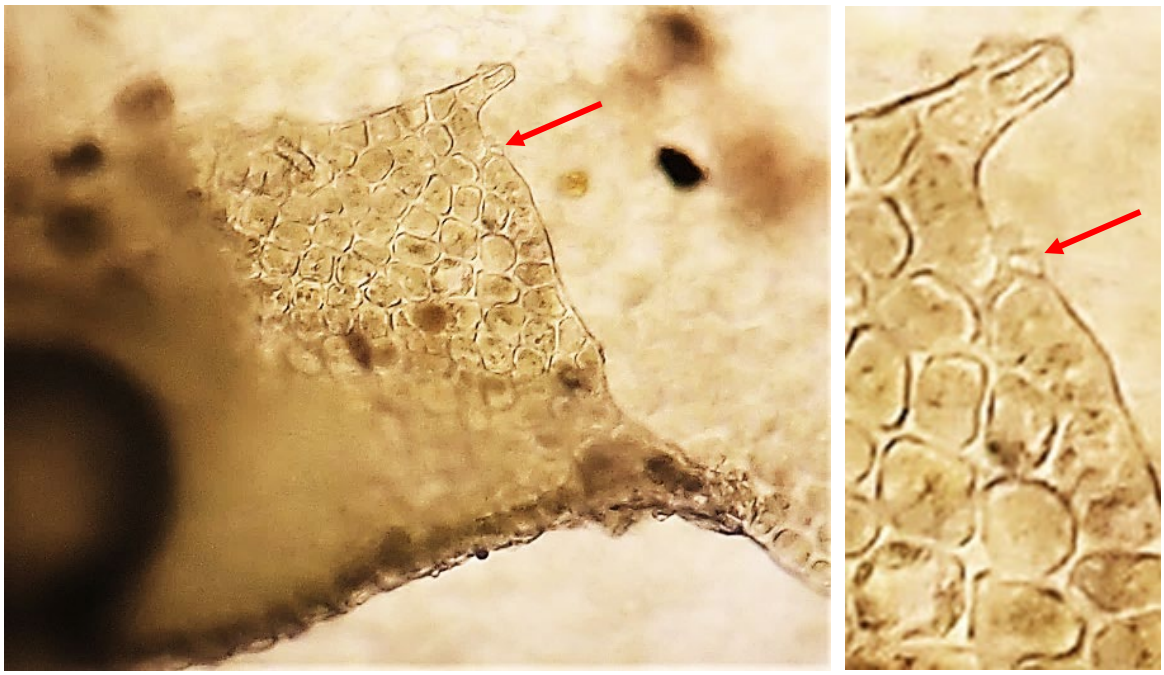
Cheilolejeunea stenoschiza. Dorsal and ventral views of plants, Ko‘olau Range, O‘ahu, Ross 2020 (BISH). Note that the minute bifid underleaf sinus is not or only barely visible at this resolution. Photos by Mike Ross: https://www.inaturalist.org/observations/226119153, with permission.

Plants are almost 2 mm broad. Scale in mm. Volcano, Hawai‘i Island, Freire and Judziewicz 22-548 (BISH).

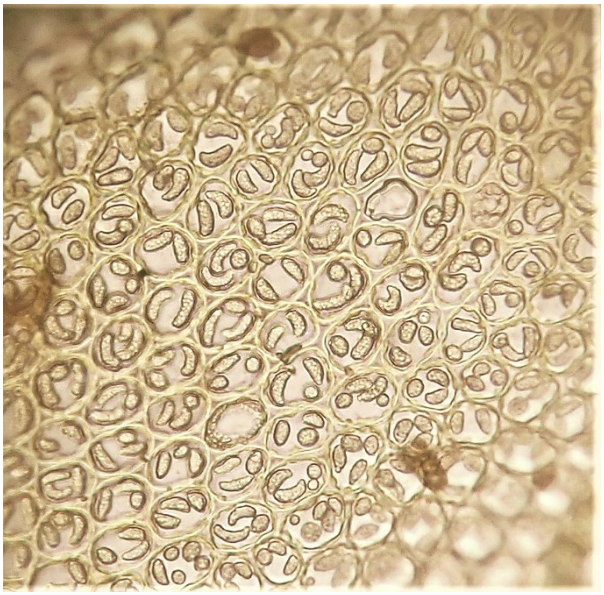
Cheilolejeunea stenoschiza. Leaves spreading at almost right angles, lobules rather rectangular and large; leaf cells have large oil bodies; and underleaves are large, about 5 times as broad as the stem. Volcano, Hawai‘i Island, Freire & Judziewicz 22-548 (BISH).



Cheilolejeunea stenoschiza. Upper left: Underleaves are large and orbicular, contiguous to overlapping. Upper right: Note the inconspicuous "slit-like" sinus. Bottom: Underleaf apex with a short notch and slightly overlapping lobes (arrow). Upper left and bottom: Volcano, Hawai'i Island, Freire & Judziewicz 22-548 (BISH). Upper right: Thomas et al. 537 (including Freire & Judziewicz) (BISH), Pu'u Ka'ala, O'ahu. Photo by E.J. Judziewicz.



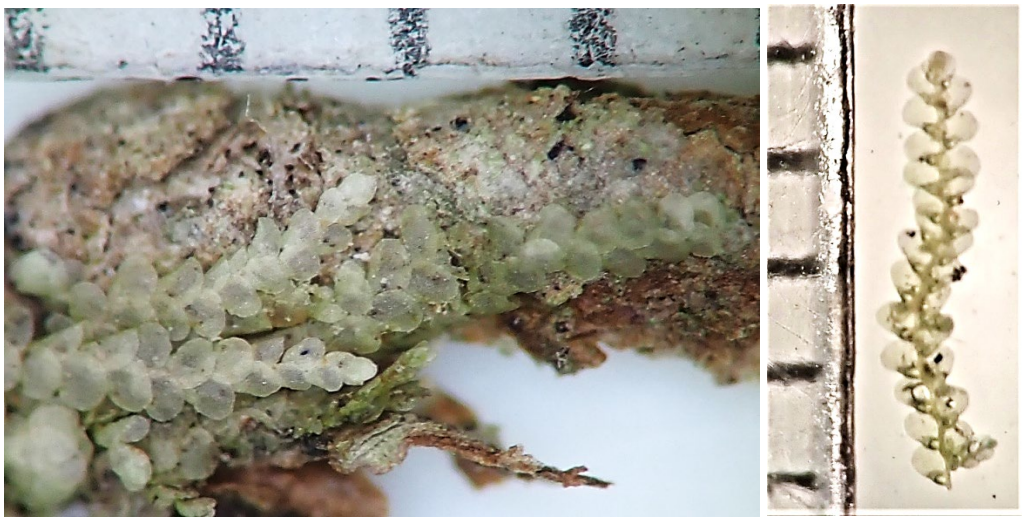
Detail of 2-celled lobule tooth and distal slime papillae (pointed by arrow). Volcano, Hawai‘i Island, Freire & Judziewicz 22-548 (BISH).



Cheilolejeunea stenoschiza, Cells with small trigones and 2-3 large oil bodies. Pu‘u Ka‘ala, O‘ahu, Thomas et al. 537 (including Freire & Judziewicz) (BISH). Photo by E.J. Judziewicz.

5. *Cheilolejeunea* species 1.

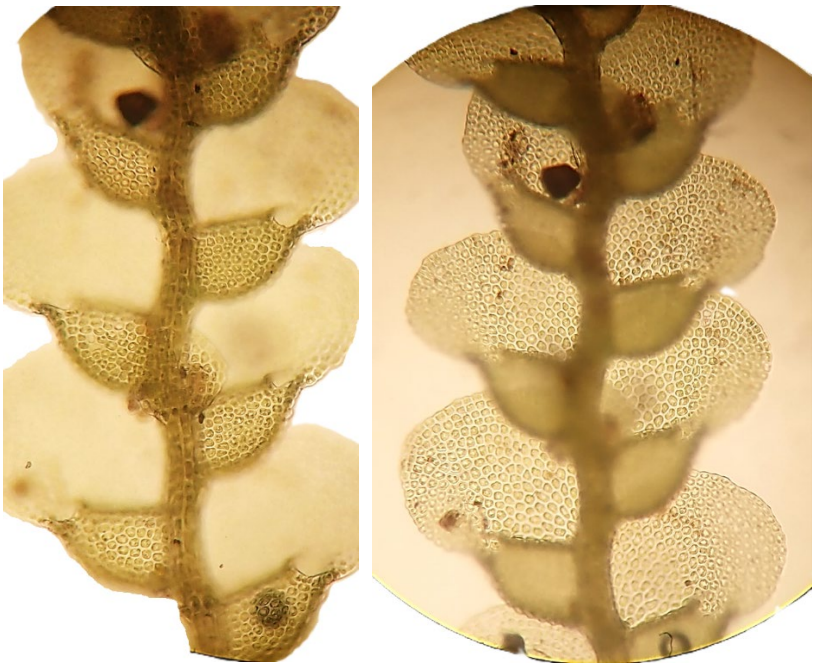
This species was collected on Kauaʻi by K. Faccenda and in the Saddle region of Hawaiʻi Island by us and, later, D. Tucker (https://www.inaturalist.org/observations/258711417).
This is certainly a new report for Hawaiʻi and could be a new species. It is recognized by its leaf lobule with a prominent hooked tooth and by the thick-walled leaf cells that lack trigones. The lower leaf margin is almost straight, not bent or "kinked". It resembles *Cheilolejeunea decursiva,* but *C.* sp. 1 has a tooth that is rounded at the tip rather than ending in a sharp point, and its leaves are not kinked. Trigones are absent.



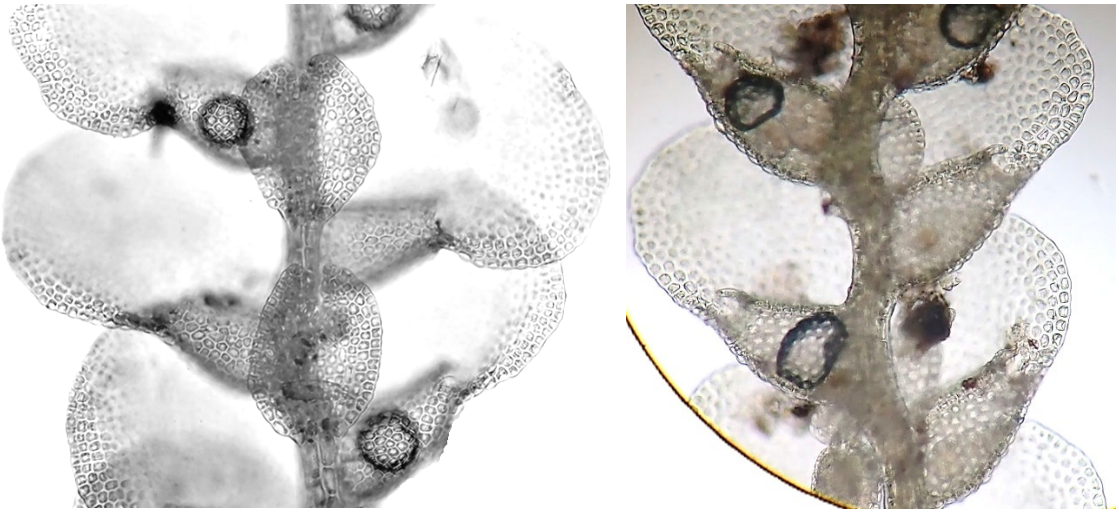
Plants are light in color and creep closely appressed to bark. They are less than 1 mm wide. Hawaiʻi Island, Freire & Judziewicz 21-1043 (BISH).

Cheilolejeunea species 1. Plant with some lateral branches. Saddle area, Hawaiʻi Island. Freire & Judziewicz 21-1043 (BISH).

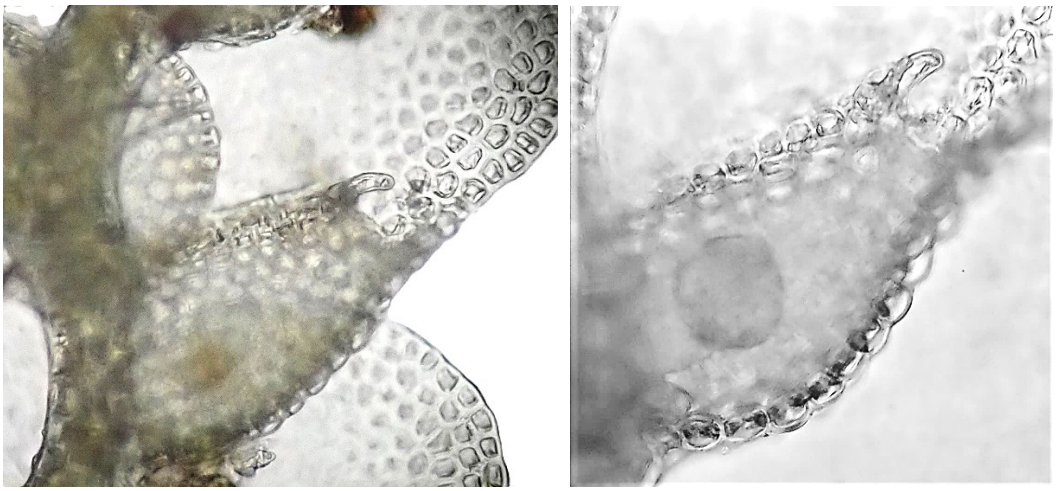
Plants showing large, inflated lobules with a prominent tooth and leaves with a more or less straight lower margin. Note the distant underleaves. Hawai‘i Island, Freire & Judziewicz 21-1043 (BISH).



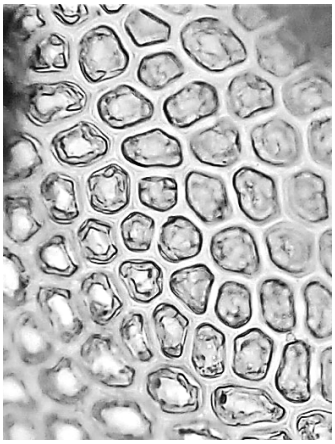
Cheilolejeunea species 1. Note the inflated lobules with prominent teeth. Lobe cells are thick-walled. Alaka‘i Plateau, Kaua‘i, Faccenda 3879b (BISH). Photos by E.J. Judziewicz.



Left: Underleaves are longer than broad, distant, and have a short sinus. Right: Leaf lobules are inrolled and have a large, curved tooth. Hawai‘i Island, Freire & Judziewicz 21-1043 (BISH).



Detail of curved lobule tooth. Note the bulging lobule cells. Most lobules are occupied by invertebrates. Hawai‘i Island, Freire & Judziewicz 21-1043 (BISH).



Cheilolejeunea species 1. Leaf cells are thick walled and lack trigones. Saddle area, Hawai‘i Island, Freire & Judziewicz 21-1043 (BISH).

6. *Cheilolejeunea* species 2.

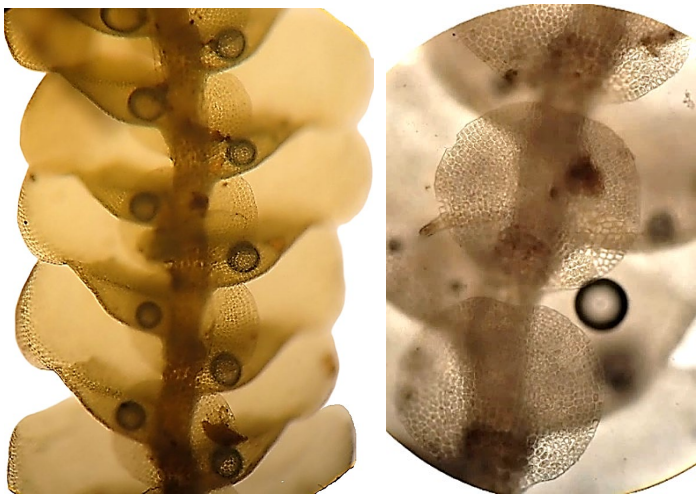
Occurring on the boggy summit of Kawaikini, Kauaʻi (5,000-5,200 ft.), K.R. Wood, T. Flynn & B. Nyberg 18546 (PTBG, with a duplicate reportedly at F), where it is an epiphyte on twigs of *Metrosideros polymorpha* Also on the summit bog of Mt. Waiʻaleʻale, Kauaʻi, Faccenda 3346 (BISH, PTBG); see Judziewicz, Faccenda & Freire (2025: 69-71). Also found in the Saddle area of Hawaii Island, Freire & Judziewicz 21-1025a (BISH). The most distinctive character is the presence of entire, unlobed underleaves, without a sinus (holostipous).

Resembling *C. stenoschiza*, but differing from it in the smaller plant size, the holostipous underleaves (the most relevant difference), the more inflated lobules, and the larger leaf trigones. Another distinctive feature is the pale color (both fresh and dried). The leaves have somewhat inflexed lobes and evident trigones; the lobules are large and rectangular, with a broad and straight, truncate apex with a single short tooth or occasionally a hint of a second, more proximal tooth. We could not find slime papillae. The oil bodies appear to be large and few per cell. Note the abundant ribbed perianths.

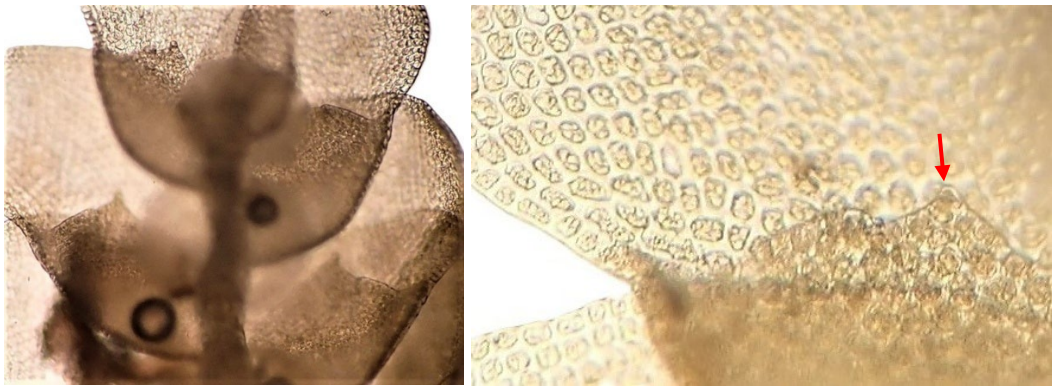
Cheilolejeunea species 2. Photo courtesy of National Tropical Botanical Garden/Ken Wood, who reports it as common and with a “tan to yellow-green” color. Note the abundant keeled perianths. Wood et al. 18546 (PTBG).


Left: Photo courtesy of National Tropical Botanical Garden/Ken Wood. Wood et al. 18546 (PTBG). Note the tan color. Scale in mm. Right: Plants have spreading leaves, with large lobules, and are often branched. Note the keeled perianth. Wood et al. 18546 (PTBG), photo by E.J. Judziewicz.

Leaf lobules are large and rectangular. Note perianths (right). Wood et al. 18546 (PTBG), photos by E.J. Judziewicz.

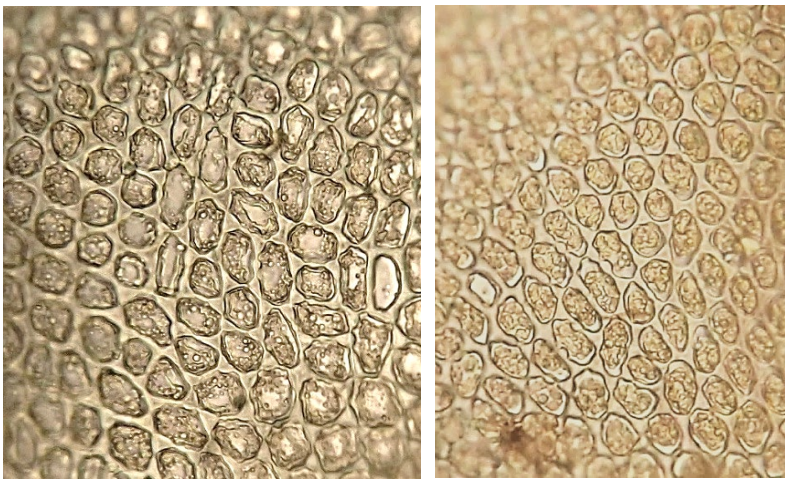


Cheilolejeunea species 2. Left: Section of plant showing contiguous underleaves. Kauaʻi, Faccenda 3346 (BISH, PTBG). Right: Underleaves are holostipous, about five times wider than the stem, and slightly wider than long. Kauaʻi, Wood et al. 18546 (PTBG). Photos by E.J. Judziewicz.



Left: Lobules are large, rectangular, with a broadly truncate apex that bears a small tooth. Kauaʻi, Wood et al. 18546 (PTBG). Right: Detail of lobule margin with small unicellular tooth (arrow). Kauaʻi, Faccenda 3346 (BISH, PTBG). Photos by E.J. Judziewicz.

Perianths are keeled, winged and beaked. Kauaʻi, Wood et al. 18546 (PTBG). Photo by E.J. Judziewicz.

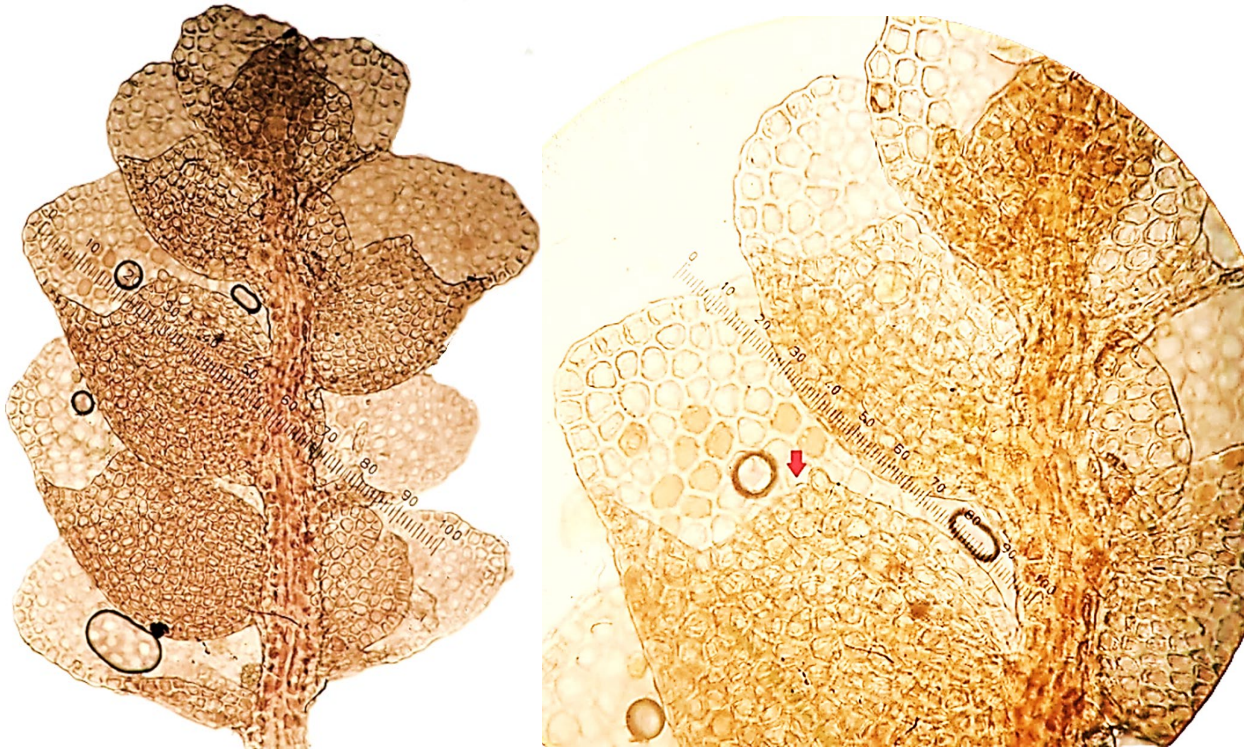


Cheilolejeunea species 2. Left: Leaf lobe cells have evident trigones and some intermediate thickenings. Kauaʻi, Wood et al. 18546 (PTBG). Right: Leaf cells showing oil bodies (4 per cell) and well-developed trigones. , Kauaʻi, Faccenda 3346 (BISH, PTBG). Photos by E.J. Judziewicz.

7. *Cheilolejeunea* species 3.
Found only at Onomea, six miles north of Hilo, Hawai‘i Island, as an epiphyte on an orchid stem in a forest of exotic trees, at an elevation below 100 ft. (Freire & Judziewicz 19-154a, in 2019). We only know of it as a tiny fragment, mixed with *Lejeunea laetevirens* and *Diplasiolejeunea* species 1. We returned to the collecting area several times but failed to find more material.

The orange-brown color and large leaf lobules are distinctive and diagnostic. We did not study the fresh oil bodies. The lobes appear to have slightly irregular margins. The lobules are over half the lobe length and width and have a small tooth. Note that the lower lobules become irregular in size and shape. Underleaves are round and have a triangular sinus, but we cannot draw conclusions about their appearance on more mature portions of the plant.

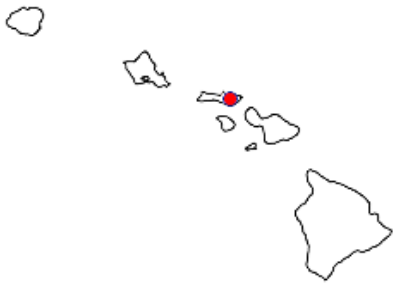
Searching the literature, we have not found any species of *Cheilolejeunea* with such long and broad lobules. However, we have not been able to match it with any other genus of Lejeuneaceae.



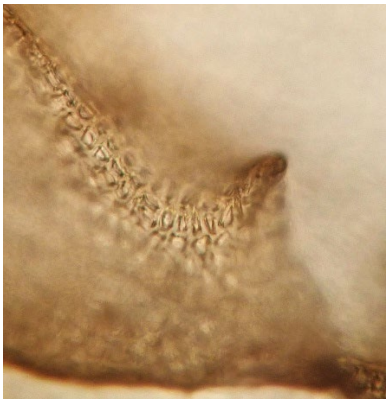
Cheilolejeunea species 3: Left: Plants are ca. 0.5 mm wide, orange-brown, and have large, flattened leaf lobules. Note the irregularly shaped lower lobules. Right: Leaf lobules bear a small tooth and a slime papillae distal to the tooth (towards lobe apex; red arrow). Note the darkened lobe cells to the left of the arrow; could these be ocelli? They are not consistently darkened. The underleaves are round and bifid to about ½ of their length. Onomea, Hawai‘i Island, Freire & Judziewicz 19-154a.

8. *Cheilolejeunea* sp. 4.

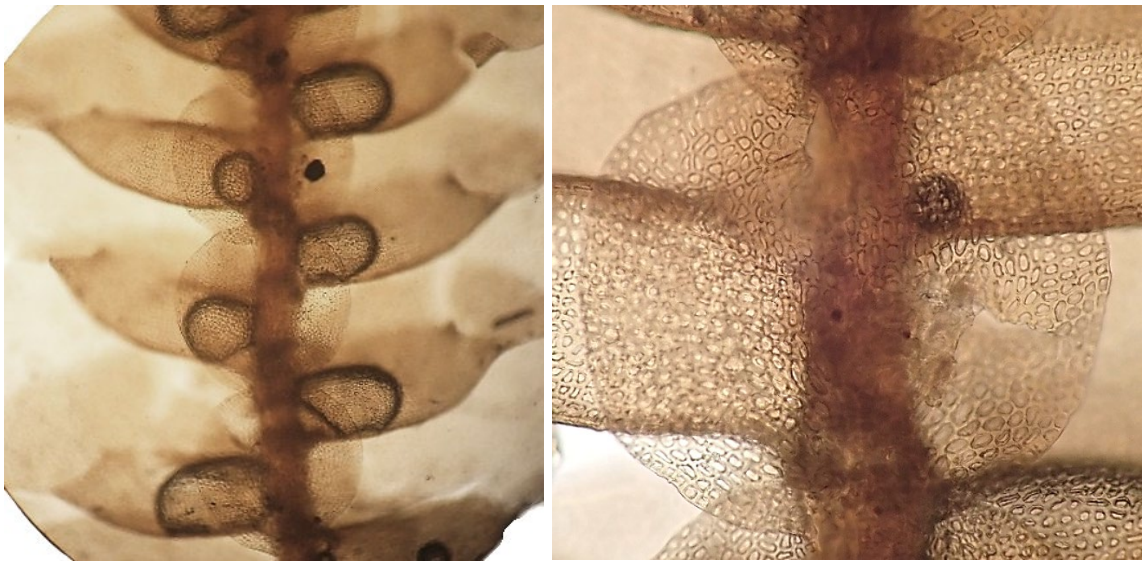
Known only from Molokaʻi Swamp below Kaunuohua, 4,200 ft., 30 May 1953, Miller & Lamberton 3564 (MU), photos below. The specimen was unidentified, but we recognize it as a new report for Hawaiʻi. The plants are 1.8 mm wide, the lobes have trigones, and the underleaves do not or only slightly overlap and are 1/3 bifid. Most striking are the inflated lobules which are a bit over 1/2 as long as the lobes. They are horizontally elongated, with an oblique and truncate apex; they lack a tooth but may have a point formed by an apical fold. The median leaf cells have thick walls and confluent trigones, with intermediate thickenings.



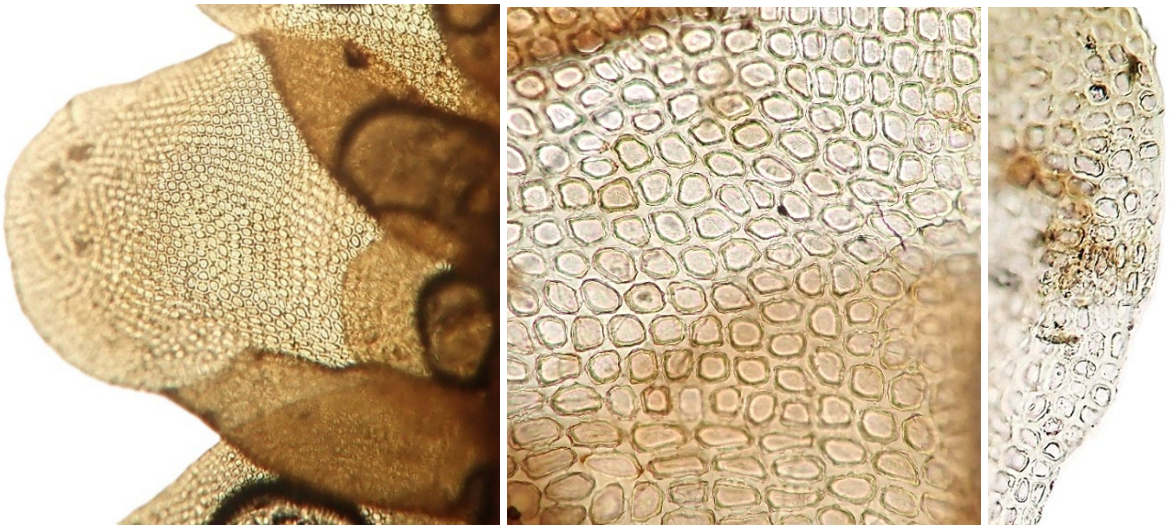
This species grows closely appressed to its substrate; plants are at least 7-8 mm long and 1.5-1.8 mm wide. Photos by E.J. Judziewicz (left) and A.V. Freire (right).



Cheilolejeunea species 4. Leaves spread broadly, overlap, have truncate to rounded apices and large, horizontal lobules. These are rectangular, inflated, sausage-like, and have an oblique, truncate apex. Some may have a fold that forms a point, but we do not interpret this as a tooth (right). Molokaʻi Swamp, Miller & Lamberton 3564 (MU). Photos by A.V. Freire.



Underleaves are contiguous to slightly overlapping, orbicular, 4-5 times as broad as the stem. They are notched by a narrow sinus, about 1/3 deep; the lobes are often connivent. Photos by E. Judziewicz (left) and A.V. Freire (right).



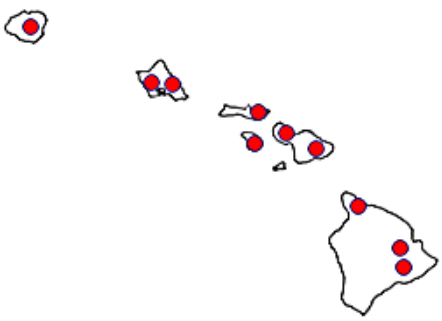
Cheilolejeunea species 4. Median leaf cells are thick-walled, with confluent trigones and at least some intermediate thickenings. Leaf marginal cells are thick-walled, small, and quadrate (right). Moloka‘i Swamp, Miller & Lamberton 3564 (MU).

Chiastocaulon Carl (Plagiochilaceae)

One species in Hawai‘i, 19 species worldwide.

Chiastocaulon has opposite, succubous leaves with their bases prolonged to the stem midline, where they meet to form a characteristic “V”-shaped decurrency that is more pronounced on the dorsal side. The similar (but not closely related), rarer *Syzygiella eatonii* also has opposite leaves but they are much broader at their base and more rounded (the apex is never acute) and the plants are often reddish.

1. *Chiastocaulon combinatum* (Mitt.) J.D.F. Patzak, M.A.M. Renner, Schäf.-Verw. & Heinrichs. **Endemic.** Treated as *Plagiochilion combinatum* (Mitt.) Inoue (Staples & Imada, 2006); see Patzak et al. (2016: 492); Judziewicz & Freire (2023c: 169). *Plagiochila oahuna* is a synonym according to Inoue (1962), see discussion later in this treatment. Found on all major islands (700-5,500 ft.). An occasional species of wet forests. It resembles and is related to the common genus *Plagiochila*, but that genus has alternate rather than opposite leaves.



Plants are olive-green or green, 4.5-5 cm long and (3)4-5 mm wide, projecting horizontally or hanging from their substrate. Stems are strong, firm and wiry, sparingly branched, with few intercalary ventral branches, stoloniferous. Leaves are succubus, opposite, distant to contiguous or imbricate; either narrowly oblong (elongate-linear) or oblong-elliptical to obovate. When narrowly oblong, the long blades have nearly parallel sides (ribbonlike), are 2.5-4(5) times longer than broad, 1.2-1.5 mm long by 0.5-0.6 mm broad, with truncate to acute apices, these usually bidentate, or sometimes with no teeth or with 4-5 jagged teeth; some teeth may also extend to 1/3(2/3) of the upper leaf margin, or a few teeth may occasionally be found on the lower margin. When oblong-elliptical to oblong-obovate, the leaves are 2-2.5(3) times longer than broad (the broadest portion at their middle or above), 2-2.8 mm long by 1-1.1 mm broad, with rounded to truncate or occasionally pointed apices, usually without teeth, but sometimes with 1-2(3-4) small and inconspicuous apical teeth. Adjacent leaf bases of both leaf morphologies join or nearly join to form a “V” on both the dorsal and ventral stem surfaces. This “V” is much longer and conspicuous on the dorsal side where the leaves are more decurrent. Leaf cells are elliptical to isodiametric, sometimes rectangular, 25-51 µm long by 15-25 µm broad. Cell walls are thin but have prominent nodular trigones that can be confluent. Marginal cells are slightly smaller and do not form a distinct border, but can sometimes have strongly thickened walls (observed on broadly elliptical leaves). Oil bodies are large, ellipsoidal and granular.

