

FILMY FERNS (HYMENOPHYLLACEAE) AS HIGH-CANOPY EPIPHYTES

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INTRODUCTION

Hymenophyllaceae, the filmy fern family, comprises more than 600 species of delicate ferns that are most abundant in humid tropical forests, but extend in humid shady habitats into temperate regions (Iwatsuki 1990). The family comprises two major monophyletic lineages, traditionally separated into the genera *Hymenophyllum s.l.* and *Trichomanes s.l.* based on indusial characters, although up to 42 separate genera have been recognized (Copeland 1938, Morton 1968, Pryer *et al.* 2001). Although *Hymenophyllum s.l.* and *Trichomanes s.l.* both contain roughly the same number of species, *Hymenophyllum s.l.* is morphologically and ecologically much more homogeneous, including mainly epiphytic and some epipetric species, whereas *Trichomanes s.l.* displays a high diversity in terms of morphology and habitats, ranging from terrestrial and saxicolous species to epiphytic ones (Dubuisson *et al.* 2003). Filmy ferns lack cuticles (or have highly reduced cuticles), differentiated epidermises, and stomata, causing dependence on high environmental moisture because no barrier exists to prevent unregulated loss of water (e.g., Gessner 1940, Härtel 1940). Hymenophyllaceae are therefore strongly hygrophilous and generally perceived as plants restricted to constantly humid microhabitat (Kelly 1985, Hietz & Hietz-Seifert 1995, Johnson *et al.* 2000). Shady conditions do not appear to be obligatory for these ferns, because at least some species are poikilohydric and thus able to withstand repeated desiccation (Benzing

1990, Iwatsuki 1990). While some studies have focussed on the ecophysiology of the family (Härtel 1940, Gessner 1940, Proctor 2003) and its general ecology (e.g., Dubuisson *et al.* 2003), very little is known about the vertical distribution of tropical species within the forest strata. The only quantitative study of such habitat preferences was made in a tropical lowland forest by Zotz & Büche (2000). Our paper intends to expand the knowledge on the vertical distribution patterns and site-specificity of filmy ferns in tropical submontane and montane forests, with a focus on high-canopy species.

METHODS

Study sites. The study was conducted at three different sites on the eastern slopes of the Andes in the Department of La Paz and Cochabamba, Bolivia, the so called “Yungas” (Fig. 1). The first study site is near the village of Sapecho (450 m; 15°27′–32′ S, 67°18′–23′ W), at the northeastern base of the Serranía Marimónos. Temperature averages 24–25°C and annual rainfall varies from 1500 mm in the valley to >2000 mm on the mountain slopes, with a 3-month dry period. The natural vegetation is an evergreen or semi-evergreen submontane forest comprised of 30–40-m-tall trees and with a well-developed shrub layer; tree diversity averages 120 species per ha (Krömer & Gradstein 2003).

The second study site (16°13′ S, 66°24′ W) was located at 1300–1600 m on the isolated Serranía de Mosetenes in Parque Nacional y Área Natural de Manejo Integrado (PN-ANMI) Isiboro Sécore. No climatic stations exist in the vicinity of the study area,

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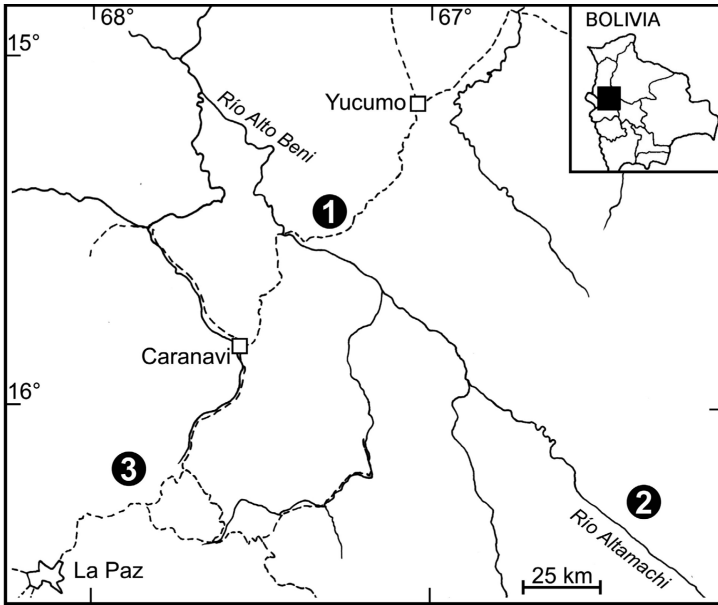


