

A checklist of the mosses and liverworts of the Parc National de Marojejy, northeastern Madagascar

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Abstract

Floristic and phytogeographic surveys of bryophytes collected in the Parc National de Marojejy, northeastern Madagascar, were conducted during bryological expeditions in 1990, November 2009 and October 2021. Field collections, and a survey of publications, brings the total number of bryophyte species and infraspecific taxa reported from the protected area to 364 (212 liverworts and 152 mosses), representing 52 families and 100 genera. Eleven percent of these 364 taxa are endemic to Madagascar. A phytogeographical analysis of known bryophyte distribution patterns indicates that the bryophyte flora of the Marojejy Massif has a strong African affinity (40%).

Keywords: bryophytes, diversity, tropical mountain, rainforest, Madagascar

Résumé détaillé

Le présent travail apporte un enrichissement des connaissances sur la flore des bryophytes Malgache, un groupe taxonomique qui contrairement aux plantes supérieures est peu documenté dans la littérature scientifique. Ainsi, une check-list des bryophytes du Parc National de Marojejy a été élaborée avec une analyse de leur affinité phytogéographique. Cette check-list est basée sur une compilation de données dans la littérature (principalement Marline, 2018), données issues d'herbier en ligne et de récentes collections écologiques et floristiques résultant principalement des expéditions de Pócs *et al.* 1990, Bryolat 2009 et Marline 2021.

Au total, 364 espèces et taxons infra-spécifiques (212 hépatiques et 152 mousses) répartis dans 100 genres et 52 familles ont été enregistrés, avec un taux d'endémisme de 11 %. La famille des Lejeuneaceae (21 genres et 107 espèces et 4 taxons infra-spécifiques) est la plus représentée dans le Parc National de Marojejy suivi de la famille des Dicranaceae (quatre genres et 29 espèces et 3 taxons infra-spécifiques). La flore des bryophytes de Marojejy montre une forte affinité africaine (40 %), ce qui démontre l'origine surtout africaine de la bryoflore de Madagascar.

Neuf espèces sont reportées pour la première fois pour Madagascar : *Syrrhopodon crenulatus* (Tixier) W.D. Reese (Calymperaceae), *Taxithelium lindbergii* (A. Jaeger) Renaud & Cardot, *Brittonodoxa subpinnata* (Brid.) W.R. Buck, P.E.A.S. Câmara & Carv.-Silva (Sematophyllaceae), *Thamniopsis utacamundiana* (Mont.) W.R. Buck (Pilotrichaceae), *Hydrogonium orientale* (F. Weber) Jan Kučera (Pottiaceae), *Racopilum capense* Müll. Hal. ex Broth. (Racopilaceae), *Sphagnum obtusiusculum* Lindb. ex Warnst. (Sphagnaceae), *Radula flaccida* Lindenb. & Gottsche (Radulaceae), et *Telaranea diacantha* (Mont.) J.J.Engel & G.L. Merr. (Lepidoziaceae).

Mots clés : bryophytes, diversité, montagne tropicale, forêt humide, Madagascar

Introduction

Bryophytes are chlorophyllose (that have chloroplasts within their cells) land plants that do not possess roots and lack lignified vascular tissues. The

bryophytes are divided into three groups: mosses, liverworts, and hornworts, which diverged (by divergent evolution) from each other by 515–470 Mya (Morris *et al.*, 2018). Bryophytes play an important role in the ecosystem, as they actively participate in nutrient cycling, water retention, and soil stabilization (Ah-Peng *et al.*, 2017). Because of their ecological, anatomical and physiological characteristics, such as poikilohydry (inability to regulate their water content), characteristics that allow desiccation resistance and bacterial symbiosis, they can maintain, modify, and even create habitats for other species.

While the vascular plant flora of Madagascar has received significant attention over the last four centuries, the bryophytes have received relatively little focus despite representing 9% of the Malagasy flora and 4% of the endemic plant species (Marline *et al.*, 2022a). In spite of numerous bryological explorations, inventories, and taxonomic work, knowledge on the bryophyte flora of Madagascar is far from complete. In this paper, we present a checklist of the bryophytes of the Parc National de Marojejy, as well as a phytogeographical analysis of the local flora.

Materials and methods

Study area

The Parc National de Marojejy, located in the SAVA Region of northeastern Madagascar, is an IUCN Category I protected area. With an area of 55,500 ha, the national park encompasses the entire massif of the same name. With the summit at 2130 m, its rugged topography forms diverse habitats that are often directly related to changes in altitude (Humbert, 1955).

Marojejy's vegetation is characterized by contrasting plant formations, which vary with altitude (Goodman, 2000; Messmer *et al.*, 2000; Tahinarivony, 2023, herein), moving from lowland evergreen moist forest (< 800 m) to a medium altitude moist evergreen forest (800–1400 m) and montane shrub (> 1800 m). This is one of the healthiest montane shrubs left in Madagascar; the vegetation on all other high mountain peaks has been degraded by fire (Goodman, 2000; Garreau & Manantsara, 2003).

