DISTRIBUTION, ECOLOGY, AND SYSTEMATICS OF THE FILMY FERNS (HYMENOPHYLLACEAE) OF MOOREA, FRENCH POLYNESIA

JOEL H. NITTA

Department of Integrative Biology, University of California, Berkeley, California 94720 USA

Abstract. Ferns present an interesting case in island biogeography because of their unusually high dispersal ability. A general survey of the filmy ferns (Hymenophyllaceae) of Moorea, French Polynesia was undertaken by observing distribution in the field, conducting tests of desiccation tolerance, and inferring a phylogeny based on morphological characters. A total of 12 filmy fern species (including three species previously unreported in the literature for Moorea) were found to occur in moist, well-covered habitats throughout the island, with distinct sets of high elevation and low elevation species. Five species were included in an experiment to determine relative degree of desiccation tolerance; results indicate that terrestrial species have lower desiccation tolerance than epiphytic or epipetric species. In order to place the Moorea filmy ferns in the larger archipelago context, eight additional Society Island species were included in the phylogeny for a total of 20 taxa based on 21 morphological characters; interspecies relationships reflect the taxonomy of Hymenophyllaceae sensu lato. Filmy fern species are widely dispersed throughout the Society Islands, and there is no indication of an adaptive radiation on Moorea.

Key words: Filmy Ferns; Hymenophyllaceae; Moorea, French Polynesia; Society Islands; desiccation tolerance; systematics; island biogeography

INTRODUCTION

Ferns are interesting plants to consider from a biogeographical perspective because of their extremely high dispersal capability. The spores of most fern species are small, lightweight, and can remain viable for months in an air-dry condition; these characteristics have enabled ferns to become widely dispersed, even to oceanic islands located thousands of kilometers from the mainland (Tryon 1970). Ferns on remote islands are of particular significance because they represent a disharmonic subset of the source flora (Whittaker 1999). Although many potentially colonizing fern species may disperse their spores over a wide area, only those that can tolerate the conditions of the new habitat will be able to survive and successfully establish a population (Wolf et al. 2001).

One such group of ferns that seems to be restricted in its potential habitat is the filmy ferns (Hymenophyllaceae). These ferns derive their name from their extremely thin lamina, which is only one cell layer thick. In addition, filmy ferns also lack any differentiated epidermis or stomata. Thus, they are highly dependent on environmental moisture and occur only in moist (but not completely wet) areas. The filmy ferns have diversified extensively within this niche, displaying an amazing degree of variation in both morphology (erect to long-creeping rhizome, robust roots or rootless, simple to divided fronds, overall size minute to large) and growth habit (terrestrial, epipetric, epiphytic, and liana) (Dubuisson et al. 2003a). These characteristics make filmy ferns an ideal model system for studying processes of evolutionary adaptation and dispersal.

Although the fern flora of many Pacific islands such as the Hawaiian Islands has been extensively studied (Robinson 1914, Palmer 2002), those of the Society Islands have received relatively little attention. The most comprehensive review of the ferns of the

Society Islands is Copeland's (1932) *Pteridophytes of the Society Islands*, however, extensive taxonomic revisions since that time have rendered it nearly unusable. More recently, Murdock and Smith (2003) compiled a checklist for ferns on Moorea based on field work, a literature review, and a survey of herbarium specimens. Two additional filmy fern species were described on the island just last year (Ranker et al. 2005)

This study was conducted on the island of Moorea, French Polynesia at the University of California, Berkeley Gump Research Station. My goal was to describe the diversity of Hymenophyllaceae on Moorea by 1) observing distribution throughout the island, 2) conducting tests of desiccation tolerance, and 3) inferring a phylogenetic tree based on morphological characters that can serve as a framework to interpret distributional and experimental data. In order to place the Moorean filmy ferns in a larger Society Island context, herbarium samples from various locations outside Moorea are also included in the tree.

Family Characteristics

Filmy ferns are an ancient group, with putative fossils dating back to the Triassic (Axsmith et al. 2001). They occupy a basal position in the leptosporangiate clade, sister to the most basal family Osmundaceae (Pryer et al. 1995). The Hymenophyllaceae family is highly diverse (>600 species).

Members of the Hymenophyllaceae family are characterized by their simplified lamina, which is only a single cell thick and lacks any differentiated epidermis or stomata. Filmy ferns also have unique sori. Unlike many ferns which bear sori on the underside of the leaf, filmy fern sori occur at the edge of the leaf, on the tips of veins. The sori are contained within involucres (synonymous with indusia for this family). The receptacles that bear the sporangia may either be exserted or included. Although the family contains a range of morphological diversity, many filmy ferns are reduced in size, with fronds reaching lengths of less than 2 cm (reviewed in Dubuisson et al. 2003a).

FIG. 1. Mat-like covering of *Crepidomanes minutus* on a tree branch halfway up the trail to Mt. Mouaputa summit. Photo by Joel Nitta.
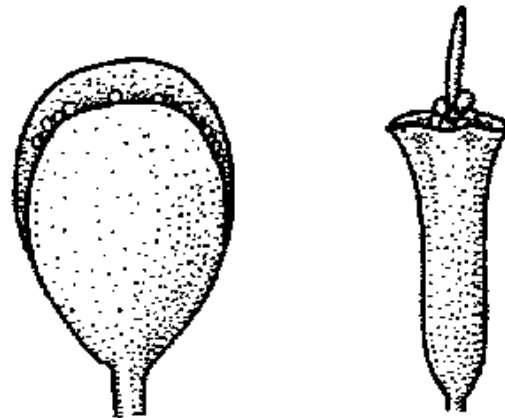

FIG. 2. Bivalved (left) vs. tubular (right) involucres. Involucres of most species are no more than a few mm long. Adapted from Palmer 2002.

The ecology of filmy ferns reflects their morphology. The thin lamina of filmy ferns dries out quickly, so they are restricted to perennially moist habitats. Most filmy ferns are either epiphytic or epipetric, with a few terrestrial and liana species. If the habitat is favorable, ferns may occur in a dense mat of interweaving rhizomes and cover the substrate (Fig. 1).

Taxonomy of the Hymenophyllaceae

Although the monophyly of Hymenophyllaceae as a family is undisputed, there has been a great deal of debate concerning intrafamilial relationships. Two main genera have been traditionally recognized based on involucre morphology,

Trichomanes having tubular involucres and *Hymenophyllum* having bivalve involucres (Fig. 2). Over the years, several modifications have been proposed to this bigeneric scheme. Morton (1968) added four monotypic genera, and defined multiple subgenera, sections, and subsections within *Trichomanes* and *Hymenophyllum*. Iwatsuki (1984) contended that involucre morphology within the family actually varies over a range from tubular to bivalve, and proposed eight genera to match this finer gradation in morphology. Other classification schemes have involved upwards of 30 to 40 different genera (Copeland 1938a, Pichi-Sermolli 1977).

Recent molecular phylogenetic studies have shed new light on systematic relationships within the family. A molecular phylogeny based on the plastid RBCL gene contains two large monophyletic lineages, which correspond to the traditional *Trichomanes* / *Hymenophyllum* split (Pryer et al. 2001). Other studies have elucidated relationships within genera (Dubuisson et al. 2003b, Ebihara et al. 2004), and Ebihara et al. have proposed yet another classification system based on monophyletic groupings found using RBCL data (Ebihara et al. 2006).

As the taxonomy of this group is still in flux, I have chosen to use Ebihara's recently published revised taxonomy of the family, which is supported by molecular data. This taxonomy largely retains the *Hymenophyllum* genus sensu lato, while splitting the Trichomanoid group into several genera.

Prior to this study, a total of nine species of filmy ferns were known to occur on Moorea (Copeland 1938b, Murdock and Smith 2003,

Family Hymenophyllaceae
    Genus *Abrodictyum*
        Subgenus *Abrodictyum*
            Abrodictyum caudatum (Brack.) Ebihara & K. Iwats.
        Subgenus *Pachychaetum*
            Abrodictyum dentatum (Bosch) Ebihara & K. Iwats.
    Genus *Callistopteris*
        Callistopteris apiifolium (C. Presl) Copel.*
    Genus *Crepidomanes*
        Subgenus *Crepidium*
            Crepidomanes humile (G. Forst.) Bosch
        Subgenus *Crepidomanes*
            Section *Crepidomanes*
                Crepidomanes bipunctatum (Poir.) Copel.
                Section *Gonocormus*
                    Crepidomanes minutum (Blume) K. Iwats.
                    Crepidomanes saxifragoides C. Presl
    Genus *Didymoglossum*
        Subgenus *Didymoglossum*
            Didymoglossum tahitense (Nadeaud) Ebihara & K. Itwats.
    Genus *Hymenophyllum*
        Subgenus *Mecodium*
            Hymenophyllum polyanthos (Sw.) Sw.
        Subgenus *Pleuromanes*
            Hymenophyllum pallidum (Blume) Ebihara & K. Iwats.
        Subgenus *Sphaerocionium*
            Hymenophyllum digitatum (Sw.) Fosberg**
    Genus *Polyphlebium*
        Polyphlebium endlicherianum (C. Presl) Ebihara & K. Iwats.

FIG. 3. Taxonomic relationships of the filmy ferns of Moorea sensu Ebihara et al. (2006). * *Trichomanes apiifolium* is listed as *Trichomanes societense* in Murdock and Smith (2003), but they report that the two are very similar and most likely the same species. ** *H. digitatum* is also listed as *H. taeniatum*, but this is most likely a species complex.

Ranker et al. 2005). I discovered three filmy ferns previously unreported in the literature for Moorea, bringing the total to 12. The Moorean filmy ferns are a diverse group, representing six of Ebihara's nine genera. Classification of the Moorean filmy ferns following Ebihara's system is outlined in Figure 3.