Inoue (1964) describes and illustrates leaves that are linear-oblong, narrow and long with parallel margins and mostly with 1-4 apical teeth that may continue along the upper margins. Mitten’s protologue (1871) describes *Plagiochila combinata* as having two leaf morphologies: oblong-elliptical with bidentate apices and some teeth on the dorsal(?) margin; and elongate-linear leaves without mention of teeth. Interestingly, the type for *Plagiochila oahuna* (synonymized by Inoue to *P. combinata*), has a mixture of plants with narrow and linear leaves and plants with much broader and elliptical ones. We have seen populations with narrowly linear and also with elliptical-oblong to obovate leaves. We have also seen both types of leaves on the same plant, the narrowly linear leaves usually on innovations or on shoot tips. Usually, plants with both types of leaf shapes lack jagged, prominent teeth, and plants with at least some broader leaves seem to be larger, with thicker marginal cells and larger trigones (but these alleged differences need to be checked on many more specimens). At this point, we are considering these two leaf morphologies and variation of their teeth as expressions of the same species.

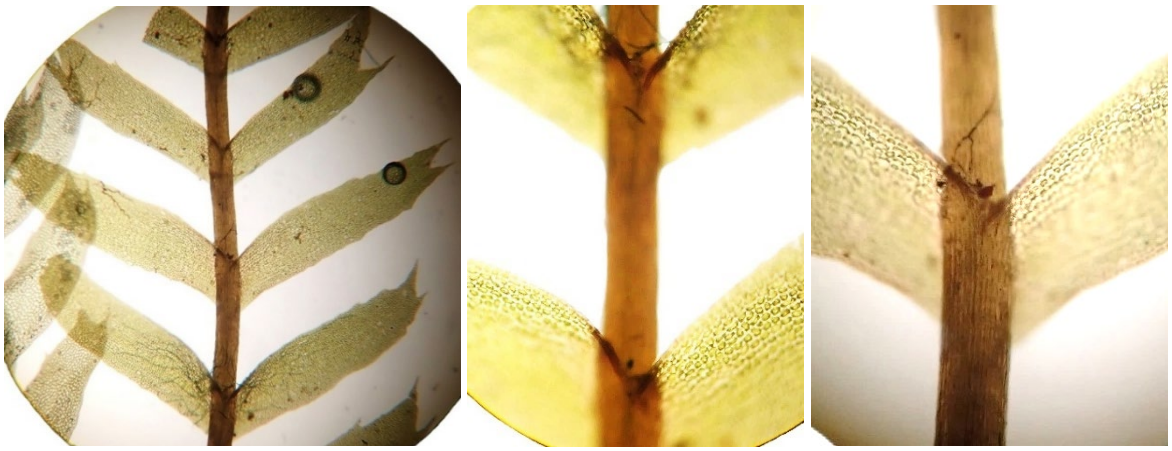
Examples of plants with narrowly oblong or oblong-linear leaves:

Plants form dense mats and project horizontally or hang from their substrate. This species is also known from the East Rift Zone Kīpuka, and Nāhuku on Hawai‘i Island. ‘Ōla‘a Tract, Hawai‘i Volcanoes National Park, Freire & Judziewicz 21-146 (HAVO).

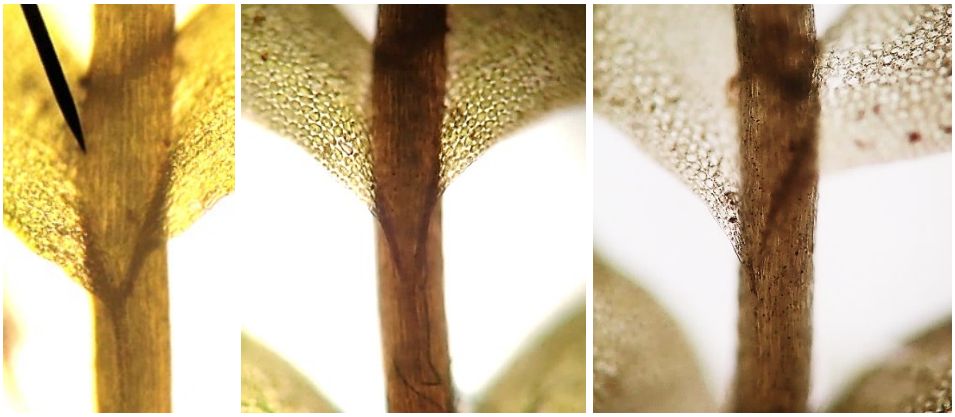
Chiastocaulon combinatum. Note opposite distant leaves with prominent apical teeth, and robust stems. Ko‘olau Range, O‘ahu; photo by Miles K. Thomas, with permission.

Plants pendant from their substrate. Note the branches with narrower and smaller leaves; compare them with the larger plant at the upper center of the left picture. Right: Note teeth extending to leaf upper (closer to the apex) margins. Koʻolau Range, Oʻahu, photos by Miles K. Thomas, with permission.

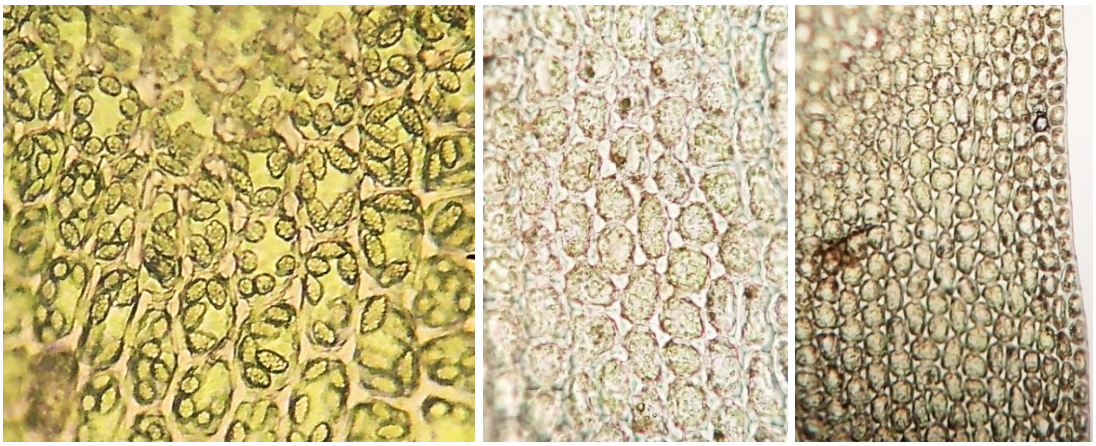
Chiastocaulon combinatum. Plants have robust stems and opposite, distant, oblong-rectangular leaves with jagged apical teeth. Note leaf base decurrency on the dorsal side and teeth on the upper margins (right). Scale in mm. Left: Koʻolau Range, Oʻahu, Ross 2013 (BISH). Photo by A.V. Freire. Right: Koʻolau Range, Oʻahu, photo by Miles K. Thomas, with permission.



Leaf bases are shortly decurrent on the ventral side of the stem, confluent or nearly so. They form a short "V". Ko'olau Range, O'ahu, Ross 2013 (BISH). Photos by A.V. Freire.



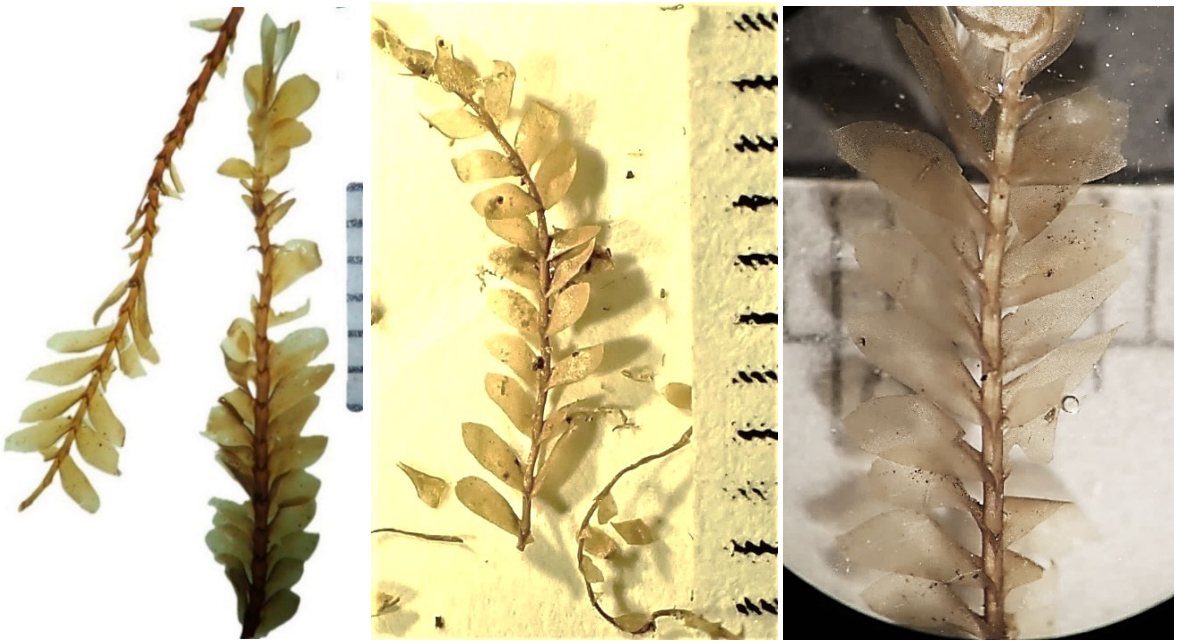
Dorsal view of decurrent leaf bases extending to the stem midline to form a deep "V". Detail of leaf decurrency (right). Left: Freire & Judziewicz 21-146 (HAVO). Center and right: Ross 2013 (BISH). Photos by A.V. Freire.



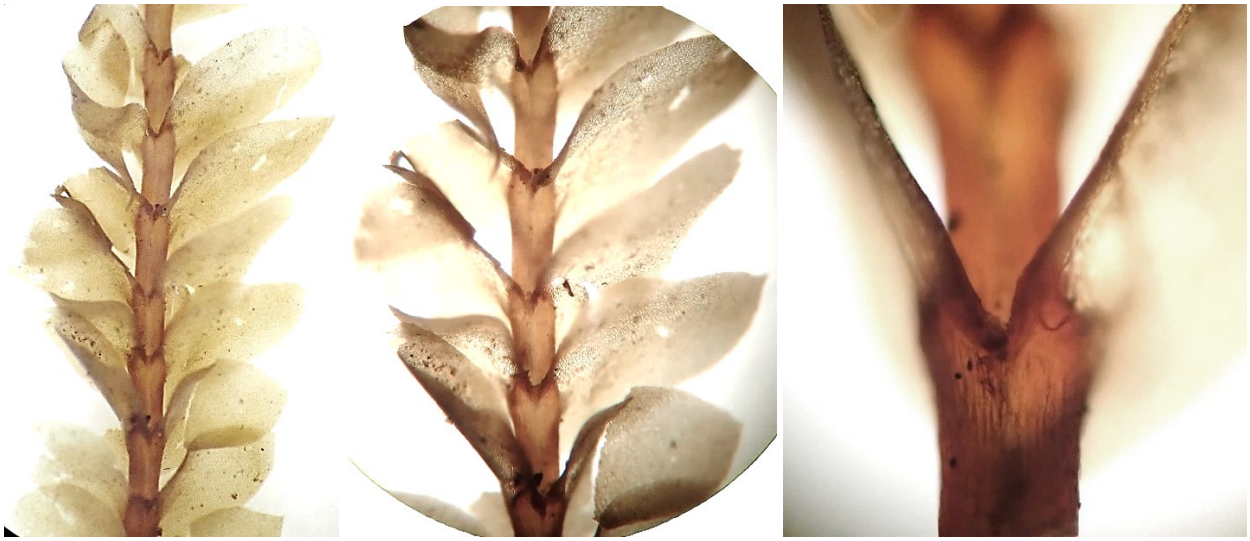
Chiastocaulon combinatum. Left: Large, ellipsoidal, granular oil bodies. 'Ōla'a Tract, Hawai'i Volcanoes National Park, Freire & Judziewicz 21-146 (HAVO). Center: Isodiametric to elongate cells, with thin walls and prominent nodular trigones that can be confluent. Right: Marginal cells are slightly smaller. Center and Right: Ko'olau Range, O'ahu, Ross 2013 (BISH). Photos by A.V. Freire.

Examples of plants with oblong elliptical to oblong-obovate leaves:

The "broad-leaved" morphology of *Chiastocaulon combinatum* could be confused with the very rare Hawaiian endemic *Syzygiella eatonii*, known from high elevation bogs in Kauaʻi and West Maui. However, *Syzygiella eatonii* leaves have broader bases, mostly lack apical teeth, and the ventral insertion line does not form a "V".

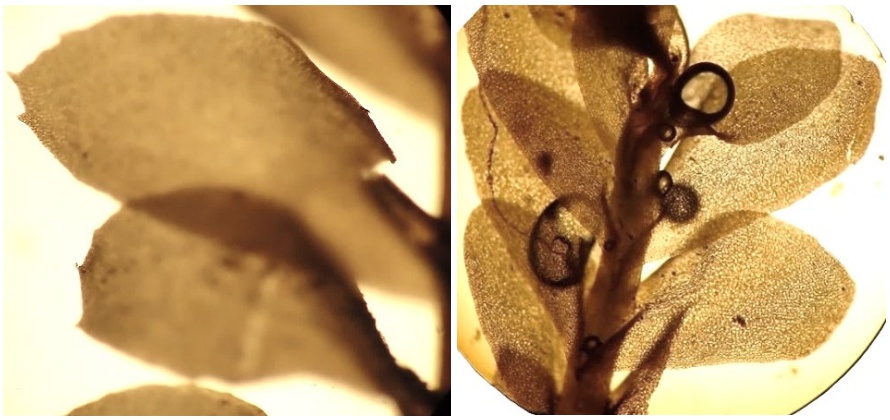


Plants are large, with robust, wiry stems. Leaves are distant, contiguous, or imbricate, with rounded to obtuse-pointed apices. Left: Oʻahu, Doty s.n. (MU). Photo by A.V. Freire. Center: Puʻu Kaʻala, Oʻahu, Iwatsuki & Hoe 2055a (BISH). Photo by E.J. Judziewicz. Right: Molokaʻi, Miller & Lamberton 3780 (MU). Photo by A.V. Freire. All scales in mm.

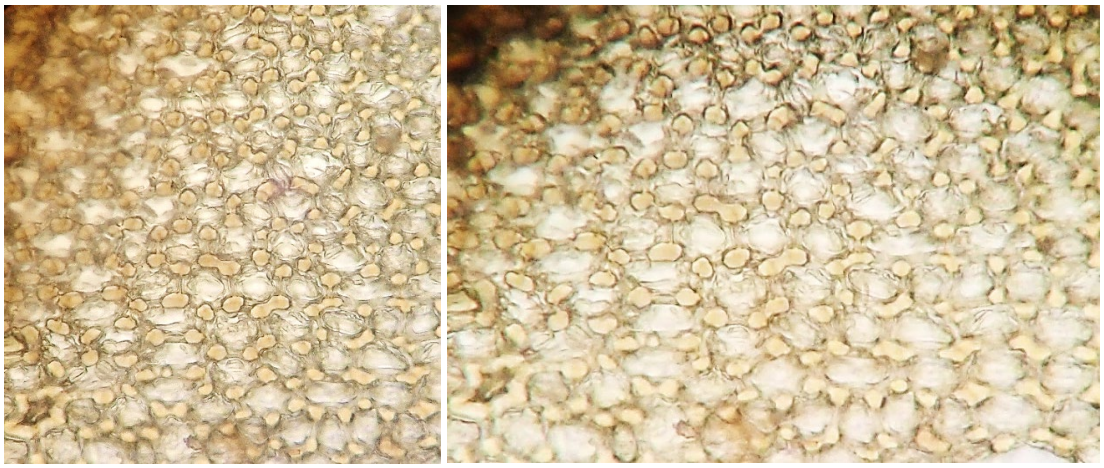


Chiastocaulon combinatum. Ventral side of plants showing the confluent base of opposite leaves with reflexed margins, forming a well-defined "V". Puʻu Kaʻala, Oʻahu, Doty s.n. (BISH). Photos by A.V. Freire.

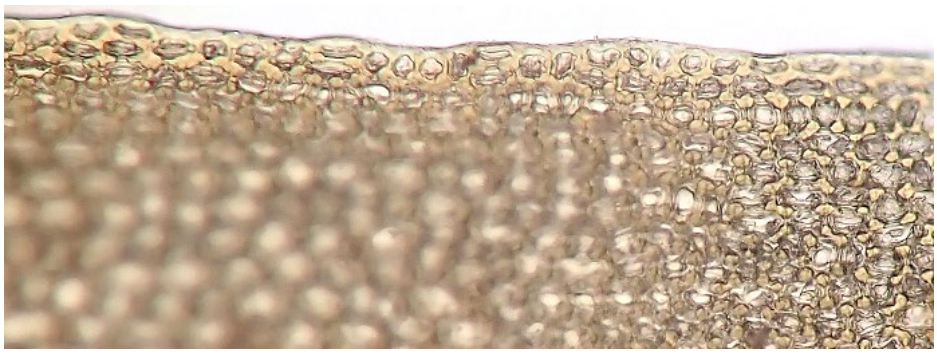
Dorsal view of plant showing confluent decurrent leaf bases forming a well-defined “V” (this longer than on ventral side). Puʻu Kaʻala, Oʻahu, Doty s.n. (BISH). Photo by A.V. Freire.



Broad leaves may have a few, small apical teeth. Apices can be rounded or obtusely pointed (right). Molokaʻi, Upper Waikolu Valley, 4,000 ft., Miller & Lamberton 3780 (MU). Photos by E.J. Judziewicz.



Chiastocaulon combinatum. Cells are mainly isodiametric, with thin walls and very prominent nodular trigones that are sometimes confluent. Puʻu Kaʻala, Oʻahu, Doty s.n. (BISH). Photos by A.V. Freire.

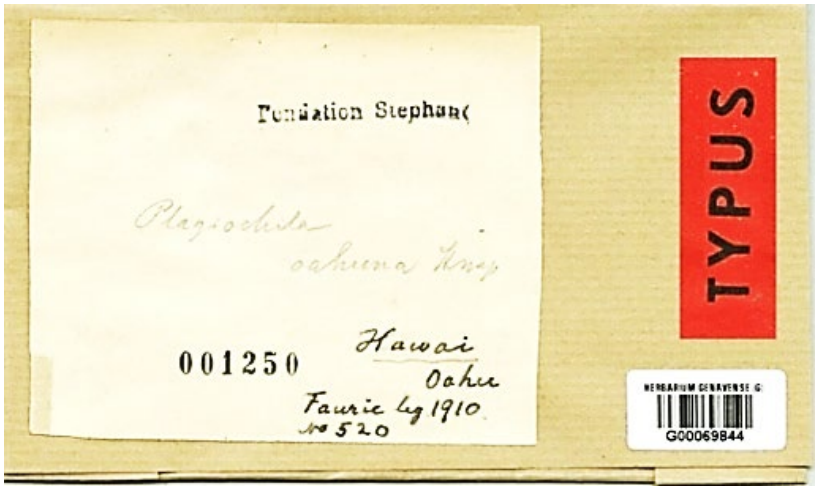


Leaf border of thick-walled cells. Pu‘u Ka‘ala, O‘ahu, Doty s.n. (BISH). Photo by A.V. Freire.

Kaua‘i, Faccenda 3896 (BISH), Kevin Faccenda photos:
(https://www.inaturalist.org/observations/254804145), with permission.

Chiastocaulon combinatum. Showing abrupt transition from broad to narrow leaves on the same shoot, Alaka‘i Wilderness Preserve, Kaua‘i, Faccenda 3896 (BISH). Photo by E.J. Judziewicz.

Plagiochila oahuna Steph. was reduced to a synonym of *Plagiochilion combinatum* by Inoue (1962). We did not study the type of *P. oahuna* from Geneva, but downloaded pictures from the CJBG, Geneva Herbarium Catalogue (https://www.ville-ge.ch/musinfo/bd/cjb/chg/index.php?lang=en). Faurie 520 has a mix of plants with long, ribbon-like leaves with parallel sides and plants with broader, ellipsoidal leaves. Some leaves seem to be damaged, probably missing their apical portion. Stephani's protologue fits the description for *C. combinatum*.



Plagiochila oahuna Steph. Type (G). Some plants with broad leaves are present (left); plants with elongate, narrow leaves are also present (right).
Photos from: https://www.ville-ge.ch/musinfo/bd/cjb/chg/index.php?lang=en.

Chiloscyphus Corda (Lophocoleaceae)

Five or six species in Hawai‘i. Thirty species worldwide.

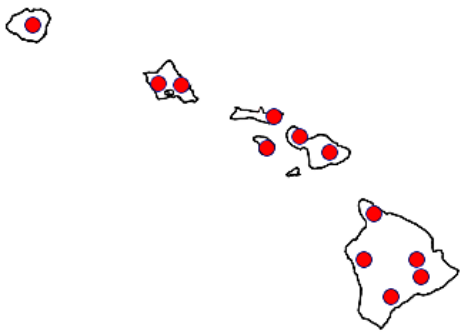
Species of *Chiloscyphus* in Hawai′i are medium to large, with succubous leaf insertion and prominent underleaves with 4 or, less commonly, 6-8 toothlike lobes. It resembles *Lophocolea* but differs from it in its smooth perianths produced terminally on short lateral branches, rather than the 3-keeled perianths, terminal on long shoots, observed in *Lophocolea* (Lee & Gradstein, 2021; Thouvenot, 2023). Leaves are usually opposite to sub-opposite, with the underleaves fused to one or both adjacent leaves. *Lophocolea*, on the other hand, has alternate leaves with no or just a narrow connation of the underleaves to one of the leaves. Median leaf cells are thin-walled, and trigones are absent or small, excepting *C. laceratus* which has prominent trigones. Antheridia are produced on normal-looking shoots (Thouvenot, 2023).

Söderström et al. (2016: 190) note that “it is unclear if [these] taxa [of *Chiloscyphus*; among them all Hawaiian species: *C. greenwelliae, C. laceratus, C. lambertonii,* and *C. skottsbergianus*] belong to *Cryptolophocolea, Lophocolea*, or some other genus of Lophocoleaceae” [such as *Heteroscyphus*].

Using the key to New Caledonian Lophocoleaceae presented by Thouvenot (2023: 5-7), all Hawaiian species would key to the genus *Heteroscyphus*; *Chiloscyphus laceratus* keys to near *Heteroscyphus splendens*. Using the key in Engel & Glenny (2019a: 207-214) for Aotearoa/New Zealand, *Chiloscyphus skottsbergianus* keys to near *Cryptolophocolea spinifera*; *Chiloscyphus greenwelliae* to *Heteroscyphus oblongifolius*; and *Chiloscyphus lambertonii* to *Heteroscyphus planiusculus*.

1. Leaves apically rounded, without teeth ……..……..…..…… **2**
   2. Underleaves round and large, much broader than the stem, with (4)6-8(-10) teeth; leaf trigones present ……. ***C. laceratus***
   2. Underleaves quadrate and small, as broad to slightly broader than the stem, with 4 teeth; leaf trigones absent ……..……...……...……..…..… ***C. lambertonii***
1. Leaves not apically rounded, with two teeth …….……...……. **3**
   3. Leaf apex broadly truncate, with 2 tiny ciliate teeth; underleaves 1-2 times as wide as the stem; widespread …...……...…….……..… ***C. greenwelliae***
   3. Leaf apex acute to narrowly truncate, with 2 long teeth; underleaves over 2 times wider than the stem; of restricted distribution ……..……...…....……...……...… **4**
      4. Leaf apical teeth broad, triangular, clearly unequal in size; underleaves with more than 4 teeth, over 3 times broader than the stem; Kohala, Hawai‘i Island ....……. ***C. skottsbergianus***
      4. Leaf apical teeth narrow, hairlike, equal or slightly unequal in size; underleaves with 4 teeth, 2.5 to 3 times broader than the stem; Haleakalā, Maui .....…… ***C.* species 1**

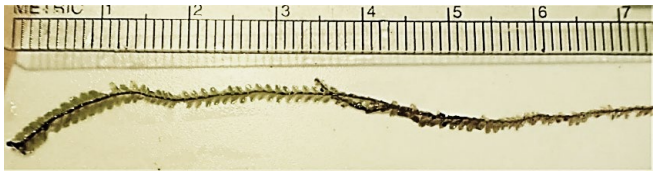
1. *Chiloscyphus greenwelliae* (H.A. Mill.) H.A. Mill. **Endemic.** Common in wet montane forests on all major islands (500-5,800 ft.). It is often seen trailing on bark or hāpuʻu stipes but is sometimes found on soil or rocks. Plants are creeping, closely attached to their substrate, large, up to 8 or more cm long and 3-5 mm wide; green and sparingly branched. Leaves are opposite, large, 1-2.3 mm long, broad at their base and slightly tapering to a broadly truncate apex. The upper leaf margins form right angles with the stem, while the lower ones are decurrent, oblique, and form up to a 45º angle with the stem. The leaf apex has two short, triangular teeth at its corners. Underleaves are small, up to twice the stem diameter, connate with both adjacent leaves, 4-6 lobed, with two larger and divergent triangular apical teeth separated by a "V"-shaped sinus, and 2-4 smaller, triangular lateral teeth. Cells are thin-walled, without trigones or with tiny triangular ones. We only studied sterile material. See also Thomas (2022) and Judziewicz et al. (2025b).



This species bears a resemblance to the Aotearoa/New Zealand endemic ***Heteroscyphus oblongifolius*** (Hook. f. & Taylor) Schiffn. (Engel & Glenny, 2019a: 437-441), an older name than *C. greenwelliae*.

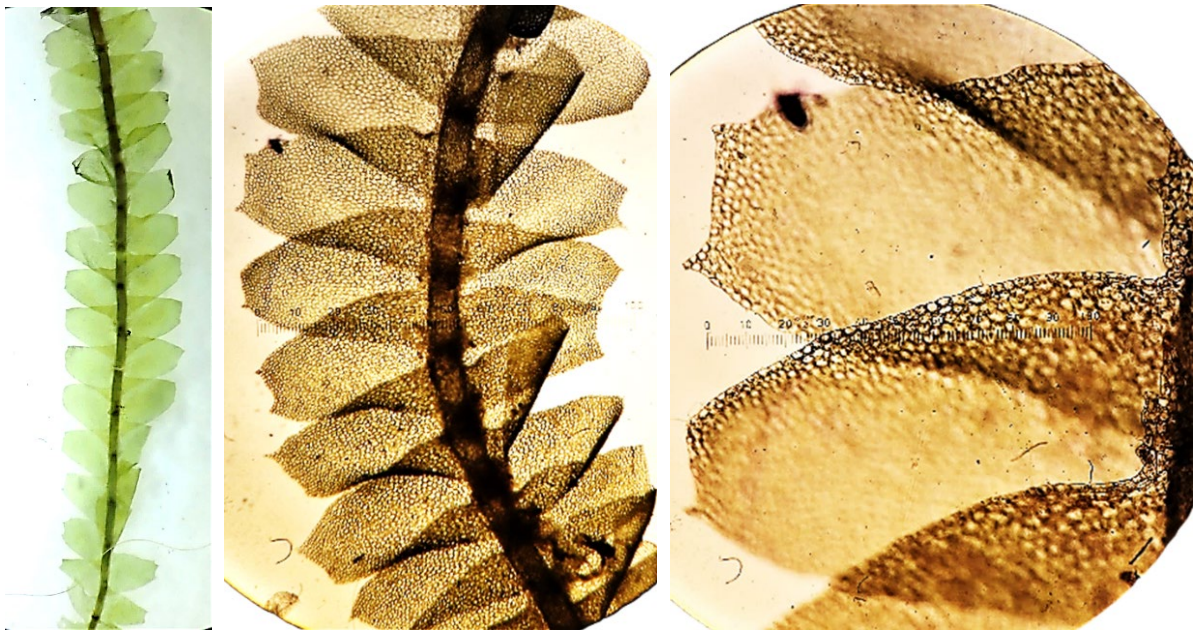
Bakalin et al. (2022a) cite the pantropical species ***Cryptolophocolea connata*** (Sw.) L. Söderstr. & Váňa as occurring in Hawaiʻi, based on Baldwin 66 (4,500 ft.) from West Maui (based on material housed at the Yale University and University of Michigan Herbaria, neither seen by us). However, at least the BISH specimens of Baldwin 66 are *Chiloscyphus greenwelliae*; leaf trigones are absent.

Plants are long, trailing on bark and hāpuʻu (*Cibotium* species) fern stipes. Nāhuku Lava Tube, Hawaiʻi Island. Photo by A.V. Freire.



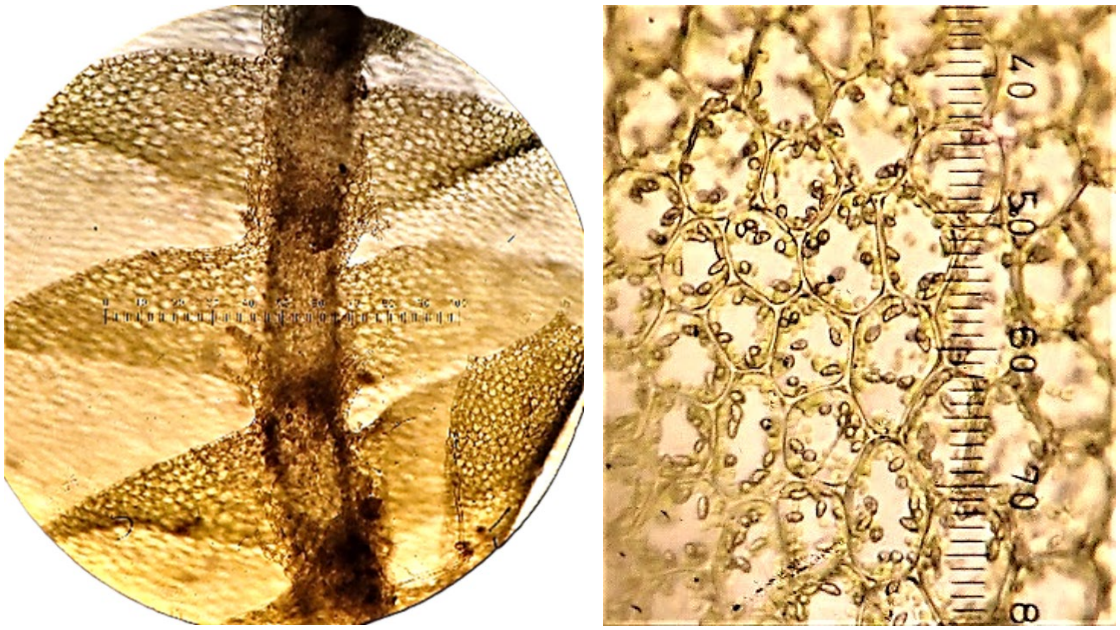
Chiloscyphus greenwelliae. Plants are long and rarely branched. Scale in mm. Nāhuku, Hawaiʻi Volcanoes National Park, Freire & Judziewicz 22-557 (HAVO).

Left: Dorsal view showing succubous insertion and opposite leaves with truncate apices and small teeth at the corners. Right: Ventral view showing small underleaves and small leaf apical teeth. ʻEleao summit, Central Koʻolau Range, Oʻahu, Thomas 228 (BISH). Photo by Miles K. Thomas, with permission.



Left: Leaves are opposite to sub-opposite, broad at their base, with truncate apices. Nāhuku, Hawaiʻi Volcanoes National Park, Freire & Judziewicz 22-557 (HAVO). Center: The truncate apices have two tiny teeth at their corners. Note the small underleaves. Scale units = 26 µm. Right: Detail of truncate leaf apices with small teeth. Scale units = 9.7 µm. Center and right: Freire & Judziewicz 22-557 (HAVO).

Ventral view showing small underleaves and small leaf apical teeth. ʻEleao summit, 2,654 ft., Central Koʻolau Range, Oʻahu, M.K. Thomas 228 (BISH). Photo by Miles K. Thomas, with permission.



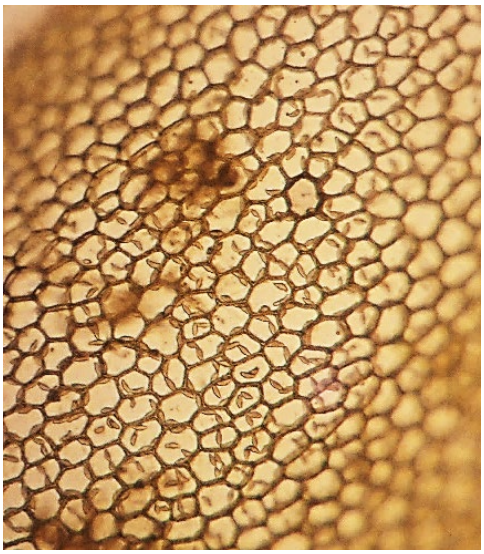
Chiloscyphus greenwelliae. Left: Underleaves are small, connate with both adjacent leaves, with two long toothlike apical lobes separated by a broad "V"-shaped sinus, and 2-4 smaller, lateral teeth. Scale units = 9.7 µm. Right: Median leaf cells have thin walls and few tiny, triangular trigones. Note the small, elongate, and segmented oil bodies. Scale = 5.1 µm. Hawaiʻi Volcanoes National Park, Freire & Judziewicz 22-55 (HAVO).

Chiloscyphus* cf. *greenwelliae, Judz. & A.V. Freire. Variant from Puʻu Kaʻala (Oʻahu) with longer leaf apical teeth; flexuous and reflexed underleaves with parallel rather than divergent apical teeth and usually with an irregular number of lateral teeth. Likely a variant of *C. greenwelliae* warranting segregation at the subspecies level. Plants are light green, large, up to 4 mm wide. Stems are stout, green, with some terminal branching. Leaves are opposite, large, fragile looking, about 2 mm long, broad at their base and slightly tapering to a broadly truncate apex.

The upper leaf margin spread from the stem at almost 90˚, and is long decurrent above to join the underleaf, while the lower leaf margin is oblique and can form up to a 45º angle with the stem. The leaf apex has two triangular to filiform teeth at its corners. Underleaves are mainly reflexed, fragile-looking, small, up to twice the stem diameter, connate to both adjacent leaves, (4)5(6) lobed, with two larger and parallel (but sometimes divergent) apical teeth separated by a "U"- or "V"- shaped sinus, usually with one small lateral tooth on one side and two on the other. Cells are thin-walled, without trigones or with tiny triangular ones.

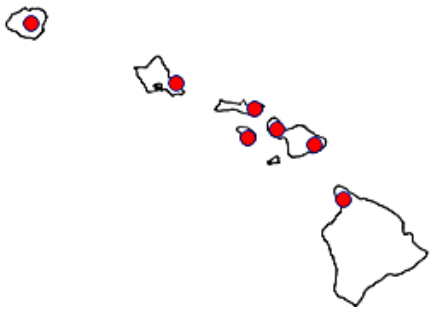
Chiloscyphus cf. *greenwelliae.* Scale in mm. Left: Robust plants. Right: Leaves with unusually long teeth at the corners of the broad truncate apex. Thomas et al. (including Freire & Judziewicz) 529 (BISH). Photos by E.J. Judziewicz.

Underleaves small, fused to both adjacent leaves, with long, linear, parallel apical teeth and 3 or 4 shorter lateral teeth. Puʻu Kaʻala, Oʻahu, Thomas et al. 529 (including Freire & Judziewicz) (BISH). Photo by E.J. Judziewicz.



Chiloscyphus cf. *greenwelliae.* Median leaf cells lacking or with only tiny trigones. Note the elliptical and granular oil bodies. Puʻu Kaʻala, Oʻahu, Thomas et al. 529 (including Freire & Judziewicz) (BISH). Photo by E.J. Judziewicz.

2. *Chiloscyphus laceratus* (Steph.) J.J. Engel & R.M. Schust. **Endemic.** Found on all major islands (1,400-4,000 ft.); rare but common on the Koʻolau Range, Oʻahu; see Miller (1963: 506); Thomas (2022); and Judziewicz et al. (2025b). This is a large, distinctive, leafy liverwort that may resemble a species of *Cuspidatula*; but that genus lacks well-developed underleaves, while they are large and prominent in *C. laceratus.* This species is recognized by its large, imbricate, erect or semi-erect leaves and by its large, orbicular, fimbriate underleaves that are unique among Hawaiian succubous liverworts. The leaf margins are often "encrusted" with yellow gemmae that resemble teeth in need of cleaning... May we suggest the common name niho lepo (dirty teeth)?