Checklist compilation

This checklist is a compilation of data from the literature (Grolle, 1974, 1984, 1985; Jones, 1992; La Farge, 2002a, 2002b; Pócs & Schäfer-Verwimp, 2006; Marline *et al.*, 2012; Pócs & Váña,

2015; Pócs, 2021; Gradstein & Reeb, 2022), online platforms (GBIF and Tropicos) and recent floristic and ecological collections. It is mainly based on the groundwork of Marline (2018), who examined the structure of epiphytic bryophyte assemblages along an elevational gradient in the Parc National de Marojejy, and the 2009 BRYOLAT project expedition (the project aimed to compare the distribution patterns of bryophytes and ferns along elevational gradients, and across a latitudinal gradient of islands, in the southwestern Indian Ocean region).

Ecological and floristic sampling of bryophytes on Marojejy

In 1990, T. Pócs, R. Magill, C. La Farge-England, and their team took part in a collecting trip in Marojejy. Liverworts collected during this trip were identified by T. Pócs and some of these records are published for the first time in the present work.

In November 2009, bryophytes were studied on the eastern slopes of the Marojejy Massif by a multinational group of bryologists following a hierarchically nested sampling design (Figure 1). Bryophytes were collected along an elevational transect, at 200 m intervals, along the Mandena-summit trail and from 250 m to 2050 m (10 sites in total). Sampling was undertaken at four hierarchical levels: elevational interval, plots, quadrats, and microhabitat (Ah-Peng *et al.*, 2007, 2012; Gabriel *et al.*, 2014; Marline *et al.*, 2020). In addition, collections made by Marline in October 2021, during a floristic inventory along the Mandena-summit trail, are also included.

Species identification

Species identification was performed using binocular and compound microscopy. Since there is no available key for the bryophytes of Madagascar, available literature and herbarium collections were used as reference material. Ecological samples (heterogeneous samples composed of multiple species) from the BRYOLAT project are currently stored at the Bolus herbarium (BOL). Floristic specimens are currently stored at the Association Vahatra and duplicates will be deposited at the Tsimbazaza National Herbarium (TAN).

Phytogeographic affinities

To analyze the phytogeographic affinities of Malagasy bryophytes, each taxon was assigned to a group based on its global distribution (Table 1). Distributions

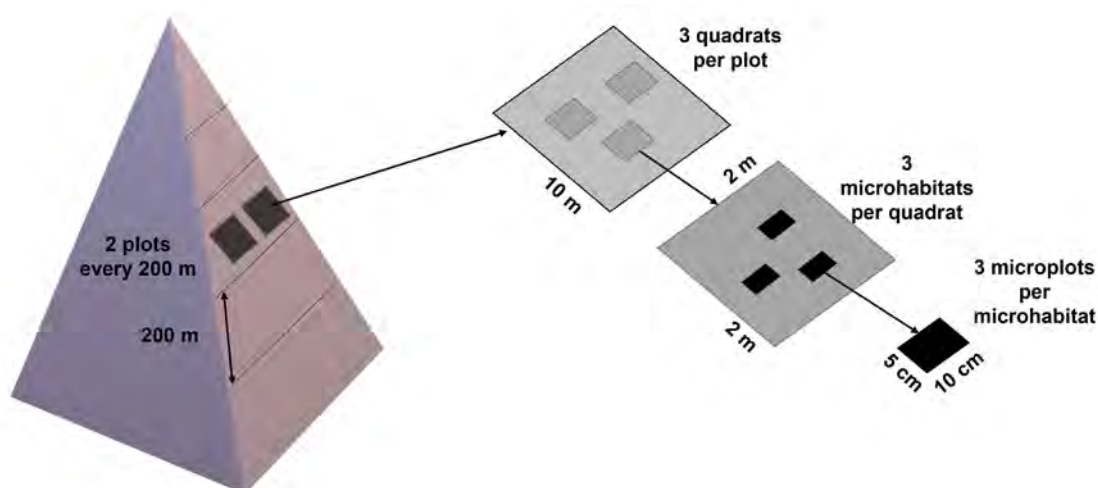


Figure 1. Bryophyte sampling design along an elevational gradient (Marline *et al.*, 2020).

were assessed by information available in the literature, the GBIF platform, and the Madagascar Catalogue (2023). The phytogeographic groups are adapted from those used by Pócs and Geissler (2002).

Table 1. Distribution of Malagasy bryophyte taxa among nine phytogeographic groups.

Phytogeographic affinities	Number of taxa		
	Total	Liverworts	Mosses
1. Endemic to Madagascar (End)	40	21	19
2. Malagasy Region (sub-endemic) (Emr)	51	25	26
3. African (Afr)	137	78	59
4. Paleotropical (Pal)	38	26	12
5. Pantropical (Pan)	51	25	26
6. Tropical Afro-American disjunct (Af-am)	26	19	7
7. Asian (Af-as)	2	2	0
8. Sub-cosmopolitan (Sco)	9	7	2
9. Pattern unknown (na)	10	9	1

Format of the list

Synopses of families, and species nomenclature follow The Bryophyte Nomenclator (Brinda & Atwood, 2023). For the annotated list, taxa are arranged alphabetically within Marchantiophyta (liverworts) and Bryophyta (mosses), and in a parallel manner within each family. Scientific names appear in *italic* font, followed by authors. For each taxon, we indicate the phytogeographical affinities in **bold** after author names (see Table 1 for abbreviations). Elevational ranges for each taxon are given in parentheses (when available). For some taxon, information about the elevational range is missing because it is not mentioned in the data associated with the specimen. In such cases, “na” is used when phytogeographic affinities and elevational ranges are unknown. The

acronym of the herbarium where specimens are housed is given in **bold** after the elevational range. Herbarium acronyms follow Thiers (2010).

