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A TAXONOMIC STUDY OF HAWAIIAN MARCHANTIA

BY

TERRI L. ROBERTS
B.S., University of Central Florida, 1984

THESIS

Submitted in partial fulfillment of the requirements
for the Master of Science degree in Biological Sciences
in the Graduate Studies Program
of Arts and Sciences
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Abstract

The genus Marchantia occurs world-wide. The greatest diversity of described species occurs in the tropical Pacific. Fourteen species of Marchantia have been reported at different times from the Hawaiian Islands but when this study began seven species were recognized. A new technique for clearing thallus material enabled me to see and compare ambiguous characters. From studies of types and numerous additional collections from the islands, I determined that the seven species accepted actually belong to three taxa and one previously undescribed species was discovered. Comparison of Hawaiian plants with specimens, drawings and descriptions of extra-Hawaiian Marchantiae showed clearly that the Hawaiian species are predominantly like those of New Guinea and the Indo-Pacific region. However, one tropical American species, Marchantia paleacea, does occur in Hawaii.

ACKNOWLEDGEMENTS

I am grateful to Dr. Harvey A. Miller for encouraging me to study Marchantia. Thank you, Dr. Miller, for providing numerous specimens and equipment and for the enduring patience required to help me complete this study. I am also grateful to Dr. Henry O. Whittier and Dr. David H. Vickers, members of my committee, for their support in this endeavor.

My sincerest thanks to my parents, Florence and Dallas Roberts, for their continuous emotional and financial support.

I wish to acknowledge the Bishop Museum (BISH) for the loan of many specimens of Marchantia. Portions of types were made available from the herbarium at Geneva, Switzerland (G) and from Yale University (YU). I also thank Dr. Allen Harrington for his assistance and the British Museum of Natural History for allowing me to study there during the summer of 1985. This study was funded in part by a grant from the National Science Foundation, BSR 8215056, Harvey A. Miller, Principal Investigator.

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INTRODUCTION

The cosmopolitan genus Marchantia is the classical textbook example of a liverwort. Marchantia is easy to propagate and responds predictably to environmental changes making it a valuable research organism. The name Marchantia was used by Linnaeus (1753) in the first edition of *Species Plantarum*. The name Marchantia was dedicated to Nicolas Marchant, director of the botanical Garden of Gaston d'Orleans in Blois, France, in 1713 making it one of the earliest in hepatics to have a modern name.

Historical Account

Marchantia polymorpha, especially, may be well-known and used by researchers for a diversity of studies, but taxonomy of the genus has been little studied for the Pacific. No monographs have been written for Pacific Marchantiae and the few reports of the genus in Hawaii are scattered over a period of one hundred and fifty years. William J. Hooker (1837) reported Marchantia trichocephala from Hawaii, which is now correctly named Dumortiera hirsuta. William Mitten (1871) reported Marchantia nitida from collections by Macrae and Hillebrand. Two new species, M. crenata and M. innovans, were described by Coe F. Austin (1874) from collections made by Horace Mann and William T. Brigham. Later M. innovans was correctly placed under the

name Asterella innovans. Austin (1874) also reported M. polymorpha collected by William Hillebrand. David D. Baldwin (1877) listed the three species previously reported by Austin and added M. disjuncta to the list. Also in 1877, H. W. Reichardt reported M. chenopoda from Kauai. He was not confident that the specimen was in fact M. chenopoda and suggested that if it was a new species it should be named M. sandvicensis, now a nomen nudum. Alexander W. Evans (1891) listed only three species of Marchantia from Hawaii: M. polymorpha, M. crenata, and M. disjuncta. Evans stated that several other species provisionally named by Austin were in too small a quantity to describe as new. Franz Stephani (1897) reported the same three species as Evans, M. polymorpha, M. disjuncta, and M. crenata, and also M. nitida which had not been reported since Mitten (1871). Schiffner (1898) also reported M. nitida. He considered specimens called M. paleacea from Hawaii to be M. nitida. In 1900, Stephani described M. furciloba and M. crenata, both new species from Hawaii. Evans (1914) cited M. polymorpha as one of the Hawaiian elements common with the Alaskan bryoflora, but without listing a specimen. Over twenty five years later Nicholson (1942) reported M. crenata collected by S. Berggren in Hilo, Hawaii. Three new Hawaiian species were described by Stephani (ex Bonner, 1953): M. antiqua, M. cuspidisquama, and M. marginata.

Another new species, M. punaluana was described as being from Japan. However, the type specimen, Faurie 503, is actually from Punaluu on Oahu and M. punaluana was based upon a Hawaiian collection. Miller (1963) transferred Fimbriaria rechingeri to the genus Marchantia and also reported M. cuspidisquama, M. crenata and M. antiqua. Miller et al. (1983), the most recent publication containing information on Hawaiian Marchantiae, considered the following species to occur in the Hawaiian Islands: M. antiqua, M. crenata, M. cuspidisquama, M. furciloba, M. marginata, M. paleacea, and M. rechingeri. All other previously reported species are accounted for as misidentifications or synonyms. The purpose of my study was to review all reports and, to the extent possible, the specimens upon which those reports were based, and to study many unreported collections to delimit and describe Hawaiian Marchantia species.

MORPHOLOGY

Thallus Structure

The thallus of Marchantia consists of an epidermis surrounding an internally complex body comprised of a chlorenchyma layer and mostly parenchymatous ventral tissue. The epidermis has mostly uniform, isodiametric, parenchymatous cells occurring in one or two layers. Epidermal cells become distinctly smaller from the middle of the thallus outward to the smallest marginal cells. Cell size may also vary depending on environmental conditions. The chlorenchyma is produced in subepidermal chambers where most photosynthesis occurs. The erect chlorenchyma filaments may be only three to five cells high up to ten to fifteen cells high depending on the species and the microclimate. The major internal component of the thallus is the ventral tissue. The ventral tissue consists of mostly isodiametric cells which are sometimes pigmented green, red, or brown. The ventral tissue layer may be eight to ten cells thick to as much as twenty-five to thirty cells thick, depending on the species and environmental conditions. Also in cross-section, an area of decidedly smaller cells is found just above the rhizoid furrow and between the perpendicular bundles of rhizoids. These cells are the same as other ventral tissue cells and are not

taxonomically significant. Often sclerids are found scattered throughout the ventral tissue. The location of sclerids in the ventral tissue does not seem to be taxonomically significant, however there does appear to be some correlation between species and sclerid morphology.

The thalli cleared with KOH revealed verrucose cells, a character previously unrecognized for Marchantia. Verrucose cells occur in the ventral tissue. These may be the "oil cells" of other authors but tests with Sudan stains were negative indicating that normal lipids were not present. The cells are isodiametric and have conspicuous, lumpy cell walls. The presence of verrucose cells does not appear to be correlated with any particular species.

Some species of Marchantia may have air spaces which can be seen in cross-section in the ventral tissue. These air spaces may vary somewhat in size, but they seem to be consistently present or absent within a species.

Epidermal Doliipores

The outstanding feature of the epidermis is the presence of the barrel-shaped epidermal doliipores (Latin dolium= barrel). The doliipore of Marchantia is comprised of two series of concentric rows of cells. The number of rows in the supraepidermal and subepidermal series is relatively stable within a taxon and may vary between species. The ventralmost row of cells in the subepidermal series surrounds the internal pore opening.

Stephani (1900) recognized four different types of pore openings. In the first type the cells bordering the opening are narrow and the opening quadrate. The second type has cells with projections which bulge into the opening. The third type is very similar to the second except that the projections are distinctly conical and the opening has a cruciate appearance. The fourth type was described for Marchantia macropora which occurs in New Zealand. This type of doliipore has a very large opening with many cells projecting into the opening but is otherwise similar to the third type.

Evans (1917) carefully studied doliipores and concluded that much of the variation in pore structure is the result of different environmental conditions. Shapes of pore openings can vary dramatically depending on the turgidity of bordering cells. Evans recognized only two types of openings, quadrate (Stephani's first type) and cruciate (Stephani's third type). Evans did not consider the type of pore found in M. macropora because it is not an American species. Quadrate and cruciate doliipores appear to be the only kinds found in Hawaiian Marchantiae. Often variation can be found in the openings of doliipores on one plant. Some specimens showed both quadrate (fig. 38) to weakly cruciate (fig. 37) pores with most other specimens being consistently only one type or the other, but still with some

variation in boundary cell inflation. If most pore openings appeared even weakly cruciate, I considered them cruciate. Species with cruciate doliipores (figs. 3-4, 17-18) seem to occur more frequently in Hawaii than species with quadrate doliipores.

