

Epiphytic bryophytes of Monteverde, Costa Rica

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Abstract: A survey of the literature and collections in the Monteverde Cloud Forest Preserve and adjacent pastureland yielded a total of 198 epiphytic bryophyte taxa (120 species of hepatics in 50 genera, 77 species of moss in 48 genera, and 1 hornwort): 178 in the primary forest, 63 in the secondary forest, and 84 in the pastureland.

Tropical montane forests support a tremendous abundance and diversity of epiphytic plants. Historically, vascular epiphytes have received more attention from researchers than epiphytic non-vascular plants (Nadkarni *et al.* 2001), and bryophytes in the tropics are generally poorly studied (Gradstein *et al.* 2001). The Monteverde Cloud Forest Reserve (MCFR) is one of one of the most studied Neotropical montane cloud forests (Nadkarni and Wheelwright 2000), and the bryoflora of MCFR is fairly well known (Reed and Robinson 1971; Gradstein 2000; Morales 2000). Epiphytic bryophytes of Monteverde have also been the focus of several ecological investigations concerning epiphytic bryophytes (Nadkarni 1984; Monge-Nájera 1989; Nadkarni and Matelson 1989, 1992; Ingram and Nadkarni 1993; Matelson *et al.* 1993;

Clark 1994; Sillett *et al.* 1995; Clark *et al.* 1998a, b; Gradstein 2000; Morales 2000; Nadkarni 2000; Nadkarni *et al.* 2000a,b; Gradstein *et al.* in press).

In this paper, we bring together data that concern work on epiphytic bryophyte species diversity across a gradient of human-induced disturbance (i.e., primary forest, 35 year-old secondary forest, and pastureland). First, a list of epiphytic bryophytes known to occur in primary forest and secondary forest of the MCFR and adjacent pastureland was compiled from the literature (Sillett *et al.* 1995; Gradstein *et al.* in press). We supplemented this with collections involving destructive sampling of trees in the primary forest and secondary forest. In primary forest, species recorded as growing epiphytically on the trunk bases (0-1 m above the ground), shrubs, and treelets in the forest understory by

Gradstein *et al.* (in press) were excluded unless the taxa were also reported as growing ≤ 3 m above the ground on tree trunks and/or on branches in the canopy by Sillett *et al.* (1995) or Merwin and Nadkarni (*unpubl. data*).

A total of 198 epiphytic bryophyte species (120 hepatics, 77 mosses, 1 hornwort) have been recorded: 178 species in the primary forest (111 hepatics, 66 mosses, and 1 hornwort), 66 species in the secondary forest (32 hepatics, 31 mosses), and 84 species in the pastureland (47 hepatics, 37 mosses) (Table 1). Most of the mosses of Monteverde are widespread species, but hepatics include several uncommon ones not previously recorded from Costa Rica (Gradstein *et al.*, 1994), including *Adelanthus carabyensis*, *Bazzania affinis*, *Calypogeia crenulata* (= *Mnioloma crenulata*), *Colura ulei*, *Frullania laxiflora*, *Lophocolea connata*, *Marchesinia robusta*, *Plagiochila deflexirama*, *P. rudischusteri*, *Prionolejeunea schlimiana*, *Radula antillana*, *R. tenera*, and *Syzygiella pectiniformis*. The Monteverde Cloud Forest is also one of the few localities of the rare Costa Rican endemic liverwort *Calypogeia rhynchophylla* (= *Mnioloma rhynchophylla*), known otherwise from only two localities on the mainland and from Cocos Island (Dauphin 1999). The rare endemic *Nowellia reedii* Robins., described from Monteverde (exact locality unknown) and not recorded anywhere else, was not found during this study.

Study Area

Research was carried out in the Monteverde Cloud Forest Reserve (MCFR) (10°18'N, 84°48'W, elevation ca. 1500 m), in the Cordillera de Tilarán, Costa Rica. The forest of MCFR is classified as tropical lower montane wet forest in the Holdridge Life Zone System (*sensu* Holdridge 1967) and further described as Leeward Cloud Forest by Lawton and Dryer (1980). Average annual rainfall is 2,000 - 2,500 mm y^{-1} , with an additional 20% contributed from mist (Clark 1994). There are three seasons: wet-misty season (November - January), dry season (February- April), and wet season (May - October). Detailed descriptions of the climate, geology, and vegetation of Monteverde are in

Nadkarni and Wheelwright (2000). Fieldwork was conducted in permanent study plots located in the Research Area of MCFR and adjacent pastureland.