Results

Species richness and compositions

A total of 364 bryophytes (355 species and 25 infraspecific taxa), comprising 152 mosses (150 species and 15 infraspecific taxa) and 212 (206 species and 10 infraspecific taxa) liverworts, from 100 genera (48 for liverworts and 52 for mosses) and 52 families (22 for liverworts and 30 for mosses) were recorded. Of these, a total of 36 species and 4 infraspecific taxa (a total of 11%) are endemic to Madagascar. Species richness increases with altitude, reaching a maximum at mid-elevation (1050-1450 m) before decreasing towards the summit. Endemic taxa (species and infraspecific) are mostly representatives of the moss family Dicranaceae (9 taxa) and the liverwort family Lejeuneaceae (15 taxa). The best represented moss families are Dicranaceae (29 taxa), Calymperaceae (19 taxa), Sematophyllaceae (15 taxa), and Orthotrichaceae (14 taxa). For liverworts, the best represented families are Lejeuneaceae (110 taxa), Lepidoziaceae (20 taxa), Plagiochilaceae (18 taxa), and Frullaniaceae (15 taxa). Nine species are newly reported for Madagascar: *Syrrhopodon crenulatus* (Tixier) W.D. Reese (Calymperaceae), *Taxithelium lindbergii* (A. Jaeger) Renauld & Cardot, *Brittonodoxa subpinnata* (Brid.) W.R. Buck, P.E.A.S. Câmara & Carv.-Silva (Sematophyllaceae), *Thamniopsis utacamundiana* (Mont.) W.R. Buck (Pilotrichaceae), *Hydrogonium orientale* (F. Weber) Jan Kučera (Pottiaceae), *Racopilum capense* Müll. Hal. ex Broth. (Racopilaceae), *Sphagnum obtusiusculum* Lindb. ex Warnst. (Sphagnaceae),

Colura hattoriana Pócs, and *Telaranea diacantha* (Mont.) J.J. Engel & G.L. Merr. (Lepidoziaceae).

Annotated list of taxa

Liverworts

ADELANTHACEAE

Adelanthus lindenbergianus (Lehm.) Mitt. **Af-am** (150-1650 m) **BOL**

Pseudomarsupidium decipiens (Hook.) Grolle **Af-am** (1050-1650 m) **BOL**

Syzygiella colorata (Lehm.) K. Feldberg, Váňa, Hentschel & Heinrichs **Pan** (1900-2130 m) **EGR**

Syzygiella manca (Mont.) J.B. Jack & Steph. **Af-am** (1250-2050 m) **BOL**

ANEURACEAE

Riccardia corbierei (Steph.) Reeb & Gradst. **Emr** (1050-1650 m) **BOL**

Riccardia longispica (Steph.) Pearson **Afr** (1650 m) **BOL**

ARNELLIACEAE

Gongylanthus sp. **na** (1450-1650 m) **BOL**

BALANTIOPSISIDACEAE

Isotachis aubertii (Schwägr.) Mitt. **Af-am** (750-2050 m) **BOL**

CALYPOGEIACEAE

Calypogeia fissa (L.) Raddi. **Afr** (1050 m) **BOL**

Mnioloma fuscum (Lehm.) R.M. Schust. **Pal** (1250-1850 m) **BOL**

CEPHALOZIACEAE

Fuscocephaloziopsis connivens subsp. *fissa* (Steph.) Váňa & L. Söderstr. **Pan** (850-1050 m) **BOL**

Odontoschisma jishibae (Steph.) L. Söderstr. & Váňa. **Af-as** (1250 m) **BOL**

CEPHALOZIELLACEAE

Cephaloziella vaginans Steph. **Afr** (1250-1450 m) **BOL**

Cylindrocolea kiaeri (Austin) Váňa **Pal** (1250-1450 m) **BOL**

Gottschelia schizopleura (Spruce) Grolle **Pal** (1850-2050 m) **EGR**

Kymatocalyx madagascariensis (Steph.) Gradst. & Váňa **Emr** (750-1400 m) **EGR**