Ventral Scales and Appendages

Several rows of scales are found on the ventral surface of Marchantia. The usual number of rows of scales is four. Only in the Subgenus Marchantia do more than four rows occur. The outermost (marginal) and middle (laminal) rows of scales are small, often ephemeral, and usually do not have appendages. I have seen a few laminal scales with small appendages but this does not seem to be the usual case and may be limited to one taxon. The centermost or median rows of scales are larger than the others and have sharply delimited appendages. The appendages are of taxonomic value in that margin, shape, and size of the appendages can frequently serve to distinguish species. Unfortunately, reproductive material was not available when some species were described with the result that the characterization derives almost entirely from appendage morphology. In at least the Hawaiian Marchantiae, material with different scale appendage margins were described as separate species. When reproductive material was examined the gametophores of the variants appeared to be identical. The general shape and proportions of appendages are more important taxonomically

than differences in marginal ornamentation. In Marchantia antiqua, e.g., a continuum of appendage size and a marginal toothing retains a consistent 1:1 to 1.3:1 length:width ratio.

Rhizoids

Rhizoids of Marchantia are of two types, smooth and tuberculate (pegged). Most rhizoids occur in a furrow between the inner ventral scales. Perpendicular bundles of rhizoids are produced near the base of median ventral scales. In Hawaiian Marchantiae the tuberculate rhizoids appear to be limited to the rhizoid furrow and the smooth rhizoids are in the scale bundles. Schiffner (1909) also recognized a correlation between the type of rhizoid and location. Evans (1917) considered the type of rhizoids and location to be useful in distinguishing some species.

Gemmae Cups

Asexual progagules, gemmae, are found in small cupules on the dorsal side of Marchantia. The gemmae are stalked, multicellular, oblong discs with notches midway on each side. They are so uniform within the genus that they have no taxonomic value at the specific level. Gemmae are drought resistant and germinate readily given adequate water and substrate. The cups show several character states of taxonomic value. Margins may be entire or dentate to ciliate and lobed with little variation within a species.

Gametophores

Archegoniophores of Marchantia are always found terminally on the thallus, and are comprised of a stalk and a receptacle. The stalk is approximately cylindrical with scales along its length. In cross-section it is possible to observe the number of rhizoid furrows and determine whether dorsal air chambers are present or absent. The receptacle disc may be attached to the stalk centrally or eccentrically. The receptacle may be symmetric or asymmetric with few to several rays. The rays may be terete to flattened. Scales occur on the ventral side of the receptacle and some are appendaged. For Hawaiian species, these have little taxonomic value. Archegonia are found within the involucre pouch which occurs between the rays. The margin of the involucre may be entire to variously ornamented.

The antheridiophore also has a stalk and receptacle and is produced terminally on the plant. The stalk has rhizoids and sometimes has air chambers, although air chambers are more frequently found in female stalks. The receptacle may be symmetric or asymmetric and the number of lobes either fixed or variable. The receptacles may have appendaged scales although most males have scales without appendages. The rays are almost always flat above but the sinus depth between lobes varies greatly among species. The antheridia

are small, white, ovoid structures set into individual cavities opening to the dorsal surface of the receptacle, usually in a row down the center of each ray.

It is important to note that immature sexual material may look much different than mature material. Immature gametophores usually have much shorter stalks, the lobes of the receptacles are often curled under, and it may be difficult to determine the sex of the material without microscopic examination.

MATERIALS AND METHODS

The principal source of material for this study, in which some one hundred and thirty specimens were examined, was air dried herbarium specimens with some collections studied thus preserved for over 50 years. In addition, portions of many specimens collected by H. A. Miller were preserved in FPA solution (1 part formalin: 1 part propionic acid: 18 parts 70% ethanol) at the time of collection. These liquid-preserved specimens were free of the distortions which sometimes occur with dried material.

Portions of dried thallus were cleared to facilitate the study of sclerids, doliipore openings, insertion patterns of ventral scales, and cell sizes. Plants were slowly heated to 60^o C in a 25% aqueous solution of KOH, and then gradually cooled. Total processing time was approximately four hours, although this varied depending on thickness of the thallus. After treatment with KOH, plants were rinsed twice in deionized water for at least twelve hours each rinse. Plants were then stored in a solution of 75% ethanol and 1% glycerol.

Dried plant material was studied with a dissecting microscope for gross morphological characters. Freehand cross-sections of water-soaked thallus and gametophore stalks were studied with a compound microscope.

Illustrations were made with the aid of camera lucida and a microprojector, although some features were hand-sketched as seen through the dissecting microscope. Photomicrographs were made to record some structural details.

TAXONOMIC TREATMENT

The genus Marchantia is characterized by an internally complex, dichotomously branched thallus that is dorsiventrally flattened. The dorsal surface has epidermal doliipores. The ventral surface has 4 to 12 rows of scales with the median row of scales bearing appendages. Gemmae cups on the dorsal surface distinguish it from all other genera except for the rare Preissia not known from the old world tropics. Marchantia is dioicous with both the antheridiophores and archegoniophores comprised of terminal stalks bearing an elevated disc containing gametangia.

Marchantia was first divided into two sections by Nees (1838) based on the symmetry of the female receptacles. His Section Astromarchantia included species with the female receptacle attached to the stalk in a central position as seen in Marchantia polymorpha. Section Chlamidium included species with the female receptacle attached excentric to the stalk. The two sections were used by Gottsche, Lindenberg and Nees (1846) but Astromarchantia was renamed Stellatae. Dumortier (1874) changed Astromarchantia to Marchantiotypus. Schiffner (1893) used the same two sections but returned to the name Astromarchantia for the first. Evans (1917) also followed this system but added new characters such as presence or absence of sclerids, number of bands of rhizoids

and air cavities in the cross-sections of receptacle stalks, and margins of involucre and gemmae cups, to the description of the sections.

Stephani (1900) used a much different system based on symmetry of female receptacles, morphology of the rays and structure of the epidermal doliipores. He did not give his two groups names other than to call the first group with symmetrical receptacles "a" and the second group with asymmetric receptacles "b". Stephani also included a third group, "c", of plants that had variable symmetry, or archegoniophores were not available. Stephani's system did not work well and often the same species was described as new in totally different groups. This system has not been accepted by anyone else.

Evans' sections were used by Haessel de Menendez (1963) for the Latin American species. Grolle (1976), following the rules of nomenclature, used the section name Marchantia for Section Astromarchantia (Stafleu et al. 1975, ICBN Art 22.1) because the type of the genus is in this section. Bischler (1982) added more characters and elevated the sections to the rank of subgenus. Most recently, Bischler (1984) more clearly defined some of the subgeneric characters of Marchantia.

Subgenus Marchantia has ventral tissue without sclerotic cells. The ventral scales cover 75-100% of the ventral surface in 4-10 rows. Appendages of medium scales

are ovate or orbicular, and never acuminate at the apex. The male receptacles are peltate, nearly symmetric and shallowly dissected into broad, rounded lobes. The female receptacles are deeply dissected into terete rays. Gemmae cups have margins with ciliate lobes and papillae on the outer surface.

Subgenus Chlamidium has ventral tissue often with sclerotic cells. The ventral scales cover 25-60% of the ventral surface, in 4 rows. The appendages of median scales are orbicular, ovate or triangular, usually acuminate, acute or apiculate. The male receptacles are palmate or peltate, asymmetric or symmetric and often with narrow rays. The female receptacles are shallowly or deeply dissected with lobes or rays that are flat at least at the apex. Gemmae cups have ciliate or nearly entire margins, seldom with ciliate lobes, and papillae are usually absent from the outer surface.

All Hawaiian species belong to Subgenus Chlamidium. Representative specimens of each taxon are cited following the description.

Key to Species

1. Median ventral scale appendages round to ovate with tips rounded to broadly obtuse, marginal cells differentiated from median cells; epidermal doliipores cruciate . . . 2.

- 2. Scale appendage margins irregularly crenulate; gemma cup teeth dentate, usually with a uniseriate tip of 1-2 short cells; supraepidermal cells of the doliipores usually in three rows; male receptacles peltate the margin shallowly crenately lobed Marchantia paleacea
- 2. Scale appendage margins erose-dentate; gemma cup teeth lacinulate, usually with a uniseriate row of three cells; supraepidermal cells of the doliipores usually in four rows; male receptacles asymmetric, deeply dissected into distinct digitate rays M. antiqua
- 1. Median ventral scale appendages ovate to triangular, tips acute to acuminate, marginal cells not differentiated from median cells; epidermal doliipores quadrate 3.
- 3. Scale appendages ovate, usually auriculate and occasionally appendiculate, appendage tips often narrowly attenuate; doliipores usually with 4 rows of supraepidermal cells; archegonial involucre irregularly fimbriate M. fimbriatula
- 3. Scale appendages ovate to lanceolate, and without appendiculae, appendage tips usually acute to acuminate; doliipores usually with 3 rows of supraepidermal cells; archegonial involucre regularly dentate M. crenata

1. Marchantia paleacea Bertol. Opus. Sci. Bologna 1: 242.

1817.