Populations creeping, closely or loosely attached to their substrate, forming spare or dense colonies, often intermixed with other leafy liverworts. Plants are light green to brownish, large, about 3.5 mm wide and at least 1.2-1.4 cm long, with a julaceous appearance. Stems sparingly branched. Leaves are erect to patent, entire, imbricate, sub-opposite to alternate, rounded to ovate, truncate to slightly cuspidate, concave, with a strongly reflexed lower margin as to appear inflated and giving a julaceous (fleshy) look. Leaf cells are isodiametric, 25-30 µm in diameter, with well-developed trigones. Underleaves are large, 3-3.5 as broad as the stem, fused to both adjacent leaves, orbicular, with 4-8(10) ciliate teeth, the two apical ones parallel, long and filiform, separated by a narrow "U"-shaped sinus; lateral teeth are smaller, radially spreading and variable in number, 2-8 per underleaf. Oil bodies are small, elongated, several per cell, and segmented. Spherical yellow to green gemmae are frequently and abundantly produced at leaf apices. Gemmae were not reported in Stephani's protologue (1922).

While rare on other islands, Miles Thomas reports it to be "extremely common in native wet forest here, especially from 1,400-3,000 ft." in the Koʻolau Range, Oʻahu (pers. comm.). The type was collected at Hānā, Maui by Faurie 266 (isotype BR, P, online images) in Sept. 1909. Other Hawaiian collections include Kauaʻi (Susan Fawcett photo, https://www.inaturalist.org/observations/253460930) and Wood 19,703 (PTBG), Molokaʻi (Pēpēʻōpae Bog, Skottsberg 5087, 5188, 5245, all S and not seen by us); Lānaʻi (Freire & Judziewicz 22-378, 22-475; Herbst 3916b, BISH), West Maui (Skottsberg 5136, S, not seen by us); and Hawaiʻi Island (Kohala; Fagerlind & Skottsberg 6901, MU, S, not seen by us). Photos of this species, unless otherwise indicated, are by Miles K. Thomas (Thomas 221, BISH) on Puʻu Kōnāhuanui, Oʻahu (3,000 ft.), on *Metrosideros polymorpha* in wet forest (Thomas, 2022). Also collected on Oʻahu by Bishop s.n. in 1963 (BISH) and several more times by Thomas (305, 307, 315, BISH) in the Koʻolau Range.

This species appears to be close to ***Heteroscyphus splendens*** (Lehm & Lindenb.) Grolle, which ranges from tropical East Africa, Madagascar, and tropical Asia to New Guinea, New Caledonia, Aoteoroa/New Zealand, and Sāmoa (Pocs, 1976; Piippo, 1985; Thouvenot, 2023), the Hawaiian species differing in the presence of leaf margin gemmae.

Left: Plant habit. Waimano, Koʻolau Range, Oʻahu. Photo by Miles K. Thomas, with permission. Right: Plants creeping on bark. Here with *Cuspidatula labrifolia* (arrow). Kauaʻi, photo by Susan Fawcett, with permission: https://www.inaturalist.org/observations/253460930.

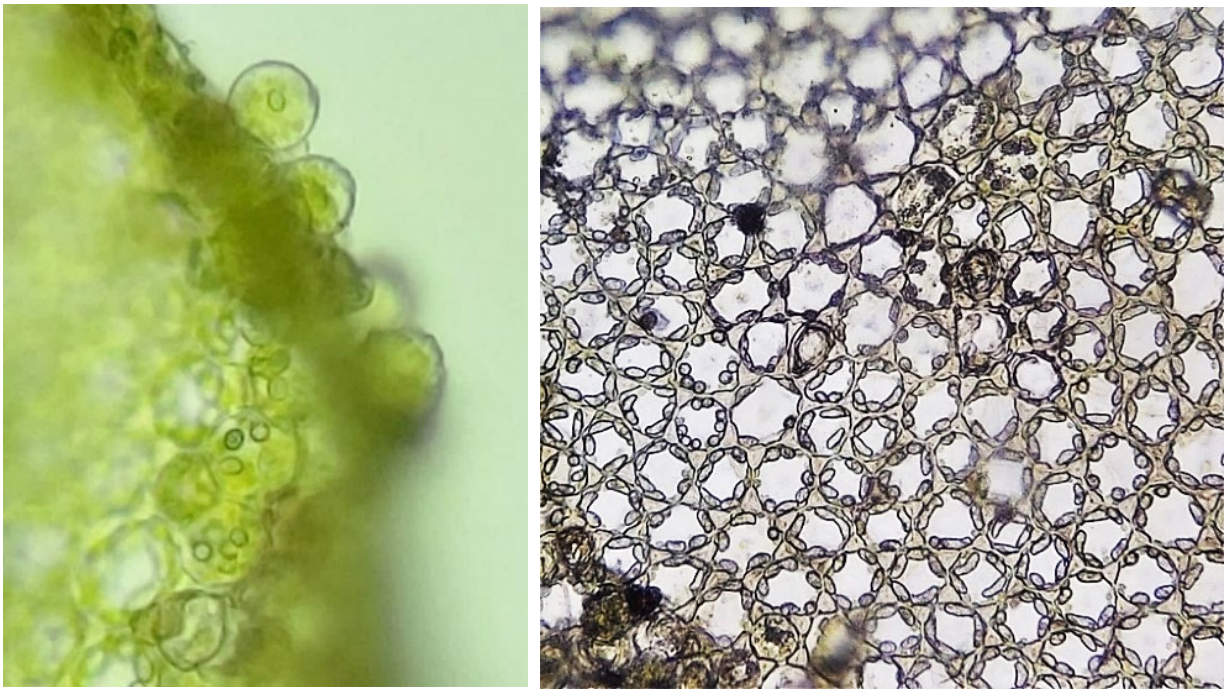
Chiloscyphus laceratus. Detail of creeping plants with leaf marginal gemmae. Kauaʻi, photos by Susan Fawcett, with permission: https://www.inaturalist.org/observations/253460930.

Chiloscyphus laceratus. Top: Leaves are erect, with reflexed margins, giving the plant a cylindrical shape, similar to *Cuspidatula labrifolia* (but the latter species lacks prominent underleaves). Bottom: Plants with semi-erect, succubous, concave leaves with reflexed margins giving the plant a fleshy look. Puʻu Kōnāhuanui, Oʻahu, photos by Miles K. Thomas (Thomas 221, BISH), with permission.

Plants are large, about 3.5 mm wide. Note gemmae clusters at leaf apices. ʻŌpaeʻula, Koʻolau Range, Oʻahu, M.K. Thomas s.n. (BISH). Photos by A.V. Freire.

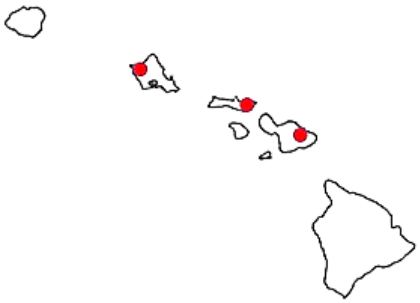
Chiloscyphus laceratus. Left: Ventral view showing large, round, fimbriate underleaves with 8 or even 10 long teeth. Center: the apical teeth are longer than the rest, parallel to each other, separated by a small "U"-shaped sinus (arrow). Left and center: Puʻu Kōnāhuanui, Oʻahu, photos by Miles K. Thomas (Thomas 221, BISH), with permission. Right: Underleaves are about 3.5 times as broad as the stem, and are fused to adjacent leaves. Lānaʻi, Herbst 3916b (BISH). Photo by E. J. Judziewicz.

Plants creeping on their substrate. Note the leaves with abundant leaf marginal gemmae. Crest of southern Koʻolau Range, Oʻahu, 21.32356°N, 157.7382°W, 2,410 ft., Photos by Kevin Faccenda, with permission. https://www.inaturalist.org/observations/236423336.



Chiloscyphus laceratus. Left: Marginal, unicellular gemmae, and fresh oil bodies, ʻŌpaeʻula, Koʻolau Range, Oʻahu, M.K. Thomas s.n. (BISH), photo by A.V. Freire. Right: Leaf cells with triangular trigones and elongate oil bodies. Waimano, Koʻolau Range, Oʻahu, photo by Miles K. Thomas, with permission.

3. *Chiloscyphus lambertonii* H.A. Mill. **Endemic?**
Uncommon**.** Found on Oʻahu, Molokaʻi and Maui (4,000-5,600 ft.). This species grows creeping on bark, in montane wet forests. Recognized by its entire, round leaves; and by its small and reflexed underleaves. If sterile, it resembles *Lophocolea autoica,* but the reflexed underleaves, uniform leaf apices, and lack of trigones are characteristic of *C. lambertonii*. Very similar to *Heteroscyphus planiusculus* with which it might be conspecific (see below).



Plants are large, up to10 cm long and 3 mm broad, fragile-looking, light green, loosely attached and projecting from their substrate. Stems are firm, frequently branched, branches intercalary. Leaves are alternate to sub-opposite, imbricate, prostrate but sometimes semi-erect, slightly concave, orbicular, with round apices and no hint of teeth. Underleaves are small, as broad as the stem or only slightly broader; with a curved insertion; slightly to strongly reflexed; quadrifid, with two prominent, long and parallel apical teeth that can be asymmetrical in size, separated by a narrow sinus; a much smaller lateral tooth is found on each side of the underleaf lamina, these also tend to be asymmetrical. Leaf cell walls are slightly thickened, without trigones. Oil bodies are elliptical, elongated, and granular (segmented). We only studied sterile material.

The collection from Puʻu Kaʻala, Oʻahu, Thomas et al. (including Freire & Judziewicz) 527 (BISH) fits the illustrations and protologue by Miller (1963), with minor differences: the leaves are entire rather than emarginate (Miller's drawings show entire apices but the protologue describes emarginate leaf apices). Leaves are alternate to subopposite and the underleaves are not obviously connate to adjacent leaves. Our measurements of leaves seem slightly smaller than reported in the protologue.

C. lambertonii keys to the genus *Heteroscyphus* in the Thouvenot (2023) treatment for New Caledonia, and there is great resemblance to the Aotearoa/New Zealand endemic ***Heteroscyphus planiusculus*** (Hook. f. & Taylor) J.J. Engel (Engel & Glenny, 2019a: 463-465), an older name. We strongly suspect they are conspecific and will treat this species again under *Heteroscyphus*.

Chiloscyphus lambertonii. Note orbicular leaves (center), and reflexed underleaves (right). Haleakalā, Maui, Z. Pezzillo 954 (BISH). Photos by Z. Pezzillo, with permission.
https://www.inaturalist.org/observations/239016862.

Plants are several cm long and about 3 mm broad. Scales in mm. Pu‘u Ka‘ala, O‘ahu, Thomas et al. (including Freire & Judziewicz) 527 (BISH). Photos by E.J. Judziewicz and A.V. Freire.

Left and center: Stems with rounded leaves and reflexed underleaves. Right: Underleaves are small and quadrifid. The apical teeth are large, parallel, and asymmetrical; the lateral teeth are much smaller and can also be asymmetrical. Note curved underleaf insertion. Thomas et al. (including Freire & Judziewicz) 527 (BISH). Photos by E.J. Judziewicz.

Chiloscyphus lambertonii. Left: Plants with intercalary branching. Right: Median leaf cells have thickened walls, without trigones. Oil bodies are ellipsoidal and granular. Pu‘u Ka‘ala, O‘ahu, Thomas et al. (including Freire & Judziewicz) 527 (BISH). Photos by E.J. Judziewicz.

Chiloscyphus* aff. *lambertonii.

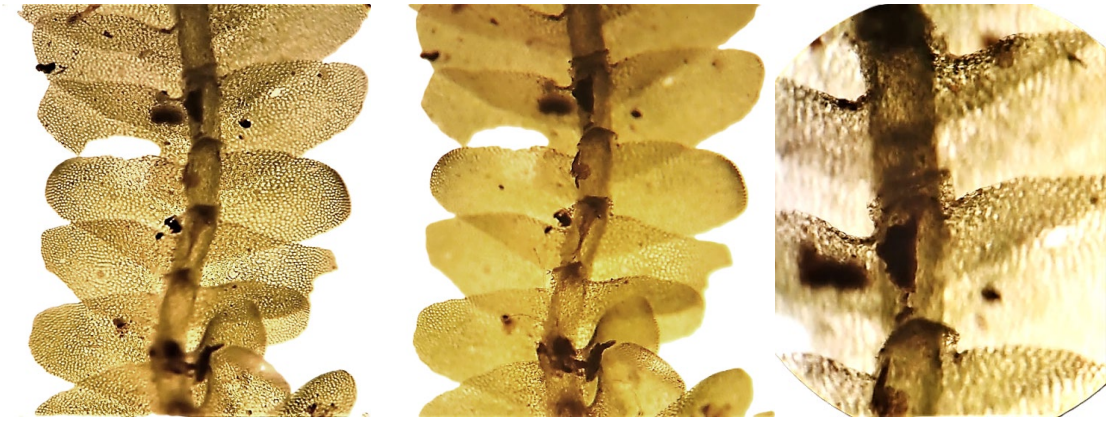
We collected several specimens, in the Hakalau Forest N.W.R. and in the Kahuku Unit of Hawai‘i Volcanoes National Park, Hawai‘i Island that have small, strongly reflexed underleaves and opposite to subopposite leaves. Initially we identified them as *C. lambertonii*, however the elongated ovate leaves with truncate apices, the underleaves clearly connate to both adjacent leaves, and the leaf cells with thin walls and tiny triangular trigones, indicate this may be a different species. We are tentatively placing them as related to *C. lambertonii* but wonder if they belong elsewhere, perhaps even in a different genus of Lophocoleaceae.

Plants are green, large, at least 3 cm long, 3 mm broad, creeping and closely attached to bark. Stems are firm and sparingly to frequently branched. Leaves are opposite to subopposite, imbricate, prostrate to suberect, flat, ovate to rectangular, longer than broad, with truncate to emarginate apices, or occasionally with a hint of blunt teeth. The underleaves are small, as broad as the stem or only slightly broader, strongly to moderately reflexed; bifid or quadrifid, with two prominent, long apical teeth and with or without shorter lateral teeth. Leaf cell walls are thin, with tiny triangular trigones. We only studied sterile material.

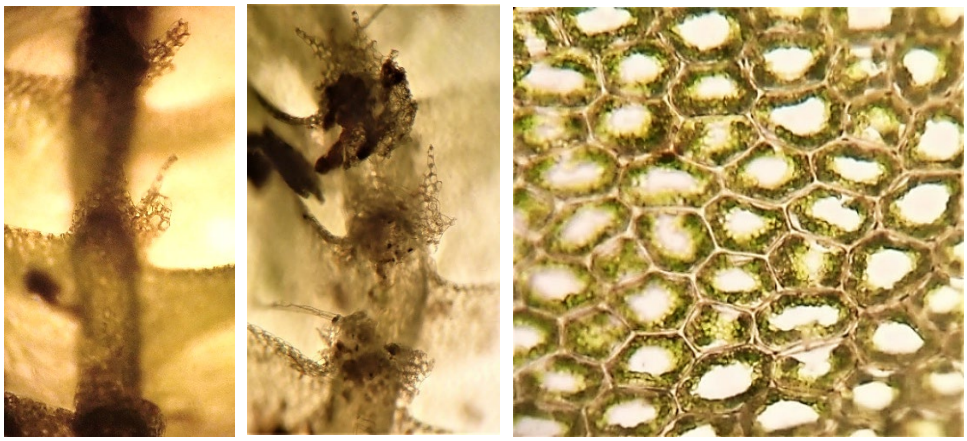
Plants creep on bark. Kahuku Unit, Hawai‘i Volcanoes National Park, Hawai‘i Island. Freire & Judziewicz 22-125 (HAVO).

Chiloscyphus aff. *lambertonii*. Plants are several cm long, up to 3 mm broad, and frequently branched. Scale in mm. Kahuku Unit, Hawai‘i Volcanoes National Park, Hawai‘i Island. Freire & Judziewicz 22-749 (HAVO).

Leaves are opposite to alternate, longer than broad, with reflexed underleaves, and leaf apices vary from truncate to emarginate, occasionally with blunt teeth (second picture, top right). Kahuku Unit, Hawai‘i Volcanoes National Park, Hawai‘i Island. Freire & Judziewicz 22-749 (HAVO).

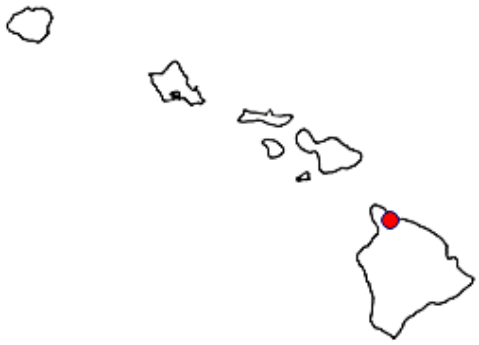


Left: Leaves opposite, elongate-ovate, with truncate apices. Center: Underleaves just slightly broader than the stem, strongly reflexed, with long apical teeth. Right: Detail of small, strongly reflexed underleaves. They connate to both adjacent leaves. Photos from Kahuku Unit, Hawai‘i Volcanoes National Park, Hawai‘i Island. Freire & Judziewicz 22-125 (HAVO).



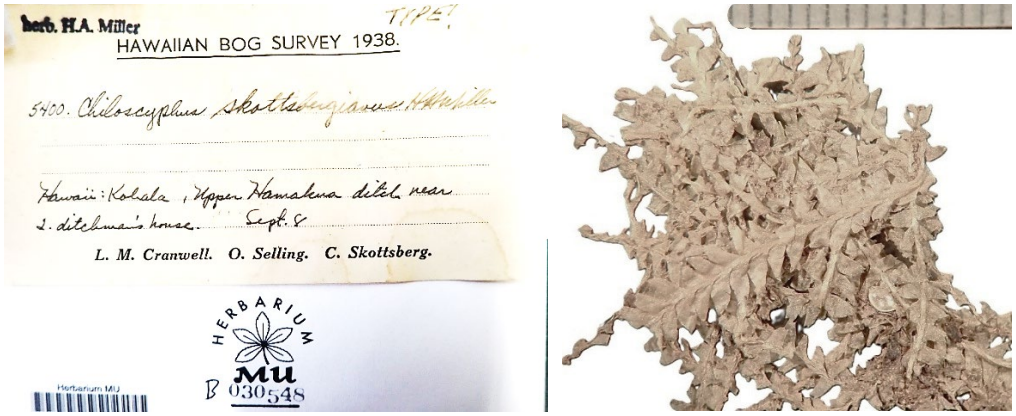
Chiloscyphus aff. *lambertonii*. Left: Underleaves without lateral teeth. Kahuku Unit, Hawai‘i Volcanoes National Park, Hawai‘i Island. Freire & Judziewicz, 22-749 (HAVO). Center: Underleaves with lateral teeth. Right: Leaf cells thin-walled, with tiny triangular trigones. Kahuku Unit, Hawai‘i Volcanoes National Park, Hawai‘i Island, Freire & Judziewicz 22-125 (HAVO).

4. *Chiloscyphus skottsbergianus* H.A. Mill. **Endemic to Hawai‘i Island.** This distinctive robust species is known only from the type specimen, from the Upper Hāmākua Ditch, Kohala, Hawai‘i Island, ca. 3,800 ft.: Cranwell et al. 5400, Miami University (MU), Stockholm Herbarium (S), and University of British Columbia (UBC) herbaria, in open bog among sedges; there are no specimens at either BISH or PTBG, but we examined an isotype at MU (all photos below from this specimen, photographed by A.V. Freire). Our failure to find this terrestrial liverwort is perhaps due to its extirpation by feral ungulates, or in competition with an invasive species of *Sphagnum* moss.



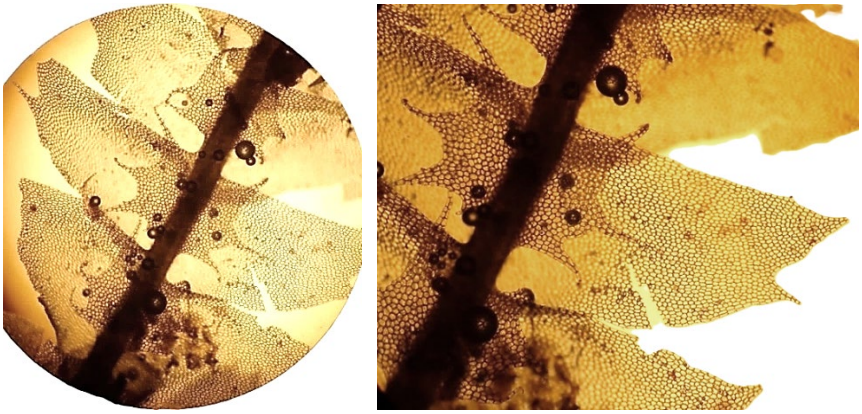
Plants grow in dense mats; they are large, 4 mm wide, and sparingly branched. Leaves are opposite, large, spreading, contiguous to slightly imbricate, flat, ovate-triangular, decurrent, with a straight upper margin and an oblique lower one, with tapering apices bearing two large and unequally sized teeth separated by a “U”-shaped sinus. Underleaves are large, about 1/3 of the plant width and with its lamina at least 5-6 times as broad as the stem; fused to one of the adjacent leaves, 6-8 lobed, with long and divergent apical teeth and lateral teeth about the same size; the line of insertion is deeply arched. The leaf cells are thin-walled and lack trigones.

Due to the lack of sexual structures, Miller tentatively placed this species in the genus *Chiloscyphus*. We wonder whether it could belong to the genus *Cryptolophocolea* because of its opposite, unequally bifid leaves and connate “asteroid” underleaves; it is a bit reminiscent of the Aotearoa/New Zealand species ***Cryptolophocolea spinifera*** (Hook. f. & Taylor) L. Söderstr. (Engel, 2010: 130), using the key in Engel & Glenny (2019a: 207-214) for Aotearoa/New Zealand, it keys near that species. *Cryptolophocolea spinifera*, however, has much broader underleaves: “the moistened plants reveal the remarkably huge underleaves, being as wide as the shoot or nearly so….” (Engel, 2010: 129); in the Kohala plants the underleaves are only about 1/3 as broad as the plant. This is a good candidate for molecular work.

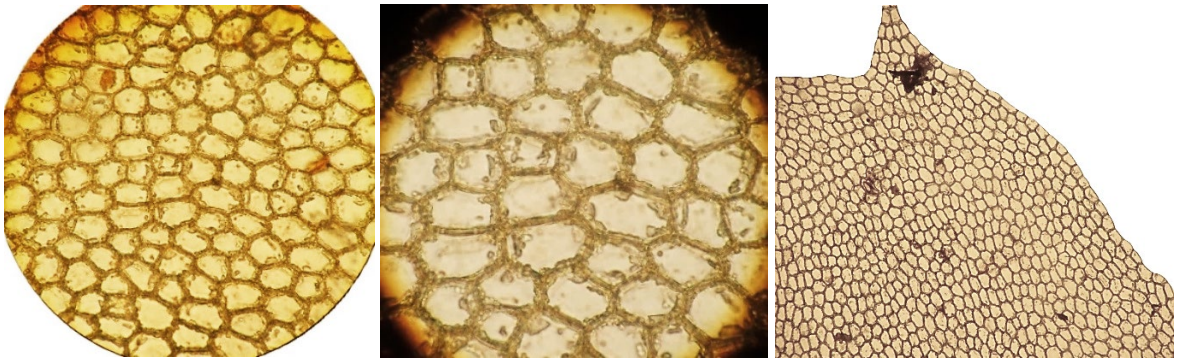


Chiloscyphus skottsbergianus. Isotype at MU. Found in wet ditch, on soil (we presume). Right: Plants are robust and form dense mats, with spreading leaves. Scale in mm. Cranwell et al. 5400 (MU), photos by A.V. Freire.

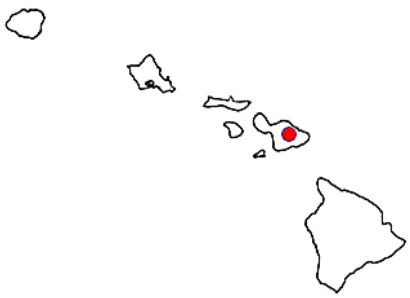
Left: Plants are sparingly branched, with spreading leaves, note the large underleaves. Scale = 6 mm. Right: Leaves are ovate-triangular, with two large and unequally sized apical teeth. Kaua‘i, Cranwell et al. 5400 (MU). Photos by A.V. Freire.



Underleaves are large, with 6-8 large teeth. The apical teeth are separated by a broad sinus. Cranwell et al. 5400 (MU). Photos by A.V. Freire.



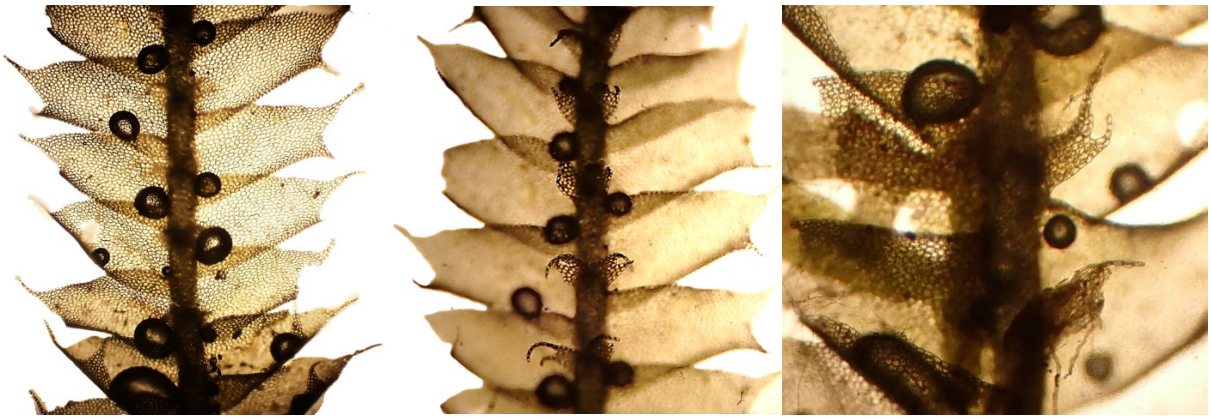
Chiloscyphus skottsbergianus. Leaf cells are thin-walled and lack trigones. There is a border of narrower and rectangular cells but this is ill defined (right). Kaua‘i, Cranwell et al. 5400 (MU). Photos by A.V. Freire.



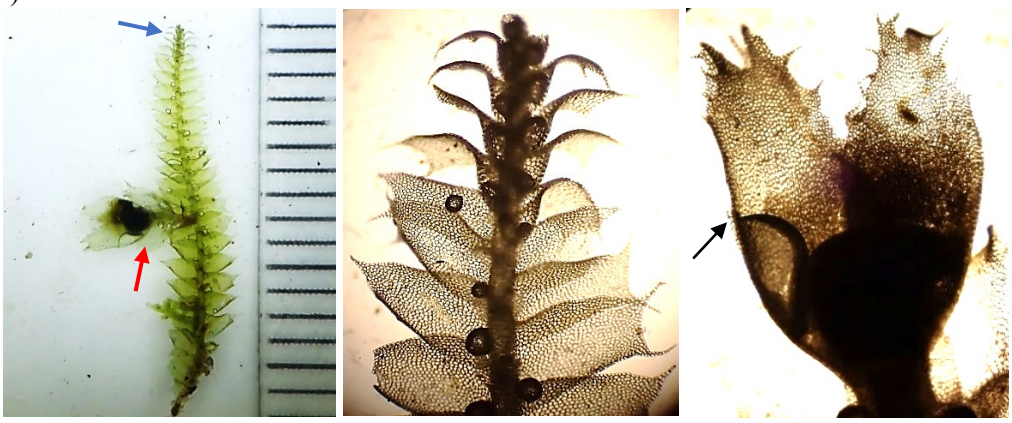
5. *Chiloscyphus* species 1, A.V. Freire & Judz. Only known from Haleakalā, Maui, at 6,100 feet. Plants grow loosely attached to their substrate and are semi-erect. They are medium-sized, up to 3 mm wide, yellow-green, and sparingly branched. Leaves are inrolled along the lower margin, subopposite, and spreading; upper leaf margin, spreading at almost 90º, lower margin spreading at 45º from the stem; they are triangular, broad at the base, narrowing toward the apex; bifid, with two hair-like teeth separated by a broadly truncate to slightly rounded sinus. Median leaf cells are thin-walled, without trigones or with tiny triangular ones; oil bodies are variable in size, narrowly ellipsoidal and granular. The underleaves are reflexed, 2-3 times larger than the stem and fused to one of the adjacent leaves; bifid, with long and narrow diverging teeth, often recurved and separated by a broad sinus. A shorter lateral tooth is present on both sides. Monoicous. Perianths not keeled, lobate, laciniate, produced on short lateral branches with reduced leaves. Antheridia produced in 2 ranks, in the axils of short saccate bracts, on compressed shoot apices.

Despite the resemblance to the genus *Cryptolophocolea*, the non-keeled perianths produced on short lateral branches, and lack of trigones are distinctive. The perianth morphology also separates it from the genus *Lophocolea*. The lack of lateral, short, antheridial branches sets it apart from the genus *Heteroscyphus*. Because of the non-keeled perianth, the short lateral gynoecial branches, and the androecia not in lateral branches, we place it in the genus *Chiloscyphus*. All pictures below from Freire & Judziewicz 23-150; Haleakalā, Maui.

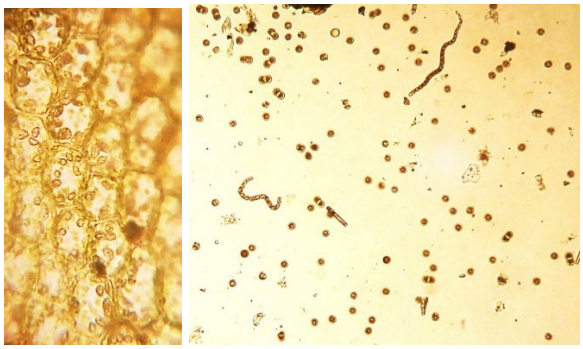
Chiloscyphus species 1. The yellow-green plants are loosely attached to their substrate; their leaves appear inflated because of the inrolled lower leaf margins. They resemble the genus *Cryptolophocolea*. Scale in mm. Photo by A.V. Freire.



Left: Leaves are sub-opposite, tapering, bifid, with long and narrow teeth and a broad truncate sinus. Center and right: Underleaves are 2.5(3) times broader than the stem, with long, divergent and often recurved apical teeth, and much shorter lateral ones. They are connate to one leaf (right). Freire & Judziewicz 23-150 (BISH).



Left: Plants are medium-sized, monoicous, with perianths on short lateral branches (red arrow), and apical androecia (blue arrow). Center: Detail of terminal androecium with two-ranked, saccate antheridial bracts. Right: Lobate, non-keeled perianth with laciniate mouth. Note small scale to the left (arrow). Freire & Judziewicz 23-150 (BISH).



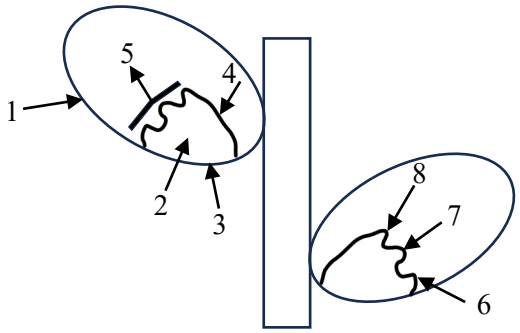
Chiloscyphus sp. 1. Left: Median leaf cells are thin-walled, without trigones or occassionally with tiny triangular ones. Oil bodies are small, elliptical and granular. Right: Tiny spores with smooth walls. They are slightly immature and still separating (2-celled clusters are present). Elaters long, robust, with 2 tightly coiled spiral thickenings. Haleakalā, Maui, Freire & Judziewicz 23-150 (BISH).

Cololejeunea (Spruce) Steph. (Lejeuneaceae)

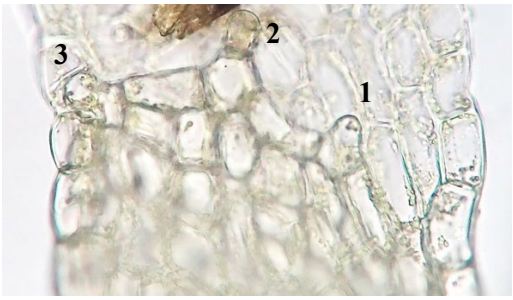
At least ten species in Hawai‘i (421 species worldwide). Alexander Evans (1900) treated this genus for Hawai‘i; the most recent world treatment is by Pierre Tixier (1985). Members of this genus are small, inconspicuous, and often overlooked. We suspect there are more, perhaps many more, species in Hawai‘i.

We regard ***Cololejeunea cookei*** A. Evans as a synonym of *Myriocoleopsis minutissima* subsp. *myriocarpa.* Two undetermined (perhaps new?) species are presented at the end of this treatment. In addition to the species reported by Staples and Imada (2006), we made several collections from cultivated trees in the Amy Greenwell Ethnobotanical Garden in Captain Cook, on the leeward side of Hawai‘i Island, that turned out to be a new record for Hawai‘i; the Asian species *Cololejeunea raduliloba* Steph. (Freire & Judziewicz 21-912 and 21-916). Pócs (2023: 7) reports ***C. spathulifolia*** (Steph.) H.A. Mill. from Hawai‘i, but with no specimen cited. We place *C. dzumacensis* Tixier as a doubtful record for Hawai‘i and reduce *C. hoeana* to *C. kapingaensis*.

Plants are small, creeping on bark, live leaves, or decaying wood, or sometimes also found on rocks. The thin stems have a hyalodermis and often have a zig-zag pattern. The leaves are spreading and are most commonly elliptical but are sometimes lanceolate or oblanceolate. The leaf lobule may have 1-3 teeth.
If more than one tooth is present, then these are numbered starting from the keel side of the lobule and proceeding towards the free margin. Underleaves are absent or rudimentary. The leaf cell walls are thin to moderately thick, and small trigones are sometimes present. Round disklike gemmae are often produced from the leaf surfaces.

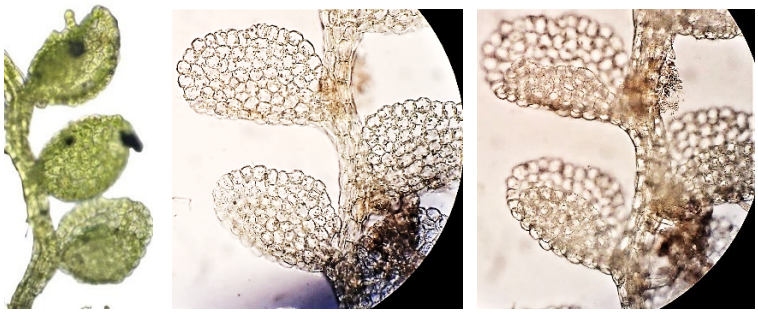


Cololejeunea with three lobular teeth. 1. Leaf lobe. 2. Leaf lobule. 3. Lobule keel. 4. Lobule free margin. 5. Lobule apex. 6. First tooth. 7. Second tooth. 8. Third tooth.



Cololejeunea hillebrandii with three teeth. 1. First tooth (near keel). 2. Second tooth. 3. Third tooth (near free margin). Southern Ko‘olau Range, O‘ahu, Faccenda & Ross 3466 (BISH). Photos by A.V. Freire.