FIG. 1. Map of central Bolivia showing the location of the study sites (1: Sapecho, 2: Mosetenes, 3: Cotapata). Continuous lines show main rivers, dashed lines main roads.

but rough estimates can be made based on comparisons with sites of physiognomically similar vegetation. Thus, mean annual precipitation is estimated at 3000–6000 mm, with a 2-month dry period, while mean annual temperatures are around 16°C at 1500 m. Forest structure in this steep and notably rocky terrain is lower than that of the previous site, with the closed canopy at 20–25 m and emergent trees 30–35 m in height. On mountain ridges, forests are stunted and only 5–15 m tall (Krömer *et al.* 2005).

The third study site was located at 1600–2200 m in the surroundings of Tuniquini Biological Station in PN-ANMI Cotapata (16°11'–13' S, 67°51'–54' W). Mean annual temperature averages 13–19°C at 1500–2500 m and mean annual rainfall is about 2500 mm, with a 2-month dry period. The very steep slopes are covered by evergreen montane forest, made up of 15–25-m-tall trees and with dense shrub and herb layers. The number of tree species per hectare is unknown but is probably lower than in Sapecho (Krömer & Gradstein 2003).

Sampling. Diversity of epiphytic filmy ferns was measured based on representative sampling of 1.0-ha plots of homogeneous forest. Five forest plots were sampled in Sapecho (600–1200 m elevation), two at Mosetenes (1300–1600 m), and three in Cotapata (1600–

2200 m). In each of the plots, four (Mosetenes) or eight (Sapecho, Cotapata) subplots of 20 x 20 m were selected for the actual sampling. In each subplot, a single mature canopy tree was selected based on the epiphyte sampling protocol of Gradstein *et al.* (2003). All trees were sampled from the bases to the outer portions of the tree crowns using the single rope technique (Perry 1978), and presence/absence of all vascular epiphyte species within the five vertical zones (Z1: trunk base, Z2a/b: lower/upper part of the trunk, Z3: lower canopy, Z4: middle canopy, Z5: outer canopy) recorded according to Johansson (1974). This procedure allows for a nearly complete inventory of epiphyte diversity in the forest canopy (Flores-Palacios & García-Franco 2001). Because the epiphyte flora on shrubs and treelets in the forest understory is usually different from that on the large canopy trees (Gentry & Dodson 1987, Shaw & Bergstrom 1997, Gradstein *et al.* 2003), epiphytes in the understory zone U were sampled within each subplot, using collecting poles and binoculars (Krömer 2003). Voucher specimens were deposited in the Herbario Nacional de Bolivia (LPB), with duplicates in the Herbarium of the University of Göttingen (GOET), Marie Selby Botanical Gardens (SEL), Missouri Botanical Garden, St. Louis (MO), and the Jepson Herbarium, University of California, Berkeley (UC).

Vertical distribution patterns. Based on their occurrence in Johansson and understory zones, epiphytic filmy ferns were classified into three ecological types (Acebey *et al.* 2003; Table 1): habitat generalists (occurring in three or more zones) and habitat specialists (occurring only in two zones, or in three continuous zones); the latter were further divided into “canopy

epiphytes” (occurring >90% in Johansson zones Z3-5) and “trunk epiphytes” (>90% in understory and Johansson zones Z1-2). To test whether the species occurred more frequently either on the trunk (incl. understory) or in the canopy, filmy ferns which occurred on at least five trees were compared with 2 x 2 contingency tables, applying Fisher’s exact test as

TABLE 1. Frequency of 27 species of Hymenophyllaceae at three study sites (Sapecho: Sa; n = 40 trees, Mosetenes: Mo; n = 8, Cotapata: Co; n = 24) in Bolivian montane forest. P-values of the two-sided Fisher’s exact test are shown for taxa with significant habitat preferences ($P < 0.05$). NS = not significant, NA = not applicable, for presence data of less than five. A total of 17 species was classified into three ecological types as habitat generalists (gen - recorded in 3 or more height zones), trunk epiphytes (trunk - recorded in up to 3 continuous zones in the forest interior), and canopy epiphytes (canopy - recorded in up to 3 continuous zones in the canopy).