(Fig. 1-14)

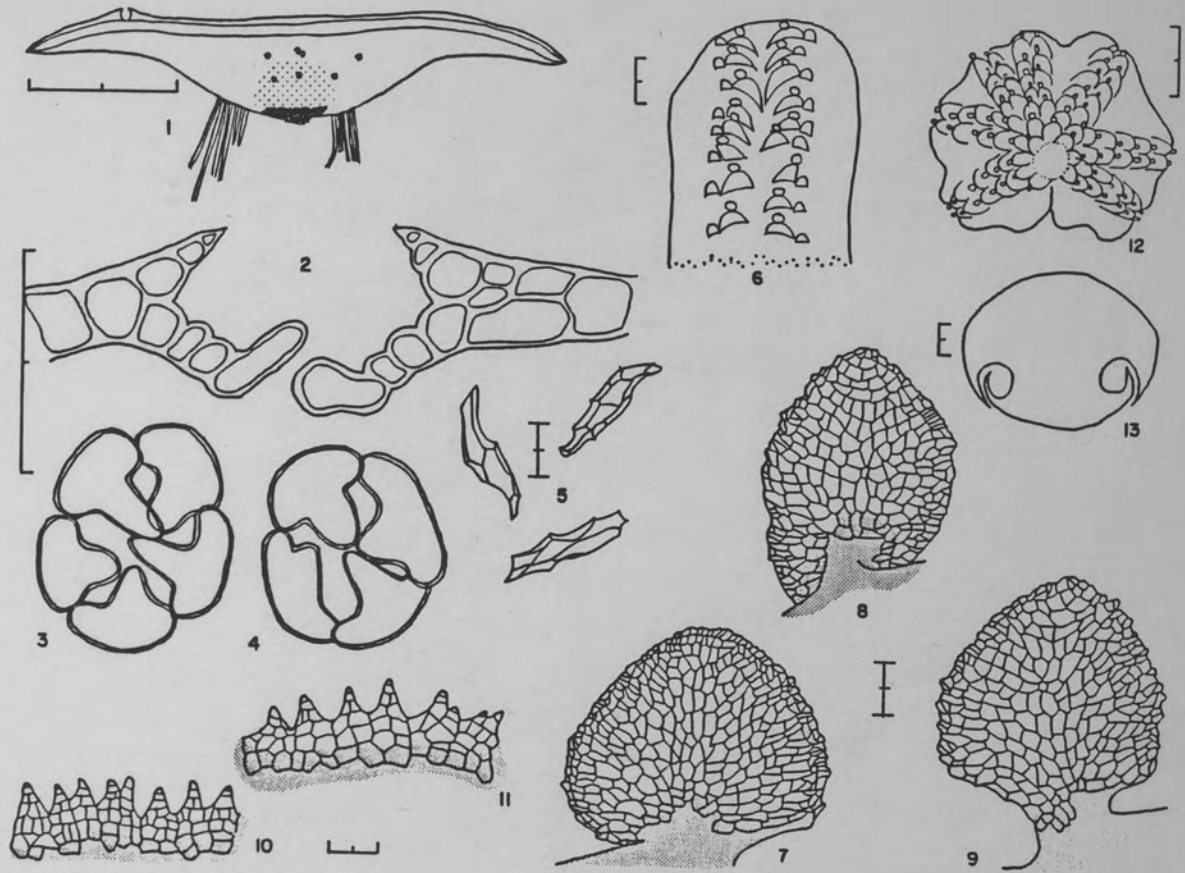
Marchantia nitida Lehm. et Lindenb. in Lehm. Pugillus

Pl. 4: 11. 1832. (fide Bischler, 1984)

Thallus soot brown (5F5) (Kornerup 1981) when dry, 4.9-5.4 mm wide; dichotomously branched with successive dichotomies about 2 cm apart. Margins green to brown and entire; usually 1 cell thick but occasionally 2 cells thick; marginal cells weakly rectangular 8-10 x 10-15 μm . Epidermal cells gradually decrease in size toward the margin. Epidermal doliipores 70-100 μm in diameter, bounded by 6-7 concentric rings of cells, 3-4 rows in the supraepidermal series, 3-4 rows in the subepidermal series. The innermost row of cells define a cruciate opening. Narrowly rhomboid, acute-angled sclerids present in ventral tissue. Ventral scales in 4 rows; laminal scales are somewhat ephemeral, ovate; median scales 5-8 x 6-10 μm ; larger than laminal scales with alternate to opposite insertion; median scale appendages subrotund to ovate, tips round to obtuse.

Antheridiophores terminal. Stalk 2.0-6.0 mm long; stalk cross section 520-650 μm in diameter; air chambers absent; 2 rhizoid furrows present. Receptacles symmetric, peltate,

Figures 1-13. Marchantia paleacea. 1. Thallus cross section.-- 2. Doliipore, cross section.-- 3-4. Doliipore opening, surface view.-- 5. Sclerids.-- 6. Thallus, ventral surface.-- 7-9. Scale appendages.-- 10-11. Gemmae cup margins.-- 12. Antheridiophore receptacle, ventral view.-- 13. Antheridiophore stalk, cross section. Scale Bars 1, 6, 12 = 1 mm; 2-5, 7-11, 13 = 100 um.



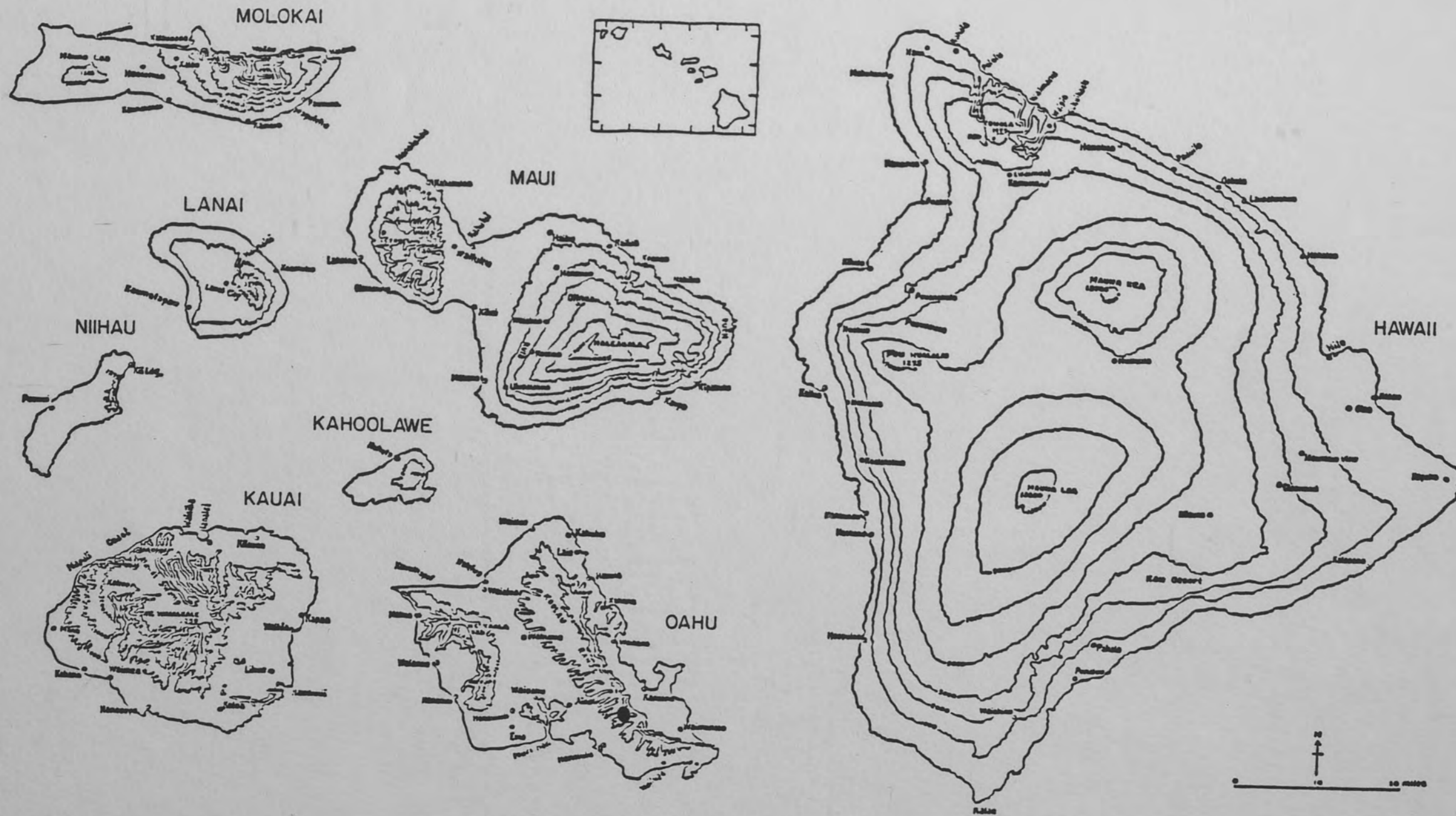


Figure 14. Distribution of Marchantia paleacea.

flattened above, scales with appendages present on the half terete ventral surface of capitulum.