Cololejeunea and *Myriocoleopsis* are the only Hawaiian genera of Lejeuneaceae that lack underleaves (they are rudimentary, if present). In Hawai‘i, *Myriocoleopsis* has inflated cells, and lobules are almost as long as the lobes, and are usually large and inflated (goblet-shaped). In *Cololejeunea*, cells are not inflated; the lobules are only slightly over ½ as long as the lobe, and they are not inflated so as to appear goblet-shaped.

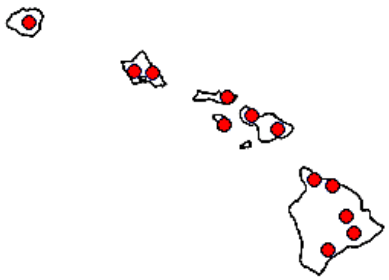


Hawaiian examples of *Myriocoleopsis*. Images showing the long lobules, almost the same length as the lobes. Also note the inflated cells. Left: Inflated, goblet-shaped lobules are almost the size of the lobe. Hawai‘i Island. Freire & Judziewicz 20-694. Center and right: Dorsal (center) and ventral (right) views of plants with a different lobule morphology, Kauai, Flynn 4243 (BISH). Photos by E.J. Judziewicz.

Artificial key to the Hawaiian species of *Cololejeunea*

1. Leaves narrow, elongate, lanceolate to ligulate, over twice as long as wide **2**
   2. Leaves more than twice as long as wide; lobule ¼-1/3 the lobe length ..... ***C. hillebrandii***
   2. Leaves slightly over twice as long as wide; lobule ½ or more the lobe length ..... ***C.* sp. 1**
1. Leaves broad, elliptical, orbicular, or broadly obovate, up to twice as long as wide **3**
   3. Leaves with a delicate hyaline border of thin-walled, quadrate and elongate hyaline cells; mostly at low elevation, below 2,000 feet **4**
      4. At least some leaf lobules per plant narrow and long, with short basal keels and free lateral margins, vertically or obliquely oriented, tending to be parallel to the stem **5**
         5. Stylus unicellular or not present, never multicellular; common ..... ***C. planissima***
         5. Stylus multicellular; rare, Hawai‘i Island ..... ***C.* sp. 2**
      4. Leaf lobules broad saccate, laterally keeled, with one free margin, horizontally oriented, perpendicular to the stem **6**
         6. Stylus lacking or unicellular; rare, O‘ahu and Lāna‘i ..... ***C. kapingaensis***
         6. Stylus multicellular (6-many-celled); Kaua‘i, O‘ahu, and Lāna‘i ..... ***C. longistylis***
   3. Leaves without a hyaline border; plants from 0-6,000 feet but more common in montane forests **7**
      7. Leaves obovate, broadest in their upper half; leaf cells with prominent trigones ..... ***C. obcordata***
      7. Leaves elliptical to orbicular, not broadest in their upper half, leaf cells without or with very small trigones **8**
         8. Leaf lobules basally keeled, with free lateral margins; erect, parallel to the stem ... ***C. raduliloba***
         8. Leaf lobules laterally keeled, with one free lateral margin; horizontal, perpendicular to the stem **9**
            9. Perianth without keels projecting as horns; plants about 1 mm wide; common ..... ***C. ceatocarpa***
            9. Perianth with keels projecting as 4 horns, plants < 1 mm wide; uncommon ..... ***C. ovalifolia***

1. *Cololejeunea ceatocarpa* (Ångstr.) Steph. **Indigenous.** A member of the subgenus *Leptocolea* (Spruce) Schiffn. (Söderstrom et al., 2016). Found on all major islands (0-6,100 ft.) and also in Asia; a common epiphyte in Hawai‘i Volcanoes National Park. Found creeping on tree trunks, hāpu‘u stipes or leaves of vascular plants. Leaves are elliptical, with a very narrow leaf insertion, with the aspect of two rows of “potatoes on a string”.

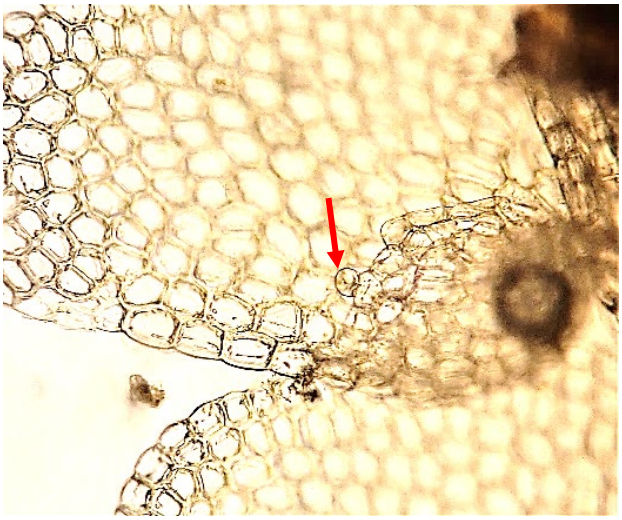


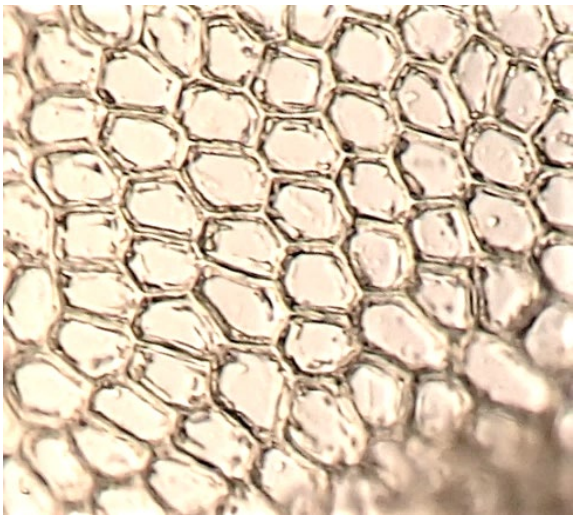
Plants are small, about 1 mm wide, light green. Stems are fragile. Leaves are from distant to contiguous, widely spreading, prostrate, alternate, elliptical, with broad and rounded apices and with a very narrow insertion to the stem. Lobule just slightly under ½ as broad as the lobe base and about 1/3 as long as the lobe; with the first tooth short, round, and single-celled. The leaf cells are smooth, with thin walls and no or very small trigones. Gemmae are round-discoidal, and are often observed on leaf surfaces.

This species is closest to *C. ovalifolia* but with a different perianth morphology. Evans (1900), describes flattened (not keeled), obovate, and “obcordate at the apex” perianths in *C. ceatocarpa*, in contrast to those of *C. ovalifolia* (see our treatment) in which the perianths are not flat, not obcordate, and have four keels that project apically into distinct horns. We were only able to examine sterile material of *C. ceatocarpa;* Study of fertile material is needed. All photos from Freire & Judziewicz 20-700, Volcano, Hawai‘i Island.

Cololejeunea ceatocarpa. Left: Plants creeping on tree bark, closely appressed to their substrate, forming radiating colonies. Right: Note short line of insertion that constricts the leaf base. Photos by E.J. Judziewicz.

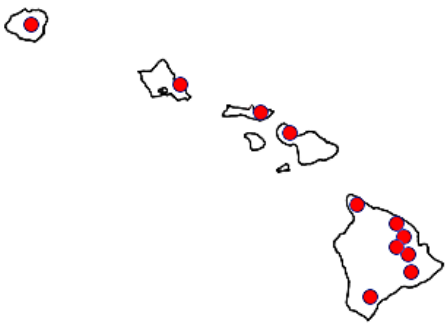
Plants are small (left, scale in mm), with approximate, elliptical, and slightly asymmetrical leaves with rounded apices and small lobules. Note the round gemmae on the surface of the lower leaves (right). Freire & Judziewicz 20-700 (BISH).





Cololejeunea ceatocarpa. Left: Lobule with two short teeth; the first tooth is 1-celled and round (arrow). Right: Cells with thin walls and very small (left) or no trigones (right). Hawai‘i Island, Freire & Judziewicz 20-700 (BISH).

2. *Cololejeunea hillebrandii* (Austin) Steph. **sensu lato (in the wide sense). Indigenous.** A member of the subgenus *Leptocolea* (Spruce) Schiffn. (Söderstrom et al., 2016). A pantropical species (Gradstein, 2021) found on all major islands except Lānaʻi (2,500-6,000 ft.). This epiphytic species has elongated leaf lobes and leaf cells without trigones. Sass-Gyarmati et al. (2023: 349) note that correcting Austin's original spelling "*hildebrandii*" is allowable under the International Code of Nomenclature since he meant to honor botanist William Hillebrand (1821-1886).



Plants are light to whitish green, creeping, closely to loosely attached; small, 0.7-0.9 mm wide. Stems are thin and fragile, irregularly branched. Leaves are flexuous, oblique spreading, distant, elongate-lanceolate, and entire. The leaf lobes are long and narrow, (2.5)3-4 times longer than broad, 0.5-0.8 mm long by 0.2 mm broad with tapering and acute to obtuse apices. In some populations, leaves may not be tapering, and the apices are rounded-obtuse. The lobules are (1/2)1/3-1/4 as broad as the base of the lobe and at least 1/3 -1/4 its length. Some populations do have larger lobules that may be almost as wide as the lobe base. They are inflated along their keel but appressed along their free margin. The lobule apices are truncate-lunulate, with two teeth, the first one with a single round cell attached to a single basal cell, while the second tooth is smaller and single-celled (perhaps with a two-celled base?). Leaf cells are isodiametric to elongated, thin- to moderately thick-walled, and lack trigones. Perianths are obovate, smooth, turbinate, and horned. Round, small to large gemmae are often observed on the surface and at the margins of leaves.

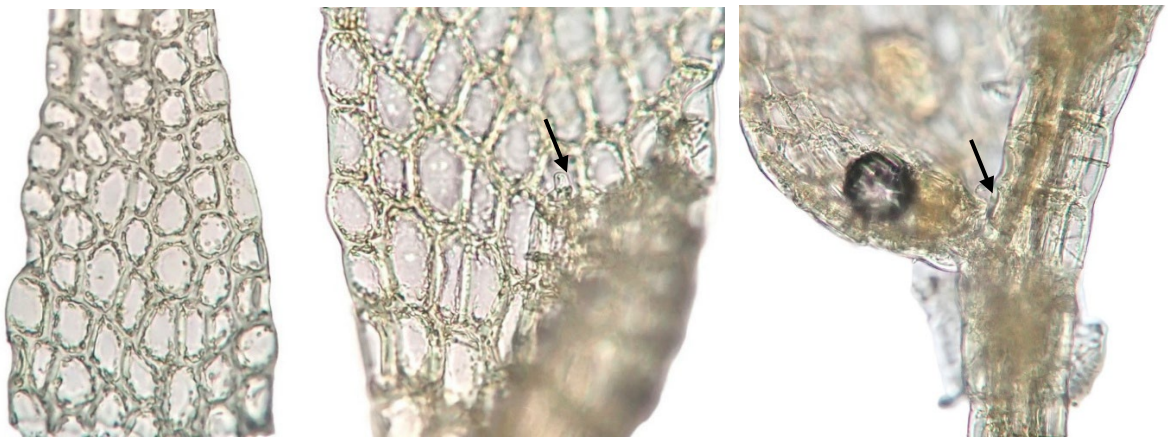
The significant variation and extreme morphologies we observed among the specimens studied are reflected in our description (above). Our treatments, below, are separated by morphological groups, with bolded subtitles. The specimen collected on Oahʻu by Forbes (2175.0, BISH), fits Evans' description and illustrations closely, excepting that the cell walls are moderately thick- rather than thin-walled. Also, several lobules have only an apical tooth, with the central tooth missing. The Kauaʻi collection by Forbes (1628, BISH) shows some variation; the leaves are not as long in proportion to their width, the lobules are larger, more leaf apices are obtuse, and leaves are not as tapering. Several more recent Kauaʻi and Hawaiʻi Island collections have a more extreme morphology with even broader lobes that do not taper towards the apex, and even broader lobules, almost as broad as the lobe base. We may be dealing with a species complex in need of elucidation. More attention needs to be given to lobule tooth morphology.

Cololejeunea hillebrandii from Evans (1904). Leaves are more acute, tapering and longer than wide, with the lobules smaller than observed by us in fresh specimens.

Forbes 2175.0, Kōnāhuanui, Oahʻu (BISH): This specimen fits the strict Evans (1900) concept of *C. hillebrandii*.

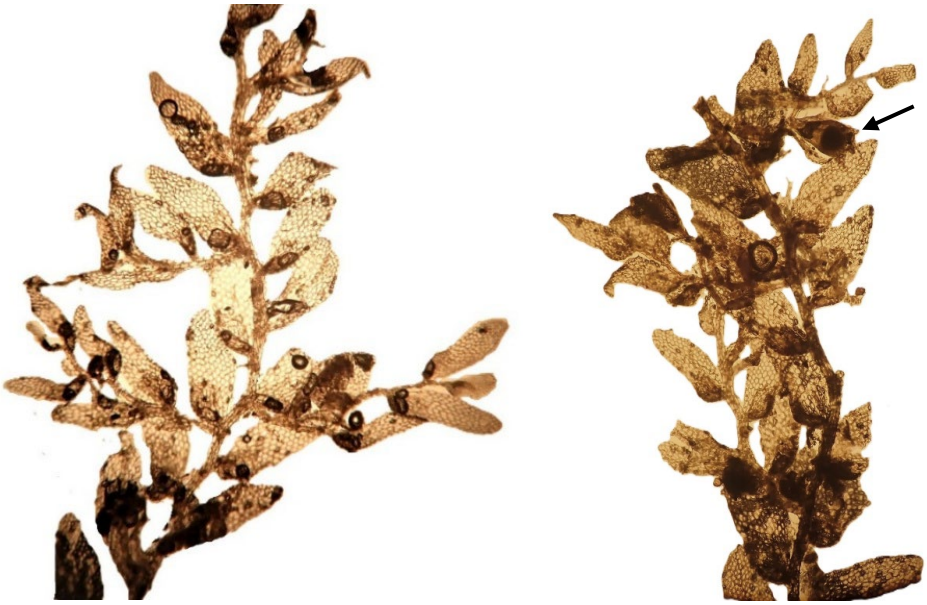
Left: Plants creeping, closely attached to substrate, small. Leaves elongate and acute, obliquely spreading. Scale in mm. Right: Detail of plant with elongate and narrow lobes with acute apices. Scale subunits = 26 µm. Kōnāhuanui, Oahʻu, Forbes 2175.0 (BISH). Photos by A.V. Freire.

Cololejeunea hillebrandii. Plants have characteristically elongated and pointed leaves. Lobules are small. Note the crowded and modified leaves at the base of branches (right). We did not see antheridia subtended by any of them. Evans describes antheridial branches as compressed units, not at the base of otherwise vegetative branches. Kōnāhuanui, Oahʻu, Forbes 2175.0 (BISH). Photos by A.V. Freire.

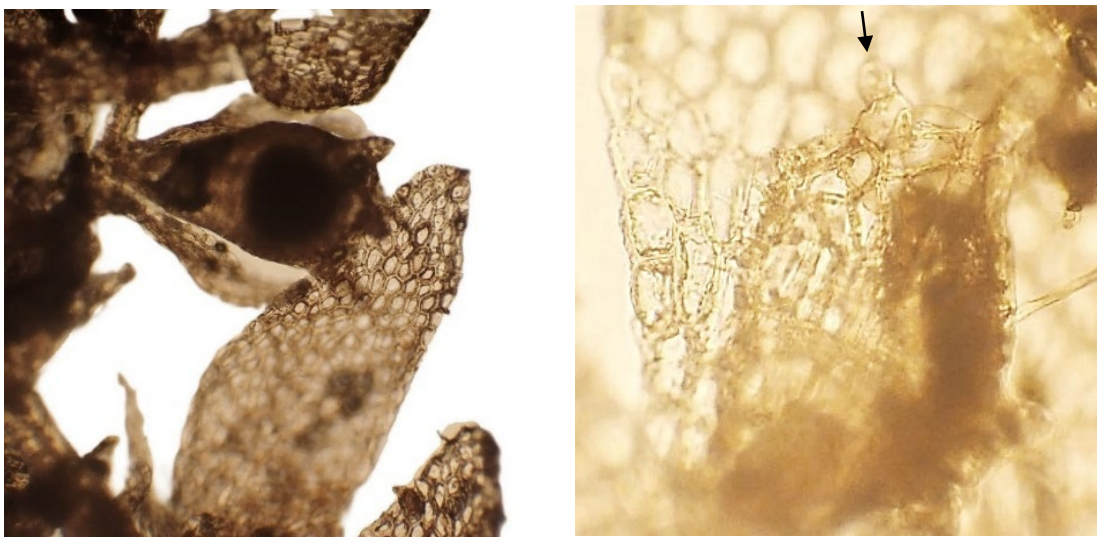


Leaf cells are variable, from elongated to isodiametric. Unlike in Evans' (1900) description, the cell walls are moderately thickened. Center: First lobule tooth. Note the two basal cells. Right: Small and single-celled stylus. Kōnāhuanui, Oahʻu, Forbes 2175.0 (BISH). Photos by A.V. Freire.

Kauaʻi, Forbes 1628 (BISH): This specimen has broader leaf lobes and lobules that taper towards the lobe apex.



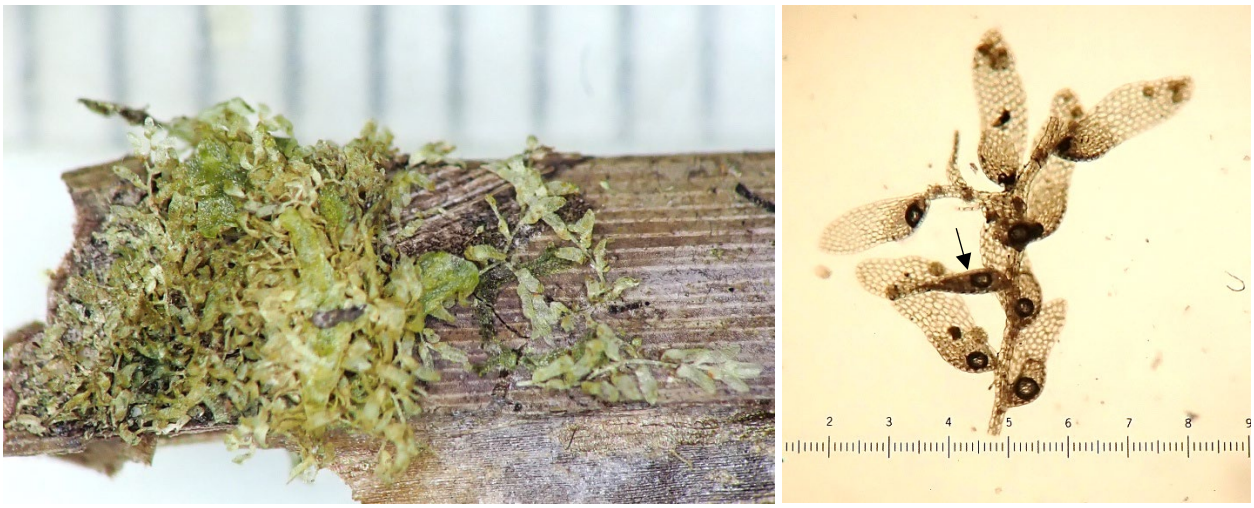
Cololejeunea hillebrandii. This specimen, collected by Forbes in Kauaʻi, is close in appearance to Evans' concept. But note broader leaves in relation to their length and the variation in leaf apices, not always tapering into an acute tip. Lobules are larger. Note perianth on top of right picture (arrow). Kauaʻi, Forbes 1628 (BISH). Photos by E.J. Judziewicz.



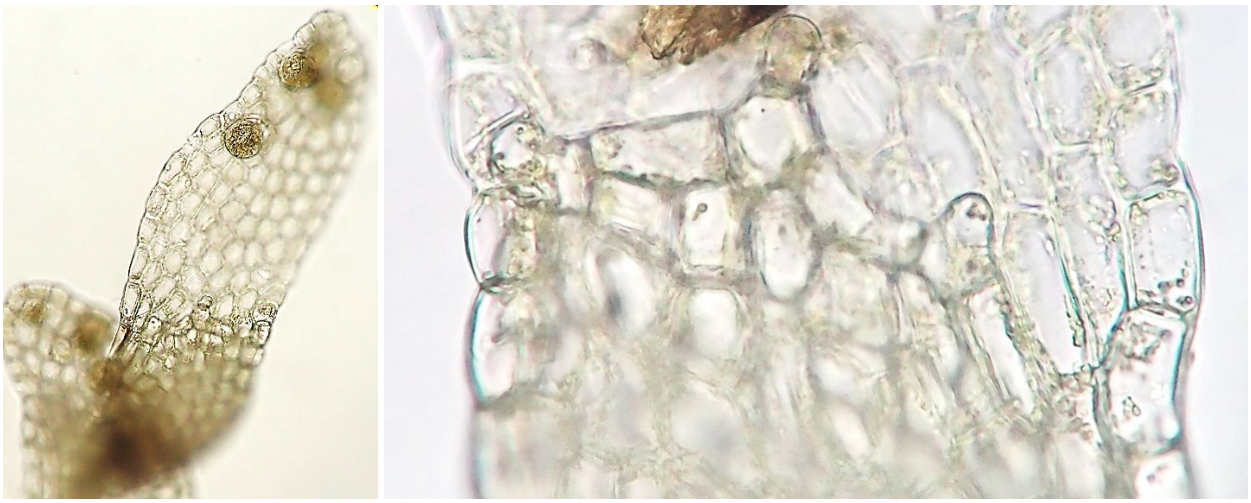
Cololejeunea hillebrandii. Left: Horned, smooth, and turbinate perianth. Right: First 2-celled tooth on lobule (arrow). Kauaʻi, Forbes 1628 (BISH). Photos by E.J. Judziewicz.

Southern Koʻolau Range, Oʻahu, Faccenda & Ross 3466 (BISH): This specimen represents a more extreme leaf morphology with broader lobes and lobules and rounded or only slightly tapering lobe apices. Perhaps a different species; we include it here as part of *C. hillebrandii* in the broad sense.

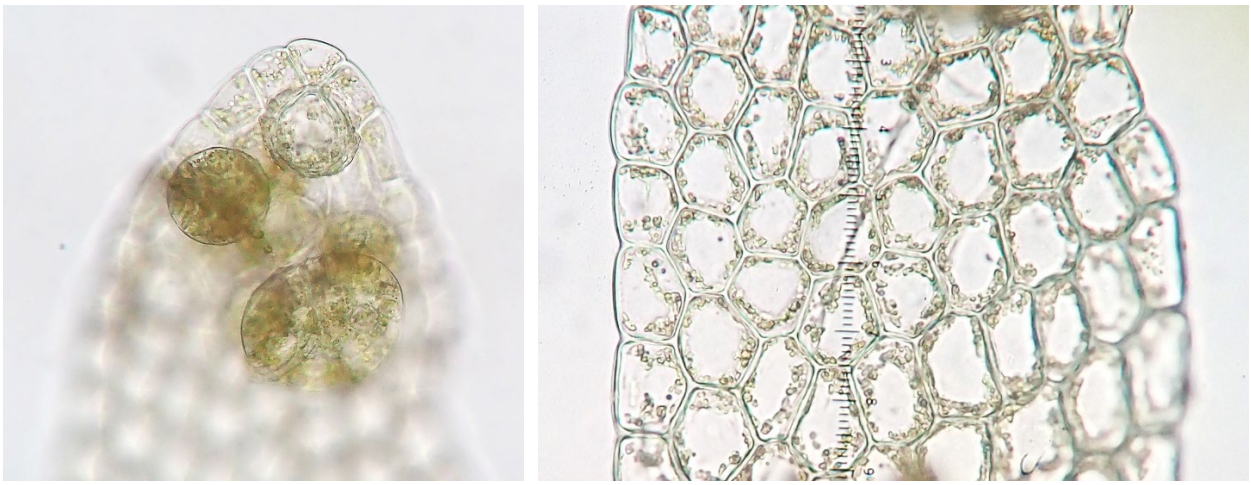
Southern Koʻolau Range, Oʻahu, Faccenda & Ross 3466 (BISH): Photo by K. Faccenda. With permission: https://www.inaturalist.org/observations/221483846.



Left: Plants are small, creeping on bark. Scale in mm. Right: Stems are fragile; leaves are elongated with acute to rounded apices. The leaf lobes are shorter in proportion to their width, less acute, and with a larger lobule than the drawing by Evans (1900) above. Note the large round gemmae and the lobule profile showing its inflated base and constricted top (arrow). Each scale subunit = 26 µm. Southern Koʻolau Range, Oʻahu, Faccenda & Ross 3466 (BISH). Photos by A.V. Freire.



Cololejeunea hillebrandii. Leaf lobules are almost as broad as the lobe base and about 1/3 of their length (the keel is on the right side in these photos, the free margin on the left side); they are tridentate, with the second tooth most prominent, round, and 2-celled. Southern Koʻolau Range, Oʻahu, Faccenda & Ross 3466 (BISH). Photos by A.V. Freire.



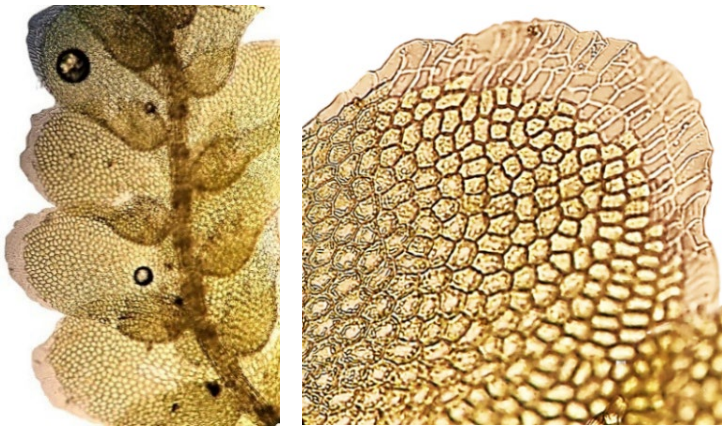
Left: Detail of large, round-discoidal gemmae. Right: Leaf cells are thin-walled and have small trigones. Each scale subunit = 2.5 µm. Southern Koʻolau Range, Oʻahu, Faccenda & Ross 3466 (BISH). Photos by A.V. Freire.

***Cololejeunea* cf. *hillebrandii*:**
Plants are characterized by a slightly constricted leaf lobe base that expands slightly where the lobule ends, before the leaf middle and towards its apex; the leaves resemble asymmetrical peanuts. Several specimens with this morphology were collected by us on Hawaiʻi Island.

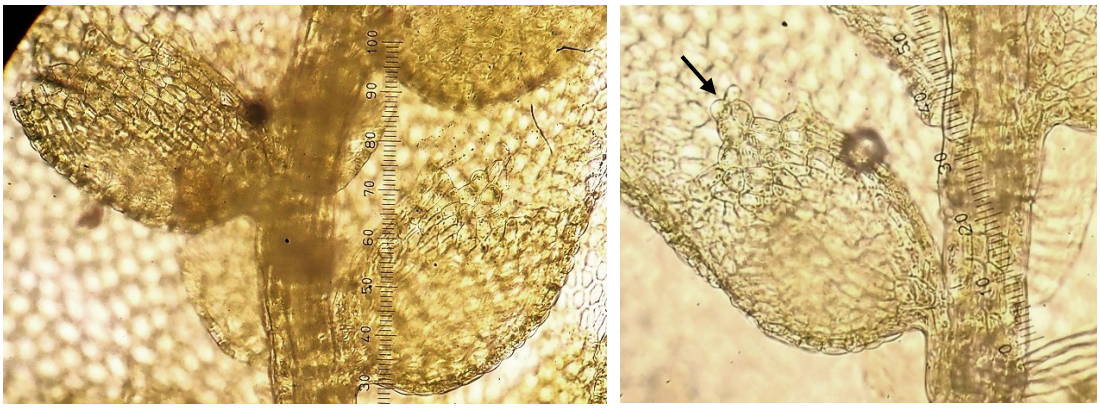
Cololejeunea cf. *hillebrandii.* Leaves are slightly constricted near the lobule apex, giving the appearance of "peanuts". Note the abundant discoid leaf gemmae. Niaulani Forest, Hawaiʻi Island, Freire & Judziewicz 20-954a (BISH).

3. *Cololejeunea kapingaensis* H.A. Mill. **Indigenous.** A member of subgenus *Pedinolejeunea* Benedix ex Mizut. (Söderstrom et al., 2016). Uncommon; rare in both the Waiʻanae and Koʻolau Ranges on Oʻahu; Maunalei Gulch, Lānaʻi; and Manukā N.A.R., Hawaiʻi Island (1,000-1,800 ft.). Micronesia, Fiji, and Hawaiʻi. Recognized by its hyaline leaf apical border; and by the ovate and inflated lobule with 2 teeth, the first multicellular and larger than the second one.

Plants medium-sized, pale green, epiphyllic, appressed to their substrate. Leaves oval, lobes with apical hyaline borders, these in 2-3 rows of cells at the leaf apex, but single-celled on the sides near the apex. Leaf cells are thin-walled and lack trigones. Leaf lobules are saccate, round, truncate, with two teeth. The second tooth is small, but the first tooth is prominent and multicellular, with some bulging cells at its apex (slime papillae?); this feature was also illustrated in the protologue of *C. hoeana* by Tixier (1985). Discoidal gemmae are sometimes present on the leaf surface. All photos below from Freire & Judziewicz 22-65b, Manukā N.A.R., Hawaiʻi Island. Based on descriptions and illustrations, we could not find significant differences between *C. hoeana* and *C. kapingaensis* and we are thus reducing ***C. hoeana*** Tixier (1985) to synonymy under the older name *C. kapingaensis* (Miller, 1956).

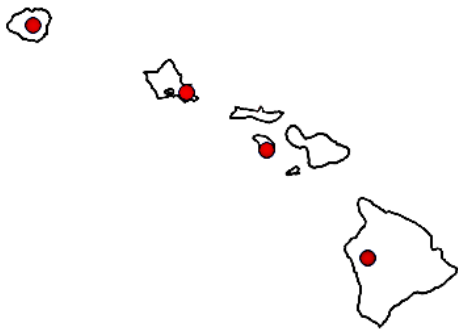


Left: Leaf lobes with a hyaline apical border; the lobules are rounded and toothed. Right: Hyaline border of lobe apex is from 1-3 cells deep. Freire & Judziewicz 22-65b (BISH).

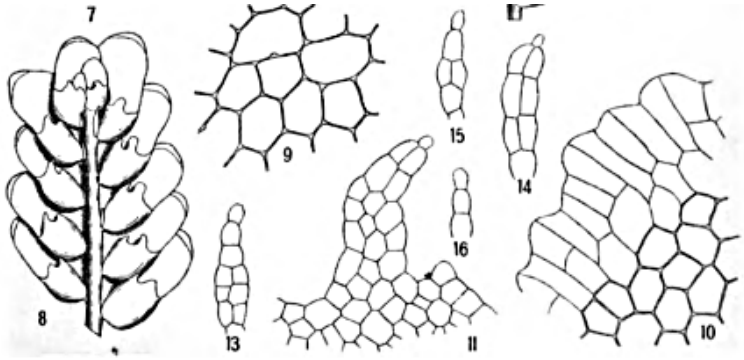


Cololejeunea kapingaensis. Lobules with two teeth, the first tooth prominent and multicellular, while the second tooth is single-celled. Right: Note the bulging cells on the first tooth (arrow). Scale units = 9.7 µm. Manukā N.A.R., Hawaiʻi Island, Freire & Judziewicz 22-65b (BISH).

4. *Cololejeunea longistylis* A. Evans. **Endemic.** Rare on Kauaʻi, Oʻahu, Lānaʻi, and Hawaiʻi Island (1,000-3,000 ft.). A member of subgenus *Pedinolejeunea* Benedix ex Mizut. (Söderstrom et al., 2016). Possible affinity (Evans, 1900): *C. stylosa* (Prantl) A. Evans, Philippines. Epiphyte. The leaves have hyaline marginal cells. The lobules are large, with a prominent, multicellular first tooth. The main distinguishing character of this species is the long multicellular stylus found at the ventral base of most leaves. Leaf cells are thin-walled and with small trigones.



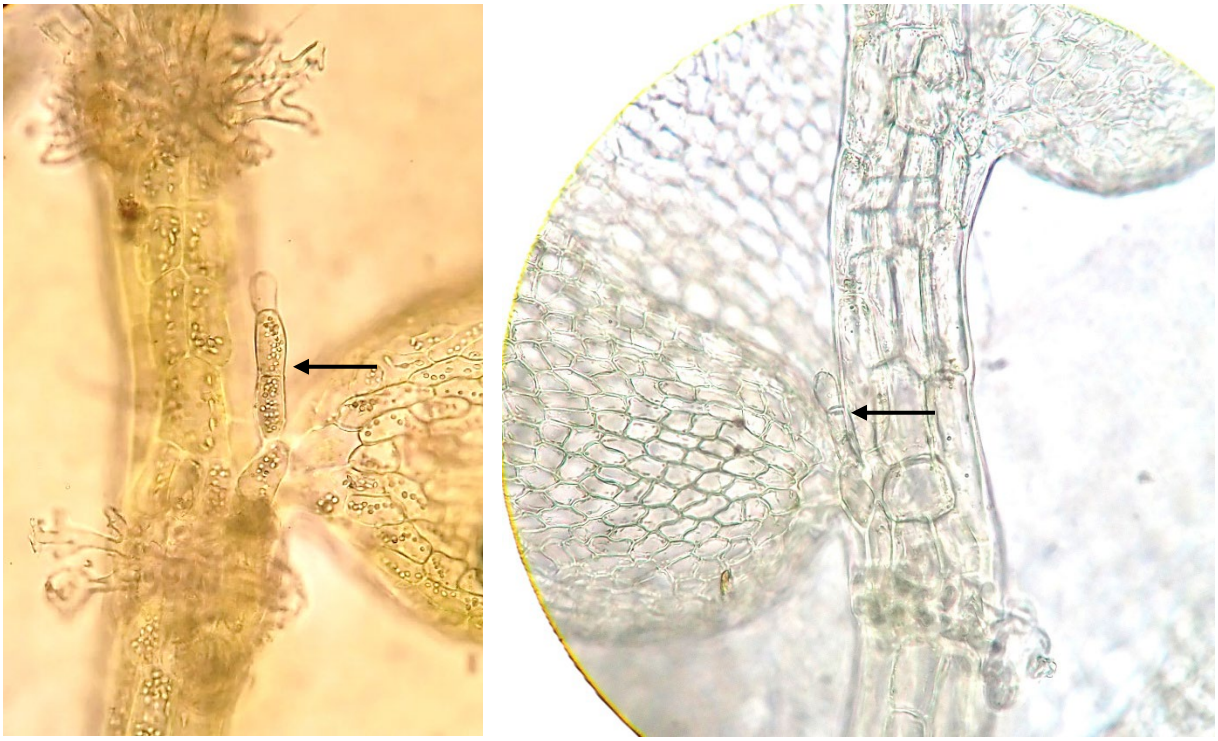
Plants are light green, closely to loosely appressed, with fragile stems, up to 7 mm long, about 1.5 mm wide. Leaves obliquely spreading, ovate-oblong, entire, contiguous to imbricate, curved on the upper margin but straight on the lower one; with hyaline marginal cells in 2-3 rows of elongate to large quadrate cells at the leaf apex and extending as a single row of smaller and quadrate cells to the upper leaf margin. Lobules are large, 1/3 to close to 1/2 as broad as the lobe's width, and about 1-2.5 times as long; they are inflated, with a prominent and multicellular first tooth and a smaller, 1-celled second tooth. A long multicellular stylus is found at the ventral base of most leaves. The stylus is (3)4-5(6) cells long and usually one cell wide but occasionally two cells wide towards the middle (according to Evans (1900): "often two cells broad at and near the middle"). Leaf cells are thin-walled and may have small trigones.