DUMORTIERACEAE

Dumortiera hirsuta (Sw.) Nees **Sco** (450-850 m) **BOL**

FRULLANIACEAE

Frullania anderssonii Aongstr. **Afr** (250-850 m) **BOL**

Frullania angulata Mitt. **Afr** (1250 m) **BOL**

Frullania apicalis Mitt. **Afr** (1050-1850 m) **BOL**

Frullania apiculata (Reinw. Blume & Nees) Nees **Pal** (850-2050 m) **BOL**

Frullania capensis Gottsche **Afr** (850 m) **BOL**

Frullania eplicata Steph. **Afr** (1250-2050 m) **BOL**

Frullania gabonensis Vanden Berghen **Afr** (780-1050 m) **BOL**

Frullania grossiclava Steph. **Afr** (1850 m) **BOL**

Frullania humbertii Vanden Berghen **Emr** (1250-1850 m) **BOL**

Frullania letestui Vanden Berghen **Afr** (1250 m) **BOL**

Frullania lindenbergii Lehm. **Afr** (850-1850 m) **BOL**

Frullania purpurea Steph. **Afr** (250-900 m) **BOL**

Frullania serrata Gottsche **Pal** (1250-1450 m) **BOL**

Frullania vandenberghenii Pócs **na** (800-1850 m) **BOL**

Frullania variegata Steph. **Afr** (1050-1850 m) **BOL**

HERBERTACEAE

Herbertus dicranus (Taylor) Trevis. **Pan** (1250-2050 m) **BOL**

Herbertus juniperoideus (Sw.) Grolle **Pan** (780-2050 m) **BOL**

LEJEUNEACEAE

Acanthocoleus madagascariensis (Steph.) Kruijt **Afr** (1050 m) **BOL**

Acrolejeunea pycnoclada (Taylor) Schiffn. **Pal** (1250 m) **BOL**

Capillolejeunea mascarena S.W. Arnell **Emr** (800-1550 m) **BOL**

Caudalejeunea africana (Steph.) Steph. **Afr** (200-500 m) **EGR**

Caudalejeunea hanningtonii (Mitt.) Schiffn. **Afr** (800-900 m) **EGR**

Caudalejeunea lewallei Vanden Berghen **Afr** (1250 m) **BOL**

Ceratolejeunea belangeriana (Gottsche) Steph. **Pal** (250-1250 m) **BOL**

Ceratolejeunea coarina (Gottsche) Schiffn. **Afr** (650 m) **BOL**

Ceratolejeunea cornuta (Lindenb.) Schiffn. **Pan** (1050 m) **BOL**

Ceratolejeunea floribunda Steph. **Afr** (1050 m) **BOL**

Ceratolejeunea papuliflora Steph. **Afr** (450-1550 m) **BOL**

- Ceratolejeunea saroltae* Pócs **End** (250-1050 m) **BOL**
- Cheilelejeunea cordigera* (Steph.) Grolle **na** (200-1800 m) **EGR**
- Cheilelejeunea cordistipula* (Steph.) Grolle ex E.W. Jones **Afr** (250-1850 m) **BOL**
- Cheilelejeunea decursiva* (Sande Lac.) R.M. Schust. **Pal** (250-1850 m) **BOL**
- Cheilelejeunea intertexta* (Lindenb.) Steph. **Pal** (250-850 m) **BOL**
- Cheilelejeunea krakammae* (Lindenb.) R.M. Schust. **Pal** (1250-1850 m) **BOL**
- Cheilelejeunea montagnei* (Gottsche) R.M. Schust. **Afr** (750-2050 m) **BOL**
- Cheilelejeunea renigastria* Pócs **End.** (1650-1850 m) **BOL**
- Cheilelejeunea rigidula* (Nees ex Mont.) R.M. Schust. **Pal** (850-1250 m) **BOL**
- Cheilelejeunea surrepens* (Mitt.) E.W. Jones **Afr** (250-1850 m) **BOL**
- Cheilelejeunea trapezia* (Nees) Kachroo & R.M. Schust. **Pal** (800-900 m) **EGR**
- Cheilelejeunea trifaria* (Reinw., Blume & Nees) Mizut. **Pan** (450-1850 m) **BOL**
- Cheilelejeunea usambarana* (Steph.) Grolle **Afr** (850-1050 m) **BOL**
- Cheilelejeunea xanthocarpa* (Lehm. & Lindenb.) Malombe **Afr** (1850-2100 m) **BOL**
- Cololejeunea andapania* Tixier **End** (450 m) **BOL**
- Cololejeunea appressa* (A. Evans) Benedix **Pan** (250-1850 m) **BOL**
- Cololejeunea capuronii* Tixier **End** (1800 m) **EGR**
- Cololejeunea cuneata* (Lehm. & Lindenb.) Herzog **Afr** (800-1800 m) **EGR**
- Cololejeunea deroinii* Tixier **End** (330-1100 m) **PC**
- Cololejeunea elegans* Steph. **Pal** (450 m) **BOL**
- Cololejeunea floccosa* (Lehm. & Lindenb.) Schiffn. **Pal** (650 m) **BOL**
- Cololejeunea hasskarliana* (Lehm.) Schiffn. **Pal** (250-850 m) **BOL, EGR**
- Cololejeunea hildebrandii* (Austin) Steph. **Af-am** (200-1800 m) **EGR**
- Cololejeunea inflectens* (Mitt.) Benedix **Pal** (800-900 m) **EGR**
- Cololejeunea leloutrei* (E.W. Jones) R.M. Schuster **Emr** (200-1050 m) **EGR**
- Cololejeunea magillii* Pócs **Afr** (800-1050 m) **BOL**
- Cololejeunea marginata* (Lehm. & Lindenb.) Pearson **Af-am** (800-900 m) **EGR**
- Cololejeunea microscopica* (Taylor) Schiffn. **Sco** (800-900 m) **BOL**
- Cololejeunea obliqua* (Nees & Mont.) Schiffn. **Pan** (800-900 m) **EGR, BOL**
- Cololejeunea obtusifolia* var. *madecassa* (Tixier) Pócs **End** (850 m) **BOL**
- Cololejeunea ocelloides* (Horik.) S. Hatt. **Pal** (na) **EGR**
- Cololejeunea peponiformis* Mizut. **Emr** (780-1250 m) **PC**
- Cololejeunea platyneura* (Spruce) A. Evans **Pan** (800-900 m) **EGR**
- Cololejeunea pteroporum* Tixier **End** (200-500 m) **EGR**
- Cololejeunea tanzaniae* Pócs **Afr** (800-1800 m) **EGR**
- Cololejeunea zenkeri* (Steph.) E.W. Jones **Afr** (450-650 m) **BOL**
- Colura digitalis* (Mitt.) Steph. **Af-am** (750-800 m) **EGR**
- Colura hattoriana* Pócs **Emr** (1800 m) **EGR**
- Colura heimii* Jovet-Ast **Emr** (200-1550 m) **EGR**
- Colura obesa* Jovet-Ast **Emr** (200-500 m) **EGR**
- Colura tenuicornis* (A. Evans) Steph. **Pan** (1800 m) **EGR**
- Dibrachiella elobulata* (Steph.) X.Q. Shi, R.L. Zhu & Gradst. **Afr** (450 m) **BOL**
- Diplasiolejeunea cavifolia* Steph. **Pan** (200-1850 m) **EGR, PC**
- Diplasiolejeunea cornuta* Steph. **Afr** (800-2130 m) **BOL**
- Diplasiolejeunea ensifera* Tixier **End** (2050 m) **BOL**
- Diplasiolejeunea ornata* Pócs & Schäfer-Verwimp **End** (200-500 m) **BOL**
- Diplasiolejeunea symoensii* Vanden Berghen **Afr** (200-900 m) **EGR**
- Diplasiolejeunea zakiae* Tixier **End** (1400-1550 m) **EGR**
- Drepanolejeunea cultrella* (Mitt.) Steph. **Afr** (1650-2050 m) **BOL**
- Drepanolejeunea madagascariensis* (Steph.) Grolle **Afr** (200-1850 m) **BOL**
- Drepanolejeunea pentadactyla* (Mont.) Steph. **Pal** (1650 m) **EGR, BOL**
- Drepanolejeunea physifolia* (Gottsche) Pearson. **Afr** (850-2050 m) **BOL**
- Drepanolejeunea pocsii* Grolle **Afr** (1830 m) **EGR**
- Drepanolejeunea trematodes* (Nees) Bischl. **Emr** (800-1400 m) **EGR**