Archegoniophores not seen.

Gemmae cup margins dentate.

Nees von Esenbeck (1838) first considered M. nitida as a synonym of M. paleacea based on specimens from Lindenberg. According to Nees, Lindenberg had not seen specimens of M. paleacea before describing M. nitida as a new species. Many authors, e.g. Evans (1917) and Bischler (1984), consider M. nitida and M. paleacea synonyms.

I have seen only one Hawaiian specimen of M. paleacea, however, this collection contained many male plants and matches Bischler's (1984) descriptions and illustrations. Marchantia paleacea appears to be very similar to M. antiqua. The most evident difference is in the antheridiophore. Marchantia paleacea has small, symmetric, peltate male receptacles and M. antiqua has large asymmetric, deeply dissected male receptacles. Unfortunately, no female plants from Hawaii were available for study.

Specimens examined: HAWAII. Oahu: Halawa

Trail, Koolau Mts., 1150-2400 ft, Miller 2774.

2. Marchantia antiqua Steph. ex Bonner. Candollea 14: 103.

1953.

(Fig. 15-34)

Marchantia marginata Steph. ex Bonner. Candollea 14: 108.

1953.

Thallus olive (3D4) to olive brown (4E5) to khaki (4D5) (Kornerup 1981) when dry, 5.0-6.0 mm wide; dichotomously branched with successive dichotomies about 2 cm apart. Margins green to brown and entire; usually 1 cell thick but occasionally 2 cells thick; marginal cells weakly rectangular 8-10 x 10-15 μm . Epidermal cells gradually decrease in size toward the margin. Epidermal doliipores 60-80 μm , bounded by 6-7 concentric rings of cells, 3-4 rows in the supraepidermal series, 3-4 rows in the subepidermal series. The innermost row of cells define a cruciate opening. Sclerids narrowly linear, acute-angled, often with truncate end walls. Lower epidermis brown, becoming reddish towards the margins. Ventral scales in 4 rows. Laminal scales are somewhat evanescent and widely ovate. Median scales 5-15 x 5-15 μm , reddish, larger than laminal scales, inserted opposite to alternate from each other. Median scale appendages subrotund to ovate, tips round to obtuse, never acute. Marginal cells of appendages much smaller than median cells usually forming a distinct band; margin entire to dentate with the teeth formed by individual cells oriented perpendicularly to median cells.

Antheridiophores terminal. Stalk 3.0-5.0 mm long; cross section 570-800 μm in diameter, air chambers absent; 2 rhizoid furrows present, each with a tendency to double. Receptacles asymmetric, 5-7 mm across; deeply dissected into

4-5 rays; rays 2.7-4.5 mm long, 1.1-1.5 mm across; sinus depth $\frac{3}{4}$ to $\frac{7}{8}$ of ray length; margin entire, scales with appendages present on ventral surface of capitulum.

Archegoniophores terminal. Stalk 18-21 mm long; cross section 600-800 μm in diameter, air chambers absent; 2 rhizoid furrows present each with a tendency to double. Receptacles symmetric, 4.8-5.5 mm in diameter; not dissected into distinct rays; usually 6 lobed with distinguishable emarginate tips; receptacle margin entire; involucre margin entire; linear scales without appendages present on ventral surface of receptacle.

Gemmae cupule margins dentate with 3-4 cells forming a base for the teeth.

2a. Marchantia antiqua var. antiqua Steph. ex Bonner.

Candollea 14: 103. 1953. (Fig. 26-27, 31, 34)

The median ventral scale appendages of M. antiqua var. antiqua fall in the middle range of size and margin dentation for the species. The appendages are ovate, 530-380 x 510-380 μm , with an irregularly dentate margin formed by a border of cells perpendicular to the median cells. At present, collections are known from Molokai, Oahu, and West Maui, with the greater number of specimens from Oahu.

Specimens examined: HAWAII. Molokai: Waikolu Canyon, Miller and Lambertson 3750. Oahu: Kawaiiki ditch trail, Koolau Mts., 1000 ft, Miller 2304, Miller 2323. South ridge of Kipapa gulch, Koolau Mts., 1800-2500 ft, Miller 2721,

Miller 2731, Miller 2748. Koolau, Punaluu, Selling 5121.

West Maui: Baldwin 87 (type G, BISH).

2b. Marchantia antiqua var. millerii var. nov.

(Fig. 28-29, 34)

Marchantia disjuncta Auct. et herb. non Sulliv. Amer. J.

Sci. II. 1: 74. 1846.

The large median ventral scale appendages, 560-500 x 600-500 um, have a distinct band of often red marginal cells. On the basis of specimens I have seen the large almost orbicular scale appendages with crenate-denticulate margins serve to differentiate this variety. At present, collections are known only from the islands of Maui and Molokai suggesting limited geographic range.

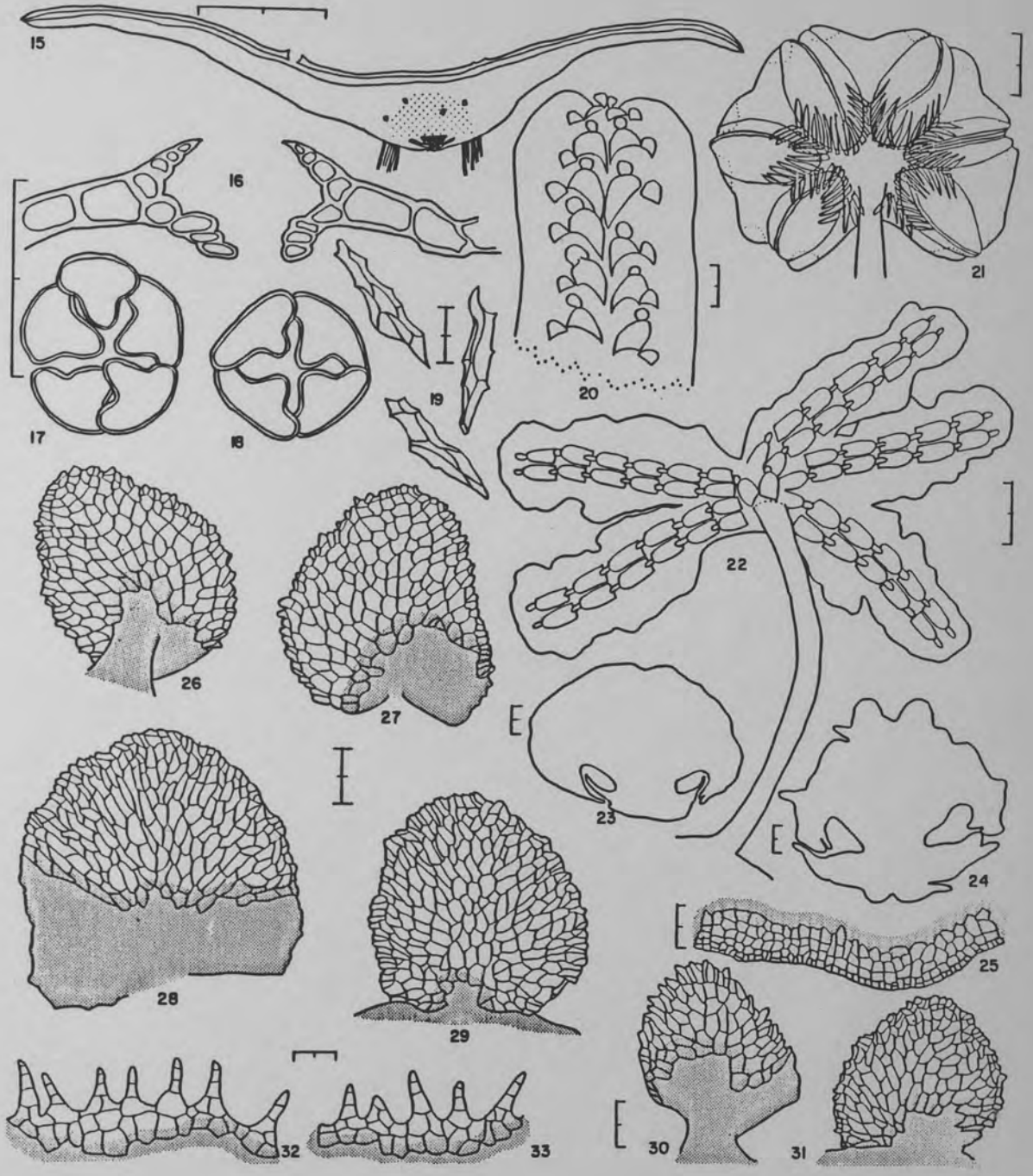
Specimens examined: HAWAII. Maui: Olinda Ditch Trail, Miller 4391, Miller 4397, Miller 4404 (type MU), Miller 4408. Makapipi Valley, Mount Haleakala, 1500 ft, Miller and Lamberton 4550. Olinda, Wilson s.n.. West Maui: Baldwin s.n. BISH. Molokai: Upper Waikolu Valley, pipe line Trail, 4000 ft, Miller and Lamberton 3763.