Desiccation Tolerance

Most animals and flowering plants cannot survive being dried to equilibrium with the air; however, many organisms under 5 mm in size posses the ability to survive complete desiccation (defined as drying to 10% or less of original water content) (Alpert 2006). Desiccation tolerance is truly a remarkable feature, as it requires complete suspension of metabolism and the preservation of organelles that are normally bathed in fluid (Hoekstra et al. 2001). Desiccation tolerance is known in a few animal species, approximately 350 species of adult flowering plants and ferns, and the majority of lichens and mosses (Alpert 2006).

Filmy ferns, although normally restricted to moist, shady areas, are also known to survive long intermittent periods of drying
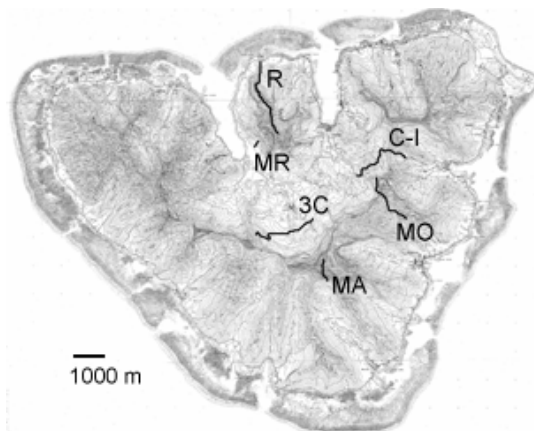

FIG. 4. Location of filmy ferns study sites on Moorea. All sites indicated by heavy black lines. Key: 3C = Three Coconuts Trail, C-I = Cross Island Trail, MA = Mahaeru Creek, MO = Mt. Mouaputa Trail, MR = Marimari Kellum's property, R = Mt. Rotui Trail. Adapted from Ministere de L'Urbanisme des Transports Terrestres et de L'Administration Generale.

due to sunlight (Shreve 1911). Filmy ferns occur in similar habitat and have even adapted similar growth forms to many mosses, so it is unsurprising that they have also evolved desiccation tolerance as well. Proctor (2003) conducted one of the only physiological studies of filmy ferns, and found two species with different overlapping ranges in south-west England to have different degrees of desiccation tolerance as measured by chlorophyll fluorescence.

The ability to tolerate drying is likely to be linked to geographic range. In this study, I have conducted desiccation tolerance experiments in the laboratory on each species to determine if they have different desiccation tolerances and how these relate to their distribution on the island.

METHODS

Distribution Analysis

Distribution analysis was primarily conducted by observing ferns near hiking trails. Filmy ferns only occur in shaded, moist areas, and are thus restricted to forests on the island's interior. There are many hiking trails traversing different parts of the interior of Moorea, ranging in elevation from sea level to 1207 m, at the top of the highest peak, Toihea. Trails I hiked included Three Coconuts Pass, Mt. Rotui, Mt. Mouaputa, and the Vaiare to Paopao cross island trail (Fig. 4). I also sampled ferns from Marimari Kellum's property and the Mahaeru stream valley on the south face of Mt. Tohiea. These areas lacked trails, but I was able to sample by hiking cross-country. Sampling involved gathering ecological data such as relative percent cover, aspect, habitat, height, and population density, as well as taking GPS coordinates for each specimen.

Desiccation Tolerance Experiment

I conducted a laboratory experiment in order to determine if the various species of filmy ferns on Moorea have different abilities to tolerate desiccation that might influence their distribution. The experiment relied on ion leakage as a measure of membrane

damage due to desiccation, a technique commonly used in mosses and lichens (Shirazi et al. 1996). In these plants, intracellular cations have been shown to leak from cells following desiccation stress; plants that are desiccation tolerant show significantly less leakage than those that are sensitive (Brown and Buck 1979). In addition, given enough time, desiccation tolerant plant species will be able to repair the damage to their membranes and ion leakage will decrease or cease completely (Leopold et al. 1981).

Due to time restrictions, it was not possible to include all 12 Moorean filmy fern species in the experiment. Instead, 5 species representing a variety of habitats and morphology were selected. Fern specimens were immediately placed in airtight containers in the field upon collection, and used within 12 – 24 h to prevent any desiccation damage before the experiment began. All samples were soaked in tap water in the laboratory overnight to insure maximum hydration prior to the experiment. Each sample consisted of a minimum of 0.015 g (wet weight) of frond material, with a maximum sample wet weight of 0.080 g. 8 samples (n = 8) were used per replicate. In order to achieve a homogenous sample containing only lamina and veins, fronds were cut so that no part of the stipe or rachis was included in the sample. Samples were washed with deionized water, blotted dry, and weighed. These were placed in airtight containers, and kept at 24°C in the dark at either 100% or 20% relative humidity. Humidity was maintained by placing deionized water or silica gel respectively inside the containers. Degree of desiccation damage and subsequent repair was measured twice, after periods of 7 and 14 days. At each of these times, fronds were removed from the containers, weighed, placed in 12.5 mL deionized water, allowed to sit for 2 hours, and removed. A Corning Checkmate II conductivity meter (Corning Inc., Corning, USA) was used to measure conductivity of the resulting solution. After this measure of membrane damage due to desiccation, samples were soaked in tap water for 24 hours in a controlled setting (63% RH, 24°C, darkness) to allow frond membranes to recover. Conductivity of the samples was then measured again following the protocol described above. Finally, samples were dried overnight in an oven at 65°C and weighed to determine dry weight.

For statistical analysis, ion leakage was expressed by dividing conductivity (uS/cm3) by dry weight (g) for each sample to correct for dependence of leakage on membrane mass. Data were found to deviate from a normal distribution by the Shapiro-Wilk test ($p < 0.0001$). A log transformation of the data still did not approximate a normal distribution ($p < 0.0001$). The Wilcoxon test was used to determine if there was any significant difference between groups in the data. Significance of difference between specific groups was determined using the Tukey test.

Morphological Phylogeny

Outgroup selection was limited because of extremely low degree of homology between Hymenophyllaceae and its sister family Osmundaceae. Instead of choosing a specific outgroup, tree rooting was based on current molecular phylogenetic studies at the sub-generic and species level (Ebihara et al. 2006).

Terminal taxa of the phylogeny include all Moorean filmy fern species observed in this study as well as several species known to occur on other islands in the Society Island archipelago.

Morphological characters were chosen based on the criteria that they be 1) heritable, 2) unique, and 3) significantly different between taxa (Brent Mishler, pers. comm.) Several characters were chosen based on those used in the morphological phylogeny of *Trichomanes* taxa by Dubuisson (1997). Character states for each Moorean filmy fern species were scored by examining specimens collected in the field. Character states for non-Moorean filmy ferns were scored by examining specimens collected on Tahiti and by examining herbarium specimens deposited at Tahiti (TA) and Berkeley (UC). After all characters were scored, a data matrix was compiled using MacClade 4.0 (Sinauer Associates Inc., Sunderland, USA).

The data matrix was loaded into PAUP 4.0 (Sinauer Associates Inc., Sunderland, USA) and hypothetical phylogenetic trees were

generated by using maximum parsimony analysis; these were then compiled into one single consensus tree.

RESULTS

Distribution Analysis

Below I describe the filmy fern occurrence at and condition of each study site. Filmy fern occurrences are summarized in Table 1.

Three Coconuts Pass - This trail leads from the Belvedre (247 m), a lookout with a vista of Mt. Rotui, to a ridge known as Three Coconuts Pass (357 m). It is mostly flat, meandering through the forest, crossing a few streams, and finally climbing near the end when the pass is reached. The habitat is typical of low- to mid-elevation Polynesian forest, dominated by *Inocarpus fagiferus* (Park.) Fosberg. and *Angiopteris evecta* (G. Forst.) Hoffm. *Cr. humile* and *Cr. bipunctatum* were common on tree trunks and rocks (the latter occurring more often on rocks). *D. tahitensis* was slightly more difficult to find, and occurred on the trunks of *Inocarpus fagiferus*.

Cross-Island Trail - This trail connects the port of Vaiare, on the west side of the island,

to the town of Paopao, located at the mouth of Cook's Bay to the north. It climbs gradually following a stream valley, then crosses the ridge (331 m) between Mt. Mouaputa and Mt. Tearai, then finally makes a long descent into Paopao. Habitat and filmy ferns observed were similar to the Three Coconuts Pass trail.

Marimari Kellum's Property - This piece of land is situated between Opunohu Bay and the eastern face of Mt. Rotui. There was no trail available, but I hiked toward Mt. Rotui until the slope became too steep to continue. Habitat and filmy ferns occurring here were again similar to the other two low- to mid-elevation sites. One difference is that this site is where I first observed *Cr. saxifragoides*, a species previously unreported in the literature for Moorea. *Cr. saxifragoides* occurs at Marimari Kellum's property on rocks within a nearly dry stream bed and on larger boulders up the hillside.

Mt. Rotui Trail - This trail starts on the coast between Cook's Bay and Opunohu Bay and climbs a north-facing ridge to the top of Mt. Rotui (899 m). Unlike the preceding three sites, it lacks a low- to mid-elevation *Inocarpus fagiferus* forest. Rather, the lower elevation hillside is mostly dry and dominated by

TABLE 1. Distribution of filmy ferns within study sites on Moorea. Data are relative abundance and elevations (m) for each species by site. Relative abundance was determined by ease with which specimens could be found in the field; white = common, grey = uncommon, black = rare. Elevation is based on GPS readings from collected specimens and field notes.