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TABLE 1. The epiphytic bryophyte taxa found in primary and secondary forest in Monteverde Cloud Forest Reserve and adjacent pastureland following Sillett et al. (1995), Gradstein et al. (in press), and M. Merwin and N. Nadkarni (unpubl.). 1 = Primary forest, 2 = Secondary forest, 3 = Pastureland.

	1	2	3
HEPATICAEE			
<i>Adelanthus carabayensis</i> (Mont.) Grolle	x		
<i>Adelanthus decipiens</i> (Hook.) Mitt.	x		
<i>Adelanthus pittieri</i> (Steph.) Grolle	x		
<i>Amphilejeunea reflexistipula</i> (Lehm. & Lindenb.) Gradst.	x	x	
<i>Anoplolejeunea conferta</i> (Meissn.) Schiffn.	x		x
<i>Bazzania affinis</i> (Lindenb. & Gott.) Trevis.	x		
<i>Bazzania denticulata</i> (Lindenb. & Gott.) Steph.	x		
<i>Bazzania gracilis</i> (Hampe & Gott.) Steph.	x		x
<i>Bazzania hookeri</i> (Lindenb.) Trevis.	x		
<i>Bazzania longa</i> (Nees) Trevis.	x		
<i>Bazzania longistipula</i> (Lindenb.) Trevis.	x		x
<i>Bazzania stolonifera</i> (Sw.) Trevis.	x		
<i>Blepharolejeunea saccata</i> (Steph.) van Slag. & Kruijt	x		
<i>Brachiolejeunea laxifolia</i> (Tayl.) Schiffn.	x		
<i>Bryopteris filicina</i> (Sw.) Nees	x	x	x
<i>Cephalozia crassifolia</i> (Lindenb. & Gott.) Fulford	x	x	x
<i>Ceratolejeunea cornuta</i> (Lindenb.) Steph.	x	x	x
<i>Ceratolejeunea filaria</i> (Tayl. ex Lehm.) Steph.	x	x	x
<i>Ceratolejeunea patentissima</i> (Hampe & Gott.) Evans		x	
<i>Cheilolejeunea adnata</i> (Kunze) Grolle	x		x
<i>Cheilolejeunea inflexa</i> (Lehm.) Grolle		x	x
<i>Cheilolejeunea rigidula</i> (Mont.) Schust.	x	x	x
<i>Cheilolejeunea trifaria</i> (Reinw. et al.) Mizut.			x
<i>Colura ulei</i> Jov.-Ast.	x		
<i>Cyclolejeunea convexistipa</i> (Lehm. & Lindenb.) Evans	x		
<i>Cyclolejeunea luteola</i> (Spruce) Grolle	x		
<i>Cyclolejeunea peruviana</i> (Lehm. & Lindenb.) Evans	x		
<i>Cyrtolejeunea holostipa</i> (Spruce) Evans	x		
<i>Dicranolejeunea axillaris</i> (Nees & Mont.) Schiffn.	x		
<i>Diplasiolejeunea alata</i> Jov.-Ast.	x		
<i>Diplasiolejeunea cavifolia</i> Steph.	x		
<i>Diplasiolejeunea johnsonii</i> Evans	x		
<i>Diplasiolejeunea pellucida</i> (Meissn. ex Spreng.) Schiffn.	x		
<i>Drepanolejeunea cf. bidens</i> Steph.	x		x
<i>Drepanolejeunea inchoata</i> (Meissn.) Evans	x		
<i>Drepanolejeunea lichenicola</i> (Spruce) Steph.	x		
<i>Echinocolea dilatata</i> (Evans) Schust.	x		
<i>Frullania apiculata</i> (Reinw. et al.) Nees	x	x	x
<i>Frullania arecae</i> (Spreng.) Gott.	x	x	