2c. Marchantia antiqua var. marginata (Steph. ex Bonner) comb. nov. (Fig. 30, 34)

Marchantia marginata Steph. ex Bonner Candollea 14: 108. 1953.

The median ventral scale appendages of this variety are smaller than the others, 360-380 x 360-390 um, and almost orbicular with an errose dentate margin. The marginal cells

Figures 15-33. Marchantia antiqua. 15. Thallus cross section.-- 16. Doliipore, cross section.-- 17-18. Doliipore openings, surface view.-- 19. Sclerids.-- 20. Thallus, ventral surface.-- 21. Archegoniophore receptacle, ventral view.-- 22. Antheridiophore receptacle, ventral view.-- 23. Antheridiophore stalk, cross section.-- 24. Archegoniophore stalk, cross section.-- 25. Involucre margin.-- 26-31. Scale appendages.-- 32-33. Gemmae cup margins. Scale bars 15, 20-22, = 1 mm; 16-19, 23-33 = 100 μ m.



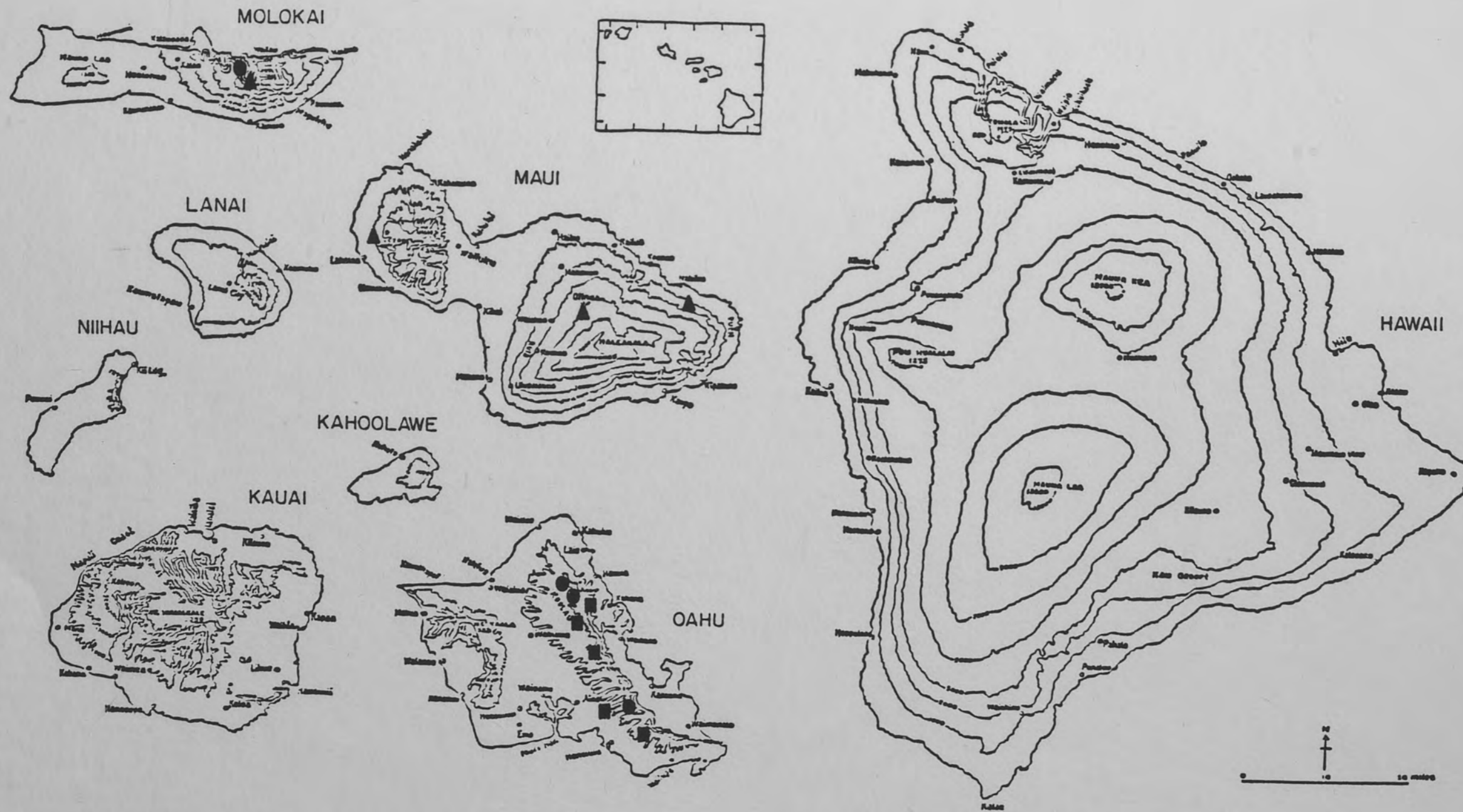


Figure 34. Distribution of *Marchantia antiqua*. ● = *var. antiqua*; ▲ = *var. millerii*;
 ■ = *var. marginata*.

are longer than wide and perpendicular to the median cells. All known collections are from Oahu, with the exception of the type specimen which is from Hawaii.

Specimens examined: HAWAII. Hawaii: Honolulu, Faurie 544 (type G). Oahu: South ridge of Kipapa gulch, Koolau Mts., 1800-2500 ft, Miller 2713. Halawa Trail, Koolau Mts., 1200-2400 ft, Miller 2769, Miller 2771. Mt. Tantalus, Trail 2, Koolau Mts., 1800 ft, Miller 3302. Kohana Waiana Uka Divide, Koolau Range, 2400 ft, Wagner 5107. Waikani-Schofield Trail at approach to Junction #7 and #9, Lohman L-0 -51. Kaliuwaa Valley, Sacred Falls, Bryan s.n..

²
The descriptions and illustrations of M. antiqua and its synonyms seem to match those of M. subgeminata, described from the Celebes. The type specimen of M. subgeminata must be examined to determine whether it is in fact synonymous with M. antiqua. If they are the same, M. subgeminata has nomenclatural priority.

3. Marchantia crenata Austin. Bull. Torrey Bot. Club 5(3):

14. 1874.

(Fig. 35-59)

Marchantia furciloba Steph. Spec. Hep. 1: 189. 1900.

Marchantia cuspidisquama Steph. ex Bonner. Candollea 14:

105. 1953.

Marchantia punaluana Steph. ex Bonner. Candollea 14: 110.

1953.

Fimbriaria rechingeri Steph. Spec. Hep. 6: 16. 1917.

Marchantia rechingeri (Steph.) Miller. Ark. Bot. 2, 5: 529.
1963.

Thallus color variable: bamboo (4C4), olive (3E4), olive brown (4E5), khaki (4D4), or goose turd (3F3) (Kornerup 1981) when dry, 5.1-5.8 mm wide; dichotomously branched with successive dichotomies about 2 cm apart. Interior of thallus containing air spaces. Margins green to brown, entire and very repand; usually 1 cell thick but occasionally 2 cells thick; marginal cells weakly rectangular 8-10 x 10-15 um. Epidermal cells gradually decrease in size toward the margin. Epidermal doliipores 60-80 um in diameter, bounded by 6-7 concentric rings of cells, 3 rows in the supraepidermal series, 3-4 rows in the subepidermal series. The innermost row of cells define a quadrate to slightly cruciate opening. Narrowly linear to narrowly rhomboid, obtuse-angled to acute-angled sclerids present in ventral tissue. Ventral scales are in 4 rows. Laminal scales are somewhat ephemeral, ovate in shape. Median scales 6-10 x 10-20 um, larger than laminal scales, rows generally with opposite to subopposite insertion. Median scale appendages ovate to triangular with the tip acute to acuminate.

Antheridiophores terminal. Stalk 4.0-5.0 mm tall; cross section 470-550 um in diameter, air chambers present in 2 ridges; 2 rhizoid furrows present. Receptacles

asymmetric, 4.8-12.0 mm wide, deeply dissected into 4-5 lobes which are 2.3-8.0 mm long; sinus depth 1.9-6.0 mm. Scales with appendages present on the ventral side of the receptacle.

Archegoniophores terminal. Stalk 3.2-5.0 mm long; cross section 520-700 um in diameter, air chambers present in 2 distinct ridges; 2 rhizoid furrows present. Receptacles globular in appearance, 2.3-3.5 mm in diameter. Involucre margin dentate.

Gemmae cup margins ciliate with the cilia 3-4 cells long.

3a. Marchantia crenata var. crenata Austin. Bull. Torrey Bot. Club 5(3): 14. 1874. (Fig. 47-50, 56, 59)

Marchantia punaluana Steph. ex Bonner. Candollea 14: 110. 1953.

Fimbriaria rechingeri Steph. Spec. Hep. 6: 16. 1917.

Marchantia rechingeri (Steph.) Miller. Ark. Bot. 2, 5: 529. 1963.