- Drepanolejeunea vandenberghenii* Buchb. & Eb. Fisch **Afr** (1250 m) **BOL**
- Drepanolejeunea vesiculosa* (Mitt.) Steph. **Pal** (780-1850 m) **BOL**
- Lejeunea abyssinica* (Gola) Cufod. **Afr** (250-1050 m) **BOL**
- Lejeunea adpressa* Nees **Sco** (850 m) **BOL**
- Lejeunea capensis* Gottsche **Afr** (250-850 m) **BOL**
- Lejeunea conformis* Nees & Mont. **Afr** (650-1050 m) **BOL**
- Lejeunea eckloniana* Lindenb. **Afr** (250-1250 m) **BOL**
- Lejeunea exilis* (Reinw., Blume & Nees) Grolle **Pan** (1550 m) **EGR**
- Lejeunea flava* (Sw.) Nees **Pan** (250-1850 m) **BOL**
- Lejeunea flava* subsp. *tabularis* (Spreng.) S.W. Arnell **Pan** (250-1850 m) **BOL**
- Lejeunea furcicornuta* (Grolle) G.E. Lee & Pócs **End** (1300 m) **EGR** Type locality
- Lejeunea helenae* Pearson **Afr** (850 m) **BOL**
- Lejeunea isophylla* E.W. Jones **Afr** (450-1850 m) **BOL**
- Lejeunea lomana* E.W. Jones **Afr** (1450 m) **BOL**
- Lejeunea obtusata* Gottsche **Afr** (1050-1650 m) **BOL**
- Lejeunea ramosissima* Steph. **Afr** (650-1650 m) **BOL**
- Lejeunea villaumei* (Steph.) Grolle **Afr** (200-500 m) **EGR**
- Lejeunea vojtkoi* Pócs **End** (850 m) **BOL**
- Leptolejeunea epiphylla* (Mitt.) Steph. **Pan** (200-900 m) **EGR**
- Leptolejeunea maculata* (Mitt.) Schiffn. **Pan** (250 m) **BOL**
- Lopholejeunea eulopha* (Taylor) Schiffn. **Pan** (850-1850 m) **BOL**
- Lopholejeunea lepidoscypha* Kiaer & Pearson **End** (2050 m) **BOL**
- Lopholejeunea minima* Vanden Berghen **Emr** (850 m) **BOL**
- Lopholejeunea multilacera* Steph. **Emr** (250-2050 m) **BOL**
- Lopholejeunea nigricans* (Lindenb.) Schiffn. **Pan** (250-1050 m) **BOL**
- Lopholejeunea onraedtii* Vanden Berghen **End** (850-1050 m) **BOL**
- Lopholejeunea paramultilacera* Vanden Berghen **Emr** (250-850 m) **BOL**
- Lopholejeunea subfusca* (Nees) Schiffn. **Pan** (250-1050 m) **PC**
- Metalejeunea cucullata* (Reinw., Blume & Nees) Grolle **Pan** (1800 m) **EGR**
- Microlejeunea africana* Steph. **Afr** (250-1250 m) **BOL**
- Microlejeunea ankasica* E.W. Jones **Afr** (1050-1650 m) **BOL**
- Microlejeunea dispar* Jovet-Ast **Emr** (780-1050 m) **EGR**
- Microlejeunea inflata* Steph. **Emr** (850-1850 m) **BOL**
- Microlejeunea oblongistipula* (Gottsche) Pearson **Emr** (1250 m) **BOL**
- Odontolejeunea lunulata* (F. Weber) Schiffn. **Af-am** (200-500 m) **EGR**
- Odontoschisma jishibae* (Steph.) L. Söderstr. & Váňa **Sco** (na) **EGR**
- Otolejeunea moniliata* Grolle **End** (800-1550 m) **EGR** Type locality
- Prionolejeunea grata* (Gottsche) Schiffn. **Afr** (250-1650 m) **BOL**
- Schiffneriolejeunea pappeana* (Nees) Gradst. **Afr** (1250-1650) *Schiffneriolejeunea polycarpa* (Nees) Gradst. **Af-am** (650-850 m) **BOL**
- Thysananthus auriculatus* (Wilson & Hook.) Sukkharak & Gradst. **Af-am** (850-1850 m) **PC**
- Thysananthus spathulistipus* (Reinw., Blume & Nees) Lindenb. **Pal** (250-1250 m) **BOL**
- LEPIDOZIACEAE
- Amazoopsis diplopoda* (Pócs) J.J. Engel & G.L. Merr. **Emr** (200-1400 m) **BOL**
- Bazzania comorensis* Steph. **Emr** (1250-1450 m) **BOL**
- Bazzania decrescens* (Lehm. & Lindenb.) Trevis. **Afr** (1050-2050 m) **BOL**
- Bazzania decrescens* subsp. *curvidens* (Steph.) Gyarmati **End** (1050-1250 m) **BOL**
- Bazzania decrescens* subsp. *molleri* (Steph.) E.W. Jones **Afr** (1050-2050 m) **BOL**
- Bazzania decrescens* subsp. *pumila* (Mitt.) Pócs **Afr** (1050-2050 m) **EGR**
- Bazzania mascarena* (Steph.) Herzog **Emr** (1650 m) **BOL**
- Bazzania nitida* (F. Weber) Grolle **Pan** (250-1650 m) **BOL**
- Bazzania orbani* Pócs **End** (1250-1650 m) **BOL**
- Bazzania praerupta* (Reinw., Blume & Nees) Trevis. **Afr** (1250-2050 m) **BOL**
- Bazzania roccatii* Gola **Afr** (850-1250 m) **BOL**
- Kurzia capillaris* (Sw.) Grolle **Af-am** (780-2050 m) **BOL**
- Kurzia capillaris* subsp. *stephanii* (Renauld ex Steph.) Pócs **Afr** (1650-1850 m) **BOL**