Species	Study site	Present on trunk	Absent on trunk	Present canopy	Absent canopy	P	Ecol. type
<i>Hymenophyllum apiculatum</i> Mett. ex Kuhn	Sa	2	38	6	34	NS	gen
<i>Hymenophyllum axillare</i> Sw.	Co	4	20	7	17	NS	gen
<i>Hymenophyllum elegans</i> Spreng.	Mo	2	6	0	8	NA	
<i>Hymenophyllum fendlerianum</i> J.W. Sturm	Sa, Mo, Co	0	72	19	53	< 0.001	canopy
<i>Hymenophyllum fragile</i> (Hedw.) C.V. Morton	Co	8	16	0	24	0.004	trunk
<i>Hymenophyllum fucoides</i> (Sw.) Sw.	Co	12	12	0	24	< 0.001	trunk
<i>Hymenophyllum hirsutum</i> (L.) Sw.	Sa	3	37	0	40	NA	
<i>Hymenophyllum interruptum</i> Kunze	Mo, Co	17	15	1	31	< 0.001	trunk
<i>Hymenophyllum microcarpum</i> Desv.	Mo, Co	16	16	5	27	0.007	trunk
<i>Hymenophyllum polyanthos</i> (Sw.) Sw.	Sa, Mo, Co	20	52	14	58	NS	gen
<i>Hymenophyllum speciosum</i> Bosch	Co	0	24	7	17	0.009	canopy
<i>Hymenophyllum tegularis</i> (Desv.) Proctor & Lourteig	Sa	0	40	1	39	NA	
<i>Hymenophyllum trichomanoides</i> Bosch	Mo, Co	3	29	4	28	NS	gen
<i>Hymenophyllum undulatum</i> (Sw.) Sw.	Mo, Co	2	30	12	20	< 0.001	canopy
<i>Hymenophyllum</i> spec. 1 (THO 1302)	Co	0	24	1	23	NA	
<i>Trichomanes angustatum</i> Carm.	Sa, Mo, Co	14	58	0	72	< 0.001	trunk
<i>Trichomanes ankersii</i> C. Parker ex Hook. & Grev.	Sa	4	36	0	40	NA	
<i>Trichomanes debile</i> Bosch	Mo	2	6	0	8	NA	
<i>Trichomanes herzogii</i> Rosenst.	Mo	4	4	0	8	NA	
<i>Trichomanes krausii</i> Hook. & Grev.	Sa	14	26	0	40	< 0.001	trunk
<i>Trichomanes pilosum</i> Raddi	Sa	0	40	5	35	0.055	(canopy)
<i>Trichomanes plumosum</i> Kunze	Sa, Mo	8	40	0	48	0.006	trunk
<i>Trichomanes polypodioides</i> L.	Sa, Co	10	54	0	64	0.001	trunk
<i>Trichomanes punctatum</i> Poir.	Sa	27	13	0	40	< 0.001	trunk
<i>Trichomanes radicans</i> Sw.	Mo, Co	3	29	0	32	NA	
<i>Trichomanes</i> cf. <i>reptans</i> Sw.	Co	3	21	0	24	NA	
<i>Trichomanes rupestre</i> (Raddi) Bosch	Co	2	22	0	24	NA	