Drawings from Evans (1900). Captions: 8. Sterile plant on ventral side. 9. Cells from middle of lobe. 10. Hyaline cells from lobe apex. 11. Lobule middle teeth. 13-16. Different morphology of multicellular stylus.

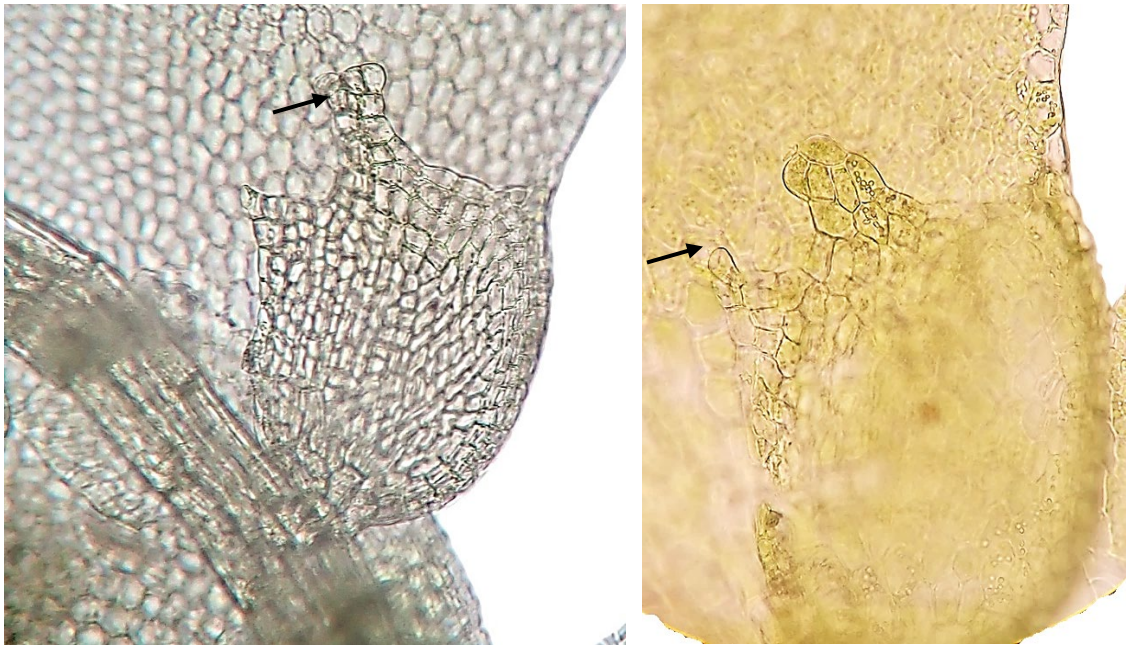
Plants are epiphytes, light green, closely to loosely appressed. Note the leaves with hyaline margins, Hawaiʻi Island, Judziewicz 17,056a (BISH). Photo by E. J. Judziewicz.

Left: Scale in mm. Photo by E. J. Judziewicz. Right: Leaves are imbricate to contiguous, with large lobules. Note the prominent first lobule tooth. Stems are fragile. Each scale subunit = 26 µm. Judziewicz 17,056a (BISH). Photo by A.V. Freire.

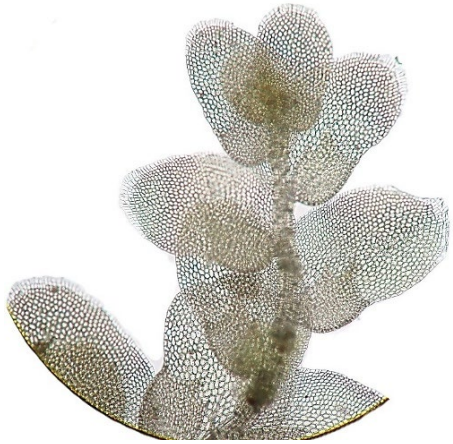


Cololejeunea longistylis. Stylus is up to 5 cells long and one cell wide. Left: Stylus 5 cells long. Photo by E.J. Judziewicz. Right: Stylus 4 cells long. Photo by A.V. Freire. Hawai‘i Island, Judziewicz 17,056a (BISH).

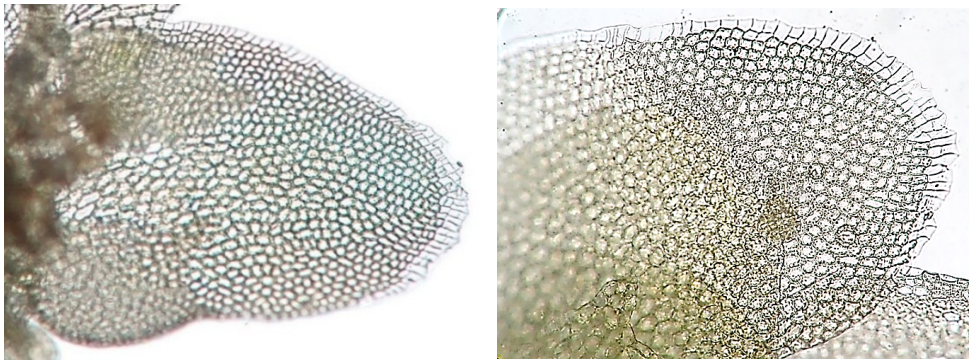
The stylus is two cells wide in its upper region (arrow). This was rarely observed by us, but Evans (1900) often observed two cells-wide styluses. This photograph is close to the plant apex. Judziewicz 17,056a (BISH). Photo by A.V. Freire.



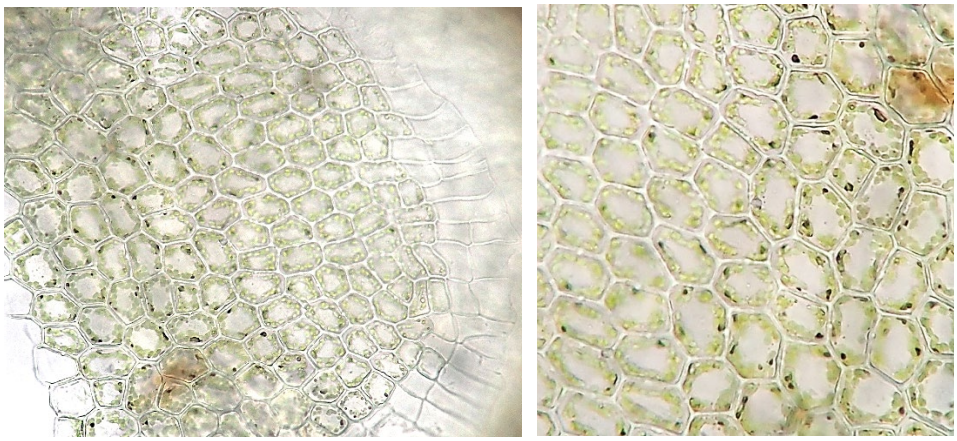
Cololejeunea longistylis. Left: The first lobule tooth is large, multicellular and very prominent (arrow). Photo by A.V. Freire. Right: The second lobule tooth is small and single-celled (arrow). Photo by E.J. Judziewicz. Hawai‘i Island, Judziewicz 17,056a (BISH).



Leaves with hyaline apical margins that extend along the upper lobe margin. Judziewicz 17,056a (BISH). Photo by A.V. Freire.

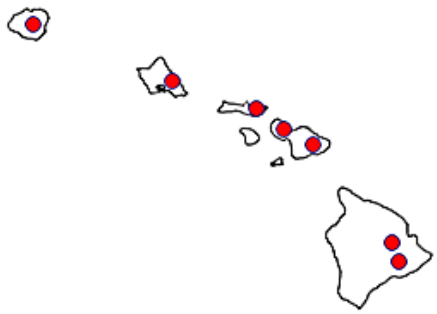


Hyaline marginal cells are mostly elongated and in 2-3 strata at the apex of the leaf. They extend as a single layer of quadrate cells along the leaf upper margin. Judziewicz 17,056a (BISH). Photos by A.V. Freire.



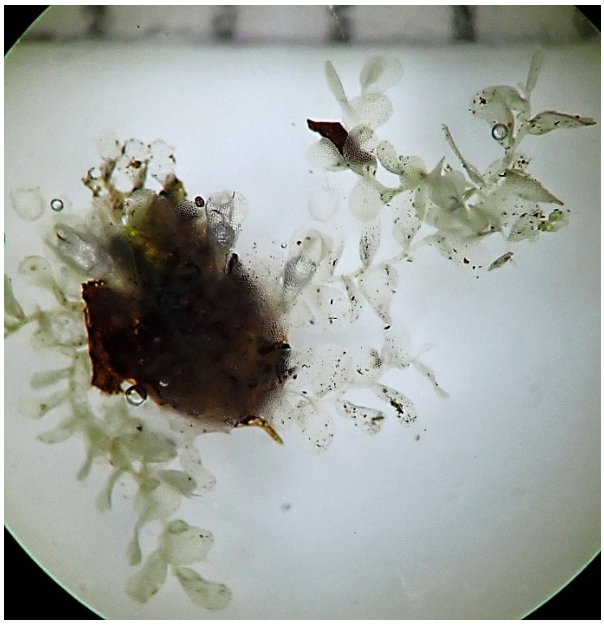
Cololejeunea longistylis. Leaf cells are thin-walled, sometimes with tiny trigones, or occasionally with tiny intermediate thickenings. Note the hyaline border (left photo). Hawai‘i Island, Judziewicz 17,056a (BISH). Photos by A.V. Freire.

5. *Cololejeunea obcordata* (Austin) A. Evans. **Endemic.**
A member of the subgenus *Leptocolea* (Spruce) Schiffn. (Söderstrom et al., 2016). Found on all major islands except Lānaʻi (2,500-5,500 ft.). Plants are small, creeping among other bryophytes or on fern fronds or bark. The suberect leaves are distinctive; they are obovate with lobes broad above but narrower at the base; the lobules have 2(3) small teeth and proximal slime papillae, and the leaf cells have large trigones.

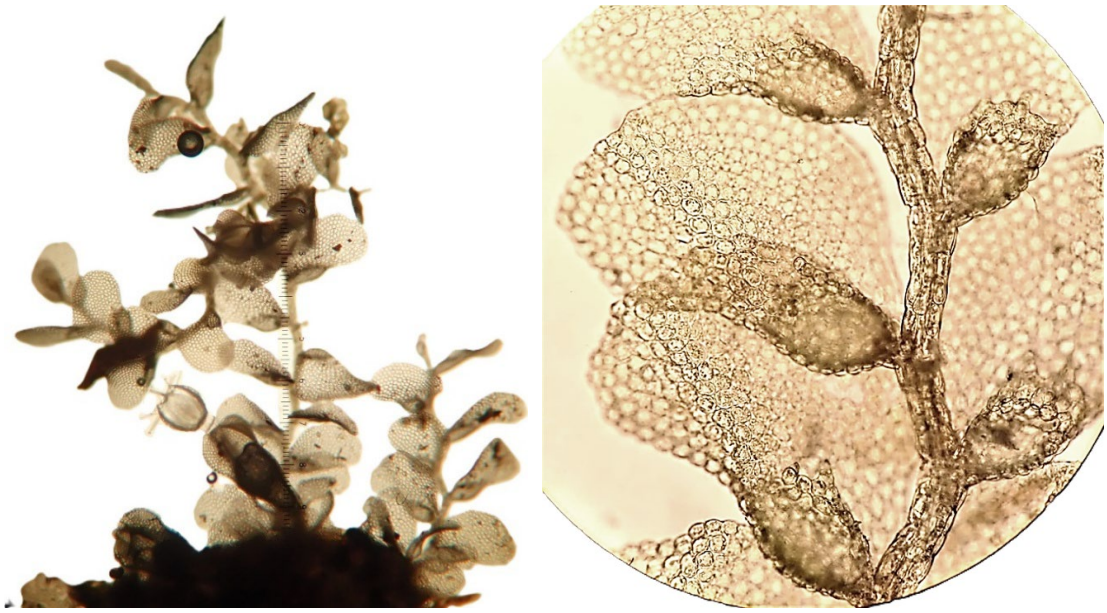


Plants are creeping, small, about 1 mm wide, yellowish-green, with fragile stems. Leaves are contiguous to slightly imbricate, spreading, usually suberect, entire, rounded on the upper margin, oblique and straight on the lower margin; obovate, broadest in their upper half and tapering towards the base. Leaf lobules are small, inflated, with 2-3 small teeth and with proximal slime papillae. Leaf cells are isodiametric, with prominent trigones. Males are produced on short, lateral, globose (inflated) innovations. Perianths are produced on short lateral branches with a sterile innovation, and with four flattened keels that resemble wings in profile.

Our specimen fits the description and illustrations by Evans (1900) and Tixier (1985) in most characters, except that the strong emargination at the perianth apex that suggests a heart shape in profile (perhaps the character used to name the species) was not observed in ours. This is concerning! This species somewhat resembles *C. ceatocarpa* but has distinct nodular leaf trigones. Photos below, Puʻu Makaʻala N.A.R., Hawaiʻi Island, Freire & Judziewicz 22-177 (BISH).

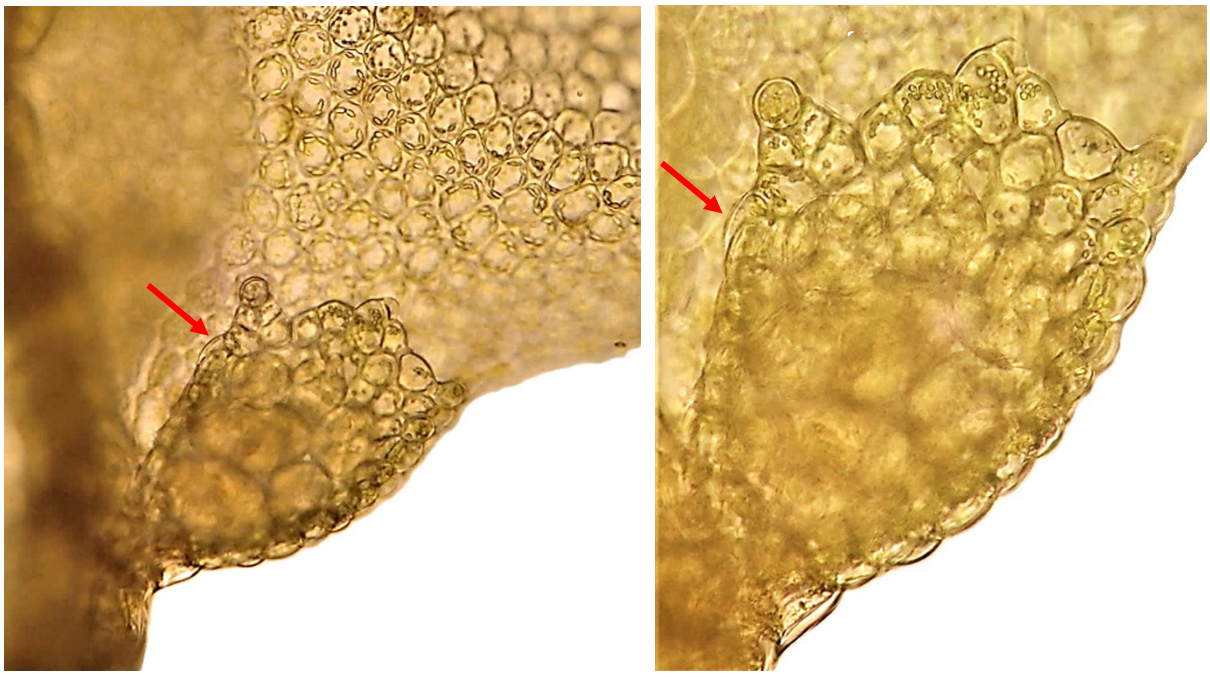


Cololejeunea obcordata, Left: Plants creeping on fern frond. They are yellow-green, with semi-erect leaves. Note keeled perianth below pointer. Right: Plants are small, about 1 mm wide. Scale in mm. Puʻu Makaʻala N.A.R., Hawaiʻi Island, Freire & Judziewicz 22-177 (BISH).

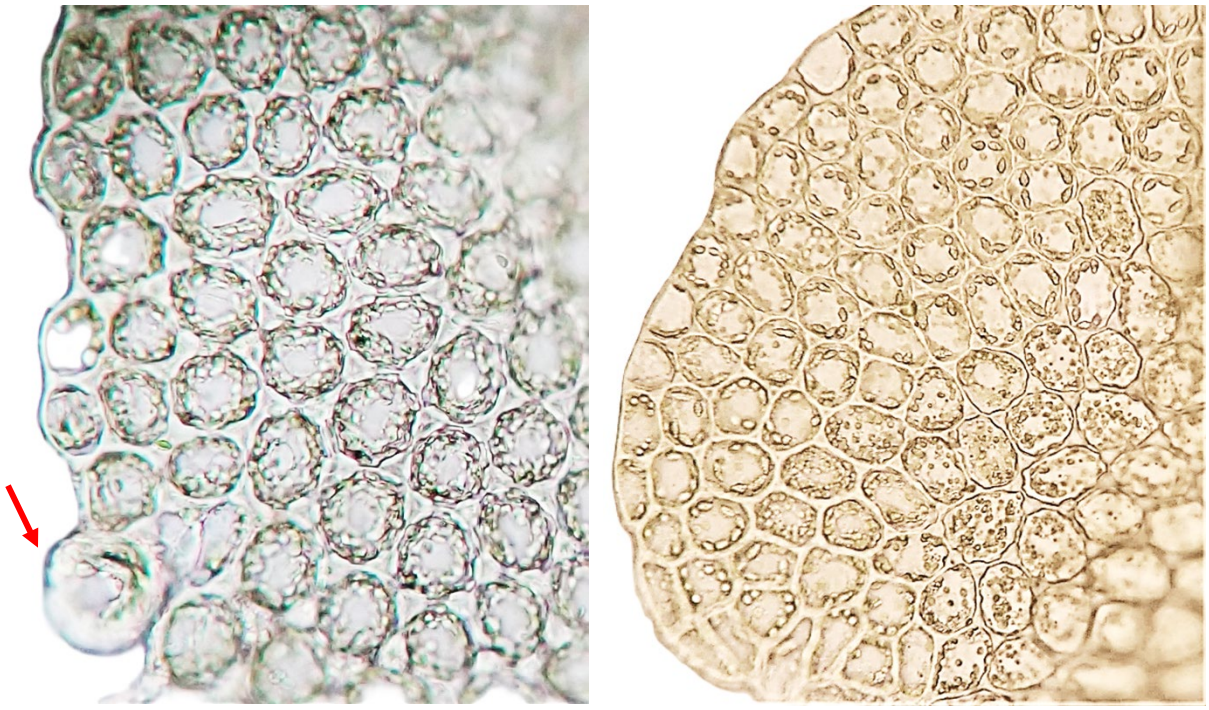


Left: Plants showing semi-erect leaves. Scale subunits = 26 µm. Right: Plant showing spreading lobes with narrow bases, rounded upper margins, small lobules, and thin stems with a zig-zag pattern. Freire & Judziewicz 22-177 (BISH).

Cololejeunea obcordata. Left: Males in short, globose lateral branches; perianths produced on short lateral branches. Note keeled, cuneate perianths with 4 conspicuous keels. Right: Detail of keeled perianth with shortly emergent, dehisced capsule with elaterophores. All pictures on this page from Pu‘u Maka‘ala N.A.R., Hawai‘i Island, Freire & Judziewicz 22-177 (BISH).

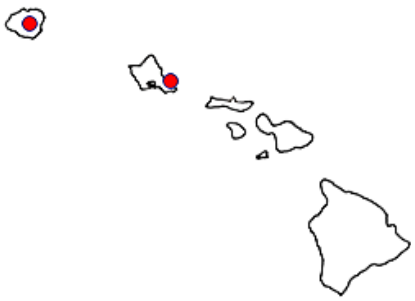


Lobule with two teeth; the second tooth is larger. The slime papilla is proximal, basal to the second tooth, on the lobule's free margin (arrows). Note that the lobule is "occupied" by several dormant invertebrates (probably rotifers). Freire & Judziewicz 22-177 (BISH).



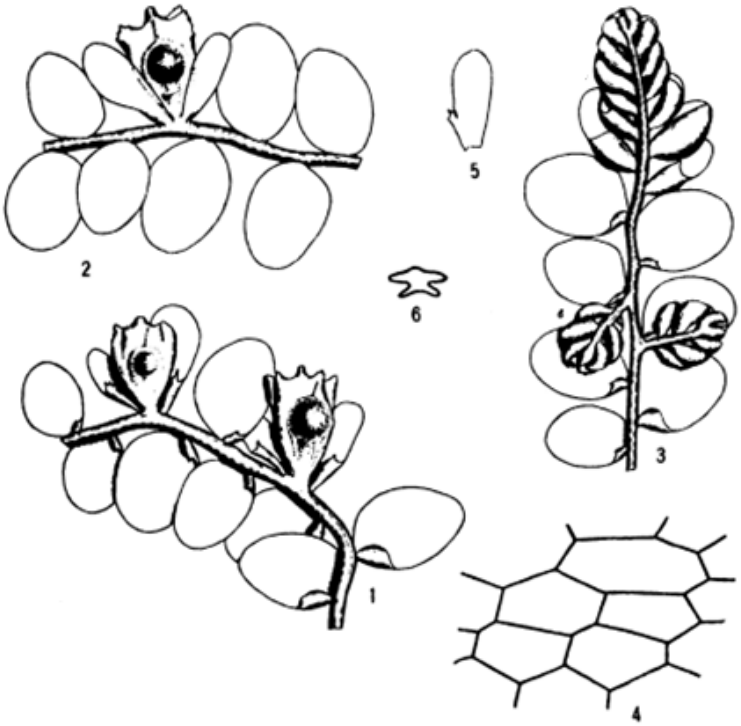
Cololejeunea obcordata, Leaf cells with prominent trigones. What we interpret as a discoid, unicellular marginal gemma is observed at the bottom left (arrow). All pictures on this page from Puʻu Makaʻala N.A.R., Hawaiʻi Island, Freire & Judziewicz 22-177 (BISH).

6. *Cololejeunea ovalifolia* A. Evans. **Endemic.** A member of subgenus *Leptocolea* (Spruce) Schiffn. (Söderstrom et al., 2016). A rare epiphyte found on Kaua‘i and O‘ahu (ca. 2,000-4,000 ft.). Not seen by us in the field. This species is closest to *C. ceatocarpa* but is smaller, with smaller lobules and more orbicular leaves. They reportedly often grow together. Unlike the perianths of *C. ceatocarpa*, *C. ovalifolia* produces keeled perianths with keel extensions that form prominent horns. These were not observed by us.



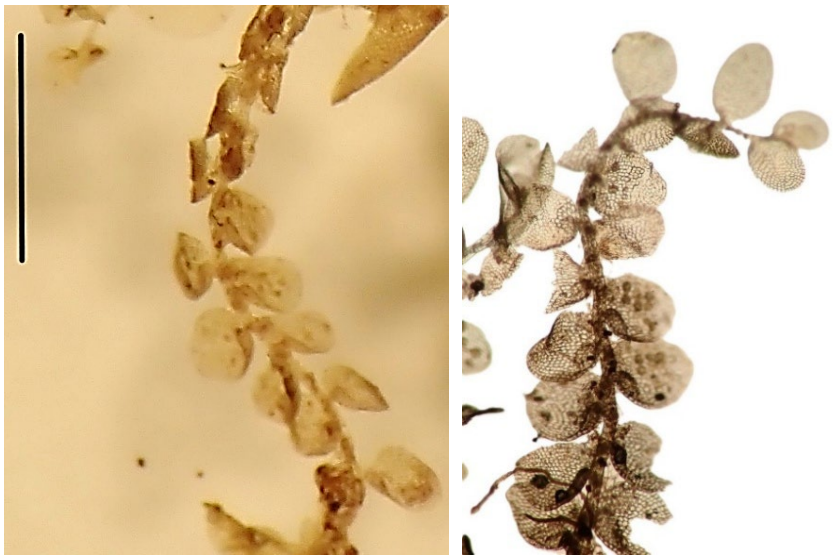
Plants are tiny, less than 1 mm wide, closely appressed to their substrate, with fragile stems. Leaves are slightly concave, spreading, entire, distant to contiguous, shortly elliptical, or almost orbicular, rounded at the apex, and basally narrowly attached to the stem. The lobules are small, 1/3-1/4 the width of lobe base and 1/3-1/4 the lobe length, oval, inflated below (along the keel), with a small tooth. Leaf cells lack trigones. Discoidal gemmae are abundantly produced on the leaf surface.

The plants studied and photographed by us fit the description by Evans (1900) but seem to be smaller. We were not able to study the distinctive perianths, and our description is based on a limited number of plants. New collections, hopefully with perianths, are needed to better understand this species.

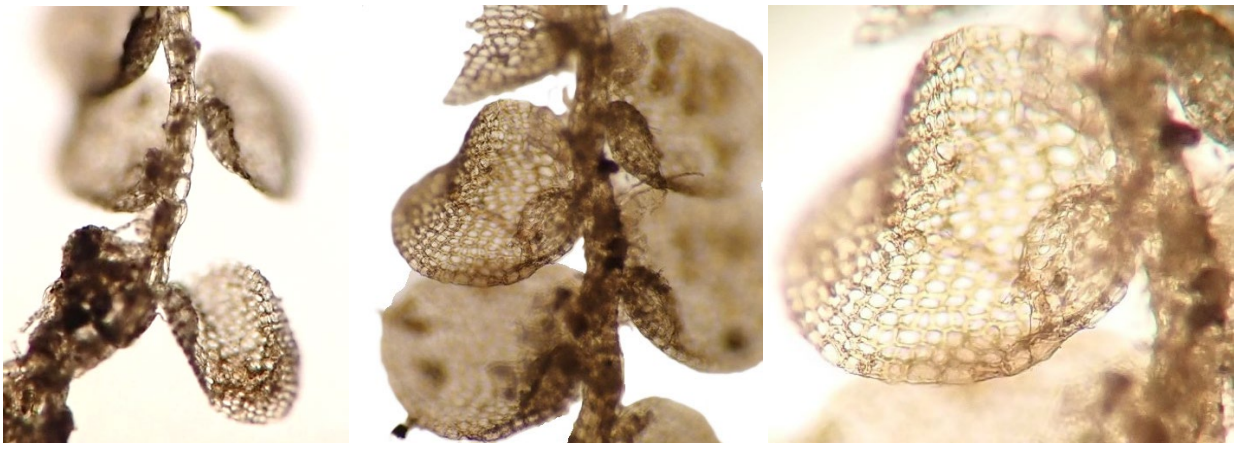


Cololejeunea ovalifolia. Plate by Evans (1900). 1. Plant with 2-keeled and horned perianths in ventral view. 2. Plant with perianth in dorsal view. 3. Plant with male branches. 4. Leaf cells lacking trigones. 5. Bract. 6. Cross section of perianth.

Isotype. Cooke s.n., Nu‘uanu, O‘ahu, July 1898 (MU).

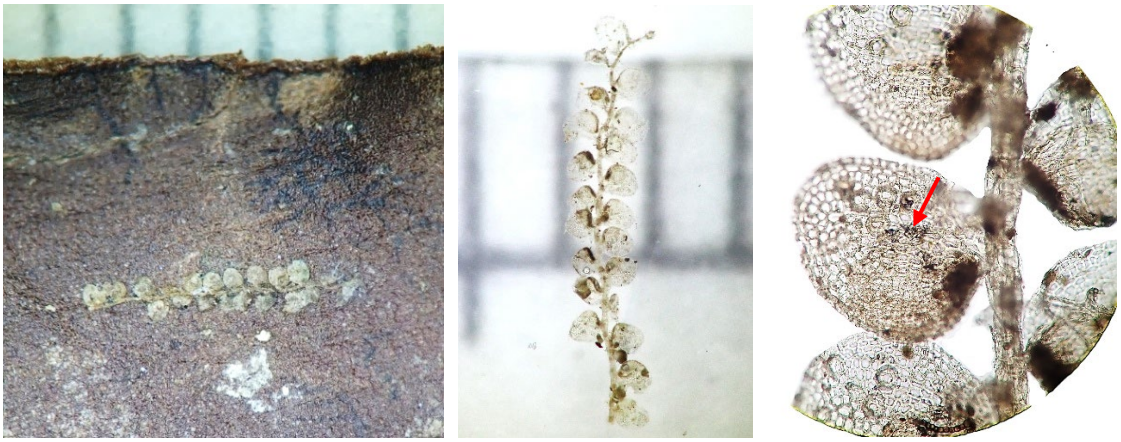


Left: Plants are tiny, less than 1 mm wide. Scale = 1 mm. Right: Leaves are rounded, distant, with small lobules and leaf surface gemmae. Isotype. Cooke s.n., Nu‘uanu, O‘ahu, July 1898 (MU). Photos by A. V. Freire.

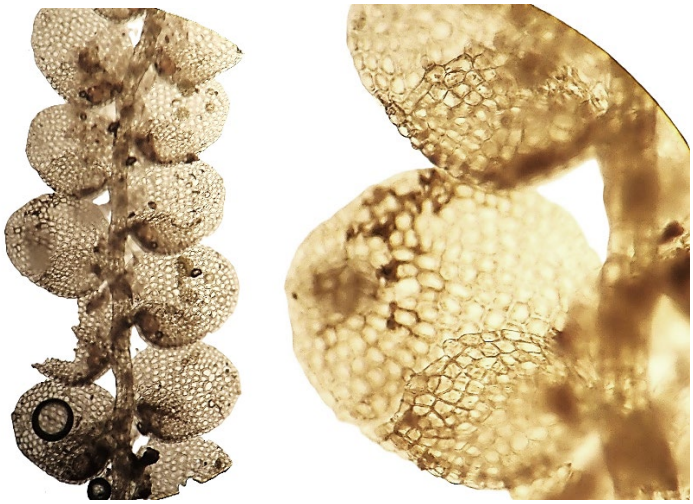


Cololejeunea ovalifolia. Left: Fragile stem with hyalodermis. Center: Small, inflated lobules. Right: Detail of lobule with first tooth. Isotype. Cooke s.n., Nu‘uanu, O‘ahu, July 1898 (MU). Photos by A.V. Freire.

Below: *Cololejeunea* aff. *ovalifolia*: This *Cololejeunea* is very similar to *C. ovalifolia* but with much larger lobules, at least ½ the lobe width and almost ½ its length. It is likely a different species. We observed it from collections from Kauaʻi by Cooke (1903) and in a 2024 collection (Faccenda 3791, BISH) from the Alakaʻi Preserve. Also: Perhaps this species, from the Saddle Area, Hawaiʻi Island, Daniel Tucker, and Randall Mindell. All specimens are in need of detailed study.
https://www.inaturalist.org/observations/257385155.
https://www.inaturalist.org/observations/255994114.

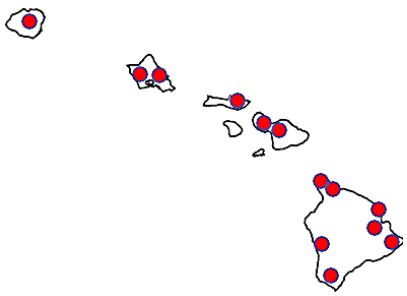


Plants are tiny, less than 1 mm wide. Lobules are more than half the lobe width, and half or more their length (arrow). Keʻākū, Kauaʻi, Cooke 36 (BISH). Photos by A.V. Freire.

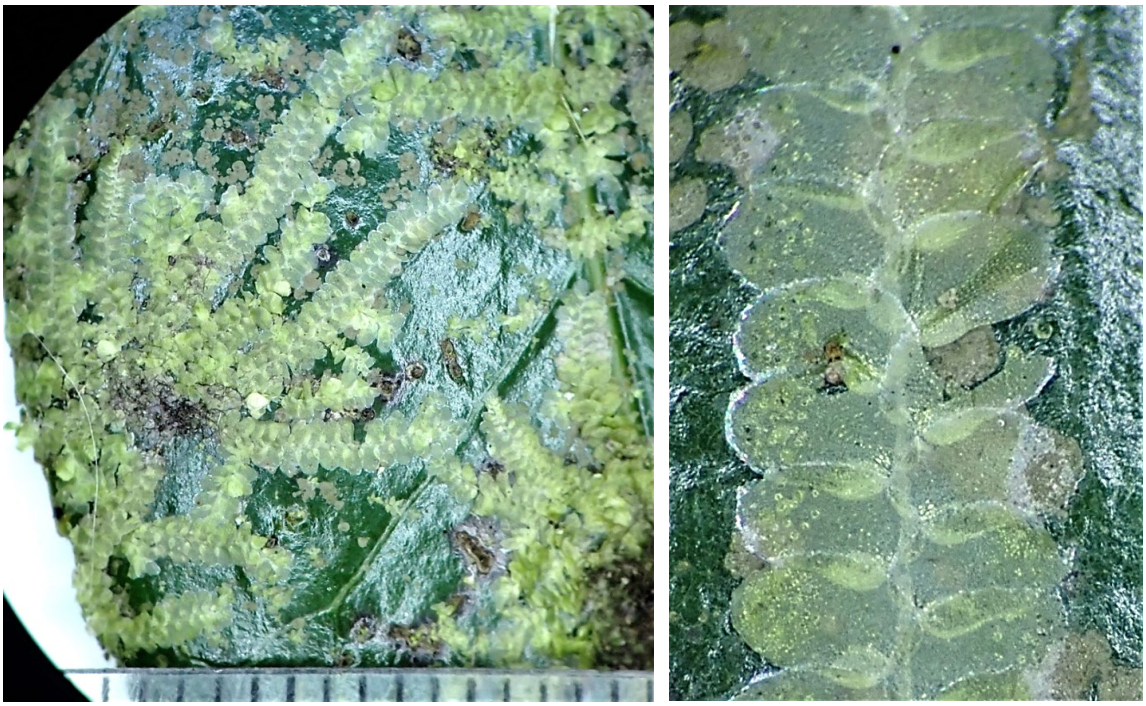


Cololejeunea aff. *ovalifolia*. Plants with large lobules, note the two teeth (right). Alaka'i Swamp, Kauaʻi, K. Faccenda 3791 (BISH). Photos by E.J. Judziewicz.

7. *Cololejeunea planissima* (Mitt.) Abeyw. **Indigenous.** Treated as *Cololejeunea lanciloba* in Staples & Imada (2006). A member of subgenus *Pedinolejeunea* Benedix ex Mizut. (Söderstrom et al., 2016). Found on all major islands except Lānaʻi (0-2,000 ft.); see Judziewicz & Freire (2023c: 153); also in Asia, Australia and Oceania. Common, typically very closely appressed to bark and leaves. The plants often appear to be literally "painted" onto their leafy substrate. Recognized by the hyaline leaf margins and by having at least some vertical and plane lobules with a short basal keel and free lateral margins. In lowland forests, on indigenous and exotic trees.