Lepidozia cupressina subsp. *africana* (Steph.) Pócs
Pan (1650 m) **BOL**

Lepidozia stuhlmannii Steph. **Afr** (1650 m) **BOL**

Lepidozia succida Mitt. **Afr** (850 m) **BOL**

Telaranea bischleriana Pócs **Emr** (850-1250 m) **BOL**

Telaranea coactilis (Spruce) J.J. Engel & G.L. Merr.
Afr (250-1250 m) **BOL**

Telaranea diacantha (Mont.) J.J. Engel & G.L. Merr.
Af-am (200-1050 m) **BOL**

Telaranea nematodes (Gottsche ex Austin) M. Howe
Af-am (1450 m) **BOL**

LOPHOCOLEACEAE

Conoscyphus trapezioides (Sande Lac.) Schiffn. **Pal**
(1250-2050 m) **BOL**

Heteroscyphus dubius (Gottsche) Schiffn. **Afr** (250-
1250 m) **BOL**

Heteroscyphus sp. **Emr** (1050-2050 m) **BOL**

Heteroscyphus spectabilis (Steph.) Schiffn. **Afr**
(1050-1450 m) **BOL**

Heteroscyphus splendens (Lehm. & Lindenb.) Grolle
Pal (750-1850 m) **BOL**

Lophocolea difformis Nees **Afr** (450 m) **BOL**

Lophocolea muricata (Lehm.) Nees **Pan** (450-1850
m) **BOL**

Lophocolea onraedtii Grolle **na** (1200 m) **BOL**

Lophocolea muhavurensis (S.W. Arnell) S.W. Arnell
ex Pócs **na** (2050 m) **BOL**