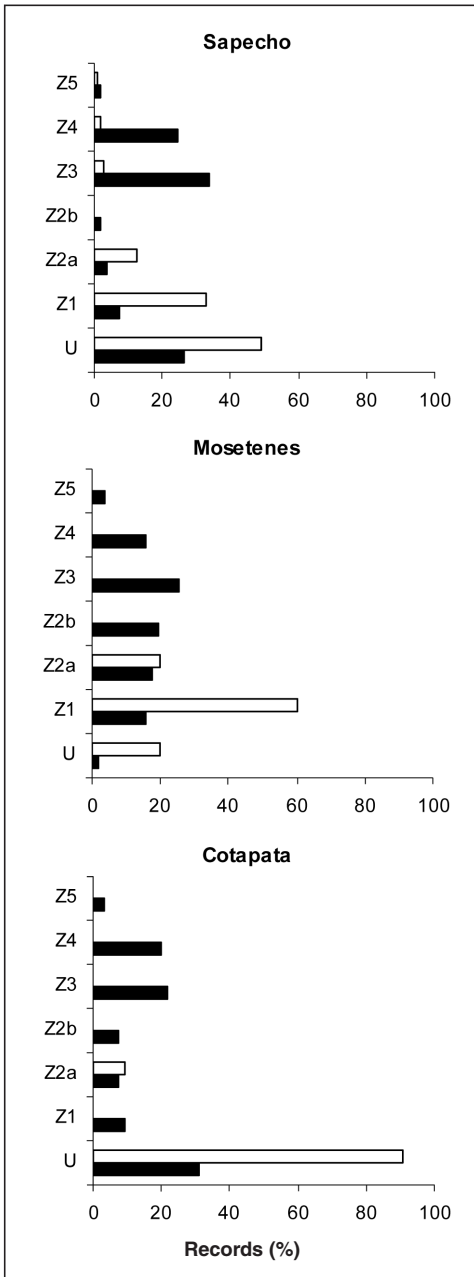


FIG. 2. Percentages of records of all species within the genera *Hymenophyllum s.l.* (black bars) and *Trichomanes s.l.* (white bars) in the seven height zones (U = understory, Z1–Z5 = tree bases to outer canopy) in primary forests at three sites in the Bolivian Andes.

recommended by Zar (1999). Table categories were determined by the presence or absence of each species in both habitats. A total of 17 species (9 from Sapecho, 7 from Mosetenes, 12 from Cotapata) were included in this analysis (Table 1).

RESULTS AND DISCUSSION

In the 10 forest plots we recorded a total of 27 species of Hymenophyllaceae (15 *Hymenophyllum s.l.*, 12 *Trichomanes s.l.*) with altogether 367 (236, 131) individual subplot records. Of these, at Sapecho we found 12 species (5, 7) with 163 (53, 110) records, at Mosetenes 12 species (7, 5) with 61 (51, 10) records, and at Cotapata 16 species (11, 5) with 143 (132, 11) records. The submontane Hymenophyllaceae assemblages of forests at Sapecho were thus dominated by the genus *Trichomanes s.l.*, whereas those of montane forests at Mosetenes and Cotapata were dominated by *Hymenophyllum s.l.*, both with respect to species richness and abundance. This elevational stratification of the two Hymenophyllaceae genera is typical of tropical mountain forests worldwide, although a wide elevational zone of overlap exists between the two major groups (Kessler *et al.* 2001).

At all three study sites there was also a vertical stratification of the two genera within the forest strata (Fig. 2). *Hymenophyllum s.l.* was found in all growth zones and achieved high relative abundances (45–60% of all records) in the Johansson zones Z3–5, corresponding to the inner to outer canopy. Of the 17 species of Hymenophyllaceae that were common enough to allow a classification into habitat generalists or specialists, 4 of 11 species of *Hymenophyllum* were generalists (e.g., *H. polyanthos*), 4 trunk epiphytes, and 3 canopy epiphytes (e.g., *H. fendlerianum*), whereas 5 species of *Trichomanes* were classified as trunk epiphytes (e.g., *T. punctatum*, Fig. 3) (Table 1). All 12 specialists were significantly more frequent within their preferred habitat (Fisher's exact test, $P < 0.05$). We therefore documented that only 4 of 11 species of *Hymenophyllum s.l.* were exclusively recorded in the forest interior, while no less than 7 species were regularly or preferentially found in the forest canopy. In contrast, the genus *Trichomanes s.l.* was almost exclusively restricted to the lower tree trunks (Z1–2a) and to treelets and shrubs in the forest understory (Fig. 2). Contrary to *Hymenophyllum s.l.* which is mainly epiphytic and has few saxicolous representatives, *Trichomanes s.l.* includes numerous primarily terrestrial and/or saxicolous species (Dubuisson *et al.* 2003).