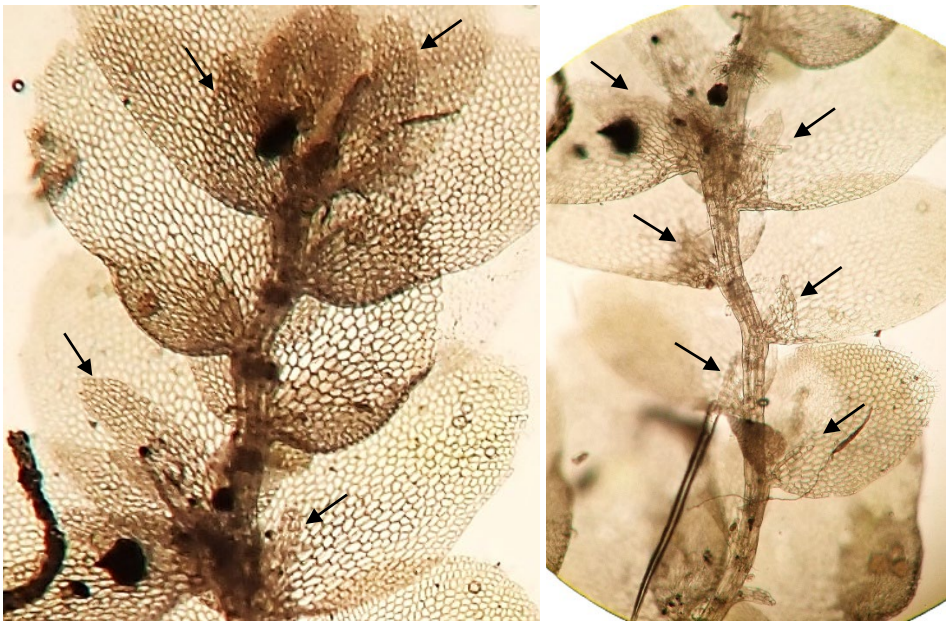
Plants are large, over 10 mm long, and 2 mm wide or wider; light green, translucent, closely appressed, frequently branched. The leaves are elliptical, plane, imbricate, spreading, with a curved upper margin that extends well beyond the stem and a straight and slightly oblique lower one; with rounded apices and a hyaline border that extends from the apex to the upper leaf margin and partially to the lower one. Two kinds of lobules are observed on the same plant, intermixed or on different regions of the plant; each kind can be rather variable. Saccate lobules are more abundant, found mainly on most leaves of main stems and sometimes on lower portions of branches; they are horizontally oriented with long keels, with truncate apices bearing 2-3 teeth, usually with a multicellular and larger first tooth. Plane lobules, vertically or obliquely oriented, often nearly parallel to the stem, triangular, ligulate or mitten-shaped, with a short basal keel and free lateral margins, sometimes toothed, are found mainly on apical plant regions or intermixed on branches. Perianths obovate, emarginate, and beaked. Leaf cells often have small trigones and intermediate thickenings. Discoidal leaf gemmae are present and abundant.



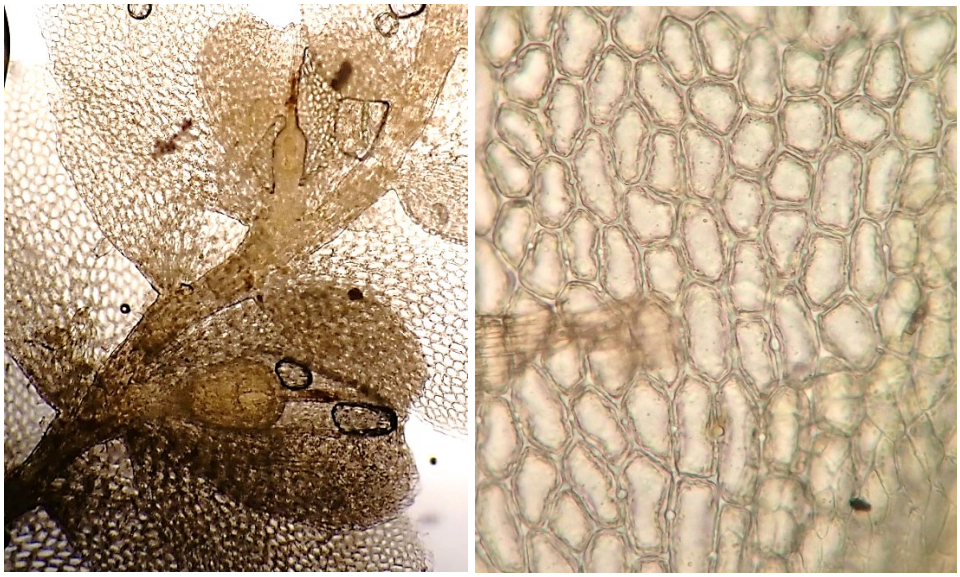
Cololejeunea planissima. Epiphyll on exotic fruit tree, plants closely appressed (left); with hyaline borders and disk-shaped leaf gemmae (right). Kurtistown, Hawaiʻi Island, Freire & Judziewicz 23-24 (BISH).

Portion of plant with saccate lobules, some with large, multicellular first teeth. Note abundant discoidal gemmae on leaf surfaces. Freire & Judziewicz 23-24 (BISH).

Cololejeunea planissima. Left: Branch with intermixed lobules. Kurtistown, Hawai‘i Island, Freire & Judziewicz 23-24 (BISH). Right: Leaf lobes with hyaline border. Note two kinds of lobules; the upper are flat, triangular, and vertical (red arrow); the lower are broad, horizontal, with a long keel (black arrow). Lower Limahuli Valley, Kaua‘i, Flynn 9107 (PTBG), photos by E. J. Judziewicz.

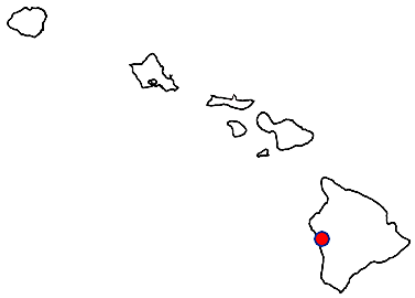


Detail of variable, vertical, plane lobules (arrows). Freire & Judziewicz 23-24 (BISH).



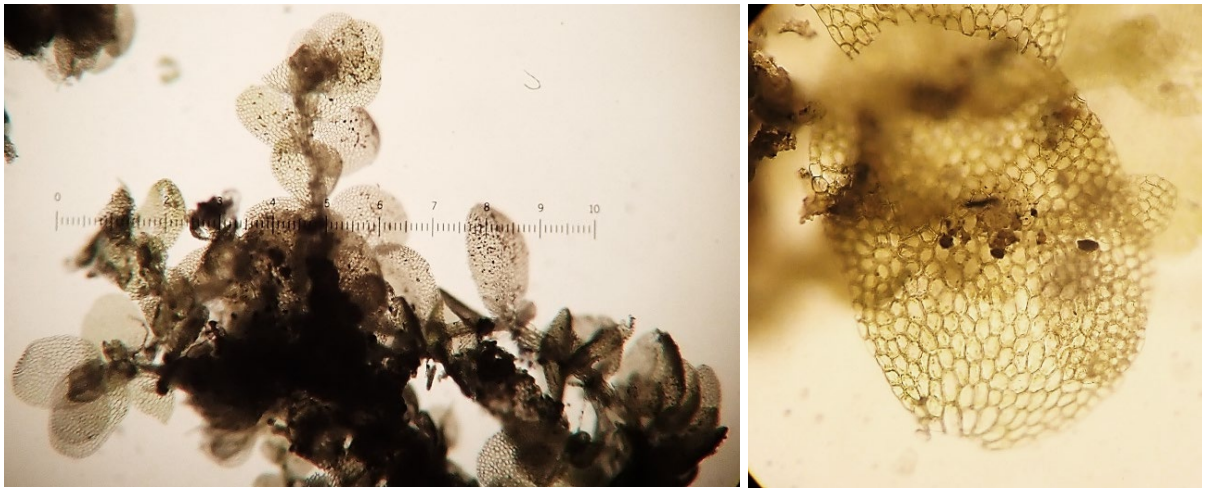
Cololejeunea planissima. Left: Plant with emarginate perianths. Hanakāpīʻai Valley, Kauaʻi, Tangalin 4522a (PTBG), photo by E.J. Judziewicz. Right: Leaf cells with some small trigones and intermediate thickenings. Kurtistown, Hawaiʻi Island, Freire & Judziewicz 23-24 (BISH).

8. *Cololejeunea raduliloba* Steph. **Indigenous.** A tropical Asian and Oceania species ranging east to New Caledonia (Thouvenot et al., 2011: 313) and Fiji (Söderström et al., 2011: 412). Rare; a new report for Hawai‘i. We collected it once, on exotic trees at the Amy B. Greenwell Ethnobotanical Garden in Ka‘awaloa (Captain Cook), el. 1,500 ft., on 9 Oct. 2021 (Freire & Judziewicz 21-916, BISH, all photos below; Judziewicz et al., 2025b). Shevock 48203 (CAS), from 1,500 ft. in Waimea Canyon, Kaua‘i, also appears to pertain to this species; it was collected from a volcanic boulder in filtered light in a dry, mixed non-native forest. It had abundant gemmae.

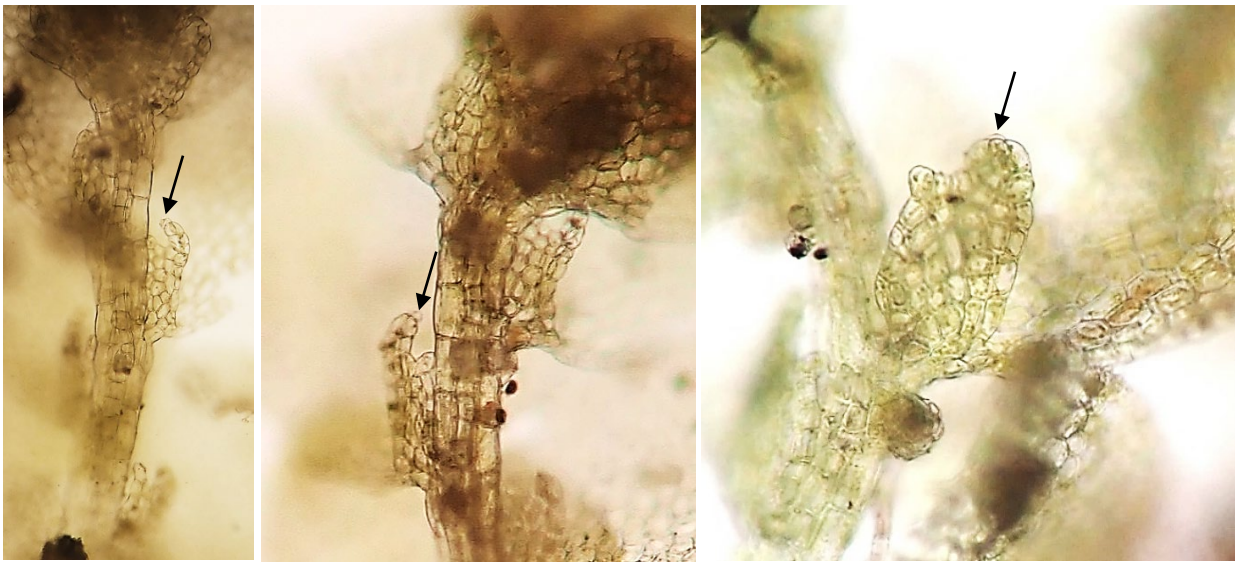


The leaves have small, narrow, erect lobules like those of *C. planissima*, but unlike that species, the leaves lack a hyaline margin. See Tixier (1985). Plants are small, 0.7-0.8(0.9) mm wide, up 1 cm long, green, with fragile stems and a conspicuous hyalodermis. They form small clumps loosely attached to their substrate. Leaves are oval, entire, imbricate, spreading, concave, semi-erect. Lobules are plane, erect, rectangular, narrow, vertically oriented, parallel to the stem, with a short basal keel and free lateral margins; asymmetrically bilobed, variable in shape, with an apical slime papilla topping the larger lobe. Leaf cells have moderately thickened walls, with small triangular trigones and few intermediate thickenings. Keeled perianths and discoid gemmae are abundantly produced. Antheridia are produced on short lateral branches. Rudimentary underleaves are present.

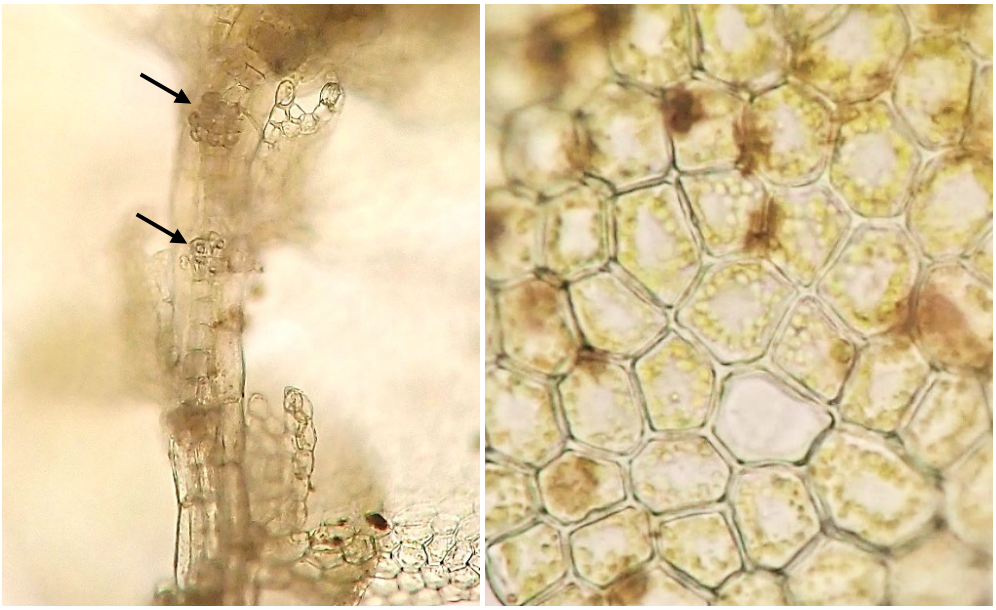
Although maintained as a member of subgenus *Pedinolejeunea* Benedix ex Mizut. according to Söderström et al. (2016: 336), these authors also note (2016: 320) that molecular evidence presented by Yu et al. (2013) instead support its placement in subgenus *Chlorolejeunea* Benedix.



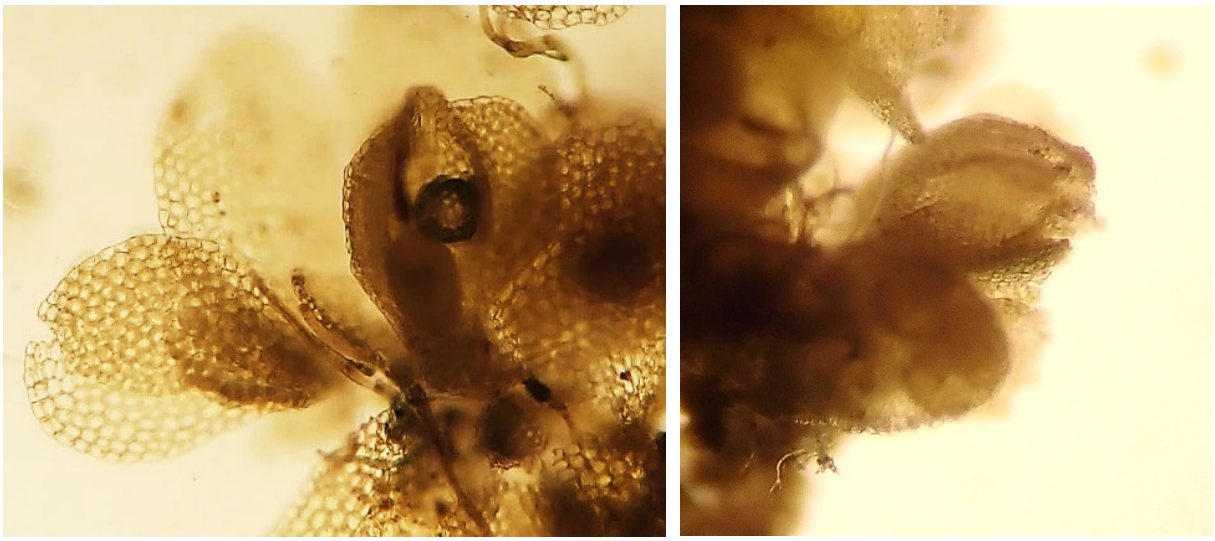
Cololejeunea raduliloba. Left: Plants are small and loosely attached to their substrate. Scale subunits =26 µm. Right: Leaves are oval and concave. Amy B. Greenwell Ethnobotanical Garden, Ka‘awaloa (Captain Cook), Hawai‘i, Freire & Judziewicz 21-916 (BISH).



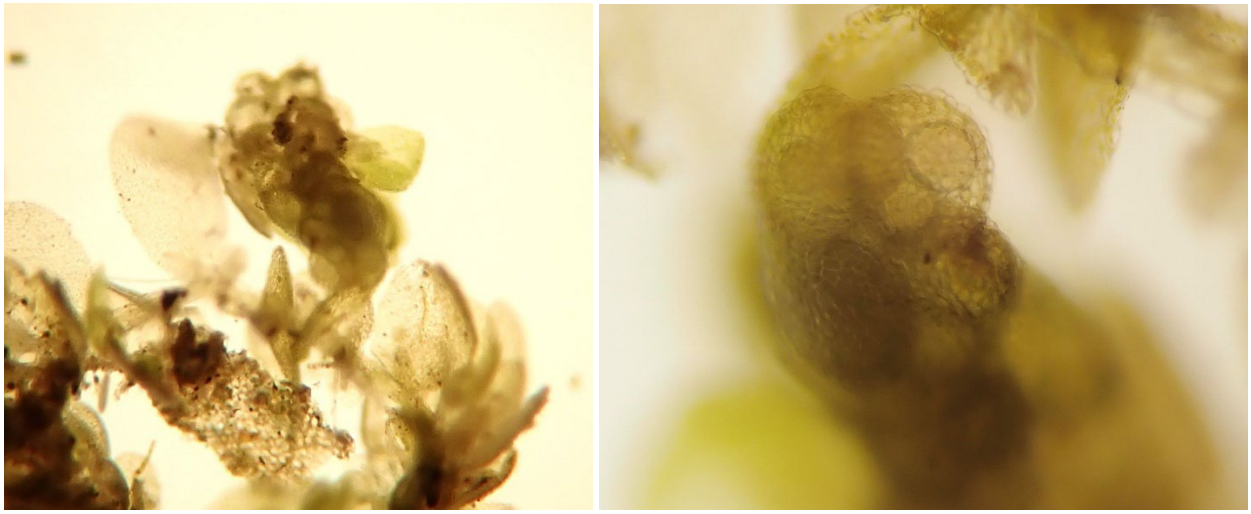
Left and center: Leaf lobules are erect, parallel to the stem, with a short basal keel and free margins. Note bilobed asymetrical apex. The largest lobe is topped by a slime papilla (arrows). Freire & Judziewicz 21-916 (BISH).



Cololejeunea raduliloba. Left: Vestigial underleaves (arrows). Right: Leaf cells have moderately thickened walls with small trigones and few intermediate thickenings. Amy B. Greenwell Ethnobotanical Garden, Ka‘awaloa (Captain Cook), Hawai‘i, Freire & Judziewicz 21-916 (BISH).



Perianths are 4-keeled. Note male branch in right photo. Freire & Judziewicz 21-916 (BISH).



Cololejeunea raduliloba. Left: Male branch with concave bracts bearing antheridia. Right: Detail of antheridia, with more than one per bract. Amy B. Greenwell Ethnobotanical Garden, Kaʻawaloa (Captain Cook), Hawaiʻi, Freire & Judziewicz 21-916 (BISH).

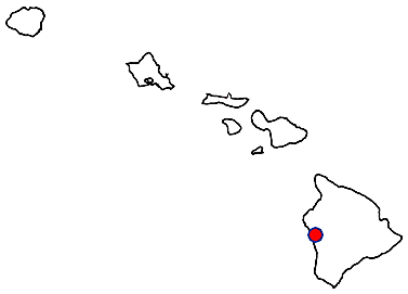
9. *Cololejeunea* species 1:
We collected a population with unique morphology from the Martha Hoverson tract, Mauna Loa Estates, Volcano, Hawai‘i Island (Freire & Judziewicz 23-409a, BISH). The plants have leaves with very short lobes with lobules over ½ the lobe length and almost as broad as the lobe width. The lobes have a border of elongated cells, while the lobules have a 2-celled tooth with an elongated apical cell. We have not been able to identify it so far; it may be a new species and needs thorough study.

The leaves are almost parallel to the stem, with short and narrow lobes. Note mm scale on right.

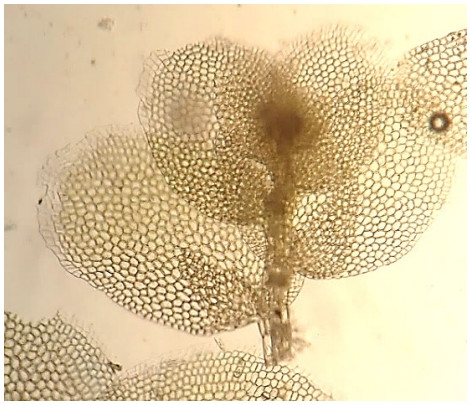
Cololejeunea species 1. Note gemmae at lobe apices, and lobule slightly more than one-half the length of the lobe; arrow indicates two-celled tooth on lobule with top cell rather elongated. Right: Note unicellular slime papilla (arrow) at base of leaf. Volcano, Hawai‘i Island, Freire & Judziewicz 23-409a (BISH).

10. *Cololejeunea* species 2.

This specimen from the Amy B. Greenwell Ethnobotanical Garden in Ka‘awaloa (Captain Cook), el. 1,500 ft., on 9 Oct. 2021, Freire & Judziewicz 21-908 (BISH) is a species unknown to us. It is unique in having hyaline margins, plane and erect lobules, and multicellular 4-6 celled styluses. The latter are not present in *C. planissima* nor in *C. dzumacensis* (see our discussion on next page; according to Tixier, 1985), the other two Hawaiian species with similar lobules.



Plants are 0.9-1.2 mm wide and have hyaline leaf lobe margins; the lobules are plane, triangular, obliquely spreading from the stem, with a short basal keel and free lateral margins with 1 to several teeth, with a slime papilla at the apex. The stylus is multicellular and unistratose or occasionally with paired cells around its middle. Perianths are keeled and truncate, and the male branches have inflated antheridial bracts. The specimen needs thorough study to clarify its identity (and to determine whether it is a novel species).



Leaves have hyaline margins and plane, triangular lobules with free lateral margins and a short basal keel. Freire & Judziewicz 21-908 (BISH).

Lobules may have from 1 to several teeth. Note the multicellular styluses to the right (arrows). Freire & Judziewicz 21-908 (BISH).

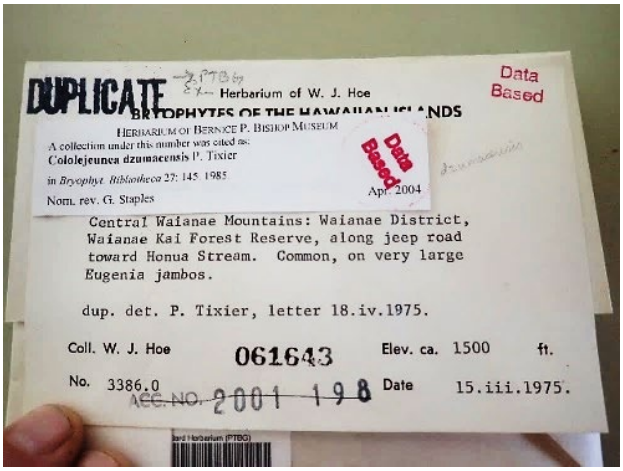
Doubtful record:

Cololejeunea dzumacensis Tixier. **Indigenous.** Rare epiphyll (on *Syzygium jambos*) in the Wai‘anae Range, O‘ahu (1,500-1,700 ft.). A member of the subgenus *Pedinolejeunea* Benedix ex Mizut. (Söderstrom et al., 2016: 333); Söderstrom et al. note that the species is “probably conspecific with *C. lanciloba*, but the type has not been localized”. This species is also found in New Caledonia. Tixier annotated and cited Hoe 3386.0 (PTBG) and Hoe 3398 (BISH) from Hawai‘i in his protologue as specimens studied (Tixier, 1985).

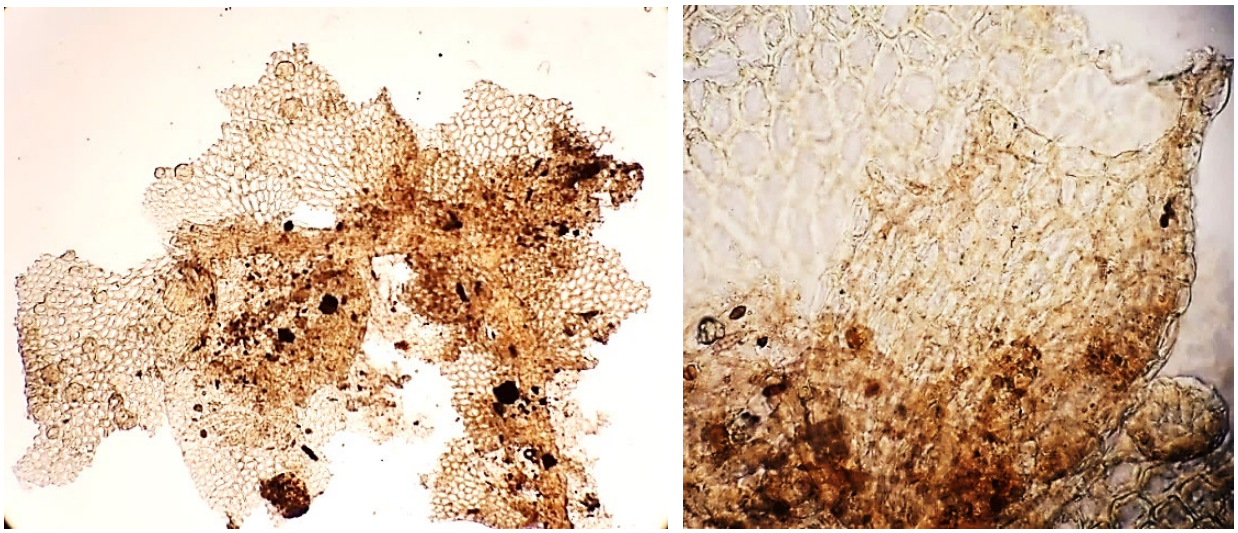
According to Tixier, the leaves of *C. dzumacensis* are orbicular, with narrow and long (ligulate) lobules, attached to the lobe by a very short and basal keel, leaving the rest of the lobule free standing. We studied Hoe 3386.0 (the PTBG duplicate); the specimen is sparse and in poor condition, and these fragments do not follow the description of the species. We found the same issues with Hoe 3386 (BISH) and Hoe 3398 (BISH). None of the plants studied fit Tixier’s drawings or description. Both collection numbers by Hoe are reported by Tixier as specimens studied and are annotated by him (1985).

We did not find any other herbarium collections labelled *C. dzumacensis*, nor collected any specimens that resemble the diagrams and description of Tixier (1985). We question the presence of this species in Hawai‘i and suspect it is erroneously reported. Or is *C. dzumacensis* perhaps conspecific with *C. planissima*?

Hoe 3386.0 (PTBG duplicate):
This specimen was originally determined by Tixier as *C. kapingaensis* in 1975; he later cited this collection number as *C. dzumacensis* (Tixier, 1985). Although the specimen is in poor condition and only fragments were available, we concluded that the lobule morphology does not fit the protologue of *C. dzumacensis* and is likely *C. kapingaensis* as originally identified by Tixier.



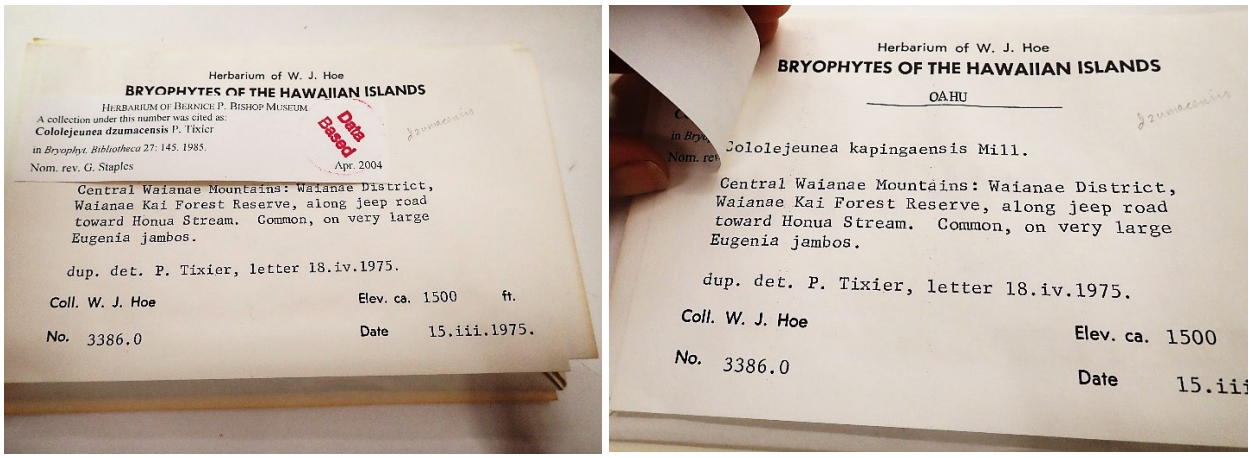
Hoe 3386.0 (PTBG duplicate). The specimen was originally annotated as *C. kapingaensis* by Tixier (letter, 1975). Then it was annotated as *C. dzumacensis* by Staples in 2004, based on the publication by Tixier (1985). We studied fragments around the punch hole to assure it was the same material originally sampled by the collector; but it remains unclear whether Tixier actually examined this duplicate specimen.



Hoe 3386.0 (PTBG duplicate). Left: Fragments of leaves showing discoidal surface gemmae. Right: The lobule morphology fits *C. kapingaensis*.

Hoe 3386 (BISH):

Tixier's determination as *C. kapingaensis* and later citation as *C. dzumazensis* (Tixier, 1985) were applied also to this duplicate deposited at BISH. The material we studied does not fit the description of *C. dzumazensis*, and we do not agree with the original determination either but are aware that Tixier likely did not study this specimen (identified by letter). One can never be sure that the same species end up in all duplicate packets unless they were carefully prepared. Mixed collections could explain discrepancies between these two duplicates. The protologue for *C. kapingaensis* describes lobules with small teeth. The plants studied have a very prominent first lobule tooth. Lobules transition within the same plant from inflated with long side keel to plane, triangular, free lateral-margined lobules with a short bottom keel. Styluses are inconspicuous. Cells have small trigones. Because of the varied lobule morphology, we identify this specimen as *C. planissima*, but the very long and multicellular central tooth seems more prominent on this specimen.



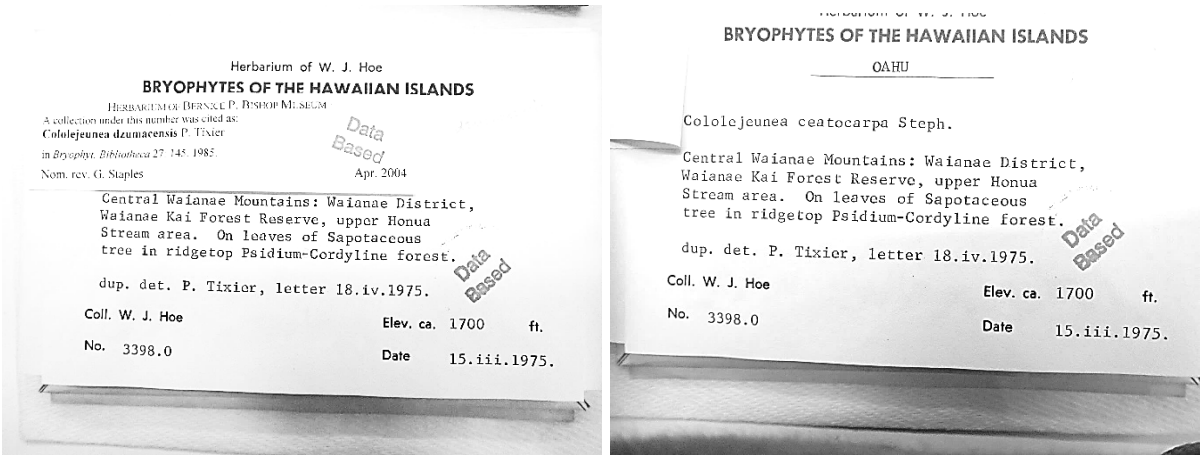
Hoe 3386 (BISH) and the previous (Hoe 3386 PTBG) are duplicates, both originally identified as *C. kapingaensis* and later cited as *C. dzumacensis*. The plants in this specimen have a different morphology than the PTBG duplicate (see below).

Plants with inflated laterally-keeled lobules. Note the very large first lobule tooth and leaf surface gemmae. Hoe 3386 (BISH). Photos by A.V. Freire.

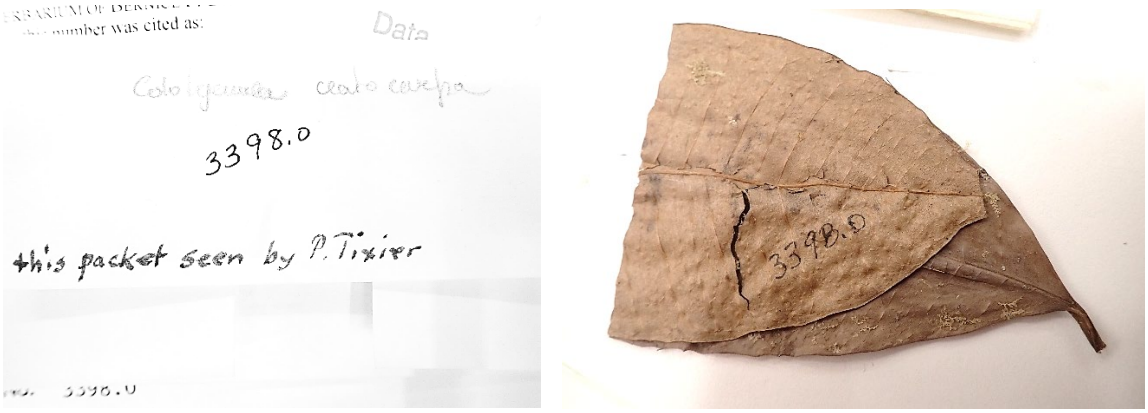
Cololejeunea planissima. Detail of hyaline apical margin of leaves. Note the long and prominent first lobular tooth, Hoe 3386 (BISH). Photos by A.V. Freire.

Cololejeunea planissima. At least some plants have a transition from laterally-keeled, inflated lobules to bottom-keeled, triangular ones. Hoe 3386 (BISH). Photos by A.V. Freire.

Hoe 3398 (BISH):
Hoe 3398 (BISH), was originally determined by Tixier as *C. ceatocarpa* (by letter, 1975) but he later cited it as *C. dzumazensis* (1985). The specimen does not fit the description for *C. dzumazensis* but rather we agree that it is *C. ceatocarpa*.



Hoe 3398 (BISH) was determined as *C. ceatocarpa* by Tixier but was later annotated by Staples as *C. dzumacensis*, based on Tixiers publication from 1985.



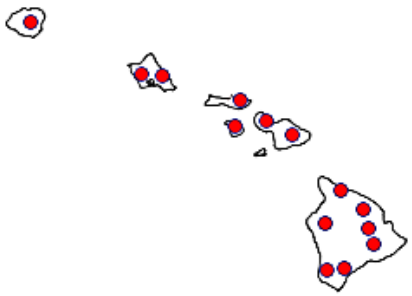
There is evidence to suggest that this specimen was studied by Tixier.

Cololejeunea ceatocarpa Left: Note elliptical leaves, with short insertion, rounded apices and inflated lobules. Right: Note round, single-celled, first lobule tooth and lobe cells with small trigones. Hoe 3398 (BISH). Photos by A.V. Freire.

Colura (Dumort.) Dumort. (Lejeuneaceae)

One species in Hawai‘i. Other Pacific Islands such as Fiji (Söderström et al., 2011) have as many as 14 species; it seems odd that additional species have not yet been recorded in Hawai‘i. 86 species worldwide.