Median ventral scale appendages for this variety are some of the smallest in the genus. The ovate scale appendages, 250-540 x 110-210 um, have acute to acuminate tips that are almost always one cell wide. Specimens of M. crenata var. crenata are known from Hawaii, Oahu, and Kauai.

Specimens examined: HAWAII. Hawaii: Kilauea crater, 1200 m.s.m., Skottsberg 1288. Hilo, Mann and Brigham s.n. (type, YU). Punaluu, Faurie 503 (M. punaluana type, G).

Mauna Loa, Rock 44 (M. rechingeri type, G) Oahu: North fork of Kamatnanui stream, Koolau Range, Waimea, 700 ft, Wilson and Lambertson 308. Pohakea Pass, Waianae Mts., 2000-2400 ft, Miller 2443. Kaawa Gulch, Puu Kaala, Kamananui oapuaa, 2000 ft, Miller 2508. Mt. Tantalus, Koolau Mts., Trail no. 2, 1800 ft, Miller 3303. Lyon Arboretum, Manoa Valley, Whittier et al. s.n.. Kauai: Long Nualolo Trail to Na Pali coast, 2800-3500 ft, Miller 2975. Long Nualolo Trail, Kokee to Na Pali coast, 1000 ft, Miller 2980, Miller 2981, Miller 2985, Miller 2987, Miller 2988. Wainiha Valley, 750 ft, Miller 3275, Miller 3280, Miller 3282, Miller 3284.

3b. Marchantia crenata var. cuspidisquama (Steph. ex Bonner) comb. nov. (Fig. 52, 54-55, 59)

Marchantia cuspidisquama Steph. ex Bonner. Candollea 14: 110. 1953.

Marchantia crenata var. cuspidisquama has median ventral scale appendages that fall midway in the range of size variation. The scale appendages are 350-510 x 200-330 um with acute tips that occasionally are two cells wide rather than the usual one cell wide. At present, most collections are known from Hawaii although type collection is from Maui.

Specimens examined: HAWAII. Hawaii: Mauna Loa above Pahala, 1200 m.s.m., Skottsberg 1367, Skottsberg 1368. Kohala, upper Hamakua ditch trail, Kamuela, Skottsberg 5356. Maui: Hana, Faurie 315 (type, G).

3c. Marchantia crenata var. furciloba (Steph.) comb. nov.

(Fig. 51, 53, 59)

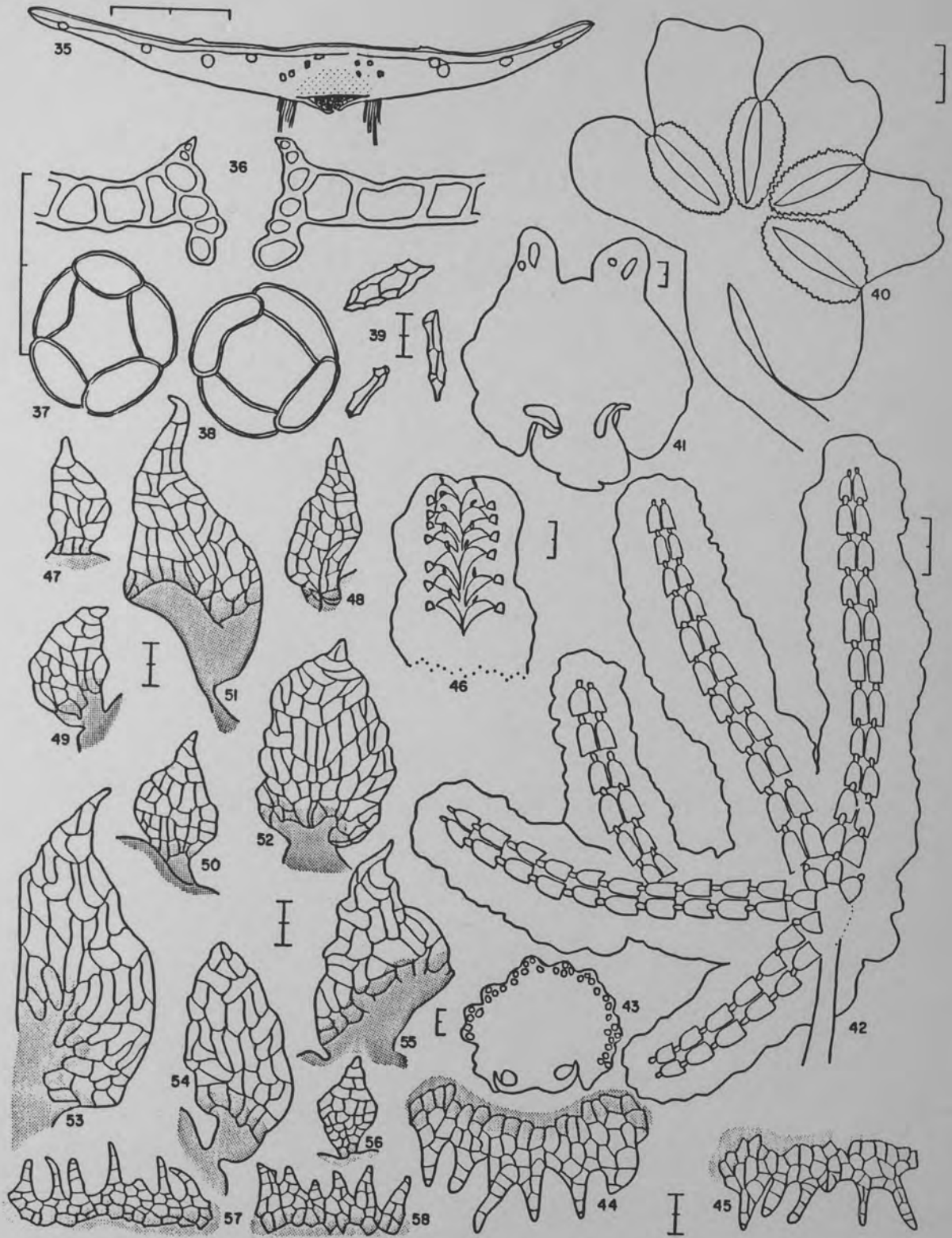
Marchantia furciloba Steph. Spec. Hep. 1: 189. 1900.

The large median ventral scale appendages, 850-750 x 210-330 um, distinguish M. crenata var. furciloba from the other varieties. The appendages have long acuminate tips that are almost always only one cell wide. At present, collections are known from Hawaii, Maui, West Maui, and Oahu.

Specimens Examined: HAWAII. Hawaii: Below Kamuelo P.O. and 1 ditch house, Selling 5051. Kohala, upper Hamakua ditch trail, Kamuela, Skottsberg 5346. Maui: Olinda Ditch Trail, Miller and Lamberton 4394, 4444, Miller 4410. Olinda Ditch Trail 4000 ft, Greenwell B-2 212. West Maui: Baldwin s.n. (type, G). Honokawai Gulch, 1500 ft, Miller and Lamberton 3367. Oahu: Kaawa Gulch, Puu Kaala, Kamananui oapuaa, 2000 ft, Miller 2527.

Marchantia crenata, M. furciloba, M. rechingeri, M. punaluana, and M. cuspidisquama were all originally described as Hawaiian endemics. All five type specimens appear to belong to the same taxonomic complex. The major differences between the type specimens are in the size of median ventral scale appendages. Marchantia crenata, M. rechingeri, and M. punaluana all have very small appendages; M. cuspidisquama has intermediate size appendages; and M. furciloba has very large appendages. The shape of the

Figures 35-58. Marchantia crenata. 35. Thallus cross section.-- 36. Doliipore cross section.-- 37-38. Doliipore openings, surface view.-- 39. Sclerids.-- 40. Archegoniophore receptacle, ventral view.-- 41. Archegoniophore stalk, cross section.-- 42. Antheridiophore receptacle, ventral view.-- 43. Antheridiophore stalk, cross section.-- 44-45. Involucre margins.-- 46. Thallus, ventral surface.-- 47-50. Marchantia crenata var. crenata scale appendages.-- 51. Marchantia crenata var. furciloba scale appendage.-- 52. Marchantia crenata var. cuspidisquama scale appendage.-- 53. Marchantia crenata var. furciloba appendage.-- 54-55. Marchantia crenata var. cuspidisquama scale appendages.-- 56. Marchantia crenata var. crenata scale appendage.-- 57-58. Gemmae cup margins. Scale bars 35, 40-42, 46 = 1 mm; 36-39, 43-45, 47-58 = 100 μ m.