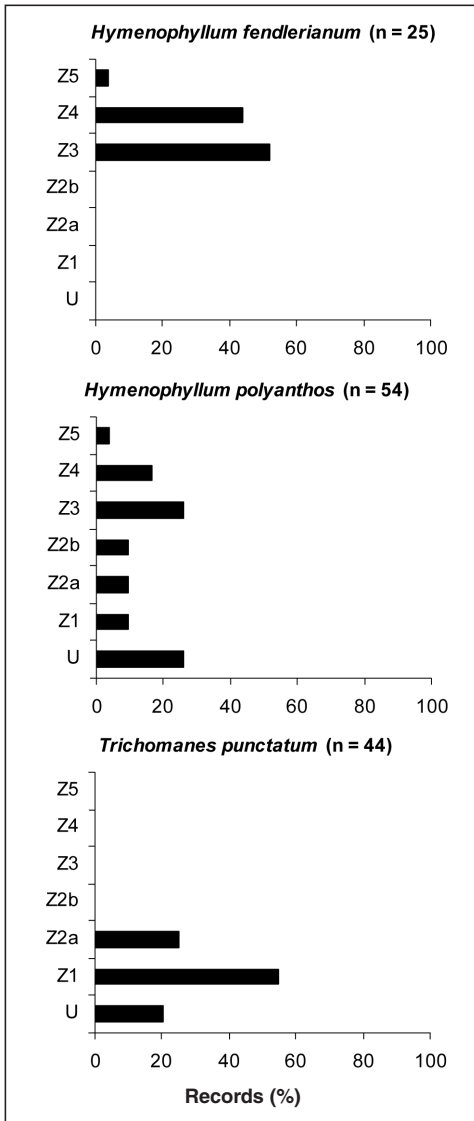


FIG. 3. Percentages of records of selected filmy fern species in the seven height zones (U = understory, Z1–Z5 = tree bases to outer canopy) in primary forests in the Bolivian Andes.

The only exception to the absence of *Trichomanes s.l.* in the canopy in our study was presented by *T. pilosum* Raddi, which was found five times at Sapecho, always in the canopy zone, although the Fisher's exact test was only marginally significant ($P = 0.055$).

Previous observations of Hymenophyllaceae in the forest canopy are rare. Van Leerdam *et al.* (1990) describe unidentified species of *Hymenophyllum s.l.* as typical elements of the epiphyte vegetation in the canopy of a Colombian cloud forest. Single records in the high canopy in the Neotropics have been reported for *Hymenophyllum brevifrons* Kunze in Costa Rica and Panama (Grayum & Churchill 1989, Zotz & Büche 2000), *H. crassipetiolatum* Stolze in Venezuela (Engwald 1999), and *Trichomanes crispum* L. in Costa Rica (Grayum & Churchill 1989). Both *Trichomanes crispum* and *T. pilosum* belong to subgenus *Achomanes* (Morton 1968). In the Old World, Dubuisson *et al.* (2003) mention the occurrence of species of *Trichomanes s.l.* in the subgroups *Crepidomanes* and *Gonocormus* on tree branches, and of *Hymenophyllum s.l.* on high canopy branches, although details are lacking. Several of these authors pointed out that the species are probably more common in such situations than the available records suggest. Our observations support this assumption and suggest that the paucity of records of Hymenophyllaceae in the high canopy is primarily a result of difficult access to the canopy, and the inconspicuous nature of the species in question.

Our data show that Hymenophyllaceae in the forest canopy are mostly found in zones Z3 and Z4, corresponding to the major branches of the canopy interior, where, in accordance with observations by van Leerdam *et al.* (1990), they mostly grow on thick mats of detritus and in moss mats. These substrate mats provide rooting grounds, nutrients, and water storage (Freiberg 2001), not only for the Hymenophyllaceae but also for other vascular epiphytes, so that these zones are generally the most species-rich epiphyte zones (ter Steege & Cornelissen 1989, Nieder *et al.* 1999). In contrast to the study of Moran *et al.* (2003), where low-trunk fern epiphytes exhibited significant differences on tree ferns in comparison to angiosperm trees, no such host preference was observed in this study. We found, however, that some angiosperm tree species, such as *Tetrageastris altissima*, *Poulsenia armata*, *Podocarpus rusbyi*, *Ficus* spp., and *Protium* spp., generally exhibited a heavy load of epiphytes, presumably as a result of their size, architecture, and longevity (Krömer 2003). This phorophyte specificity applied to the epiphyte load as a whole, and did not imply that certain epiphyte species were specialized to growing on these trees. According to Ibisch (1996), phorophyte specificity is more pronounced in dry forest habitats, where the epiphytes grow in direct contact with the host tree's bark, whereas in humid forests,