Colura tenuicornis (A. Evans) Steph. **Indigenous.** A member of section *Colura* (Söderström et al., 2016). A proposal has been made by Söderström et al. (2023) to conserve this name over *Lejeunea ceratophora* Nees. *Colura tenuicornis* is a pantropical species found on all major islands (900-5,700 ft.), as a branch epiphyte or epiphyll, sometimes on exotic species like coffee. The leaves have a distinctive “horn”, formed by the narrowed, apical prolongation of the lobule.



Plants are epiphytes, on twigs and leaves, creeping, loosely attached to their substrate, small, and yellow green. Stems thin, translucent, and fragile. Leaves prominent, up to 1 mm long, erect, alternate, distant, complicate bilobed, with very enlarged and inflated lobules that end in a long, narrow, hornlike structure; the base of the lobule is saccate and has an opening. Underleaves one per leaf, deeply bifid, with divergent, elongate, filiform lobes. Leaf cells are conspicuously mamillose, rectangular or polygonal, thin-walled, and lack trigones. Oil bodies are small, elongate, and homogeneous. Perianths turbinate, with five horned keels, these abundantly produced; several per plant are commonly observed. Sporophytes are shortly emergent. The capsules are globose, their walls unpigmented and splitting into four valves. Seta with a thickened ring close to the capsule. Elaters protrude from the dehisced capsules. Gemmae are sometimes present at the tips of the horns.

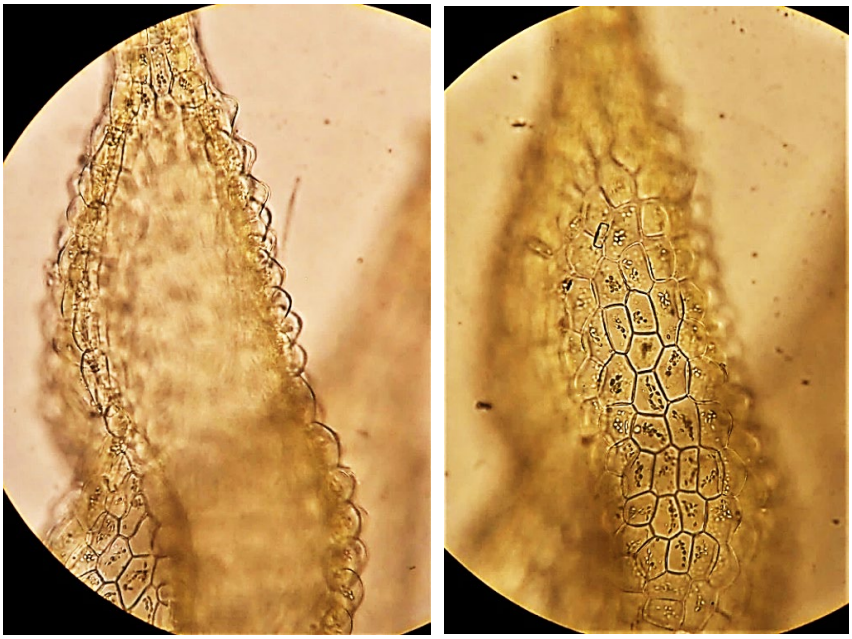
Inflated lobules can act as traps to capture and digest invertebrates. We have videos of a live nematode trapped in a lobule (see photo below); *C. zoophaga* Eb. Fisch., an Asian species, has been shown to be carnivorous (Barthlott et al., 2000) and it is likely that the Hawaiian species is too.

Colura tenuicornis. Left: Yellow green population growing at the base of a coffee leaf. Right: Perianths with five horned keels (pointed by arrows). Volcano, Hawai‘i Island, Freire & Judziewicz 20-497a (BISH).

Left: Plants are small, with elongate leaves up to 1 mm long. Scale = mm. Volcano, Hawai‘i Island, Freire & Judziewicz 22-558a (BISH). Right: Several perianths can be produced per plant. Scale units = 26 µm. Freire & Judziewicz 20-542 (BISH).

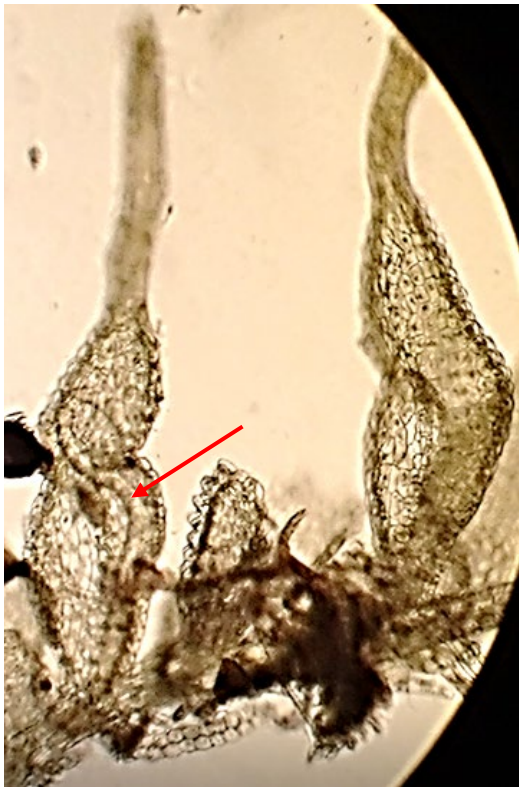
Colura tenuicornis. Shortly emergent sporophyte. The capsule splits into four valves and lacks pigmentation (what we see as spheres within capsules are air bubbles). Note the ring on the seta (center, black arrow) and the elaterophores with elaters (see Pocs & Eggers, 2007) protruding from the capsules (red arrows). Volcano, Hawai‘i Island, Freire & Judziewicz 20-542 (BISH).

Left: Plants have highly modified alternate leaves with inflated, horned-shaped lobules. Right: Underleaves are deeply bifid, with long, divergent, filiform lobes (pointed by arrows). Freire & Judziewicz 22-558a (BISH).



Colura tenuicornis. Inflated pouch of the lobule. Left: cells are mamillose. Right: Cells are thin-walled and without trigones. Volcano, Hawai‘i Island, Freire & Judziewicz 22-558a (BISH).

Inflated, horned lobules are much larger than the leaf lobes (red arrow). Note the opening between lobe and lobule (black arrow). Volcano, Hawai‘i Island, Freire & Judziewicz 22-558a (BISH).



Colura tenuicornis with trapped nematode (red arrow) in saccate lobule. Volcano, Hawai‘i Island, 5 June 2022. Photo by A.V. Freire.

Cryptolophocolea L. Söderstr., Crand.-Stotl., Stotler & Váňa (Lophocoleaceae)

Two species in Hawai‘i. Thirty-five species worldwide.

According to Söderström et al. (2016), Hawaiian species of *Chiloscyphus* may belong to *Cryptolophocolea*, *Lophocolea* or other genera of Lophocoleaceae. Judziewicz & Freire (2023) transferred *Chyloscyphus bartlettii* to *Cryptolophocolea bartlettii*. It seems possible that *Chiloscyphus skottsbergianus* may also be transferred to this genus.

Resembling *Lophocolea* in its 3-angled perianth, and *Chiloscyphus* in its opposite to sub-opposite leaves with confluent underleaves. Connation of the underleaves to adjacent leaves is strong in *Cryptolophocolea*, suggesting the profile of a bat in flight, we suggest the common name “batwort” to refer to species of this genus in Hawai′i. Leaves are slightly to strongly inrolled ventrally, rather than flat, giving plants a “fleshy” look. Leaf cell trigones are present; most species of *Chiloscyphus* and *Lophocolea* have thin-walled leaf cells lacking or with inconspicuous trigones. Perianths are terminal on main stems, keeled, and laciniate. Male branches are also terminal, with concave and imbricate bracts.

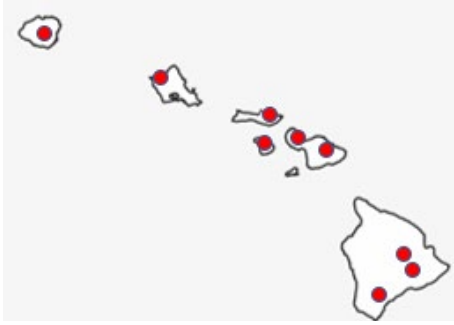
Dan Tucker and Randal Mindell collected an unusual liverwort in Kalōpā Park, Hawai‘i Island, https://www.inaturalist.org/observations/255995034, https://www.inaturalist.org/observations/255955666 16 Dec. 2024, 20.03771°N, 155.43718°W, elev. 633 m, that might be a species of *Cryptolophocolea.* The leaves are succubous, subopposite, and are slightly to considerably bilobed, and each lobe may in turn have one to several teeth. The underleaves are erect, quadrifid, and connate to both adjacent leaves. Leaf trigones appear to be present and small.

1. Leaves broad rectangular; leaf apices obtuse, mainly truncate, with or without teeth; when toothed, with one or two small teeth at the extremes of a nearly flat sinus; underleaves with prominent, divergent, and broadly triangular apical teeth ……..……..... ***C. bartlettii***
1. Leaves narrow ovate-triangular; leaf apices acute, not truncate, always toothed; with two or three long, laciniate teeth usually unequal in shape and size, with a triangular sinus; underleaves with small, slender, nearly parallel, and narrowly triangular lobes ….……..…….....…..… ***C. ciliolata***

Bakalin *et al*. (2022a) cite the pantropical species ***Cryptolophocolea connata*** (Sw.) L. Söderstr. & Váňa as occurring in Hawai‘i, based on Baldwin 66 (4,500 ft.) from West Maui (material not observed by us, housed at the Yale University and University of Michigan Herbaria). However, both the BISH and MU specimens of Baldwin 66 are *Chiloscyphus greenwelliae* (below); leaf trigones are absent.

Baldwin 66 (BISH), *Chiloscyphus greenwelliae*.

1. *Cryptolophocolea bartlettii* (H.A. Mill.) Judz. & A. V. Freire (Judziewicz & Freire 2023c: 166). **Endemic.** Treated as *Chiloscyphus bartlettii* in Staples & Imada (2006). Found on all major islands (3,500-6,160 ft.). An uncommon species, creeping on bark. The best way to recognize this species is by its broadly rectangular leaves with truncate apices that can be rounded, straight or emarginate, often with two small teeth but these may be absent. Trigones are prominent.



Plants are green, creeping, several (9-16 and probably more) mm long, about 2 mm wide. Stems are robust and sparsely branched. Leaves are imbricate, spreading at or nearly at 90˚, opposite to nearly so, rectangular, althouugh some taper slightly towards their apices; lateral margins slightly inroll ventrally, giving the leaves a "fleshy" look; apices variable, truncate, round or slightly emarginate, with two small equal teeth at the extremes of truncate to lunate sinuses; some leaves lack teeth. The underleaves are 1.5-2(2.5) times the stem width, bifid, clearly connate to both adjacent leaves ("bat-like"), with broadly triangular and usually divergent apical lobes (teeth) separated by a triangular sinus; small- to well-developed lateral teeth or "elbows" are present. Median leaf cells isodiametric, with conspicuous trigones. Oil bodies narrowly elliptical, granular. Perianths terminal, truncate, with three laciniate keels (not observed by us). Antheridial branches terminal, with imbricate and concave antheridial bracts (not observed by us).

Miller (1963) illustrated *Lophocolea bartlettii* with a keeled perianth (see below). Keeled perianths are not present in *Chiloscyphus* but are present in *Cryptolophocolea* and *Lophocolea*. Miller (1963) noticed the similarity of this species to *Lophocolea gaudichaudii* (now = *Cryptolophocolea ciliolata*). The presence of trigones; the opposite, inrolled leaves; the underleaves strongly connate to adjacent leaves; and the keeled perianth all support the placement of this species in the genus *Cryptolophocolea*.

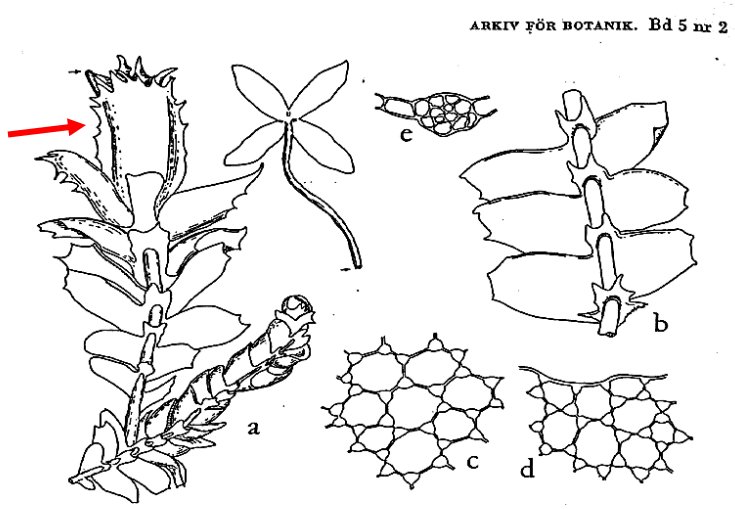


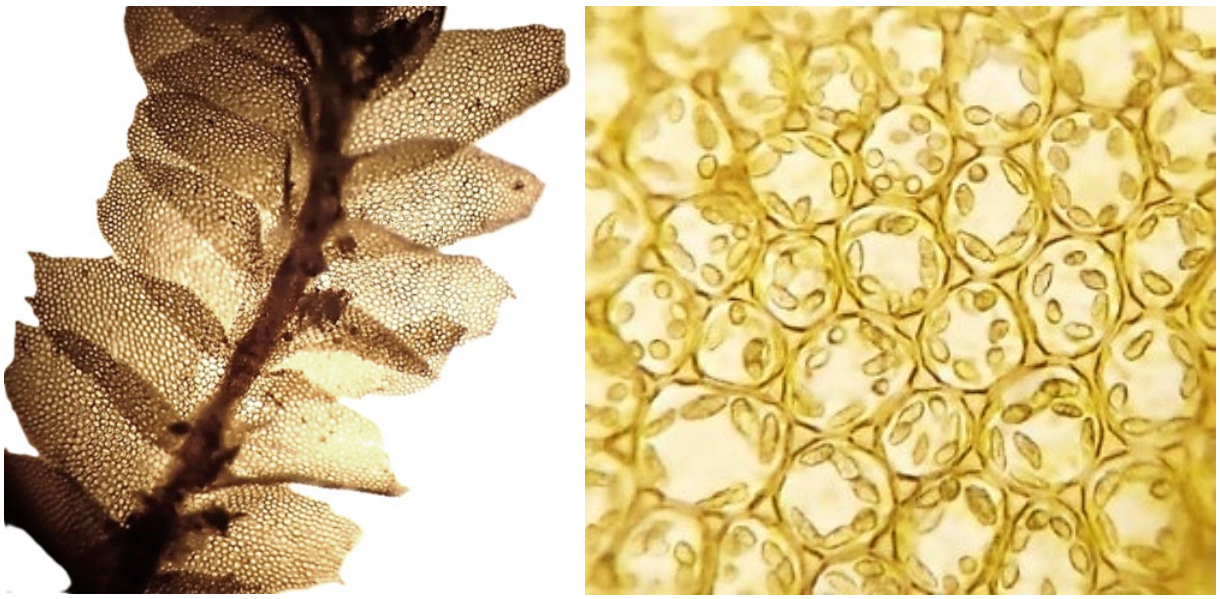
Fig. 6. *Lophocolea bartlettii* Miller n.sp. *a* ventral aspect showing sporophyte, mature perianth, and male branch, × 15. *b* ventral aspect, × 28. *c* median leaf cells, × 240. *d* antical leaf margin cells, × 240. *e* stem, cross-section, × 123. (Drawn from the type.)

Plant to the left with a perianth (red arrow), showing flat, dentate keels and the suggestion of a third one at the back. Note also the irregularly shaped leaf apices, the presence of trigones, and opposite to subopposite leaves, and the underleaves bearing divergent triangular apical teeth and clearly fused to both adjacent leaves. Figure from Miller (Arkiv för Botanik 5(2): 489–531. 1963).

Left: Plant with lateral branching. Right: Branched plant in ventral view. Note opposite, inrolled leaves. Pu‘u Ka‘ala, O‘ahu, Thomas 496 (BISH), photos by Miles K. Thomas, with permission.

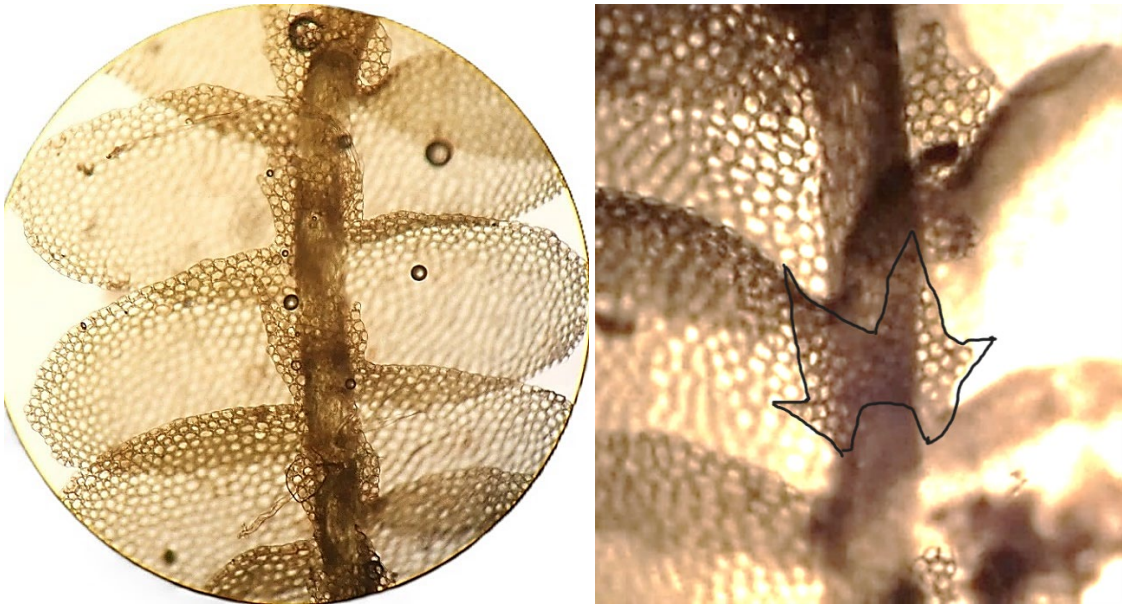
Left: *Cryptolophocolea bartlettii* (arrows; intermixed with *Cuspidatula labrifolia*). Right: Detail of plants with “fleshy” appearance due to the ventrally inrolled leaf margins. Volcano, Hawai‘i Island, Freire & Judziewicz 22-263 (BISH).

Left: Plants are about 2 mm broad and sparsely branched. Right: Note the broadly rectangular, spreading leaves with truncate apices and underleaves mostly with divergent apical teeth. Freire & Judziewicz 22-263 (BISH).



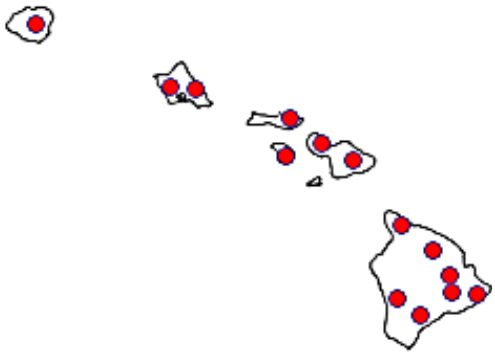
Cryptolophocolea bartlettii. Left: Note variation in leaf apices. Right: Leaf cells are isodiametric, with large trigones and elliptical, granular oil bodies. Volcano, Hawai‘i Island, Freire & Judziewicz 22-263 (BISH).

Plants with laciniate apical leaves and innovations. Left: Leaves mainly rectangular. Right: Detail of plant with slightly inrolled leaves. Freire & Judziewicz 22-263 (BISH).



Cryptolophocolea bartlettii. Left: Underleaves fused to both adjacent leaves. Note the broad sinus that separates the two broad triangular apical lobes and the lateral “elbows”. Alaka'i Preserve, Kaua‘i, Faccenda 3899b (BISH), photos by E.J. Judziewicz. Right: Typical underleaf with divergent, broadly triangular apical lobes and-well developed lateral teeth. Volcano, Hawai‘i, Freire & Judziewicz 22-263 (BISH).

2. *Cryptolophocolea ciliolata* (Nees) L. Söderstr., Crand.-Stotl., Stotl. & Váňa. **Indigenous.** Treated as *Chiloscyphus ciliolatus* by Staples & Imada (2006); see Söderström et al. (2013a: 39) and Judziewicz & Freire (2023c: 167). A variable species found on all major islands (1,500-6,100 ft.); common in wet forests in Hawai‘i Volcanoes National Park, growing on bark or shaded soil embankments. Plants are large, often loosely attached to tree trunks or rock. They have narrow triangular and strongly ventrally inrolled leaves, and small underleaves with erect, parallel, narrow apical lobes.



Plants large, up to 2-3 cm long, 1.5-2.5 mm wide, projecting horizontally from their substrate or creeping. Stems stout, sparsely branched. Leaves imbricate, somewhat sigmoid when dry, projecting at angles close to 45˚, sub-erect, flat or slightly deflexed; opposite, with strongly ventrally inrolled lateral margins, giving them a tubular look; long and narrowly triangular, acute at their apices; they are tipped by two or three unequal, elongate, prominent teeth, separated by a triangular sinus; leaf cells have a bulging aspect, and have prominent trigones. Underleaves are small, slightly broader than the stem, sometimes reflexed, the margins plane or ventrally inrolled, strongly fused to both adjacent leaves; with erect, nearly parallel, small and slender apical lobes, and small lateral protuberances (“elbows”) or slender teeth. Together with the leaves, they form the silhouette of a bat in flight. Perianths ovate, 3-keeled, laciniate.

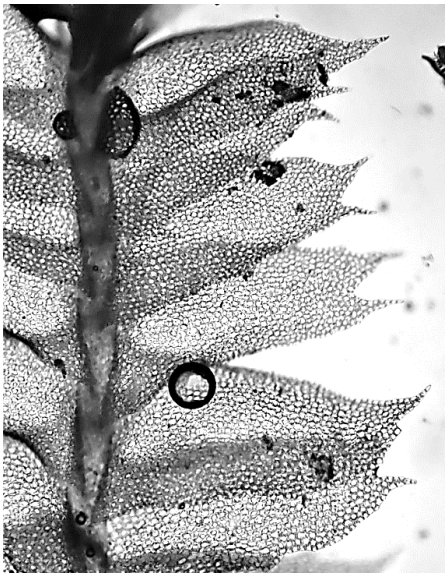
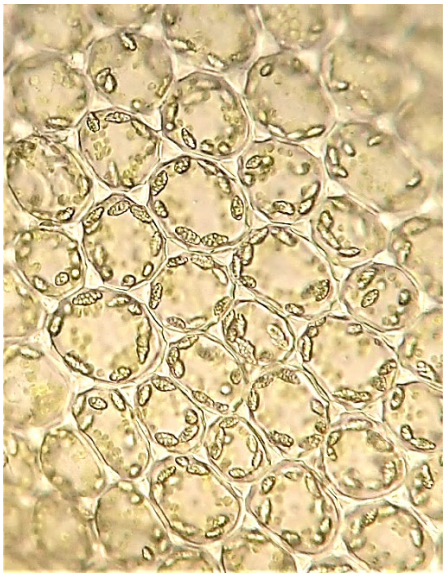
An eastern Asian species, disjunct in Hawai‘i (Sun et al., 2018: 160). Piippo (1985: 154-156) illustrates the variation in this polymorphic species, including figures of two Hawaiian synonyms, *Lophocolea gaudichaudii* Mont. and *L. beecheyana* Taylor.

Cryptolophocolea ciliolata. Note the underleaf with slender apical teeth (arrow), the shape and aspect of leaves and the laciniate gynoecial bracts. Isotype (NY) of the synonym *Lophocolea beecheyana*.

Plants projecting horizontally from their substrate. Note the deflexed leaves. Pu‘u Maka‘ala Natural Area Reserve, Hawai‘i Island. Photo by E.J. Judziewicz.

Cryptolophocolea ciliolata. Plants creeping on bark Note the flat to sub-erect leaves. Volcano, Hawai‘i Island. Photo by E.J. Judziewicz.


Left: Dorsal view of plant. Leaves are strongly tubular and slightly sigmoidal. Note the bulging aspect of the cells. Volcano, Hawai‘i Island, photos by A.V. Freire. Right: Plant with opposite, ovate, triangular leaves. Note the reflexed underleaves (above) and the antheridial branch bearing reflexed bracts (arrow). Niaulani Forest, Hawai‘i Island. Freire & Judziewicz 20-776 (BISH).

Cryptolophocolea ciliolata. Left: Dorsal view showing long, narrow, triangular, acute leaves, with elongate, teeth separated by a “V”-shaped sinus. Right: Leaf cells are isodiametric, with large trigones. Oil bodies are elliptical and coarsely granular. Volcano, Hawai‘i Island, Freire & Judziewicz 22-921 (BISH).

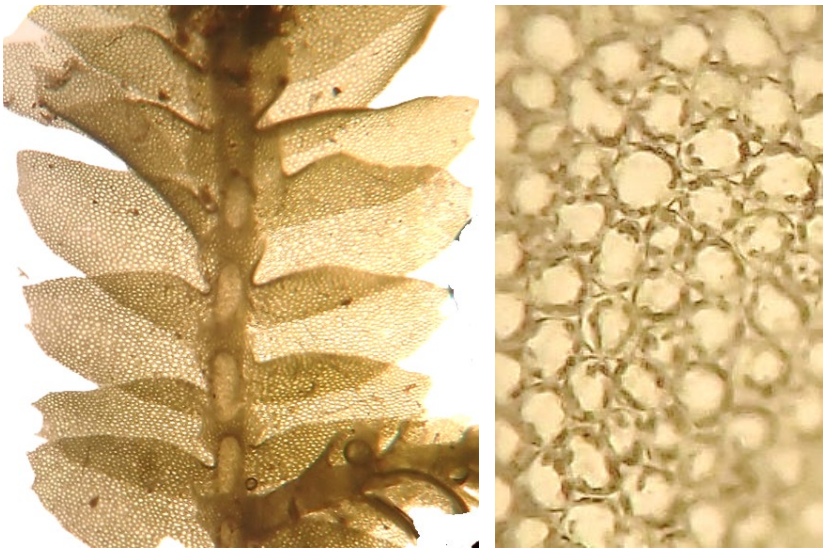
Ventral side of plant showing underleaves clearly fused to leaves on both sides. Note the silhouettes of a series of bats at flight. Niaulani Forest, Hawai‘i Island. Freire & Judziewicz 20-776 (BISH).

Cryptolophocolea ciliolata. Keeled, laciniate, ovate perianths. Note the emergent sporophytes. Ko‘olau Range, O‘ahu, Faccenda 3473 (BISH) (https://www.inaturalist.org/observations/221484677), with permission.

Cryptolophocolea aff. ***ciliolata*** (Nees) L. Söderstr., Crand.-Stotl., Stotl. & Váňa

A 2024 collection by Zach Pezzillo from the back of Waihoʻi Valley, East Maui, at ca 3,600 ft (Pezzillo 765, BISH), is puzzling and needs more study. It has leaves similar to *C. ciliolata,* but the leaf cells have less conspicuous trigones. The underleaves are mainly as in *C. ciliolata* but some are as in *C. bartlettii*. The perianths are large, inflated, globose, urn-like, and winged, but not keeled, unlike descriptions for the two species mentioned.

Left: Abundant large (3 mm long) globose, unkeeled perianths; right, plants with mm scale. Photos by E.J. Judziewicz.



Cryptolophocolea aff. *ciliolata.* Left: Opposite, asymmetrically bifid leaves connate to small quadrifid underleaves. Right: Median leaf cells are isodiametric, with small leaf trigones. Zach Pezzillo 765, Waihoʻi Valley, East Maui, ca 3,600 ft (BISH). Photos by E.J. Judziewicz.

Left: Terminal perianth (dry plant). Center: Detail of perianth showing 2 of the 3 laciniate wings and the truncate and laciniate mouth. Right: Antheridial branch with imbricate, reflexed bracts. Zach Pezzillo 765, Waihoʻi Valley, East Maui, ca 3,600 ft (BISH). Left and center photos by A.V. Freire; right photo by E.J. Judziewicz.

Cryptolophocolea ciliolata. Population with terminal, globose, winged, wide-mouthed, and laciniate perianths. This population seems to belong to the same species as the above and may represent the same collection. Photo by Z. Pezzillo, East Maui (https://www.inaturalist.org/observations/202371433), with permission.

Cuspidatula Steph. (Adelanthaceae)

A genus of three species (eight species worldwide) of montane forests on all major islands. Plants are large, usually reddish, but sometimes green when growing in the shade. Leaves are succubous, entire, commonly imbricate, prostrate to patent to erect, with round apices and evident trigones. Underleaves are typically absent, although tiny ones (soon aborted) can be present near the plant apex. The perianths are ciliate, with truncate mouths. The genus was treated as *Jamesoniella* by Staples & Imada (2006), and it is possible that Hawaiian members of this genus may be sunk into *Syzygiella* based on DNA evidence (Lee & S.R. Gradstein, 2021: 52); for example, Feldberg et al. (2010) found the placement of *Cuspidatula robusta* to be uncertain.

1. Leaves round, strongly concave, pouched or cupped ……..…… ***C. labrifolia***
1. Leaves longer than wide, plane to somewhat concave, not strongly pouched or cupped ……. **2**
   2. Leaves narrowly oblong, with parallel margins, at least twice as long as wide ..……..... ……...……***Jamesoniella coriacea****
   2. Leaves ovate, broader in their lower half, less than twice as long as broad ….....…… ***C. robusta***

* - To be transferred to *Cuspidatula*.

Grolle (1971), reduced *Jamesoniella labrifolia* (now *Cuspidatula labrifolia*) and *Jungermannia coriacea* to *Jamesoniella robusta.* We disagree with the reduction of both *C. labrifolia* and *J. coriacea*, as discussed below.

Cuspidatula populations can be strikingly luxuriant, as exemplified here by *C. robusta*. Summit of Hāʻupu Range, Kauaʻi, Flynn 9852 (PTBG). Photo courtesy of the National Tropical Botanical Garden/Tim Flynn.

1. ***Jamesoniella coriacea*** (Austin) Steph. **Basionym:** ***Jungermannia coriacea*** Austin, Proceedings of the Academy of Natural Sciences of Philadelphia 21(4): 219. 1869. To be transferred to *Cuspidatula*. **Endemic.** This species is found in montane forests (4,000-5,500 ft.) on Kauaʻi, Maui and Hawaiʻi Island. It has flat, rigid leaves, that are clearly longer than wide, with parallel margins and rounded apices; they are inserted parallel to each other. Evident trigones are present.

Grolle (1971) and Miller et al. (1983), placed *Jungermannia coriacea* in the synonymy of *Jamesoniella robusta* (*Cuspidatula robusta*). In later, unpublished work, H.A Miller recognized *Jamesoniella coriacea* as a discrete species, and we agree with his disposition. In his protolog for *Jungermannia coriacea*, Austin (1869) describes plants with firm, thick leaves, and we have seen Hawaiian populations with rigid-(coriaceous) looking leaves, at least twice as long as broad and with parallel margins. In contrast, *C. robusta* has flaccid leaves that are shorter, ovate, and lack parallel margins.

Plants are blue-green, olive-green or red; loosely attached to their substrate, prostrate to procumbent or ascending, 1.5-2 cm long, 3-3.5 mm broad. Stems are firm and frequently branched. Leaves are entire, succubous, squarrose, parallel to each other, distant to contiguous, or slightly imbricate, flat and prostrate, oblong-rectangular, with parallel margins and a rounded, obtuse apex; they are twice (or slightly more than twice) as long as broad, 1-1.5 mm long and about 0.5 mm broad; and are dorsally decurrent with the stem midline. Cells are elongate to isodiametric, 25-37 µm long by 16-22 µm wide, verrucose, with triangular trigones and large, elongate, granular oil bodies, five per cell. The leaf margins are bordered by smaller quadrate cells with thickened outer walls. Underleaves are absent.

Jamesoniella coriacea. In situ photos, Waiʻaleʻale, 5,200 ft., Kauaʻi, Kevin Faccenda, with permission: https://www.inaturalist.org/observations/201454992.

https://www.inaturalist.org/observations/254804144. Kaua‘i, Kevin Faccenda, with permission.

https://www.inaturalist.org/observations/254837229. Kaua‘i, Kevin Faccenda, with permission.

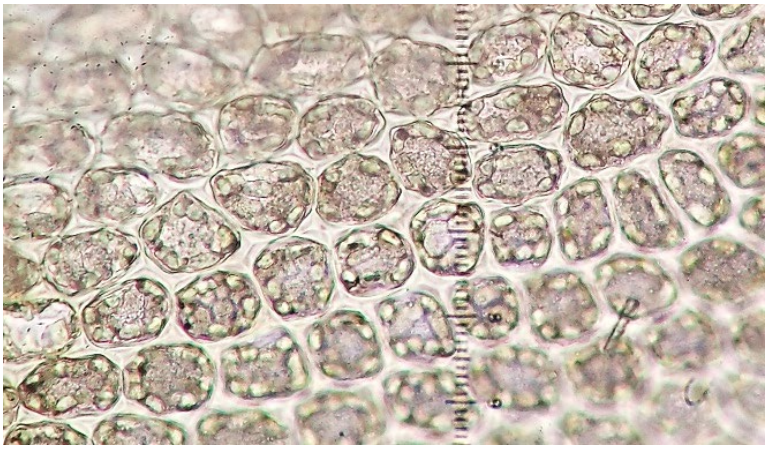
Jamesoniella coriacea. https://www.inaturalist.org/observations/202249940, Maui, Zach Pezzillo, with permission.

Plants can be blue-green, prostrate, with flat leaves that are much longer than wide, and rounded apices. Freire & Judziewicz 21-1022 (BISH).

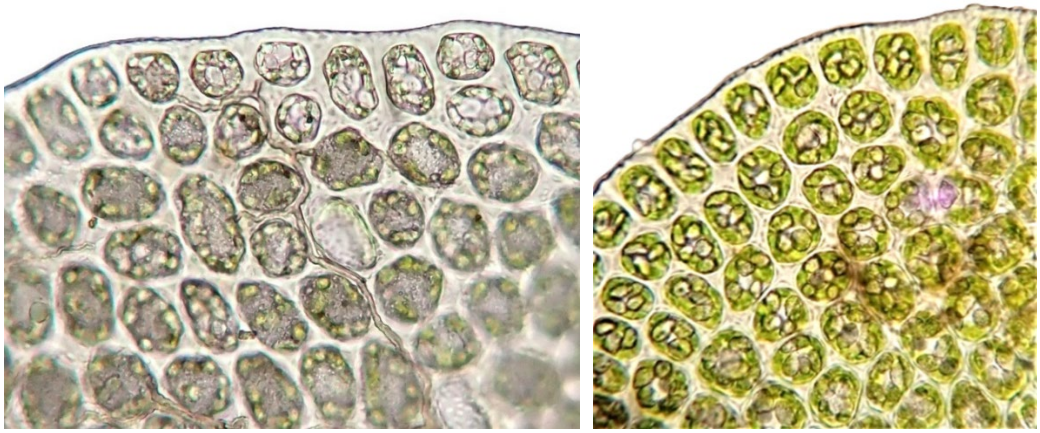
Leaves are oblong-rectangular, with rounded apices and long dorsal decurrency. Scales in mm. Freire & Judziewicz 21-1022 (BISH).

Jamesoniella coriacea. Leaves are contiguous to slightly overlapping. Volcano, Hawai‘i Island, Freire & Judziewicz 21-1022 (BISH).

Leaves are oblong-rectangular, with parallel margins. They are dorsally decurrent (left). Hawai‘i Island, Freire & Judziewicz 21-1022 (BISH).