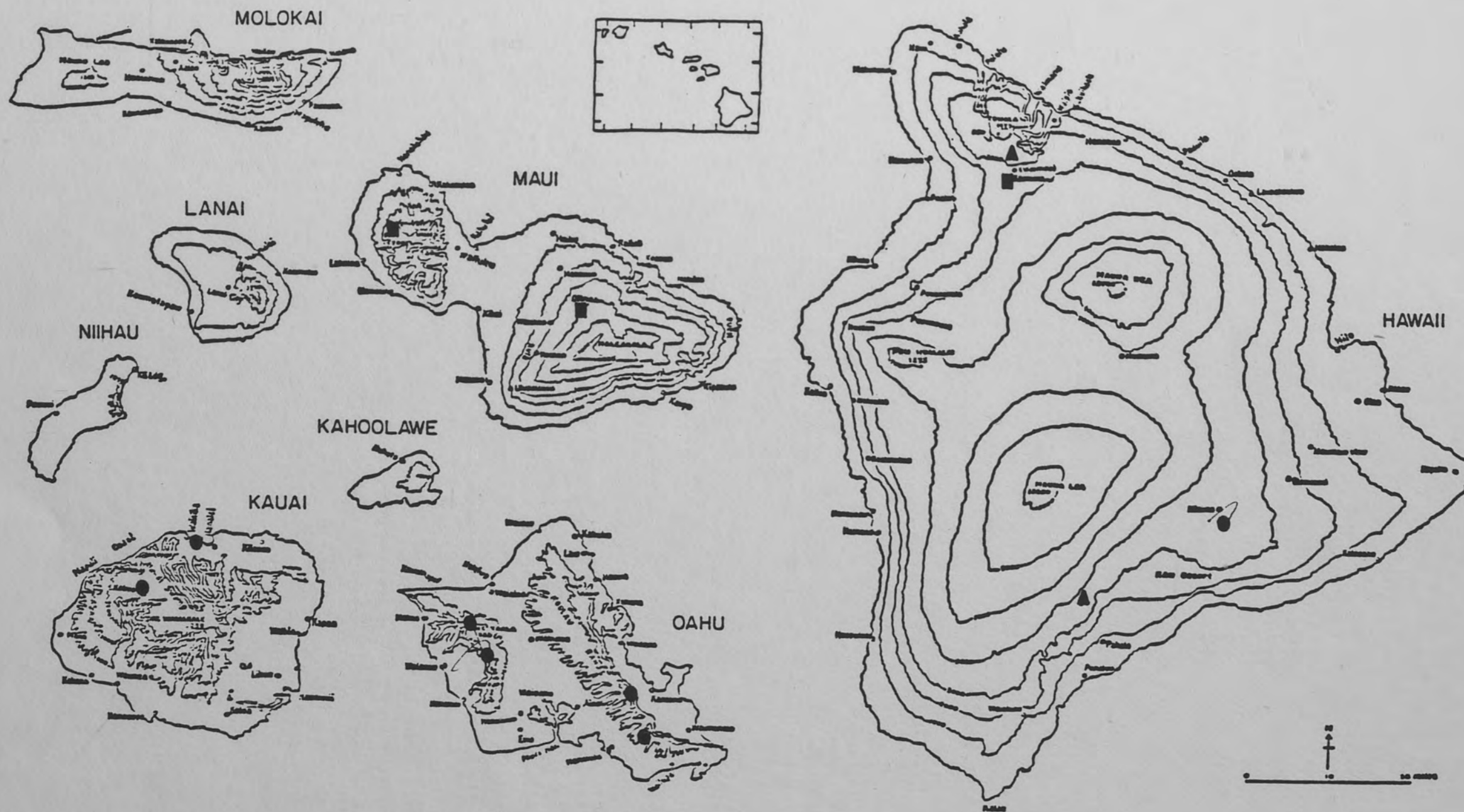


Figure 59. Distribution of Marchantia crenata. ● = var. crenata; ▲ = var. cuspidisquama; ■ = var. furcilloba.

appendages is consistently ovate with acute to acuminate tips, and the width:length ratio is usually 1:2, with the extremes being 1:1.5 and 1:3. A wide range of variation in the scale appendages must be accepted for M. crenata. Scale appendages correlate somewhat with distribution which suggests that the varieties should be recognized.

I have noted that female plants tend to have larger ventral scale appendages and male plants tend to have smaller ventral scale appendages. This was not always the case, and further study is merited when extensive fertile collections become available.

4. Marchantia fimbriatula sp. nov. (Fig. 60-75)

Thallus olive brown (4E5) (Kornerup 1981) when dry, 5.5-6.3 mm wide; dichotomously branched with successive dichotomies about 2 cm apart. Internal structure contains very large air spaces. Margins green to brown and entire; usually 1 cell thick but occasionally 2 cells thick; marginal cells weakly rectangular 8-10 x 10-15 μ m. Epidermal cells gradually decrease in size toward the margin. Epidermal doliipores 60-75 μ m in diameter, bounded by 7-8 concentric rings of cells, 3-4 rows in the supraepidermal series, 4 rows in the subepidermal series. The innermost row of cells define a cruciate opening. Narrowly linear to narrowly rhomboid, obtuse-angled to acute-angled sclerids present in the ventral tissue. Ventral scales are in 4

rows. Laminal scales are mostly ephemeral, ovate. Median scales 4-8 x 10-23 μm , larger than laminal scales, usually with opposite insertion. Median scale appendages ovate with the bases auriculate, tips acute to acuminate; occasionally an appendiculum can be found attached to the side of an appendage.

Antheridiophores not seen.

Archegoniophores terminal. Stalk 2.0-4.0 mm long; cross section 620-680 μm in diameter, air chambers present in two ridges; 2 rhizoid furrows present. Receptacles symmetric, suborbicular, 4.1 mm wide, shallowly lobed with 5-6 distinguishable truncate rays, with sinus depth 100-500 μm . Involucre hyaline with a distinctly fimbriate margin.

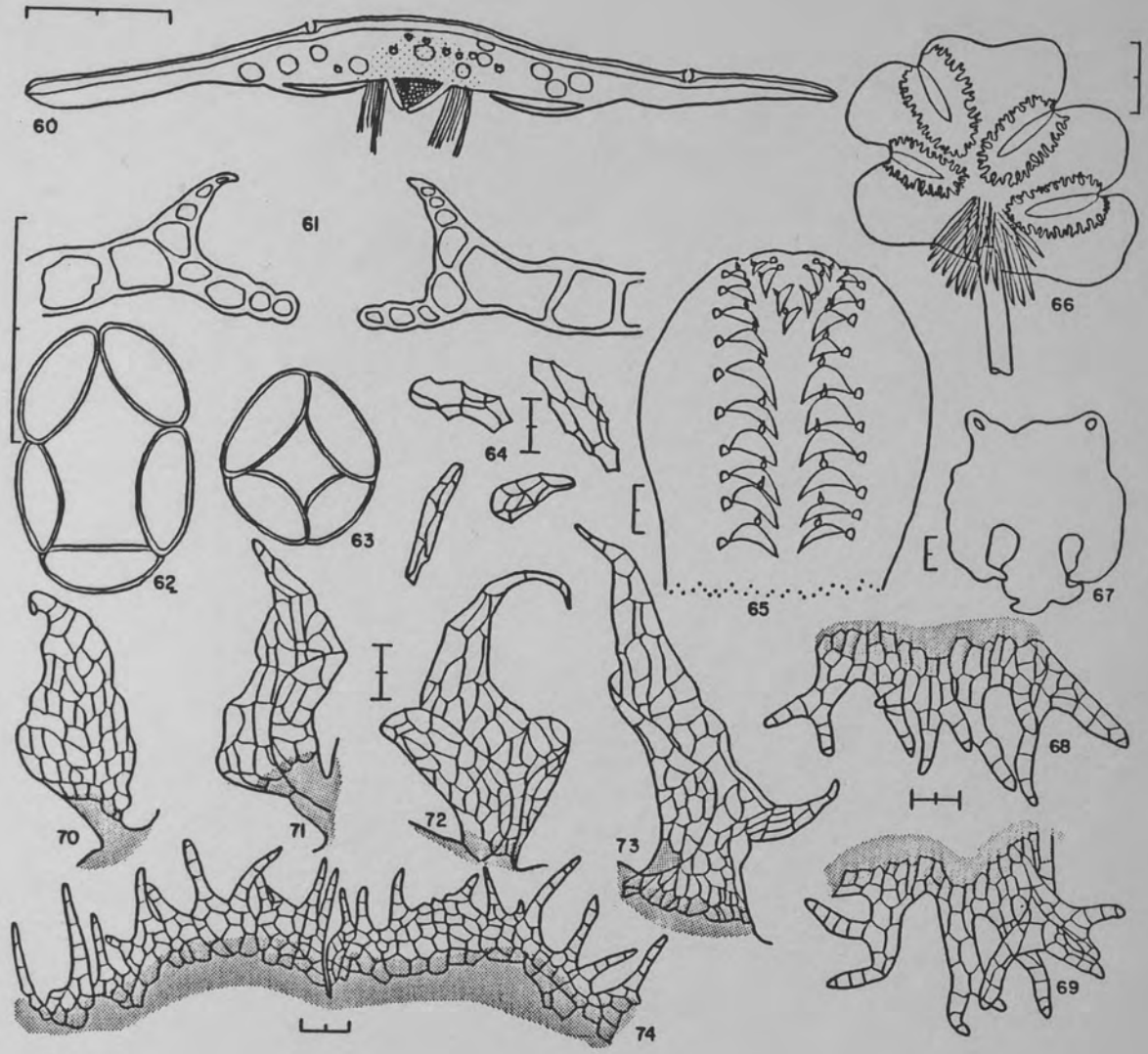
Gemmae cup margins ciliate with the cilia 4-5 cells long.