such as those studied by us, mats of bryophytes, lichens, and detritus lead to similar growth conditions on different trees.

The regular occurrence of species of Hymenophyllaceae in the canopy is a previously unrecognized phenomenon that is at odds with the common perception of this family as typical of humid, shady habitats (Zotz & Büche 2000, Dubuisson *et al.* 2003). Ecophysiological studies have shown that at least some species of Hymenophyllaceae, especially in *Hymenophyllum s.l.*, are poikilohydric and well-adapted to periodic drying (Härtel 1940, Benzing 1990, Proctor 2003). Indeed, Proctor (2003) found that *Hymenophyllum tunbrigense* (L.) Sm. and *H. wilsonii* Hook. require regular drying phases to maintain optimal photosynthetic capabilities, and that constant very high air humidity is detrimental to these plants. Rather than humidity or deep shade as such, the essential requirements of Hymenophyllaceae are probably reasonably frequent precipitation coupled with low evaporation (Proctor 2003). The first of these is a natural feature of rain forests, while the second is often a result of the high fog frequency in montane and some lowland tropical forests (Gradstein 2003, in press). Overall, the Hymenophyllaceae can be seen as the morphological and ecological pteridophyte equivalent of bryophytes, which, although also most abundant in very humid sites, are able to inhabit periodically dry habitats, including the forest canopy (Proctor & Tuba 2002).

Phylogenetically, the species of *Hymenophyllum s.l.* recorded as high-canopy epiphytes mainly belong to subgenus *Mecodium* as defined by Morton (1968), characterized by lacking blade hairs and smooth segment margins. This subgenus, now recognized to be polyphyletic, even though the Neotropical species may represent a monophyletic clade (Hennequin *et al.* 2003), is represented in Bolivia by ten species (M. Kessler & A.R. Smith, unpubl. data). Of these, no less than six have here been found to be habitat generalists or canopy epiphytes, with no species restricted to the trunk and understory. Our field experience with the remaining four species suggests that one of them (*H. brevistipes* Liebm.) is also likely to be a canopy epiphyte, while the other three (*H. ferax* Bosch, *H. lehmannii* Hieron., and *H. mathewsii* Bosch) are probably generalists. The only canopy species recorded by us that belongs to a phylogenetically distinct group in *Hymenophyllum s.l.* was *H. speciosum* Bosch in Morton's (1968) subgenus *Sphaerocionium*. This subgenus, which includes a monophyletic Neotropical clade (Hennequin *et al.* 2003), groups species with often

densely hairy and pendant blades, and is typically found epiphytically in the forest understory, as shown by *H. fragile* (Hedw.) C.V. Morton, or epipetrically on rock faces, often in sheltered sites not directly affected by rain (T. Krömer & M. Kessler, pers. obs.). In summary, it appears that in the Neotropics the colonization of the canopy habitat by Hymenophyllaceae has mainly taken place in *Hymenophyllum* subgenus *Mecodium*, with a few additional cases in *H.* subgenus *Sphaerocionium* and in *Trichomanes* subgenus *Achomanes*. In the Old World tropics, which are inhabited by a different suite of subgroups within *Hymenophyllum s.l.* and *Trichomanes s.l.* (Copeland 1938, Morton 1968, Pryer *et al.* 2001, Dubuisson *et al.* 2003, Hennequin *et al.* 2003), the situation may be different (H. Schneider, pers. comm.). Comparative ecophysiological studies of species of different subgroups within *Hymenophyllum s.l.* might reveal a physiological basis for the colonization of the high-canopy habitat by filmy ferns.

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