Site	*A. caudat.*	*A. dentat.*	*Cal. apiifol.*	*Cr. bipunct.*	*Cr. humile*	*Cr. minutus*
marimari	-	-	-	40 - 150	40 - 150	-
x island	-	-	-	40 - 330	40 - 330	-
3 cocos	-	-	-	250 - 300	250 - 360	-
mahaeru	400 - 500	400 - 500	490	130 - 300	130 - 300	400 - 500
rotui	-	-	-	-	-	600 - 800
mouaputa	600 - 830	460 - 800	400 - 830	100 - 450	100 - 450	500 - 830

	Cr. saxifra.	*D. tahitense*	*H. digitat.*	*H. polyan.*	*H. pallid.*	*P. endlich.*
marimari	40 - 150	40 - 150	-	-	-	-
x island	-	40 - 330	-	-	-	-
3 cocos	-	250 - 360	-	-	-	-
mahaeru	130	130 - 300	400 - 500	400 - 500	-	-
rotui	-	-	650 - 800	600 - 800	-	-
mouaputa	515	100 - 300	500 - 830	500 - 800	820	800

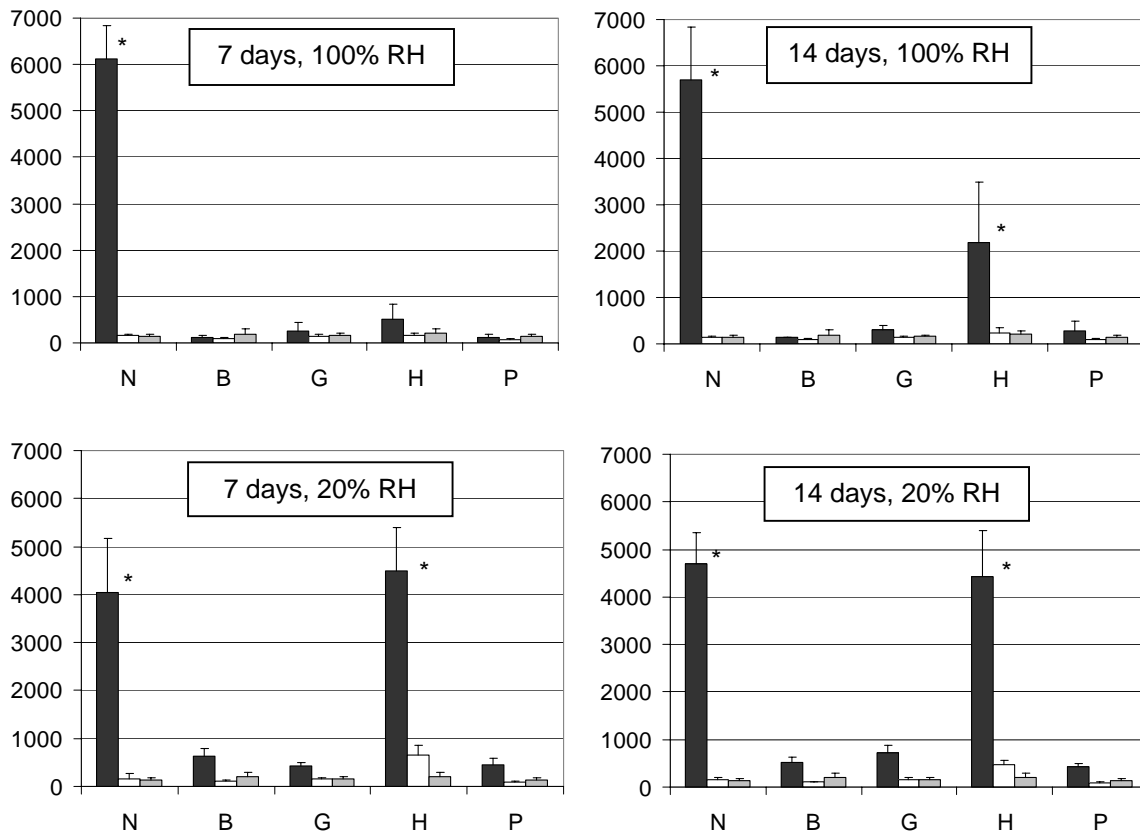Fɪɢ. 5. Results of desiccation tolerance test. Data are electrical conductivities (uS g⁻¹ dry weight) and 95% confidence intervals. Species key: B = *Cr. bipunctatum*, N = *A. dentatum*, G = *H. digitaum*, H = *Cr. humile*, P = *H. polyanthos*. For each species, the black bar is electrical conductivity immediately following desiccation, the white bar is electrical conductivity following a 24 hr recovery period, and the grey bar is control (no desiccation). * indicates results found to be significantly different from others by the Tukey test.

Psidium guajava Linn. and *Hibiscus tiliaceus* L. Thus, none of the typical low-elevation filmy ferns are to be found on this trail. Filmy ferns did not appear until higher elevations, when the habitat changes to cloud forest. The cloud forest is dominated by smaller trees and shrubs such as *Metrosideros collina* (JR & G. Forst.) A. Gray, *Weinmannia parviflora* Forster, and *Fagraea berteroana* A. Gray. *Dicranopteris linearis* (Burm. f.) Underw. dominates along the trail itself, often growing so thickly that it appears to limit the growth of other plants. *H. polyanthos* was the most common filmy fern, often occurring in mats covering tree trunks and branches. *Cr. minutus* occurred less frequently, and *H. digitatum* (previously unreported in the literature to occur on

Moorea) was occasionally spotted underneath overhanging branches or roots.

Mahaeru Creek - Mahaeru creek has its headwaters at the southern base of Mt. Tohiea. This area lacked a trail, but I followed a ridge next to the creek toward Mt. Tohiea until the slope became too steep to allow further progress. This area contained very high fern diversity. *Cr. humile* and *Cr. bipunctatum* were plentiful at low elevations near the creek, and *D. tahitense* was common on *Inocarpus fagiferus* trunks. Once I climbed above 350 m, I began to see *A. dentatum* on steep hillsides, and occasionally *A. caudatum* on tree ferns. Other high-elevation species such as those on Mt. Rotui were also present, but not as numerous.

I only saw one occurrence of *Cal. apiifolia*, mixed in with a population of *A. dentatum*.

Mt. Mouaputa Trail - This trail starts out above the town of Afareaitu (100 m) and climbs to the summit of Mt. Mouaputa (831 m). It follows a creek through a mid-elevation *Inocarpus fagiferus* forest for about 3 km, then climbs a ridge to the top of the mountain. The ridge is initially dry and dominated by *Dicranopteris linearis*, but eventually gives way to a humid cloud forest. Thus, this trail contains a variety of habitats and a high diversity of filmy ferns. Typical low elevation species were found along the creek, with the rare addition of *Cal. apiifolia* and *Cr. saxifragoides*. Upon reaching the base of the ridge (460 m), the trail enters a *Miconia calvescens* DC dominated thicket, and *A. dentatum* is common on the exposed soil. Higher up in the cloud forest, some rare species such as *H. pallidum* and *P. endlicherianum* (previously unknown in the literature to occur on Moorea) were discovered by carefully searching in the area next to the trail.

Desiccation Tolerance Experiment

Average water content following desiccation was 52.8% +/- 2.2% for samples dried at 100% RH and 13.2% +/- 2.2% for samples dried at 20% RH.

At 100% RH, electrical conductivity was significantly higher for *A. dentatum* over all other species after 7 days of drying; by 14 days of drying, *A. dentatum* still showed the greatest amount of ion leakage, but the electrical conductivity of *Cr. humile* also became significantly greater than the other three species (Fig. 5). These and other differences were found to be significant by the Tukey test at the 0.05 level, corrected for multiple tests. At 20% RH, both *A. dentatum* and *Cr. humile* had similarly high conductivity values which set them apart from the rest of the species. The electrical conductivity values for the other three species (*Cr. bipunctatum, H. digitatum, H. polyanthos*) never varied from each other significantly following desiccation after any time at either humidity.
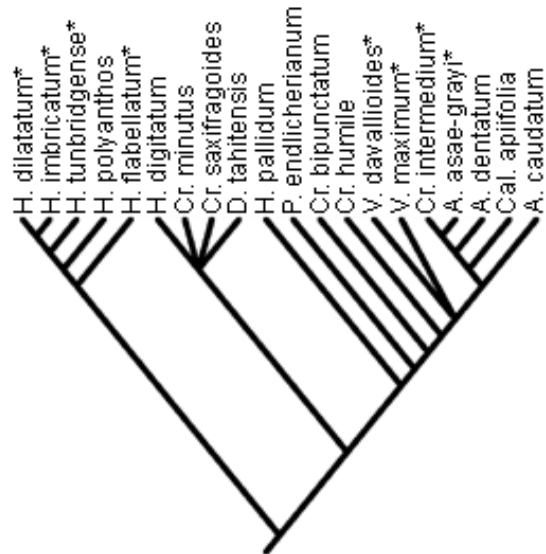

FIG. 6. Consensus tree showing evolutionary relationships between Society Island filmy fern species. * indicates non-Moorean filmy ferns.

All fern species tested were able to completely recover following desiccation (post-recovery ion leakage values were not significantly different from control values).

Morphological Phylogeny

A total of 25 morphological characters were defined and scored (see Appendix A). Some characters had to be excluded because they did not meet all three requirements mentioned above in the methods section. Characters were restricted to macroscopic features that could be seen either with the naked eye or under a dissecting microscope (up to 40x magnification). Characters included all major parts of the sporophyte: rhizome and roots, stipe, frond, and sporangia. Spore and gametophyte characters were not used.