<i>Frullania brasiliensis</i> Raddi	x	x	x
<i>Frullania convoluta</i> Lindenb. & Hampe	x		x
<i>Frullania kunzei</i> Lehm. & Lindenb.	x		
<i>Frullania laxiflora</i> Spruce	x		
<i>Frullania riojanerirensis</i> (Raddi) Ångstr.	x		x
<i>Harpalejeunea</i> cf. <i>stricta</i> (Lindenb. & Gott.) Steph.			x
<i>Harpalejeunea cinchonae</i> (Nees) Schiffn.	x		x
<i>Herbertus divergens</i> (Steph.) Herz.	x		x
<i>Herbertus juniperoideus</i> (Sw.) Grolle	x	x	x
<i>Herbertus pensilis</i> (Tayl.) Spruce	x		
<i>Jamesoniella rubricaulis</i> (Nees) Grolle			x
<i>Jubula bogotensis</i> Gott.	x		
<i>Kurzia capillaris</i> (Sw.) Grolle	x		
<i>Lejeunea cerina</i> (Lehm. & Lindenb.) Gott. <i>et al.</i>		x	
<i>Lejeunea</i> cf. <i>caespitosa</i> Lindenb.			x
<i>Lejeunea</i> cf. <i>filipes</i> Spruce	x		
<i>Lejeunea controversa</i> Gott.	x	x	
<i>Lejeunea flava</i> (Sw.) Nees	x		x
<i>Lejeunea laetevirens</i> Nees & Mont.	x		x
<i>Lejeunea phyllobola</i> Nees & Mont.	x		
<i>Lepidolejeunea involuta</i> (Gott.) Grolle	x		x
<i>Lepidozia armata</i> Steph.	x		
<i>Lepidozia cupressina</i> (Sw.) Lindenb.	x	x	x
<i>Lepidozia muenchiana</i> Steph.	x		x
<i>Lepidozia squarrosa</i> Steph.	x		
<i>Leptosciaphus porphyrius</i> (Nees) Grolle	x		x
<i>Leucolejeunea xanthocarpa</i> (Lehm. & Lindenb.) Evans	x		x
<i>Lophocolea muricata</i> (Lehm.) Nees	x		
<i>Lophocolea trapezoidea</i> Mont.	x		
<i>Lopholejeunea subfusca</i> (Nees) Schiffn.			x
<i>Marchesinia brachiata</i> (Sw.) Schiffn.	x	x	x
<i>Marchesinia robusta</i> (Mitt.) Schiffn.	x		
<i>Metzgeria albinea</i> Spruce	x	x	x
<i>Metzgeria aurantiaca</i> Steph.			x
<i>Metzgeria decipiens</i> (Mass.) Schiffn.	x	x	x
<i>Metzgeria leptoneura</i> Spruce	x	x	x
<i>Metzgeria liebmanniana</i> Lindenb. & Gott.		x	
<i>Microlejeunea acutifolia</i> Steph.	x		
<i>Microlejeunea bullata</i> (Tayl.) Evans	x		x
<i>Neurolejeunea breutelii</i> (Gott.) Evans	x	x	x
<i>Odontolejeunea lunulata</i> (Web.) Schiffn.	x		
<i>Odontoschisma longiflorum</i> (Tayl.) Steph.	x		
<i>Omphalanthus filiformis</i> (Sw.) Nees	x	x	x
<i>Omphalanthus grandistipulus</i> Steph.	x		
<i>Omphalanthus ovalis</i> (Lindenb. & Gottsche) Gradst.	x	x	x
<i>Pallavicinia lyelli</i> Hook.	x		
<i>Plagiochila adiantoides</i> (Sw.) Lindenb.	x	x	x

<i>Plagiochila aerea</i> Tayl.	X	X	X
<i>Plagiochila bidens</i> Gott.	X		
<i>Plagiochila cristata</i> (Sw.) Lindenb.	X		
<i>Plagiochila deflexirama</i> Tayl.	X		
<i>Plagiochila diversifolia</i> Lindenb. & Gott.	X	X	
<i>Plagiochila gymnocalycina</i> (Lehm. & Lindenb.) Lindenb.	X	X	X
<i>Plagiochila laxa</i> Lehm. & Lindenb.	X		
<i>Plagiochila micropteryx</i> Gott.	X	X	
<i>Plagiochila miqueliana</i> Lehm. & Lindenb.	X		
<i>Plagiochila patula</i> (Sw.) Lindenb.	X		
<i>Plagiochila raddiana</i> Lindenb.	X	X	X
<i>Plagiochila stolonifera</i> Lindenb. & Gott.	X		X
<i>Plagiochila stricta</i> Lindenb.	X		
<i>Plagiochila subplana</i> Lindenb.	X		
<i>Plagiochila tenuis</i> Lindenb.	X		
<i>Porella swartziana</i> (Web.) Trevis.	X		
<i>Radula antilleana</i> Castle	X		
<i>Radula frondescens</i> Steph.	X		
<i>Radula gottscheana</i> Tayl.	X	X	
<i>Radula javanica</i> Gott.	X		X
<i>Radula tenera</i> Mitt. ex Steph.	X	X	
<i>Riccardia fucoidea</i> (Sw.) Schiffn.	X		
<i>Scapania portoricensis</i> Hampe & Gott.	X		
<i>Symbiezidium barbiflorum</i> (Lindenb. & Gott.) Evans	X		X
<i>Symbiezidium transversale</i> (Sw.) Trevis var. <i>hookerianum</i> (Gott. et al.) Gradst. & van Beek	X		
<i>Symphyogyna brasiliensis</i> Nees	X		
<i>Symphyogyna brogniartii</i> Mont.	X		
<i>Syzygiella pectiniformis</i> Spruce	X		
<i>Taxilejeunea pterigonia</i> (Lehm. & Lindenb.) Schiffn.	X		
<i>Telaranea nematodes</i> (Aust.) Howe	X		
<i>Trichocolea flaccida</i> (Spruce) Jack & Steph.	X		
<i>Trichocolea tomentosa</i> (Sw.) Gott.	X	X	X
<i>Tylimanthus</i> cf. <i>approximatus</i> (Lindenb.) Besch.	X		
<i>Tylimanthus laxus</i> Spruce	X		