MARCHANTIACEAE

Marchantia pappeana Lehm. **Afr** (850 m) **EGR**

MASTIGOPHORACEAE

Mastigophora diclados (Brid. ex F. Weber) Nees **Pal**
(200-2050 m) **BOL**

METZGERIACEAE

Metzgeria crassipilis (Lindb.) A. Evans **Afr** (250 m)
BOL

Metzgeria furcata (L.) Corda **Sco** (450-1500 m) **BOL**

Metzgeria leptoneura Spruce **Sco** (1800 m) **EGR**

Metzgeria nudifrons Steph. **Emr** (2050 m) **BOL**

Metzgeria warnstorffii Steph. **Pal** (250 m) **BOL**

NOTOSCYPHACEAE

Notoscyphus lutescens (Lehm. & Lindenb.) Mitt. **Pal**
(2050-2130 m) **EGR**

PLAGIOCHILACEAE

Plagiochila angusta Lindenb. **Emr** (450 m) **BOL**

Plagiochila barteri Mitt. **Afr** (1250-1850 m) **BOL**

Plagiochila barteri var. *valida* (Steph.) Vanden
Berghen **Afr** (1250-1650 m) **BOL**

Plagiochila boryana Steph. **Af-am** (1150 m) **EGR**

Plagiochila drepanophylla Sande Lac. **Afr** (1000-
1400 m) **BOL**

Plagiochila fusifera Taylor **na** (1050 m) **BOL**

Plagiochila incerta Gottsche **Emr** (450-850 m) **BOL**

Plagiochila kiaeri Gottsche **Afr** (750-1250 m) **BOL**

Plagiochila macrostachya Lindenb. **End** (1050 m)
BOL

Plagiochila pectinata Willd. ex Lindenb. **Afr** (750-
2050 m) **BOL**

Plagiochila pinniflora Steph. **na** (850-1250 m) **BOL**

Plagiochila punctata var. *paucidentata* (Mont. &
Gottsche) Gradst. **na** (1000-1400 m) **BOL**

Plagiochila renauldii Steph. **Emr** (1250 m) **BOL**

Plagiochila repanda (Schwägr.) Lindenb. **Afr** (850-
1540 m) **BOL**

Plagiochila rodriguezii Steph. **End** (1300-1400 m)
BOL

Plagiochila sikorae Steph. **End** (1000-1400 m) **BOL**

Plagiochila stricta Lindenb. **Af-am** (1300-1400 m)
BOL

Plagiochila terebrans Nees & Mont. ex Lindenb. **Afr**
(450-1400 m) **BOL**

PLEUROZIACEAE

Pleurozia gigantea (F. Weber) Lindb. **Pal** (1250-2000
m) **BOL**

RADULACEAE

Cladoradula boryana (F. Weber) M.A.M. Renner,
Gradst., Ilk.-Borg. & F.R. Oliveira-da-Silva. **Af-am**
(450 m) **BOL**

Radula appressa Mitt. **Afr** (200-1050 m) **BOL**

Radula mexicana Lindenb. & Gottsche **Afr** (450 m)
BOL

Radula flaccida Lindenb. & Gottsche **Pan** (800-900
m) **EGR**

Radula fulvifolia (Hook.f. & Taylor) Gottsche, Lindenb.
& Nees **Afr** (450-1050 m) **BOL**

Radula marojezica E.W. Jones **End** (1330-1370 m)
EGR Type locality

Radula madagascariensis Gottsche **Afr** (850-1850
m) **BOL**

Radula stenocalyx Mont. **Af-am** (650-1650 m) **BOL**

Radula voluta Taylor ex Gottsche, Lindenb. & Nees
Af-am (850-1050 m) **BOL**

SCAPANiaceae

Anastrophyllum auritum (Lehm.) Steph. **Afr** (1250-2050 m) **BOL**

Anastrophyllum piligerum (Nees) Steph. **Pan** (1250-2050 m) **BOL**

Plicanthus hirtellus (F. Weber) R.M. Schust. **Sco** (1450-1850 m) **BOL**

SCHISTOCHILACEAE

Schistochila neesii (Mont.) Lindb. **Af-as** (1000-1650 m) **BOL**

Schistochila piligera Steph. **End** (800-900 m) **EGR**

Schistochila alata (Lehm.) Schiffn. **Af-am** (1500-1850 m) **EGR**

Mosses

BARTRAMIACEAE

Breutelia perrieri Thér. **Afr** (1850 m) **NY**

Breutelia stuhlmannii Broth. **Afr** (2050 m) **EGR**

BRACHYTHECIACEAE

Squamidium brasiliense (Hornsch.) Broth. **Af-am** (1250 m) **BOL**

BRYACEAE

Ptychostomum pseudotriquetrum (Hedw.) J.R. Spence & H.P. Ramsay ex Holyoak & N. Pedersen **Sco** (na) **PC**

Rosulabryum huillense (Welw. & Duby) Ochyra **Pan** (950 m) **NY**

CALYMPERACEAE

Calymperes hispidum Renauld & Cardot **Emr** (250-850 m) **BOL**

Calymperes loucoubense Besch. **End** (700 m) **MO**

Calymperes palisotii Schwägr. **Pan** (900 m) **MO**

Calymperes pallidum Mitt. **Pan** (700 m) **MO**
Calymperes taitense (Sull.) Mitt. **Pan** (250-450 m) **BOL**