21 characters were used to produce a phylogeny with 20 terminal taxa (Fig. 6). This phylogenetic tree is the consensus tree (consistency index = 0.0500) of 12 equally parsimonious trees, each with a length of 65 steps. Terminal taxa included all 12 Moorean species, plus 8 additional species that do not occur on Moorea but are described from other locations in the Society Island archipelago: *H. dilatatum* (G. Forst.) Sw., *H. imbricatum* Blume,

H. tunbrigense (L.) Sm., *H. flabellatum* Labill., *Vandenboschia. davallioides* (Gaudich.) Copel., *V. maximum* Blume, *Cr. intermedium* (Bosch) Ebihara & K. Iwats., and *A. asae-grayi* (Bosch) Ebihara & K. Iwats.

DISCUSSION

Tree Structure

The overall structure of the tree inferred using characters I selected supports the traditional bigeneric classification scheme for Hymenophyllaceae. The first split in the tree produces two monophyletic groups: *Hymenophyllum* s.l. and *Trichomanes s.l.* (Fig. 7). It is interesting to note that the *Trichomanes* s.l. clade includes both *H. digitatum* and *H. pallidum*, two species that were only recently reclassified as *Hymenophyllum* based on molecular data (Ebihara et al. 2006). It is logical that a tree based on morphological characters would reflect a classification system also based on morphology. The basal split of *Hymenophyllum* s.l. and *Trichomanes* s.l. into two monophyletic groups is also supported by the molecular data of Pryer et. al (2001). These results highlight the use of robust morphological characters as a valuable tool in taxonomic analysis of Hymenophyllaceae.

This tree also supports traditional classification schemes at the sub-generic level. Species from the same genera sensu Ebihara et al. generally appear sister to each other (*Vandenboschia*, *Abrodictyum*, *Hymenophyllum*); these species were usually considered in the same sub-genus or section by other taxonomists (Copeland 1932, Morton 1968). The few exceptions are probably due to a low sample size (only 21 characters), rather than differences in evolutionary hypotheses. In order to produce a more highly resolved tree it will be necessary to include more characters, such as those of the gametophyte and internal cell morphology.

Elevational Gradient

As I observed the filmy ferns at each study site, I noticed that species composition varied along an elevational gradient, and that this gradient was similar between sites. The
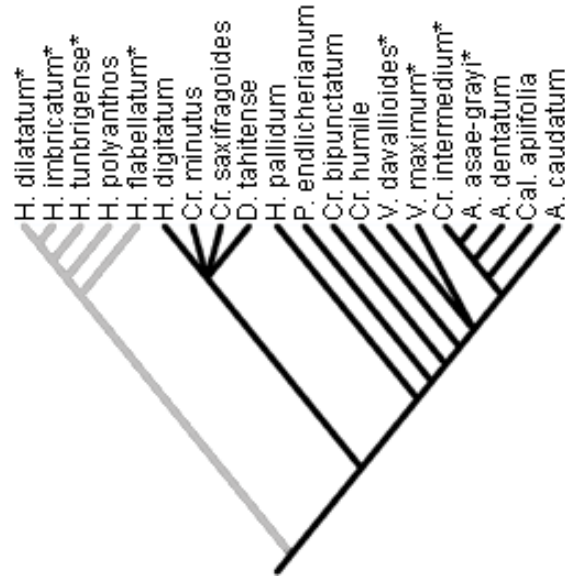

FIG. 7. Traditional classification system overlaid onto consensus tree. Grey indicates species classified under *Hymenophyllum* senso lato; black indicates species classified under *Trichomanes* sensu lato. * indicates non-Moorean filmy ferns.

Moorean filmy ferns can be split into two major groups: low elevation species occurring below 450 m and moderate to high elevation species occurring above 450 m. These two groups were largely exclusive, with little overlap in range. Low elevation species include *Cr. bipunctatum*, *Cr. humile*, *Cr. saxifragoides*, and *D. tahitense*. Moderate to high elevation species include *A. dentatum*, *A. caudatum*, *Cal. apiifolia*, *Cr. minutus*, *H. polyanthos*, *H. digitatum*, *H. pallidum*, and *P. endlicherianum*.

The physical factors responsible for determining fern distribution along the elevational gradient such as humidity and precipitation are important in determining the species composition of all plants, not just filmy ferns. There is a marked difference in plant communities between the low- to mid-elevation valley forest dominated by *Inocarpus fagiferus*, *Hibiscus tiliaceus*, and *Angiopteris evecta* and the high elevation cloud forest dominated by *Metrosideros collina*, *Weinmannia parviflora*, and a huge variety of epiphytes. This transition in plant communities is reported to occur at 400 – 500 m for Polynesian high volcanic islands (Meyer 2004),

a figure which matches the cutoff point between my two filmy fern groups. Thus, the difference in filmy fern species composition between high and low altitude reflects an overall difference in plant communities between high and low altitude.

It is interesting that the clear elevational gradient in species composition that I observed in the field did not match the mixed results of the desiccation tolerance test, however. High elevation species included in test showed both relatively high (*H. digitatum*, *H. polyanthos*) and low (*A. dentatum*) degrees of desiccation tolerance as indicated by ion leakage values. Similarly, the low elevation species also yielded mixed results; *Cr. humile* displayed a low degree of desiccation tolerance, whereas *Cr. bipunctatum* was much more tolerant. This suggests that relative degree of desiccation tolerance may only be a minimal factor in determining filmy fern distribution. In my test, all five species included were able to completely recover following desiccation, regardless of the degree of initial damage. Perhaps filmy ferns only need to survive a certain minimum amount of desiccation in the field, and relative degree of desiccation tolerance beyond this minimum is unimportant.

The results of the morphological phylogeny can also be used to interpret this elevational pattern. When elevational data from the distribution survey is overlaid on the consensus tree, it is apparent that the low elevation and high elevation species do not form monophyletic groups (Fig. 8). However, the low elevation species do form two grades each containing a pair of closely related species. This shows that low elevation species have evolved similar morphology that reflects their habitat niche. Although the filmy fern species occupying a single habitat type may not necessarily be more closely related to each other than those from different habitats, they do share at least some of the same morphological adaptations.

Growth Habit

Another pattern I noticed in the course of this study is the correlation of both distribution and desiccation tolerance with
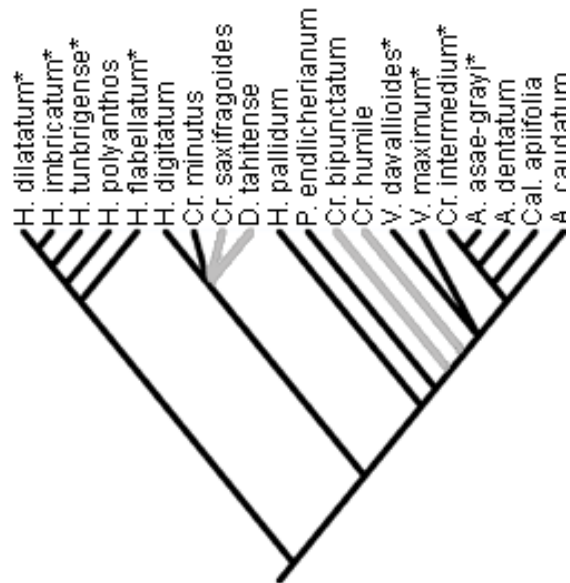

FIG. 8. Distributional data overlaid onto consensus tree. Grey indicates low elevation species; black indicates mid to high elevation species except for non- Moo'orea species noted with an asterisk, for which distribution data are lacking.

growth habit. Of the twelve Moorean filmy fern species, only two (*A. dentatum* and *Cal. apiifolia*) are terrestrial; the rest are epiphytic or occasionally epipetric. [The line between epiphytism and epipetrism is blurred in the field; I observed many species typically described as epiphytic growing on both trees and rocks. The important difference between these and terrestrial species is the habit of growing into the soil (terrestrial) versus growing spread out over the surface of some substrate (epiphytic or epipetric), not the nature of the substrate itself. Therefore, I will refer to these as "epiphytic" species with the intention of including occasional epipetrism.]

Dubuisson et al. (2003a) noted that growth habit correlates with habitat within *Trichomanes* s.l., describing terrestrial species as more widespread and epiphytic species as restricted to wet areas or cloud forests. I observed the opposite trend on Moorea, finding the two terrestrial species only at high elevation, and epiphytic species at both high and low elevations. This could be an issue of sample size; Dubuisson's study includes 193 of the 325 members of *Trichomanes* s.l., whereas my study includes only 12 species

from both *Trichomanes* s.l and *Hymenophyllum* s.l. Another possibility is that the two terrestrial species I found are relatively weak competitors in the Moorean forest environment. *Cal. apiifolia* seems to be an infrequent reproducer: of the eight specimens of *Cal. apiifolia* that I collected in the field, only two had fronds bearing sporangia. I also noticed that *A. dentatum* showed more evidence of herbivory damage than other species. These observations suggests that perhaps these species are poor competitors and became restricted to high elevation as low elevation areas became crowded with other (non-filmy) terrestrial fern species.

There is a strong correlation between growth habit and desiccation tolerance. Electrical conductivity values following initial desiccation were generally higher for the terrestrial *A. dentatum* than the other epiphytic species, indicating that terrestrial ferns have a lower desiccation tolerance than epiphytic ferns. Most epiphytic ferns do not possess true roots, and all water gain and loss occurs through frond lamina and rhizomes located near the substrate surface. Therefore, it makes sense that they would evolve countermeasures such as desiccation tolerance to survive prolonged periods of low humidity. Terrestrial species such as *A. dentatum*, however, can still rely on an extensive root system to absorb water from the ground even when atmospheric humidity is low. Thus, terrestrial species have less selection pressure to gain extensive desiccation tolerance. There was one exception to the pattern – *Cr. humile*, an epiphyte, had electrical conductivity values nearly as high or higher than *A. dentatum* after drying at 20% RH. More tests including more representatives of both terrestrial and epiphytic growth habits are needed to clarify this trend.

