

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 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. rудischusteri*, *Prionolejeunea schlimiana*, *Radula antillana*, *R. tenera*, and *Szygiella 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) ($10^{\circ}18'N$, $84^{\circ}48'W$, 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.

Acknowledgments: We thank Gregorio Dauphin, Ingo Holz, Zach Magombo, Maria Morales, Michelle Price, and Ronald Pursell for assisting with identifications. Special thanks to Bruce Allen, Steve Churchill, and Elena Reiner Drehwald for making numerous identifications. Rigo Solano, Jeremy Donaghue, Sylvia Englund, Leah Lessen, Robert Lücking, Gretchen Vos and Steve Yanoviak assisted with the fieldwork. The first author thanks the staff of the herbaria of the University of Göttingen (GOET), Missouri Botanical Garden (MO), and Universidad de Costa Rica (USJ) for assistance during research visits. Vouchers were deposited in USJ. Research was supported by National Science Foundation grants (BIR 9975110, DEB 9974035, INT 9981531, DEB 9615341).

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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
HEPATICAE			
<i>Adelanthus carabensis</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>Cheirolejeunea adnata</i> (Kunze) Grolle	x		x
<i>Cheirolejeunea inflexa</i> (Lehm.) Grolle		x	x
<i>Cheirolejeunea rigidula</i> (Mont.) Schust.	x	x	x
<i>Cheirolejeunea 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 cf. stricta</i> (Lindenb. & Gott.) Steph.			x
<i>Harpalejeunea cinchonae</i> (Nees) Schiffn.	x		x
<i>Herbertus divergens</i> (Steph.) Herz.	x		x
<i>Herbertus juniperoides</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. et al.		x	
<i>Lejeunea cf. caespitosa</i> Lindenb.			x
<i>Lejeunea cf. 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 phylllobola</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>Leptoscyphus 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 subfuscata</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 gymnocalyicina</i> (Lehm. & Lindenb.) Lindenb.	x	x	x
<i>Plagiochila laxa</i> Lehm. & Lindenb.	x		
<i>Plagiochila micropteryx</i> Gott.	x	x	
<i>Plagiochila miquelianiana</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		
<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		
<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>Acporium estrellaе</i> (Müll. Hal.) Buck & Schäf.-Verw.	x	x
<i>Acporium pungens</i> (Hedw.) Broth.	x	x
<i>Actinodontium standleyi</i> Bartr.	x	x
<i>Amphidium tortuosum</i> (Hornschr.) Robins.		x
<i>Brachymenium</i> sp.	x	x

<i>Bryohumbertia filifolia</i> (Horns.) J.-P. Frahm		x	
<i>Bryum capillare</i> Hedw.	x		
<i>Campylium praegracile</i> (Mitt.) Broth.	x		
<i>Campylopus arctocarpus</i> (Horns.) 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 chimbazensis</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 falcatulum</i> Müll. Hal.	x	x	
<i>Lepidopilum muelleri</i> (Hampe) Spruce	x		
<i>Lepidopilum scabrisetum</i> (Schwägr.) Steere	x	x	
<i>Leptotheca boliviiana</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 cf. tonduzii</i> Ren. & Card.	x		
<i>Macromitrium cirrosum</i> (Hedw.) Brid.	x		x
<i>Macromitrium parvirete</i> Bartr.	x		x
<i>Macromitrium podocarpi</i> Müll. Hal.	x	x	x
<i>Macromitrium richardii</i> Schwägr.	x		
<i>Meteoriidium remotifolium</i> (Müll. Hal.) Manuel	x	x	x
<i>Meteoriump 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> (Horns. 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 cf. 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>Rhynchosstegium 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 gaudichaudii</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 praeglaciale* (Mitt.) Broth.
Frullania exilis Tayl. = *Frullania apiculata* (Reinw. et al.) Nees
Frullania neesii Lindenb. = *Frullania kunzei* Lehm. & Lindenb.
Macromitrium mamillosum 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..