ANTHOCEROTAE

<i>Dendroceros crispus</i> (Sw.) Nees	X		
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MUSCI

<i>Acroporium estrellae</i> (Müll. Hal.) Buck & Schäf.-Verw.	X	X	
<i>Acroporium pungens</i> (Hedw.) Broth.	X		X
<i>Actinodontium standleyi</i> Bartr.	X	X	X
<i>Amphidium tortuosum</i> (Hornsch.) Robins.			X
<i>Brachymenium</i> sp.	X	X	

<i>Bryohumbertia filifolia</i> (Hornsch.) J.-P. Frahm			X
<i>Bryum capillare</i> Hedw.	X		
<i>Campyllum praegracile</i> (Mitt.) Broth.	X		
<i>Campylopus arctocarpus</i> (Hornsch.) Mitt.	X	X	
<i>Campylopus densicoma</i> (Müll. Hal.) Paris	X		
<i>Campylopus flexuosus</i> (Hedw.) Brid.			X
<i>Campylopus nivalis</i> (Brid.) Brid.	X	X	X
<i>Campylopus savannarum</i> (Müll. Hal.) Mitt.			X
<i>Caribaeohypnum polypterum</i> (Mitt.) Ando & Higuchi	X		X
<i>Daltonia gracilis</i> Mitt.	X	X	
<i>Daltonia longifolia</i> Tayl.	X	X	
<i>Ectropothecium leptochaeton</i> (Schwägr.) Buck.	X		
<i>Fissidens lagenarius</i> Mitt. var. <i>lagenarius</i>		X	
<i>Groutiella apiculata</i> (Hook.) Crum & Steere			X
<i>Groutiella chimborazensis</i> (Spruce ex Mitt.) Florsch.	X	X	
<i>Herzogiella cylindricarpa</i> (Card.) Iwats.		X	
<i>Holomitrium arboreum</i> Mitt.	X		X
<i>Holomitrium pulchellum</i> Mitt.			X
<i>Hypnella diversifolia</i> (Mitt.) Jaeg.	X		
<i>Hypnella pallescens</i> Herz.	X		
<i>Isodrepanium lentulum</i> (Wils.) Britt.	X	X	X
<i>Leiomela bartramoides</i> (Hook.) Par.	X		
<i>Lepidopilum falcatum</i> Müll. Hal.	X	X	
<i>Lepidopilum muelleri</i> (Hampe) Spruce	X		
<i>Lepidopilum scabrisetum</i> (Schwägr.) Steere	X	X	
<i>Leptotheca boliviana</i> Herzog	X		X
<i>Leucobryum antillarum</i> Besch.	X	X	X
<i>Leucobryum giganteum</i> Müll. Hal.	X		
<i>Leucoloma cruegerianum</i> (Müll. Hal.) Jaeger	X	X	X
<i>Leucoloma serrulatum</i> Brid.	X	X	X
<i>Macromitrium</i> cf. <i>tonduzii</i> Ren. & Card.	X		
<i>Macromitrium cirrosus</i> (Hedw.) Brid.	X		X
<i>Macromitrium parvirete</i> Bartr.	X		X
<i>Macromitrium podocarp</i> Müll. Hal.	X	X	X
<i>Macromitrium richardii</i> Schwägr.	X		
<i>Meteoridium remotifolium</i> (Müll. Hal.) Manuel	X	X	X
<i>Meteorium illecebrum</i> Sull.	X		
<i>Mittenothamnium lehmanni</i> (Besch.) Card.	X		
<i>Mittenothamnium reptans</i> (Hedw.) Card.	X		X
<i>Orthodontium pellucens</i> (Hook.) B.S.G.	X		
<i>Orthostichella pentasticha</i> (Brid.) Buck	X		X
<i>Palamocladium leskoides</i> (Hook.) Britt.	X		X
<i>Papillaria deppei</i> (Hornsch. ex Müll. Hal.) Jaeg.			X
<i>Papillaria imponderosa</i> (Tayl.) Broth.	X		
<i>Phyllogonium fulgens</i> (Hedw.) Brid.	X	X	X
<i>Phyllogonium viscosum</i> (P. Beauv.) Mitt.	X	X	X
<i>Pilotrichella flexilis</i> (Hedw.) Ångstr.	X		X