The importance of growth habit as an evolutionary adaptation can be seen by plotting growth habit states for each species onto the phylogeny (Fig. 9). Terrestrial species and epiphytic species each form nearly exclusive groups. This reflects both the unique morphological characters that each group has developed as well as their distinctness as evolutionary lineages. Characters related to growth habit should be
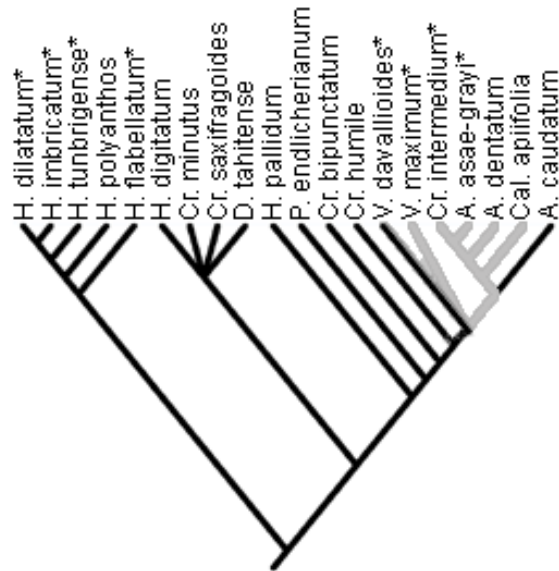

FIG. 9. Growth habit overlaid onto consensus tree. Grey indicates terrestrial species; black indicates epiphytic species. * indicates non-Moorean filmy ferns.

useful for continued taxonomic studies within the family.

Island Distribution

By including other Society Island species in the phylogeny and examining distribution data for each species, it is possible to place the Moorean filmy ferns in the larger context of an island chain. The 12 filmy ferns occurring on Moorea are also known to occur on most of the other Society Islands (Copeland 1932, Moore 1933, Copeland 1938b, Robertson 1952, Fosberg 1997, Ranker et al. 2005), and Moorea species do not form a monophyletic group within Society Island filmy ferns, as can be seen on the consensus tree (Fig. 6). This, plus the fact that Moorea filmy ferns include a wide variety of genera, suggests that filmy ferns on Moorea do not represent the result of an adaptive radiation; rather, they have probably evolved independently in other locations and subsequently become widespread throughout the Society Island archipelago. High dispersal ability conferred via lightweight, durable spores seems to be a characteristic that unites all ferns, reflected in their disproportionately high frequency in island flora and low rate of endemism (Smith

1972). This high dispersal ability does have its limits, however: although the filmy fern flora from nearby island chains such as the Marquesas or Cook Islands are reported to be similar to that of the Society Islands (Robertson 1952, Game et al. 1997), a different set of species occurs on the more distant Hawaiian islands (Palmer 2002). By sampling from a broad area representing several island chains, it should be possible to clarify biogeographical patterns within the Pacific Hymenophyllaceae in future studies.

Conclusion

The family Hymenophyllaceae contains a rich diversity of ecology and morphology, and this diversity is well represented by the filmy ferns of Moorea. Moorean filmy ferns occur from low (30 m) to high (900 m) elevations in epiphytic, epipetric, and terrestrial growth forms. They display a variety of morphological characters that have evolved to match the niche of each species including frond size, loss of roots, and rhizome habit. Within this diversity, certain patterns are evident such as a low degree of desiccation tolerance in terrestrial species and strong elevational preference. By constructing a phylogenetic tree that includes filmy ferns known from other sites within the Society Island archipelago, larger biogeographical patterns become evident. The Moorea filmy ferns do not appear to be the result of an adaptive radiation, but rather a group of species that each evolved elsewhere and immigrated to the island independently. These patterns seen in my study highlight the suitability of filmy ferns as a model system for studying processes in evolution and biogeography. It is certain that more fascinating contributions can be made to these fields by continued investigation of the family Hymenophyllaceae.

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APPENDIX A: CHARACTERS

RHIZOME

1. *Habit: 0 = erect; 1 = creeping*. An erect rhizome is no longer than 5 cm in length for the entire fern, and all fronds are clustered together with very short internode length. An erect rhizome is often associated with the terrestrial growth habit. Creeping rhizomes have no limit on growth length, and fronds are spaced out along the rhizome. Creeping rhizomes are usually associated with the epiphytic or epipetric growth habit. See Figure 10.

2. *Presence of roots: 0 = true roots present; 1 = true roots absent, root-like shoots present*. Root-like shoots are a unique character of the Hymenophyllaceae family. Root-like shoots more closely resemble an extension of the rhizome rather than a true root. Differences cited by Schnieder include thickness compared to the rhizome (true roots are half the diameter of the rhizome or less; root-like shoots range from equal to half in size of the rhizome), presence of a root cap (true roots present; root-like shoots absent), and direction of growth (true roots positive geotropic or negative heliotropic; root-like shoots plagiotropic) (Schneider 2000). This character is also closely associated with growth habit. Most terrestrial species have retained full-sized roots, whereas epiphytic species possess root-like shoots.

3. *Hairs on rhizome: 0 = hairs absent, 1 = some hairs; 2 = thick hairs*. Hairs are defined as one or more elongated single cells in a row. Some species such as Cr. humile and Cr. bipunctatum have dense hairs such that the rhizome itself cannot be seen because it is completely covered in hairs. Others still possess hairs, but not completely covering the rhizome, whereas others are hairless or nearly so. Ebihara et. al. consider this one character that sets apart *Hymenophyllum* from the other genera (those previously considered to be in *Trichomanes*) (Ebihara et al. 2006). This is an ordered character. See Figure 11.

4. *Hairs on roots: 0 = hairs absent, 1 = some hairs; 2 = thick hairs*. This character only applies to those species having true roots; those lacking roots were scored as "?". Hairs are defined as above. This is an ordered character. See Figure 11.

5. *Hairs on root-like shoots: 0 = hairs absent;, 1 = some hairs, 2 = thick hairs*. This character only applies to those species having root-like shoots; those with true roots were scored as "?". Hairs are defined as above. This is an ordered character. See Figure 11.

6. *Rhizome diameter: 0 = filiform (<1 mm thick); 1 = medium (1 – 2.5 mm thick); 2 = robust (>2.5 mm thick)*. Reduced root size is usually associated with epiphytism, but not in all cases (such as A. caudatum, other Abrodictyum species). This is discrete-state, ordered character as shown in Figure 12.

STIPE

7. *Lamina: 0 = not winged; 1 = narrow wing (average 2 cells wide;) 2 = winged (average 5 cells wide)*. An extension of the lamina at least halfway down the stipe is called the "wing." This is an ordered character. See Figure 13.

8. *Hairs on stipe: 0 = hairs absent; 1 = hairs present.* There is no case of thick hairs covering the stipe as on the rhizome; only presence or absence is coded for.

9. *Hairs on wing: 0 = hairs absent; 1 = hairs present.* In one case, hairs were found to be growing from the margin of the stipe wing. **EXCLUDED**: only occurs in a single taxon (*Cr. bipunctatum*).

10. *Type of venation: 0 = dichotomous; 1 = anadromous, 2 = catadromous.* Filmy ferns are known for being the one of the few fern families containing both anadromous and catadromous vein patterns (Dubuisson 1997). In several species, especially those which lack highly dissected fronds, the vein pattern is dichotomous. See Figure 14.

11. *Cell walls: 0 = thin, straight cell walls; 1 = thick, wavy or pitted cell walls.* In most filmy ferns, the lamina appears delicate and translucent; however, in some, the lamina is darker in color and thicker due to thick cell walls, even though it is only one cell layer. This character could only be scored on fresh specimens; lamina of all dry specimens became wavy and toughened due to desiccation.

12. *Dissection of blades: 0 = simple to slightly lobed; 1 = once to twice pinnatifid; 2 = three times or greater pinnatifid.* No filmy ferns included in this phylogeny are completely pinnate. Species with larger fronds are often more dissected. This is treated as an ordered character.

13. *Sub-marginal false vein: 0 = absent;, 1 = present.* Most species lack any sort of specialized cells in the lamina, but false veins do appear in some. False veins appear distinct from other lamina cells and may serve a purpose as supporting tissue (Boer 1962). A sub-marginal vein appears 3 cells below the margin. Sub-marginal false veins may either be continuous (as in *Cr. saxifragoides*) or discontinuous (as in *Cr. bipunctatum*). See Figure 15.

14. *False vein in between true veins: 0 = absent; 1 = present.* This type of false vein appears between true veins rather than in the sub-marginal position. **EXCLUDED**: only occurs in a single taxon (D. tahitense).

15. *Specialized marginal cells: 0 = absent; 1 = present, but not elongated as compared to non-specialized lamina cells; 2 = present, two to three times longer than non-specialized lamina cells.* This is treated as an ordered character. See Figure 16.

16. *Frond size: 0 = large (>20 cm), 1 = medium (10 – 20 cm), 2 = small (2.5 – 10 cm), 3 = tiny (< 2.5 cm).* Filmy ferns display a range of frond sizes. Most epiphytic and epipetric species are smaller, whereas most terrestrial species are larger. This is a discrete-state, ordered character as shown in Figure 17.

17. *Habit of fronds: 0 = erect; 1 = lax; 2 = adpressed.* This could only be determined based on observations in the field. Treated as an unordered character.

18. *Hairs on veins: 0 = absent; 1 = present.* Small hairs, usually only one to two cells long appear on the veins of some species.

19. *Hairs on margin: 0 = absent; 1 = present.* **EXCLUDED**: only occurs in a single taxon (H. digitatum).