Marchantia fimbriatula superficially resembles M. crenata but the marked differences warrant the description of a new species. The most obvious difference is found in the distinctive fimbriate involucre margin. Another character which I have not seen in any other species is the occasional presence of appendicula on the sides of the median ventral scale appendages. The ventral scale appendages are also strongly auriculate, unlike other Hawaiian species. I have also seen appendages on laminal scales where they are rarely observed in herbarium material

of the genus. These appendages are often reduced and usually occur near the thallus apex. The thallus cross section shows significantly larger air spaces than other Hawaiian Marchantia species.

Specimens examined: HAWAII. Oahu: Punaluu, Svihla 35-169 (type, BISH).

Figures 60-74. Marchantia fimbriatula. 60. Thallus cross section.-- 61. Doliipore cross section.-- 62-63. Doliipore openings, surface view.-- 64. Sclerids.-- 65. Thallus, ventral surface.-- 66. Archegoniophore receptacle, ventral view.-- 67. Archegoniophore stalk, cross section.-- 68-69. Involucre margin.-- 70-73. Scale appendages.-- 74. Gemmae cup margin. Scale bars 60, 65-66 = 1 mm; 61-64, 67-74 = 100 μ m.



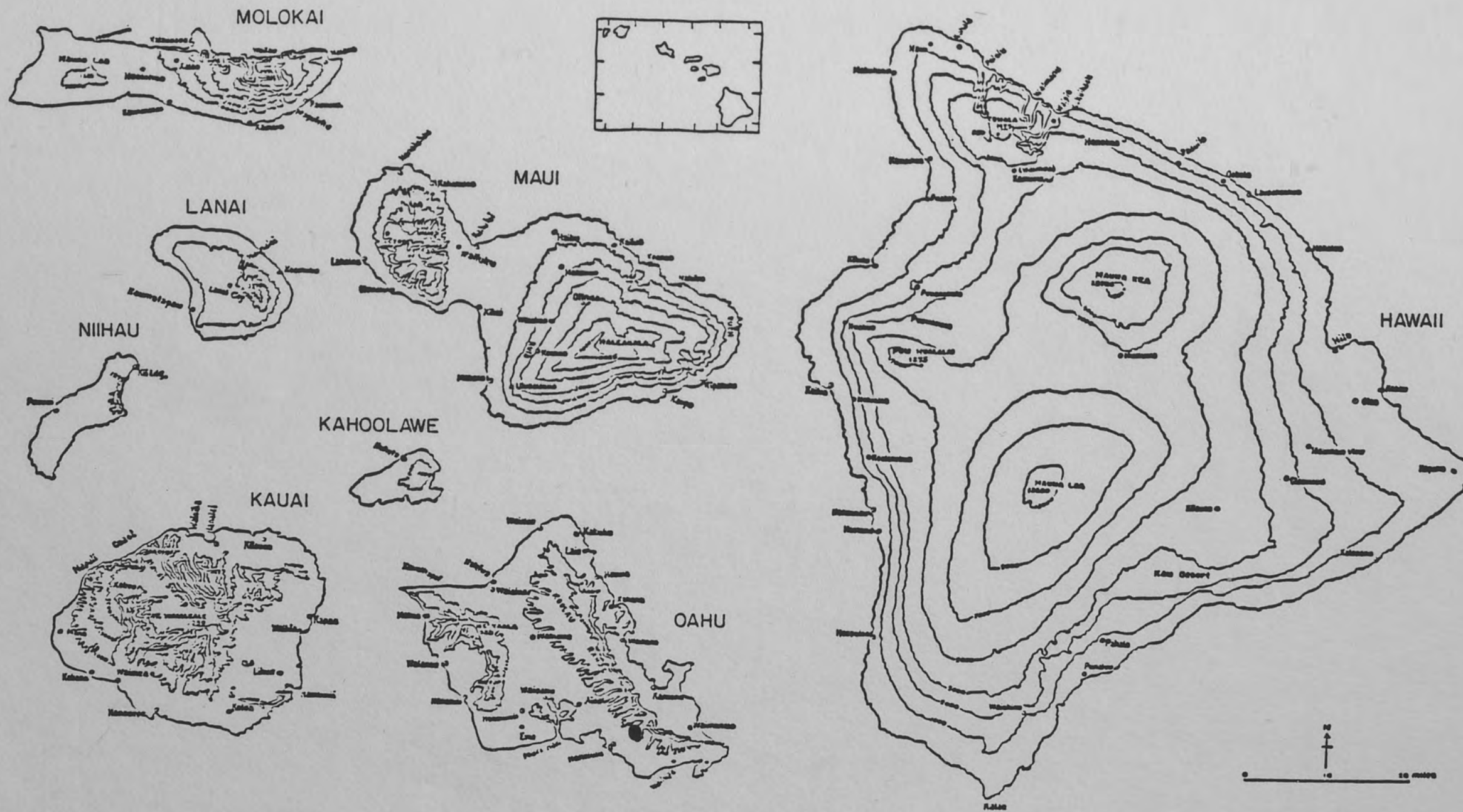


Figure 75. Distribution of *Marchantia fimbriatula*.

DISCUSSION AND CONCLUSIONS

The taxonomy of Hawaiian Marchantia has been limited to the study of small collections with species reports and descriptions of new taxa until now. Many of the old reports were based on identification errors and some described taxa have proven to be synonyms. Of the fourteen species names reported from Hawaii two, Marchantia trichocephala and M. innovans, belong to other genera. Five species, M. nitida, M. polymorpha, M. disjuncta, M. chenopoda, and M. punaluana, were treated in the literature as synonyms or misidentifications prior to my study. Of the seven remaining, I have been able to distinguish three taxa. Marchantia paleacea, a fairly common species in tropical America, apparently does occur in Hawaii, although female plants are needed for final confirmation. Marchantia marginata is reduced to a variety of M. antiqua which has three intergrading varieties. Marchantia furciloba, M. cuspidisquama, M. rechingeri, and M. crenata are considered to be synonyms of the genetically plastic M. crenata in which three varieties have been recognized. One new species, M. fimbriatula, was discovered and is here described, bringing to four the number of species now known to occur in the Hawaiian Islands.

The present high Hawaiian Islands were formed by submarine volcanoes probably near the end of the Tertiary Period in the Pliocene Epoch about seven million years ago. Each of the six major islands behaves like a miniature continent, with individual climatic patterns which contribute to a vast array of habitats.

The extreme isolation of the Hawaiian Islands in the North Pacific has led to a high frequency of endemics in both flora and fauna. The existence of three endemic Marchantia species, M. antiqua, M. crenata and M. fimbriatula, is consistent with the high level of endemism in Hawaii. Native seed plants are nearly 99 percent endemic; vascular cryptogams are over 64 percent endemic; and bryophytes are about 60 percent endemic, probably as a result of the isolation of the islands combined with the vast variety of available habitats. Although the Hawaiian bryoflora is known for its endemics, there is also an element composed mostly of Indomalayan genera and species. The Indomalayan element correlates with weather patterns which move north along the coast of Japan and Asia and bend south near Alaska and the North American continent, turning east near the equator and continuing around to the Hawaiian Islands. At present, no Indomalayan Marchantia species are confirmed to occur in Hawaii. However, if M. antiqua proves to be a synonym of M. subgeminata, described from the

Celebes, this species will be an Indomalayan one. The small but significant tropical American element in the Hawaiian flora is represented by M. paleacea. This element also corresponds to weather patterns which flow east from tropical America and move around to the islands. The varieties of M. antiqua and M. crenata correlate with limited geographic areas and may be incipient species. Based on the collections I have seen, M. antiqua var. antiqua occurs on Molokai and Oahu; M. antiqua var. millerii occurs on Molokai and Maui; and M. antiqua var. marginata occurs on Oahu. It is possible that the different varieties of M. antiqua evolved as a result of geographic isolation. A similar pattern of island isolation is seen in the distribution of M. crenata, where three of the islands have only one variety. Marchantia crenata var. crenata occurs on Kauai and Oahu with one population seen from Hawaii; M. crenata var. cuspidisquama occurs only on Hawaii; and M. crenata var. furciloba occurs on Maui and Hawaii. Thus, even though the numbers are small, the genus Marchantia reflects the patterns of geographic relationships and species endemism characteristic of the native Hawaiian flora as a whole. Comparison of the Hawaiian Marchantia species with those of islands of the tropical Pacific and the Indomalayan region will do much to contribute to our understanding of the genus in the Pacific.

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