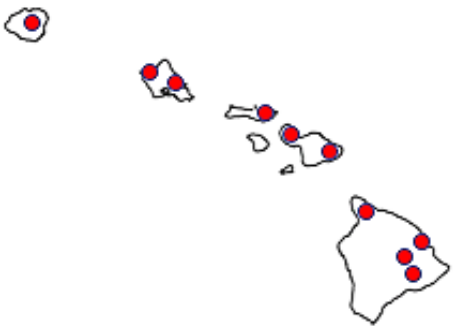


Median leaf cells (horizontally oriented). Scale units = 2.5 µm. Hawai‘i Island, Freire & Judziewicz 21-1022 (BISH).



Jamesoniella coriacea. Note verrucose leaf surface and thickened outer walls of marginal cells. Oil bodies are elliptical and granular (right). Volcano, Hawai‘i Island, Freire & Judziewicz 21-1022 (BISH).

2. *Cuspidatula labrifolia* (H.A. Mill.) A.V. Freire & Judz. **Endemic.** Judziewicz & Freire (2023c: 159); treated as *Jamesoniella labrifolia* by Staples & Imada (2006). The type locality is Mile 15 [elev. ca 3,000-4,000 ft.] on the Saddle Road on Hawai‘i Island (Miller, 1967); found on all major islands except Lāna‘i (900-8,500 ft.). Growing on tree trunks in montane rain forest. The plants are large and showy, red or usually with at least some red coloration. They are recognized by their rounded, imbricate, erect, and markedly pouched or concave leaves. Leaf cells have large, often confluent trigones.



Populations form dense mats on bark and are loosely attached; they are erect, projecting from their substrate, or occasionally appressed. Plants are large, 2 or more cm long and about 3 mm wide; they usually have at least some red coloration, but can also range from “apple-green”, yellow-green, brownish red, to orange red. Stems are stout, 0.45 mm wide, obscured by the leaves; they are scarcely branched. Leaves densely imbricate, erect, somewhat concave (pouched or cupped), round (sometimes asymmetrical), large, 1.7-2 mm long, slightly longer than broad, decurrent, with a long insertion line of almost 180˚ around the stem. Underleaves are sometimes present in the plant’s apical region; these are minute, deeply bifid, with narrow and acuminate lobes. Leaf cells elongate, irregular in shape, (30)40-45 µm long by 20-25 µm wide, with large and often confluent trigones. Marginal cells with a thick outer wall. Oil bodies are large, 4-6 per cell, gray, granular, and elliptical. Perianths are often present, abundant, dorsal, on main stems or branches, often several per plant; they are elongated, tubular, pleated, keeled, with a ciliate mouth that can be constricted, or broad and truncate; the cilia are laciniate, with broad laminas 2-3 cells long that branch into lateral teeth of 1 to a few cells in a single row. Perianths are protected by laciniate bracts but are clearly emergent. No males were observed.

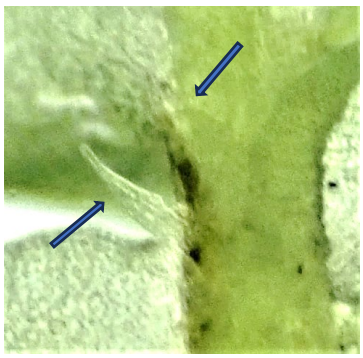
At first glance this species might be mistaken for *Pleurozia conchifolia,* but the leaves are merely cupped, not divided into a small sac-like dorsal lobe and larger ventral lobe as in *Pleurozia*. Minute, bifid, oblique underleaves can be present near the stem apex. Another superficially similar species is *Chiloscyphus laceratus*, but the large, disk-shaped, laciniate underleaves of that species are absent in *Cuspidatula labrifolia.*

Grolle (1971) synonymized *Jamesoniella labrifolia* with *Jamesoniella robusta*. He did not study the type for *J. labrifolia* but instead based this reduction on a specimen (not available to us) identified by Miller as *C. labrifolia*. Based on our study of this species, we do not accept this reduction and choose to recognize it as an endemic Hawaiian species.

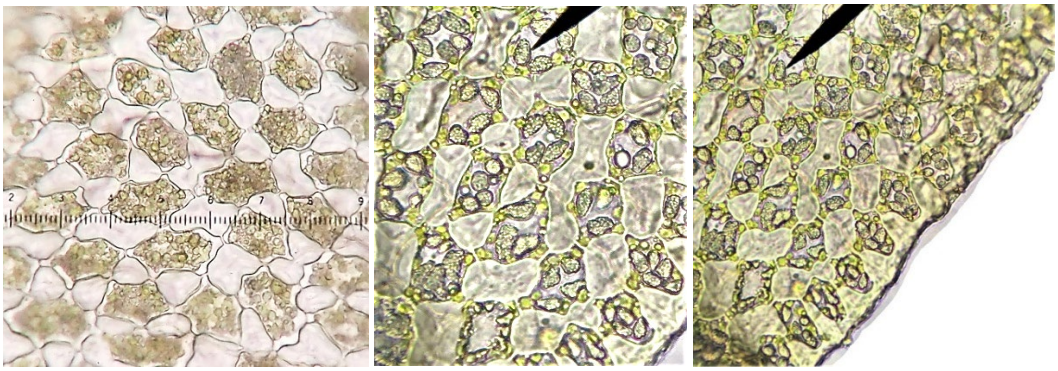
Cuspidatula labrifolia. Example of a green population. Occasional plants have brown to orange highlights. Volcano, Hawai‘i Island. Photos by E.J. Judziewicz.

Cuspidatula labrifolia. Dense population on bark of *Metrosideros polymorpha*. Plants grow either appressed or erect. Volcano, Hawai‘i Island, Freire & Judziewicz 23-449 (BISH). Right: Detail of plants with erect and strongly concave leaves; note brownish-green coloration; note *C. robusta*-like undulate leaves. Volcano, Hawai‘i Island. Freire & Judziewicz 20-509 (BISH).

Left: Leaf profile. They are very concave, imbricate, and decurrent. Center and right: Round, cupped leaves. Hawai‘i Island, Freire & Judziewicz 23-539 (BISH).

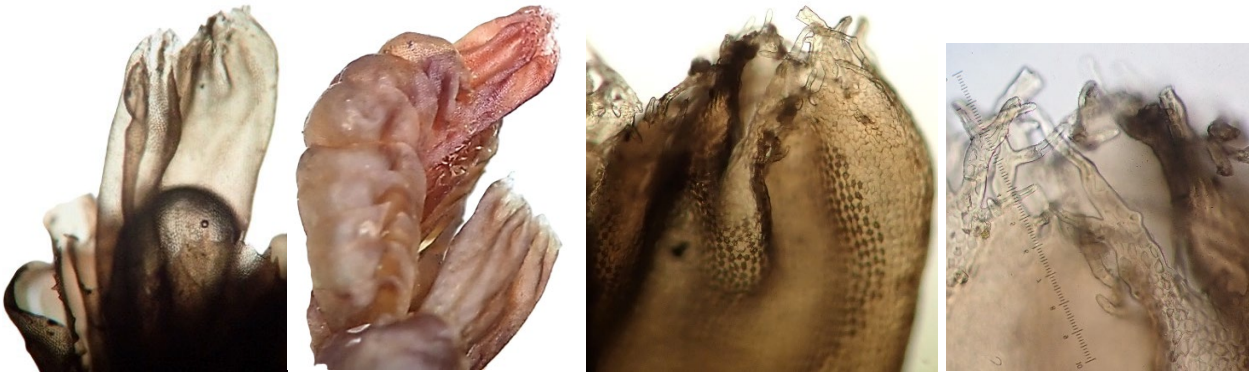


Cuspidatula labrifolia. Right: Note minute bifid underleaves (arrows point to lobes) occasionally present on some plants. Hawai‘i Island, Freire & Judziewicz 23-371 (BISH).



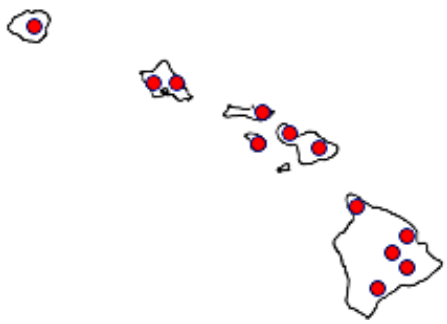
Leaf cells with very large, often confluent trigones. Note the irregular cell shape. Left: Scale units = 2.5 µm. Hawai‘i Island, Freire & Judziewicz 23-539 (BISH). Center: Live leaf cells with large, elliptical and granular oil bodies. Right: Marginal cells with a thick outer wall. Center and Right: Volcano, Hawai‘i Island. Freire & Judziewicz 20-509 (BISH).

Left: Plant dorsal view; note the keeled perianth, Kōnāhuanui, Koʻolau Range, Oʻahu, photo by Miles K. Thomas, with permission. Right: Plant with numerous dorsal perianths. Scale in mm. Hawai‘i Island, Freire & Judziewicz 23-539 (BISH).



Cuspidatula labrifolia. Left: Perianth with keels and laciniate bracts. First central image: Ciliate perianths with broad, truncate mouths. The last two pictures show details of the large, laciniate cilia (perhaps more correctly referred to as scales). Hawai‘i Island, Freire & Judziewicz 23-539 (BISH).

3. *Cuspidatula robusta* (Austin) Váňa & L. Söderström. **Indigenous.** Treated as *Jamesoniella robusta* in Staples & Imada (2006); see Váňa et al. (2013a: 36) and Judziewicz & Freire (2023c: 159). In Hawai‘i, we may be dealing with a species complex (see comments below). This is one of the largest and showiest leafy liverworts in Hawai‘i; it is found on all major islands (900-7,500 ft.), and on other islands in Oceania. In Hawai‘i Volcanoes National Park it is found in wet forests along the Escape Road and in the East Rift Zone Kīpuka; it is also found in the ‘Ōla‘a Tract.



It grows mainly as an epiphyte on ‘ōhi‘a bark, usually 1-2 meters (but occasionally up to 6 meters) above the ground. Populations form dense mats on tree trunks. The stems either creep closely appressed to bark or spread and droop from the tree trunk; sometimes plants can be erect. Plants are up to 4 cm long and about 3-4 mm wide; usually reddish-orange but can also be apple-green to yellow green in shaded places. Stems are strong and sparingly branched, about 0.3 mm in diameter. Leaves are succubous, imbricate, horizontal to patent or sometimes erect, entire, ligulate, less than twice longer than wide, (1.4)1.6-2 mm long x (1)1.5-1.9 mm broad (broadest on lower half), tapering towards their apex, rounded at the tip, and plane to slightly concave; slightly decurrent dorsally, with a short, curved insertion ventrally. Verrucose. Median leaf cells 35-47 µm long x 20-23 µm wide, with large triangular trigones. Oil bodies are elliptical, granular and gray, 6-8 per cell. Leaf marginal cells form a border, sometimes clearly hyaline, of small quadrate cells with thickened outer walls 8-9 µm thick, about 1/3-1/2 the length of marginal cells' lumen. Perianths are dorsal, smooth, furrowed close to their apex, with a truncate mouth that bears numerous cilia; they can be long tubular (up to 3 mm long) to short and globular (about 1.3-1.5 mm long). The protective bracts of the long tubular perianths are bifid; each half is lobate, and each lobe tipped by a prominent spine; for globular perianths, they are bilobed, each lobe bifid, with acute lobes (but many more perianths need to be studied to check for constancy of this correlation).

The plants have a strong peppery or turpentine-like odor when wet.

Plants size varies greatly in this species. Small plants could be mistaken for *Odontoschisma denudatum* subsp. *denudatum* but lack the reduced-leafy branches tipped with gemmae of the latter genus. The presence of two different perianth and associated bract morphologies may mean there are at least two species. Kaua‘i collections consist of more robust plants, of these we only studied sterile plants; Perianths need to be studied.

Some Hawaiian populations of *C. robusta* have evidently undulate leaves, for example from Kaua‘i (Kevin Faccenda, https://www.inaturalist.org/observations/254877299) and O'ahu (Mike Ross, https://www.inaturalist.org/observations/255936184). These populations resemble the Aoteoroa/New Zealand endemic *Cuspidatula kirkii* (Steph.) K. Feldberg, Váňa, Hentschel & Heinrichs, based on the description and drawing in Engel & Glenny (2019: 716-717) as well as images posted on iNaturalist, some verified by M.A. Renner and D. Glenny (https://www.inaturalist.org/taxa/1010954-Cuspidatula-kirkii). If one took an inclusive view and lumped these two taxa, *C. robusta* (Austin, 1869) is the older name and would have priority.

In summary, we regard *C. robusta* as a complex that needs to be elucidated with careful morphological work and DNA studies.

Orange-red population, creeping on tree bark. Volcano, Hawai‘i Island, Freire & Judziewicz 20-524 (BISH).

Cuspidatula robusta. Left: Summit of Hā‘upu Range, Kaua‘i, Flynn 9852 (PTBG). Photo courtesy of the National Tropical Botanical Garden/Tim Flynn. Right: Detail of creeping plants with patent leaves. Volcano, Hawai‘i Island. Photo by E.J. Judziewicz.

Plant with erect and imbricate leaves. Note the round apices and brownish-red coloration of the older leaves. O‘ahu, Miles K. Thomas, with permission.

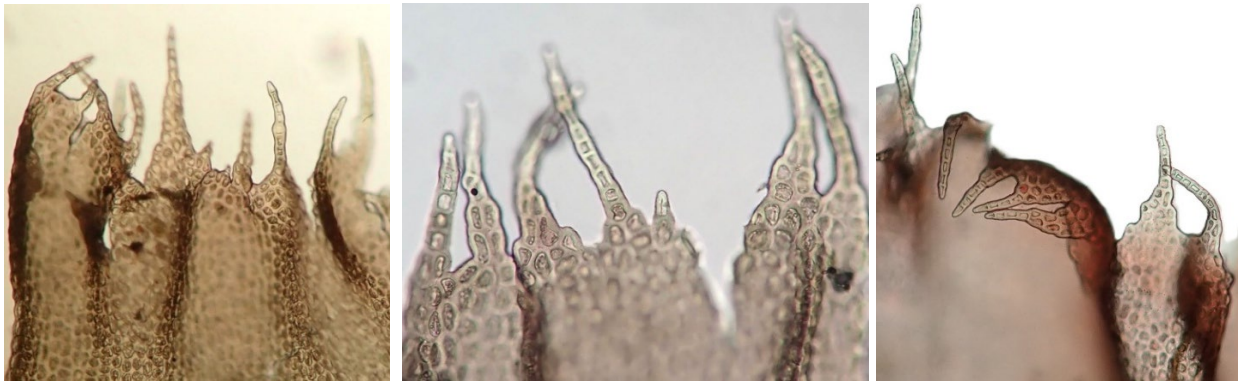
Scales in mm. Pictures 1 and 2: Hawai‘i Island, Freire & Judziewicz 23-445 (BISH). Pictures 3 and 4 (of the same plant): Kaua‘i, Flynn 9147 (PTBG). Photos by A.V. Freire.

Cuspidatula robusta. Plant, dorsal view. Leaves have a long insertion to or beyond the stem midline. Hawai‘i Island, Freire & Judziewicz 23-445 (BISH).

Leaves are ligulate, broadest at the base, and slightly longer than broad. Hawai‘i Island, Freire & Judziewicz 23-445 (BISH).

Cuspidatula robusta. Perianths. Left, above: Dry plant; perianth with closed, constricted mouth. Center, above: Dry plant; perianth with open, truncate mouth. Hawai‘i Island, Freire & Judziewicz 23-378 (BISH). Scales in mm. Right, above: Note the deeply bilobed bract immediately below the perianth. Below: Detail of bract with 4 apical lobes each tipped by a spine. Photos 1, 3 and 4: Hawai‘i Island, Freire & Judziewicz 23-445 (BISH).

Perianths can be short and globose. The ones in these images housed archegonia, with no evidence of sporophytes. Scale in mm. Bottom right: Perianth bracts are bilobed; in turn, each lobe is also bilobed - so in this photo we see one of the bilobed lobes. Hawai‘i Island, Freire & Judziewicz 23-445 (BISH).



Cuspidatula robusta. Detail of cilia at the mouth of the perianth. Left and center: Perianths with long, tubular morphology. Right: Types on the globular perianth morphology. No difference is found between the two perianth types. Hawai‘i Island, Freire & Judziewicz 23-445 (BISH).

Leaves have a border (see below) and a vittae-like region of enlarged cells at the center of the basal region. Hawai‘i Island, Freire & Judziewicz 23-445 (BISH).

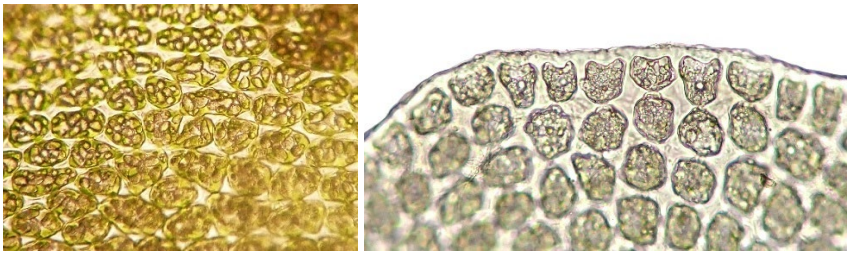
Leaf cells with large trigones. The oil bodies are long-elliptical and granular. Left: Hawai‘i Island, Freire & Judziewicz 23-445 (BISH). Right: Volcano, Hawai‘i Island, Freire & Judziewicz 22-920.

Cuspidatula robusta. Marginal leaf cells with thickened outer walls. Scale units = 2.5 µm. Hawai‘i Island, Freire & Judziewicz 23-445 (BISH).

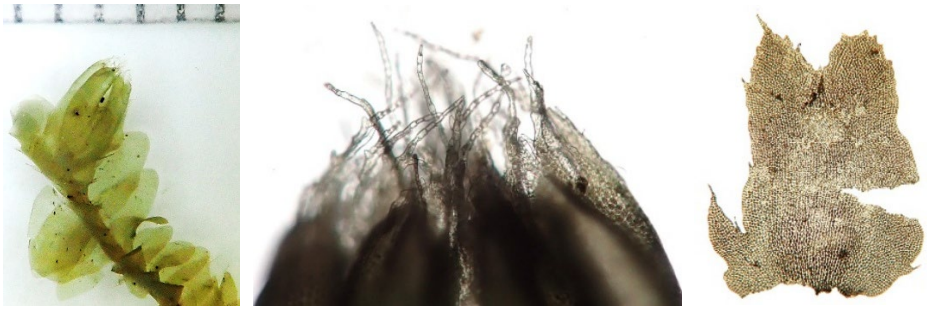
***Cuspidatula* species.** Following are images of a population growing in deep shade, from Volcano, Hawai‘i, Freire & Judziewicz 22-919 (BISH). The plants are large, green, flexuous, fragile-looking, procumbent, with patent to prostrate, decurrent leaves, with a curved dorsal insertion; the perianth bracts are bifid and laciniate. Could this be a variant of *Jamesoniella coriacea*?

Plants are loosely attached and hang from tree trunks. Scales in mm. Left: Freire & Judziewicz 22-920 (BISH).

Left: Leaves spreading, flat and elongate. Center and right: Leaves with decurrent insertion on dorsal side. Leaves tapering towards the apex, longer than broad. Note leaf insertion to beyond the stem midline.



Cell walls with triangular trigones and cells with large, elliptical, granular oil bodies. Outer wall of marginal cells is about 1/3 as thick as marginal cells are long.



Cuspidatula robusta. Perianth is furrowed, with a ciliate mouth. Perianth bracts lobed and laciniate.

Cylindrocolea R.M. Schust. (Cephaloziellaceae)

One or two species in Hawai‘i. 19 species worldwide.

Minute, creeping leafy liverworts less than 1 mm wide. The leaves are slightly obliquely (almost horizontally) inserted, and their leaf bases are noticeably constricted. The leaf insertion is short and the lobes are separated by a narrow sinus. The leaf cells are large and thin-walled. Although uncharacteristic for this genus, gemmae are sometimes present. Bakalin et al. (2024: 11) present molecular evidence that *Cephaloziella kiaeri* and *C. microphylla* (related to our *Cephaloziella* “sp. 1”) should be transferred to *Cylindrocolea*; the latter combination has not yet been made.

It is possible that we are dealing with more than one species under our concept of *C. planifolia* (green plants). A much more detailed study is needed. Randal Mindell’s record from the Saddle area (5,750 ft.) of Hawai‘i Island (https://www.inaturalist.org/observations/257671540) may also pertain to this genus.

1. Plants green; both leaf lobes with pointed apices, the cells not bulging ……..……..... ***C. planifolia***
1. Plants pinkish; one leaf lobe truncate, the other with pointed apex, the cells bulging... ***C.* aff. *planifolia***

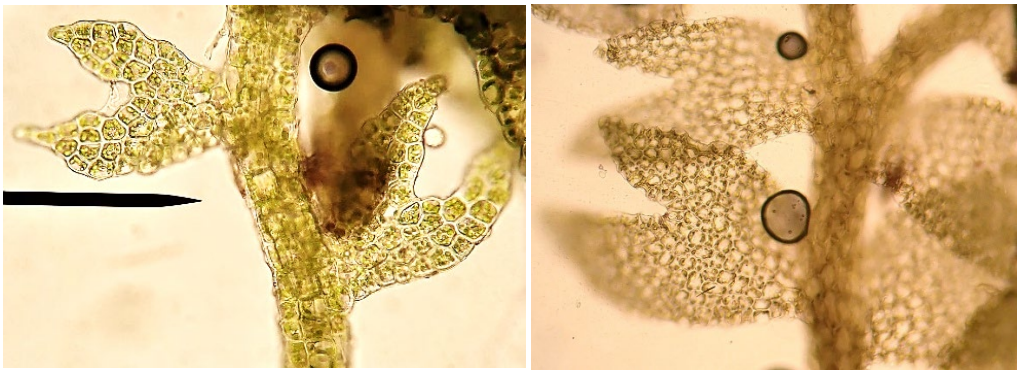
1. *Cylindrocolea planifolia* (Steph.) R.M. Schust. **Indigenous.** First report for Hawai‘i: Judziewicz & Freire (2023c: 161). A member of subgenus *Cylindrocolea* sect. *Cylindrocolea* (Söderström et al., 2016). This bright green, dry lowland to montane mesic forest species, apparently identical to the widespread American *C. planifolia*, is found on Hawai‘i Island (1,100-6,100 ft.) in Kīpukakī, Hawai‘i Volcanoes National Park and in the Pu‘u Maka‘ala N.A.R.; it is also found on rock at 1,100 ft. in Waimea Canyon, Kaua‘i, Shevock 46371 (CAS, PTBG, UWSP).

Plants are tiny, emerald-green, and rosette forming. Creeping on decaying logs, on bark of trees, or rocks. Plants small, about 0.6-0.7 mm wide, yellow-green to emerald-green, creeping, forming dense rosettes or mats, appressed to their substrate. Stems 50-60 µm wide, flexuous, sparingly branched. Leaf insertion is short, succubous, slightly oblique, but almost horizontal. Leaves are distant, contiguous or imbricate; broadly spreading, patent, flat, cuneate to obovate, 300 µm long and about as wide, slightly to markedly constricted at the base; unequally bifid, split to about 1/2 their length by an acute sinus. Leaf lobes are acute, unequally sized, one broader than the other. Leaf margins are usually irregular. Leaf cells are mostly isodiametric, 20-24 µm in diameter, slightly bulging, thin- to moderately thick-walled, without trigones. Underleaves underdeveloped when present. Antherida are stalked and sphaerical, produced at the axils of normal looking leaves that are imbricate. Perianths are terminal on main stems, large, tubular, furrowed, and slightly constricted at the mouth when immature but apically flaring and truncate when mature (our interpretation). Unicellular gemmae are occasionally present.

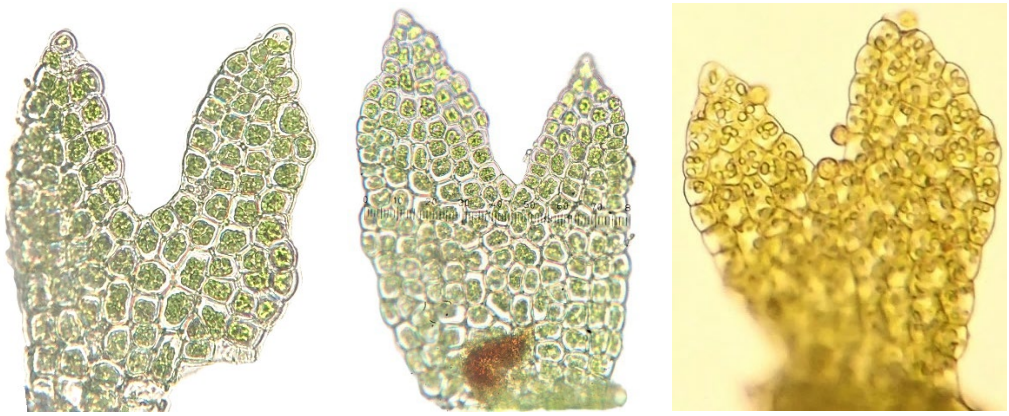
Cylindrocolea planifolia. Habit on decorticating log, Kīpukakī, Hawai‘i Island, Freire & Judziewicz 23-330 (HAVO).

Left: Emerald-green, rosette-forming plants. Hawai‘i Island, Freire & Judziewicz 23-330. Right: Bright green to yellow-green tiny plants growing appressed to their substrate. Leaves are patent. Hawai‘i Island, Freire & Judziewicz 21-334 (HAVO).

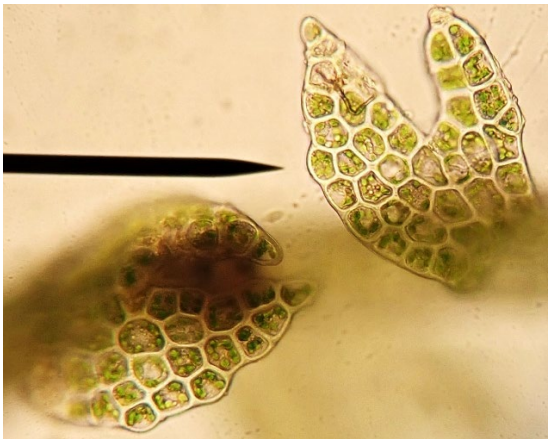
Plants have distant leaves and are sparingly branched. Here intermixed with *Cephaloziella*. Hawai‘i Island, Freire & Judziewicz 21-664 (BISH).



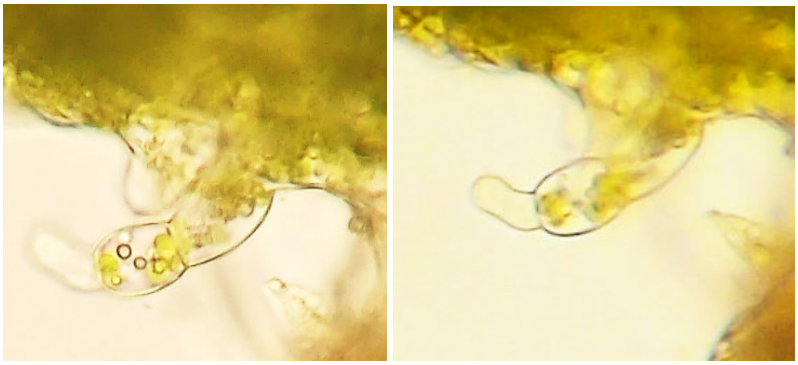
Cylindrocolea planifolia. Left: Leaves constricted at the base and almost horizontally inserted. Pu‘u Maka‘ala N.A.R., Hawai‘i, Freire & Judziewicz 21-664 (BISH). Right: Leaves can be larger, with many more cells, and can be imbricate as in this photo. Hawai‘i Island, Freire & Judziewicz 21-334 (HAVO).



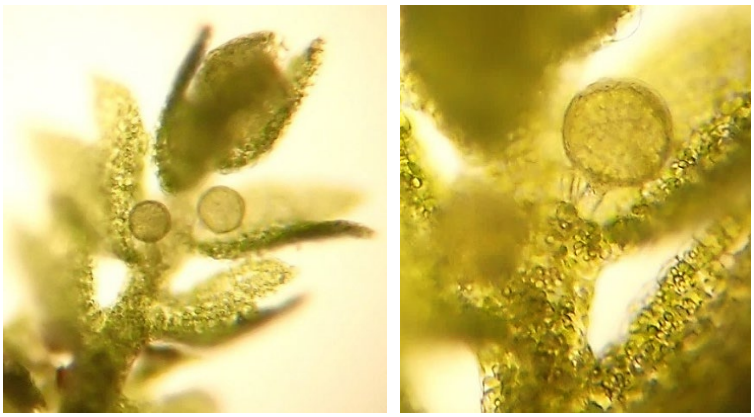
Leaves are bilobed, with an acute sinus to one-half or slightly less than one-half the leaf length. Lobes acute, unequal. Note spherical, single-celled gemmae (right). Scale units = 2.5 µm (center). Kīpukakī, Hawai‘i Island, Freire & Judziewicz 21-334 (HAVO).



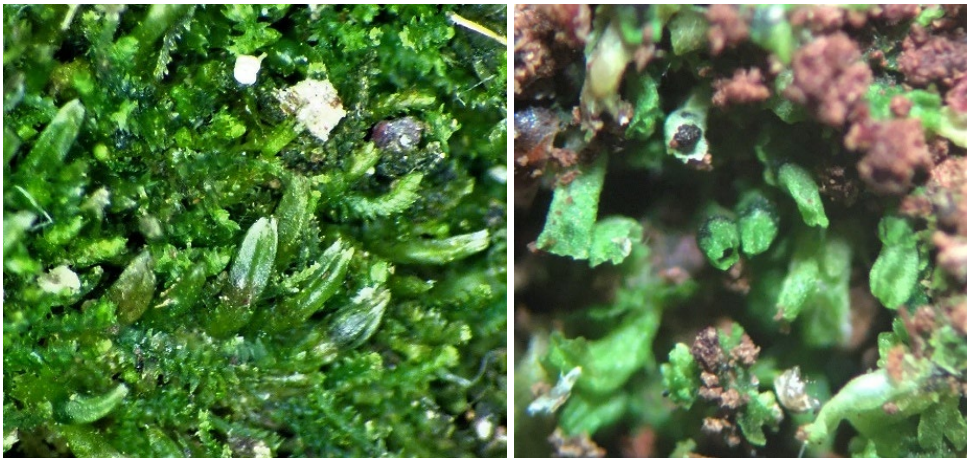
Cell walls can be thickened as in this photo. Pu‘u Maka‘ala N.A.R., Hawai‘i, Freire & Judziewicz 21-664 (BISH).



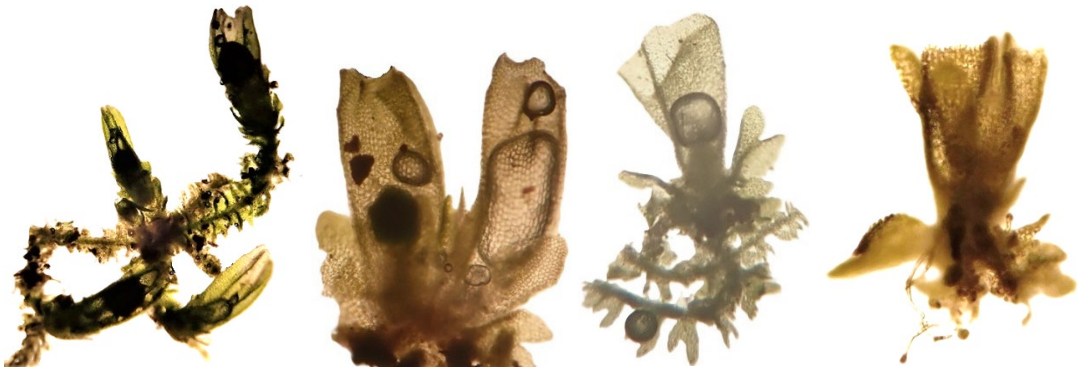
Cylindrocolea planifolia. Underleaves are rudimentary when present. Note the slime papillae (?) at the tip. Kīpukakī, Hawai‘i Island, Freire & Judziewicz 23-330 (HAVO).



Stalked antheridia are produced in the axils of leaves. Hawai‘i Island, Freire & Judziewicz 23-330 (HAVO).



Left: Perianths are large, erect, tubular, pleated, with a constricted mouth. Freire & Judziewicz 21-1032 (HAVO). Right: Perianths with constricted mouth (enclosing immature sporophyte) and broad-mouthed (mature). Kīpukakī, Hawai‘i Island, Freire & Judziewicz 21-334 (HAVO).



Cylindrocolea planifolia. Left: Plant with perianths. The upper one with a seemingly mature capsule and open mouth, Kīlauea, Hawai‘i Island, Freire & Judziewicz 21-1032 (HAVO). Left center: Tubular perianths (left with immature sporophyte), Kīpukakī, Hawai‘i Island, Freire & Judziewicz 21-334 (HAVO). Right center and right: Perianths with broad, truncate mouth, Kīpukakī, Hawai‘i Island, Freire & Judziewicz 23-330 (HAVO).

2. *Cylindrocolea* cf. *planifolia*. This plant is known from just one sterile collection in mesic forest in Kīpukakī (4,200 ft.), Hawai'i Volcanoes National Park, made in 2020. It was growing on mānele (*Sapindus saponaria*) bark with *Frullania oahuensis,* with which it can be mistaken from a distance. David Wagner (pers. comm.), authority on North American species of *Cephaloziella*, suggests that it may be a new species. This was an incidental collection without sexual structures. We returned to the collection site several times but failed to relocate it here or elsewhere in Hawai'i. Typical bright green *C. planifolia* is common in this kīpuka.

Plants are minute, reddish-black, freely branched, 1-5 mm long, ca. 0.5 mm wide. They grow closely appressed to their substrate. Stems are olive-green, ca. 70 µm in diameter. The leaves are distant, horizontal succubous, round in outline, bifid to ½ to 1/3 their length, the sinus narrow, rounded ("U"-shaped to "V"-shaped), the lobes parallel to slightly spreading, asymmetrical, one larger than the other, 6-8 cells long; the dorsal lobe obtuse, ca. 6 cells wide at the base; the ventral lobe acute, 4-5 cells wide at the base, with 1 to several clear hyaline apical cells. The leaf cells are globose, bulging, thin-walled, 18-25 µm in diameter in the middle of the leaf, lacking trigones, and have several ellipsoidal, smooth, slightly granular oil bodies. Underleaves are absent (but we had limited material). Below: Freire & Judziewicz 20-864 (HAVO).

Cylindrocolea cf. *planifolia.* Above: Green stem and bilobed leaves with unequal lobes. Below: Leaf with bulging cells and unequal lobes. Noye hyaline cell at the tip of the ventral lobe. Kīpukakī, Hawai'i Island, Freire & Judziewicz 20-864 (HAVO).

About the researchers

The authors near Nāhuku, Hawai‘i Volcanoes National Park, 14 Oct. 2021 (photo by Luciana Boisson-Meighan). Virginia received her PhD at Southern Illinois University studying the tropical American species of the thalloid liverwort *Fossombronia*. She is responsible for initiating the first bryophyte studies program in her native Guatemala and conducted the first liverwort inventory of the rich cloud forests of that country. Virginia taught at the University of Wisconsin-Stevens Point (UWSP) from 1999 to 2019. Emmet received his PhD at the University of Wisconsin studying the basal grass tribe Phareae and for many years worked on tropical American bamboos and Great Lakes islands vascular floras. He also taught at UWSP, from 2001 to 2017. Both authors are Professors Emeriti there, and Distinguished Affiliates at the Herbarium Pacificum, Bernice Pauahi Bishop Museum. The authorship order is alphabetical. Contact us at calypogeia@gmail.com or judzemmet@gmail.com.