20. *Cell shape: 0 = round; 1 = elongated.* Cell-shape is cited as a useful character at the specific level for *Hymenophyllum* s.l. (Sanchez et al. 1995). Therefore, I felt it was applicable to a species level usage across the whole family.

21. *Position of sori: 0 = sori at end of ultimate segment; 1 = sori occurs before end of ultimate segment.* Although there could have been overlap between these two states, I observed that they were mutually exclusive. Sori either occurred at the end of the segment or somewhere near the middle.

22. *Immersion of sori in lamina: 0 = immersed; 1 = not immersed.* Sori may either be immersed in the lamina, or not immersed and on a pedicel.

23. *Position of receptacle: 0 = included to slightly exserted, but not more than 2 X the length of the involucre; 1 = significantly exserted.* Sporangia are clustered around the receptacle. Bivalve involucres usually have included receptacles, and tubular involucres usually have exserted receptacles. See Figure 18.

24. *Shape of involucre: 0 = mostly bivalve; 1 = mostly tubular.* This is a debated character. Iwatsuki proposes 8 different classes representing a range from tubular to bivalve, whereas traditional classification recognizes only two states. **EXCLUDED**: correlates with position of receptacle. Included to slightly exserted receptacles are always associated with bivalve involucres, and significantly exserted receptacles are always associated with tubular involucres.

VARIOUS

25. *Rhizoids: 0 = absent; 1 = present.* **EXCLUDED**: only occurs in a single taxon (D. tahitense). This is known as an autapomorphy of the *Didymoglossum* genus (Ebihara et al. 2006).
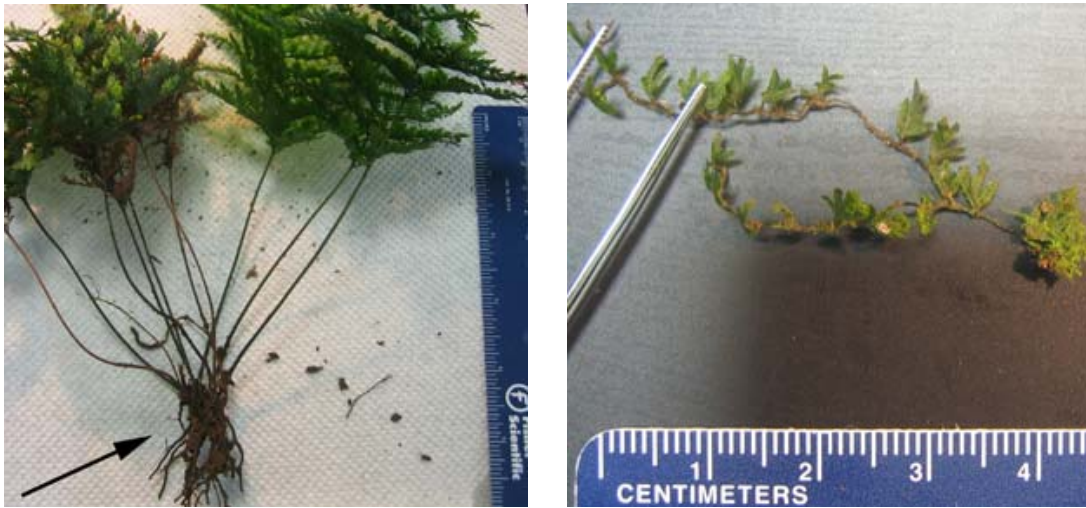
CHARACTER FIGURES

FIG. 10. Examples of erect and creeping rhizomes. *A. dentatum* (left) has an erect rhizome, indicated by the arrow. *Cr. saxifragoides* (right) has a creeping rhizome.
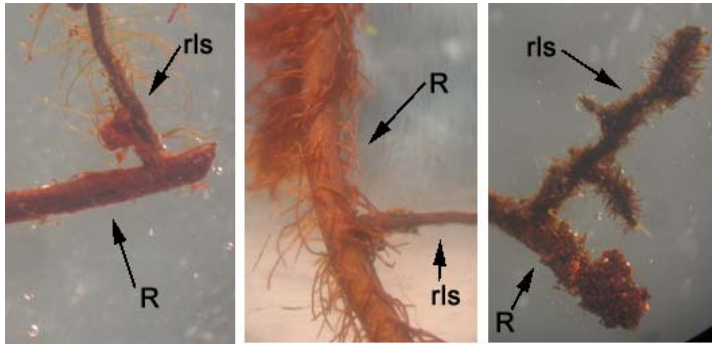
FIG. 11. Examples of hairs on rhizomes and root-like shoots. *H. polyanthos* (left) has a glabrous root and a hairy root-like shoot. *H. pallidum* (middle) has a hairy rhizome and glabrous root-like shoots. *Cr. bipunctatum* (right) has both rhizome and root-like shoots thickly covered in fuzzy, brownish black hairs. All magnification 20x. "R" with an arrow indicates the rhizome; "rls" with an arrow indicates a root-like shoot.

Species Key
A = *H. polyanthos*
B = *Cr. minutus*
C = *D. tahitense*
D = *Cr. humile*
E = *H. pallidum*
F = *Cr. bipunctatum*
G = *A. caudatum*
H = *A. dentatum*
I = *Cal. apiifolia*
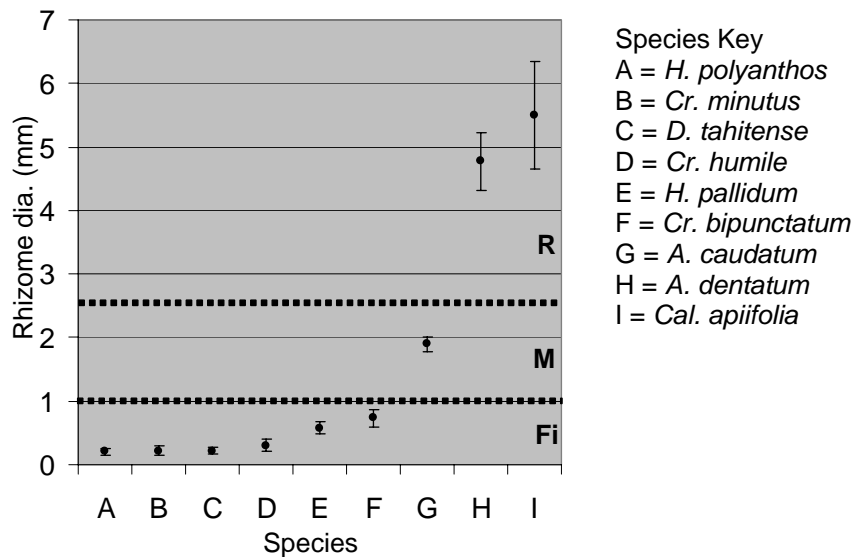
FIG. 12. Rhizome diameter data and 95% confidence intervals. Rhizomes from 9 of the 12 Moorea species were measured. Rhizomes sorted into 3 size classes, separated in the figure by dashed lines and labeled with letters. Fi = "filiform," M = "medium," R = "robust."

FIG. 13. Examples of wingless and winged stipes. *A. digitatum* (left) lacks any wing on the stipe. *A caudatum* (middle) has a stipe with a very narrow wing. *Cr. humile* (right) has a stipe with a wide wing. All magnification 20x.
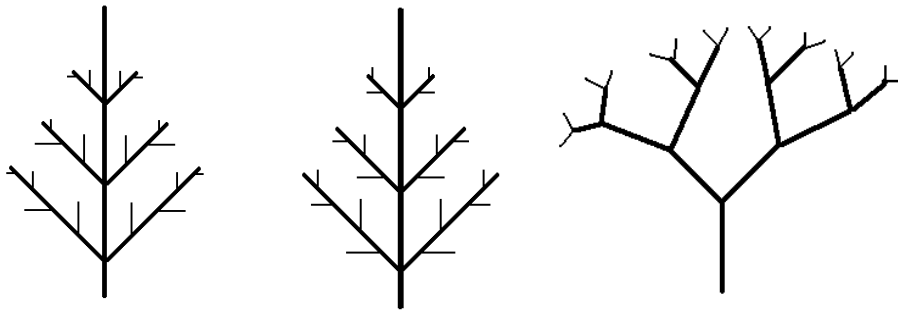
FIG. 14. Schematic diagram of vein types. In anadromous venation (left), the first vein of each costa points towards the tip of the frond. In catadromous venetion (middle), the first vein of each costa points towards the base of the frond. In dichotomous venetion (right), there is no central rachis or costa, and the vein divides in two at each junction.
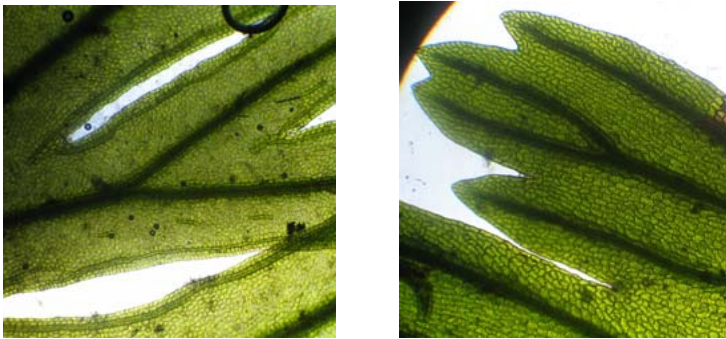
FIG. 15. Examples presence and absence of a sub-marginal false vein. *Cr. bipunctatum* (left) has a discontinuous false vein beneath the margin. *A. dentatum* (right) lacks any such specialized cells beneath the margin. All magnification 40x.