<i>Porotrichodendron superbum</i> (Tayl.) Broth.		x	
<i>Porotrichum</i> cf. <i>guatemalense</i> Bartr.	x	x	
<i>Porotrichum korthalsianum</i> (Dozy & Molk.) Mitt.	x	x	x
<i>Porotrichum longirostre</i> (Hook.) Mitt.	x		
<i>Prionodon densus</i> (Hedw.) Müll. Hal.	x	x	x
<i>Prionodon fuscolutescens</i> Hampe	x		
<i>Pterobryon densum</i> Hornsch.	x	x	
<i>Pyrrhobryum spiniforme</i> (Hedw.) Mitt.	x		x
<i>Rhegmatodon polycarpus</i> (Griff.) Mitt.	x		x
<i>Rhizogonium lindigii</i> (Hampe) Mitt.	x		
<i>Rhynchostegium serrulatum</i> (Hedw.) Jaeg.	x		
<i>Schlotheimia rugifolia</i> (Hook.) Schwägr.	x		x
<i>Sematophyllum subsimplex</i> (Hedw.) Mitt.	x		x
<i>Squamidium isocladum</i> (Ren. & Card.) Broth.	x		
<i>Squamidium leucotrichum</i> (Tayl.) Broth.	x		
<i>Squamidium livens</i> (Schwägr.) Broth.	x	x	x
<i>Squamidium nigricans</i> (Hook.) Broth.	x		
<i>Syrrhopodon gaudichaudi</i> Mont.	x		x
<i>Syrrhopodon incompletus</i> Schwägr.	x	x	x
<i>Syrrhopodon lycopodioides</i> (Sw. ex Brid.) Müll. Hal.	x	x	
<i>Syrrhopodon prolifer</i> Schwägr.	x	x	x
<i>Thuidium delicatulum</i> (Hedw.) B.S.G.	x	x	
<i>Zelometeorium allionii</i> Manuel			x
<i>Zelometeorium patulum</i> (Hedw.) Manuel	x		
<i>Zygodon liebmanii</i> Schimp.	x		

Synonyms

- Campylium hispidulum* (Brid.) Mitt. = *Campylium prae glaciale* (Mitt.) Broth.
Frullania exilis Tayl. = *Frullania apiculata* (Reinw. et al.) Nees
Frullania neesii Lindenb. = *Frullania kunzei* Lehm. & Lindenb.
Macromitrium mammosum Bartr. = *Macromitrium cirrosum* (Hedw.) Brid.
Macromitrium portoricense Williams = *Macromitrium podocarpi* Müll.
Plagiochila acanthoda Lindenb. & Gott. = *Plagiochila stricta* Lindenb.
Plagiochila bursata (Desv.) Lindenb. = *Plagiochila aerea* Tayl.
Plagiochila guilleminiana Nees & Mont. = *Plagiochila raddiana* Lindenb.
Porotrichum mutabile Hampe = *Porotrichum longirostre* (Hook.) Mitt.
Prionodon luteovirens (Tayl.) Mitt. = *Prionodon densus* (Hedw.) Müll.
Radula macrostachya Lindenb. & Gott. = *Radula javanica* Gott.
Schlotheimia jamesonii (Arnott) Brid. = *Schlotheimia rugifolia* (Hook.) Schwägr.
Thuidium antillarum Besch. = *Thuidium tomentosum* Besch..