Species Key
A = *D. tahitense*
B = *Cr. minutus*
C = *H. digitatum*
D = *Cr. humile*
E = *Cr. bipunctatum*
F = *H. polyanthos*
G = *H. pallidum*
H = *A. dentatum*
I = *A. caudatum*
J = *Cal. apiifolia*
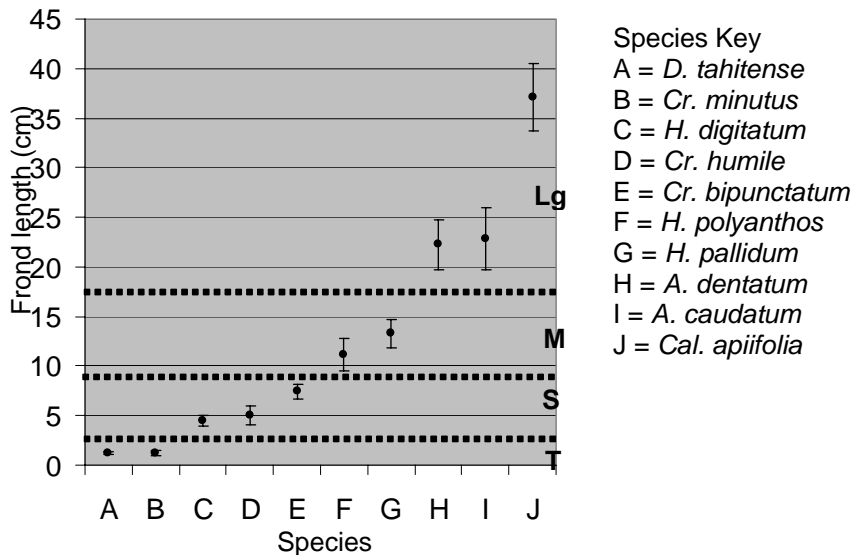
FIG. 16. Frond length data and 95% confidence intervals. Fronds from 10 of the 12 Moorea filmy fern species were measured. Fronds sorted into 4 size classes, separated in the figure by dashed lines and labeled with letters. T = "tiny," S = "small," M = "medium," Lg = "large."
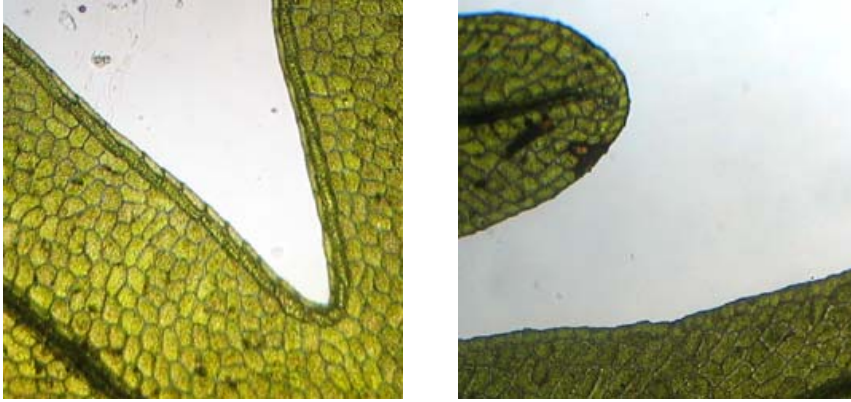
FIG. 17. Examples of specialized marginal cells. *Cr. humile* (left) has a double row of elongated marginal cells. *A. caudatum* (right) has distinct marginal cells that are the same length as other lamina cells. All magnification 40x.

FIG. 18. Examples of involucre variation. *H. polyanthos* (left) has bivalve involucres with an included receptacle (not visible). *A. caudatum* (right) has tubular involucres with an exserted receptacle.

TABLE 2. Character matrix used to infer phylogenetic tree.

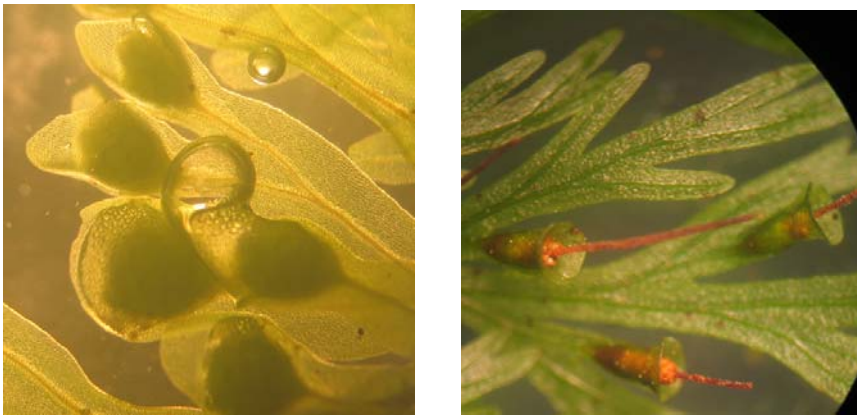|	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
A. caudatum	2	1	2	1	?	1	1	1	0	?	0	2	0	0	1	0	1	0	0	1	?	0	1	1	0
A. dentatum	0	1	2	0	?	2	0	0	0	1	0	2	0	0	0	0	0	0	0	0	1	0	1	1	0
Cal. apiifolia	0	1	2	1	?	2	0	1	?	1	1	2	0	0	0	0	0	0	0	1	1	0	0	0	0
Cr. bipunctat.	2	0	2	?	1	0	2	0	1	1	1	2	1	0	0	1	0	1	0	1	1	0	1	1	0
Cr. humile	2	0	2	?	1	0	2	1	0	1	1	1	0	0	2	1	1	1	0	1	1	0	1	1	0
Cr. minutus	2	0	2	?	1	0	0	0	?	2	1	1	0	0	1	2	0	1	0	0	0	0	1	1	0
D. tahitense	2	0	1	?	1	0	?	?	?	?	0	0	0	1	0	2	2	0	0	0	0	0	1	1	1
H. digitatum	2	0	0	?	1	0	0	0	?	2	1	1	0	0	0	2	1	0	1	1	0	0	1	1	0
H. polyanthos	2	0	0	?	1	?	0	0	?	1	1	2	0	0	0	1	0	0	0	1	0	0	0	0	0
H. pallidum	2	0	1	?	1	?	0	0	?	1	0	2	0	0	1	1	1	1	0	1	1	0	1	1	0
Cr. saxifrag.	2	0	1	?	1	0	0	1	?	2	1	1	1	0	0	3	0	1	0	1	0	0	1	1	0
P. endlicher.	2	0	1	?	1	?	1	0	0	1	1	2	0	0	0	1	1	1	0	1	1	0	1	1	0
H. flabellatum	2	0	1	?	1	?	0	?	?	1	1	2	0	0	0	0	1	0	0	?	0	0	0	0	0
A. asae-grayi	0	1	1	1	?	2	1	?	0	1	?	2	0	0	0	0	0	1	0	0	1	1	1	1	0
H. dilatatum	2	?	0	?	?	1	2	0	0	1	?	2	0	0	0	0	?	0	0	1	0	0	0	0	0
H. imbricatum	2	?	0	?	?	1	2	0	0	1	?	2	0	0	0	0	?	0	0	1	0	0	0	0	0
H. tunbrigense	2	?	0	?	?	1	1	0	0	1	?	2	0	0	0	1	?	0	0	1	0	0	0	0	0
V. davallioides	2	1	2	1	?	1	2	1	0	1	?	2	0	0	0	0	?	1	0	1	1	1	1	1	0
Cr. intermed.	0	1	2	1	?	2	1	0	0	1	?	2	0	0	0	0	?	1	0	0	1	0	1	1	0
V. maximum	1	1	2	0	?	1	2	1	0	1	?	2	0	0	0	0	?	1	0	1	1	0	1	1	0

APPENDIX B: REVISED KEY TO THE FILMY FERNS OF MOOREA, WITH DESCRIPTION OF EACH

1a. Rhizome long-creeping, growing on rocks or trees..2
1b. Rhizome erect, growing terrestrially.. 3
2a. Rhizome of moderate thickness (ca. 2 mm dia.), epiphytic on tree ferns...*Abrodictyum caudatum*
2b. Rhizome filiform (less than 1 mm dia.)..4
3a. Long reddish hairs present on stipe...*Callistopteris apiifolia*
3b. Stipe lacks hairs. Fronds dark green... .... *Abrodictyum dentatum*
4a. Sub-marginal false vein (ca. 3 cell rows beneath margin of lamina) present..................................5
4b. Sub-marginal false vein absent. 6
5a. Sub-marginal false vein continuous, fronds < 1 cm long... ....*Crepidomanes saxifragoides*
5b. Sub-marginal false vein discontinuous, fronds 3 – 8 cm long................*Crepidomanes bipunctatum*
6a. Specialized marginal cells (ca. 3x longer than others) present........................*Crepidomanes humile*
6b. Specialized marginal cells absent.. 7
7a. Fronds simple or 1-pinnatifid..8
7b. Fronds 3-pinnatifid or greater. 9
8a. Fronds peltate, tightly adpressed to substrate, stipe absent....................*Didymoglossum tahitense*
8b. Fronds not as above... 10
9a. Lamina light green, stipe and rachis black. Involucres distinctly bivalve...*Hymenophyllum polyanthos*
9b. Rachis color not different from lamina. Involucres more tubular than bivalve.........................11
10a. Fronds with wavey margins, margin hairs present...............................*Hymenophyllum digitatum*
10b. Fronds fan-shaped, margin hairs absent, < 2 cm long.................................*Crepidomanes minutus*
11a. Frond covered in fine white hairs, resulting in white sheen................. *Hymenophyllum pallidum*
11b. Frond lacks white hairs, costa often elongated with short branching along length...*Polyphlebium endlicherianum*

Abrodictyum dentatum
    Large (average frond length 22 cm) 3-pinnatifid fronds on a short-creeping, erect rhizome. Fronds dark green, with tough texture. Involucres occur in series of two parallel rows along pinnae. Occurs terrestrially at moderate to high elevations. May occur on open forest floor or under high amount of cover, often in groups of 4 – 5 individuals or more. Most common terrestrial species.

Abrodictyum caudatum
    Large (average frond length 22 cm) 3-pinnatifid fronds on a medium (2 cm diameter) long-creeping rhizome. Rhizome of this species is larger than other long-creeping species. Fronds light green, delicate. Occurs epiphytically at moderate to high elevations. This species grows exclusively on tree ferns. The roots of this filmy fern are often deeply intertwined within the adventitious roots of the tree fern rhizome, making it difficult to remove.

Crepidomanes humile
    Small (average frond length 5 cm), 2-pinnatifid fronds on a long-creeping rhizome. Laminae have specialized row of elongated marginal cells visible with a hand-lens. Fronds ovate-lanceolate, light green. In favorable conditions, will grow in a mat with interweaving rhizomes on the substrate. Common at low (30 m) to middle (450 m) elevations in forests with at least moderate (70%) cover, growing on tree trunks or rocks. Often occurs with *Cr. bipunctatum* at lower elevations.

Crepidomanes bipunctatum

Small (average frond length 7 cm), 3-pinnatifid fronds on a long-creeping rhizome. Laminae have a discontinuous sub-marginal false vein visible with a hand lens. Fronds lancelote (overall shape resembles a Christmas tree). Fronds are dark green in color, but may vary with state of desiccation. In favorable conditions, will grow in a mat with interweaving rhizomes on the substrate. Common at low elevations in forests with at least moderate cover, growing on tree trunks or rocks (occurs more often on rocks than trees). Often occurs with *Cr. humile* at lower elevations.

Crepidomanes saxifragoides

Tiny (average frond length 1 cm), 1-pinnatifid fronds on a long-creeping rhizome. Laminae have a continuous sub-marginal false vein. Fronds ovate-lanceolate, light green. In favorable conditions, will grow in a mat with interweaving rhizomes on the substrate. Rare at low elevations. Only grows on rocks, often on boulders next to stream beds. Easily confused with juvenile *Cr. humile*, but the two may be differentiated by size and specialized margin and vein structures.

Crepidomanes minutus

Tiny (average frond length 1.5 cm), fan-shaped fronds on a long-creeping rhizome. Veins split dichotomously. Stipe occasionally proliferous, producing new fronds. In favorable conditions, will grow in a mat with interweaving rhizomes on the substrate. Occurs at high elevations (> 450 m) on tree trunks and branches, often with dense moss or *H. polyanthos*.

Callistoperis apiifolia

Large (average frond length 37 cm) 3-pinnatifid fronds on an erect, short-creeping rhizome. Stipe and rachis covered with long, reddish hairs. Occurs terrestrially at moderate to high elevations. Much less abundant than *A. dentatum*, usually only found in populations of a single individual. Fertile fronds often absent in small specimens.

Didymoglossum tahitense

Small (average frond width 1.5 cm) peltate fronds lacking a stipe on a filiform, long-creeping rhizome. Fronds are adpressed to substrate, often difficult to remove. Rhizoids on underside of leaf help anchor to substrate. Fronds may overlap slightly so that rhizome is hidden from view. At first glance may appear to resemble a liverwort more closely than a fern. Does not grow in a mat like other low elevation species, but will form a line of peltate fronds as the rhizome grows along the substrate. Found on tree trunks (especially *Inocarpus fagiferus*) at low elevations.

Hymenophyllum digitatum

Delicate in appearance, with very fine, glabrous stipe and rhizome. Small (average length 4.5 cm) fronds hang lax from the substrate, often in a dense mat. Frond veins split dichotomously, up to 10 times. Fronds have characteristic wavey edges, with small hairs along margin. Fronds light green, with dark brown to black veins. Laminae turn black when severely desiccated; blackened individuals often present within populations. Involucre bivalve at ends of veins. Occurs epiphytically at mid- to high- elevations, often on underside or recessed areas of trunks or branches.

Hymenophyllum pallidum

A moderately sized fern (average frond length 13 cm), characterized by fine, whitish hairs covering the frond. Hairs are usually concentrated towards the tips and margins, and are most conspicuous on young fronds. Another unusual morphological feature is a double layer of cells 4 cells wide on either side of the veins. Frond is three times pinnatifid, oblong to ovate in shape.

Growth habit similar to other epiphytes (long-creeping rhizome which forms a mat). Occurs as a rare epiphyte at high elevations.

Hymenophyllum polyanthos

   This species contains a high degree of morphological variation. Fronds vary in length from small (5 cm) in some populations to large (15 cm) in others; light green laminae on a dark-brown to black stipe. Frond shape may be long and narrow with limited branching, or short and wide with long branching. Involucres are distinctively bivalve, with rounded wings and an included receptacle. A common epiphyte at high elevations, often growing on *Metrosideros collina*. Similar growth habit to *Cr. humile* or *Cr. bipunctatum*, with long-creeping rhizomes forming an interwoven mat.

Polyphlebium endlicherianum

   Gross morphology similar to *Cr. humile* or *Cr. bipunctatum*. Small fronds on a long-creeping rhizome. Occasionally a single costa will be elongated, with short pinnae along its length. Rare at high elevations. Found growing epiphytically with mosses and *H. digitatum*.
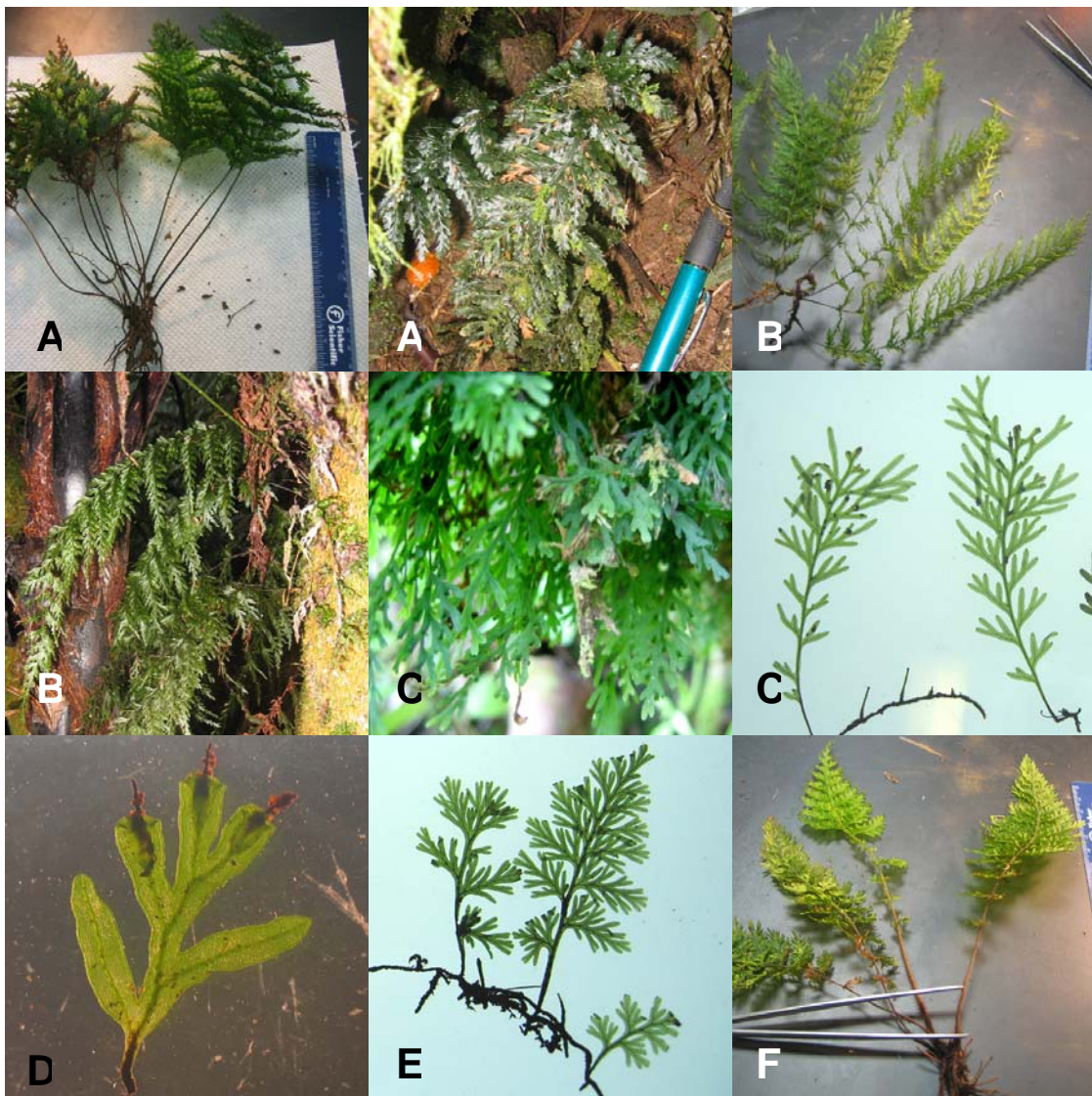

Figure 19. Species in the key. A = *A. dentatum*, B = *A. caudatum*, C = *Cr. humile*, D = *Cr. saxifragoides*, E = *Cr. bipunctatum*, F = *Cal. apiifolia*. Continues on next page.

FIG. 18 (Cont'd). F = *Cal. apiifolia*, G = *H. digitatum*, H = *Cr. minutus*, I = *H. pallidum*, J = *H. polyanthos*. K = *P. endlicherianum* L = *D. tahitense*