Calymperopsis madagascariensis (Thér.) Broth **End** (330-1100 m) **PC**

Leucophanes angustifolium Renauld & Cardot **Afr** (450 m) **BOL**

Leucophanes hildebrandtii Müll. Hal. **Afr** (450-850 m) **BOL**

Leucophanes renauldii Cardot **Afr** (250-1450 m) **BOL**

Leucophanes rodriguezii Müll. Hal. ex Renauld & Cardot **Afr** (1050 m) **BOL**

Octoblepharum albidum Hedw. **Pan** (330-310 m) **MO, PC**

Syrrhopodon albidus subsp. *integrifolius* (E.B. Bartram) L.T. Ellis **Afr** (1250 m) **BOL**

Syrrhopodon apertifolius Besch. **Af-am** (850-1650 m) **BOL**

Syrrhopodon armatissimus W.D. Reese **Afr** (na) **MO**

Syrrhopodon crenulatus (Tixier) W.D. Reese **End** (na) **MO**

Syrrhopodon gardneri (Hook.) Schwägr. **Pan** (1250 m) **BOL**

Syrrhopodon gaudichaudii Mont. **Af-am** (1250-1450 m) **BOL**

Syrrhopodon hispidocostatus Renauld & Cardot **Pan** (850-1650 m) **BOL**

Syrrhopodon prolifer var. *prolifer* Schwägr. **Pan** (1250 m) **BOL**

DALTONIACEAE

Calyptrochaeta asplenioides (Brid.) Crosby **Afr** (1300-1400 m) **NY**

Distichophyllum mascarenicum Besch. **Emr** (na) **PC**

DICRANACEAE

Dicranoloma billarderii (Brid.) Paris **Pan** (1250-1850 m) **BOL**

Dicranoloma billarderii var. *scopareolum* (Müll. Hal.) Thér. **Afr** (1250-1650 m) **BOL**

Dicranum johnstonii Mitt. **Afr** (1050-1850 m) **BOL**

Holomitrium borbonicum Besch. **Emr** (1450 m) **BOL**

Holomitrium cylindraceum (P. Beauv.) Trevis. **Afr** (1050 m) **TAN, PC**

Holomitrium gracilisetum Thér. **End** (1250 m) **BOL**

Leucoloma bifidum (Brid.) Brid. **Emr** (450-1650 m) **BOL**

Leucoloma boivinianum var. *boivinianum* Besch. **Emr** (1250 m) **BOL**

Leucoloma candidum Broth. **End** (1250 m) **BOL**

Leucoloma chrysobasilare var. *chrysobasilare* (Müll. Hal.) A. Jaeger **Afr** (450-1050 m) **BOL**

Leucoloma cinclidotioides Besch. **Emr** (1250 m). **BOL**

Leucoloma cuneifolium (Hampe ex Müll. Hal. and Geh.) C.H. Wright **Afr** (1650 m) **BOL**

Leucoloma dichelymoides (Müll. Hal.) A. Jaeger **Emr** (650-1850 m) **BOL**

Leucoloma fontinaloides Dixon **End** (1450-1650 m) **BOL**

Leucoloma fuscifolium Besch. **Emr** (na) **PC**

Leucoloma gracilescens Broth. **Afr** (1250 m) **BOL**

Leucoloma grimmoides P. de la Varde **Afr** (1250-1650 m) **BOL**

Leucoloma holstii Broth. **Afr** (450-1250 m) **BOL**

Leucoloma lepervanchei Besch. **Afr** (250-1650 m) **BOL**

Leucoloma longifolium (Brid.) Wijk & Margad. **Emr** (450-1250 m) **MO**

Leucoloma madagascariense La Farge **End** (450-1650 m) **BOL**

Leucoloma marojeziense La Farge **End** (1450-1650 m) **BOL**

Leucoloma membranaceum La Farge **Emr** (1050-1450 m) **BOL**

Leucoloma ochrobasilare Renaud **Emr** (450 m) **BOL**

Leucoloma rutenbergii (Müll. Hal.) C.H. Wright **End** (850-1050 m) **BOL**

Leucoloma sanctae-mariae Besch. **Afr** (1450-1650 m) **BOL**

Leucoloma sinuosulum Müll. Hal. ex Besch. **Afr** (500-1000 m) **PC**

Leucoloma subchrysoasilare Renaud **End** (1050-1850 m) **BOL**

Leucoloma thraustum Hampe ex Besch. **End** (250-1850 m) **BOL**

Leucoloma thuretii Besch. **End** (1850 m) **BOL**

FISSIDENTACEAE

Fissidens aristifer Brugg.-Nann. **Emr** (850 m) **BOL**

Fissidens asplenioides Hedw. **Pan** (250 m) **BOL**

Fissidens crispulus Brid. **Afr** (1050 m) **MO**

Fissidens madecassus Schimp. ex Müll. Hal. **Emr** (700 m) **MO**

Fissidens punctulatus Sande Lac **Pal** (450-850 m) **BOL**

Fissidens pellucidus Hornsch. **Pan** (na) **PC**

Fissidens planifrons Besch. **Pal** (na) **PC**

Fissidens ramulosus Mitt. **Afr** (1050 m) **MO**

Fissidens serratus var. *serratus* Müll. Hal. **Pan** (250-450 m) **BOL**

HEDWIGIACEAE

Bryowijkia madagassa Touw. **Afr** (na) **MO**

HYPNACEAE

Chaetomitrium papillifolium Bosch & Sande Lac. **Pal** (330-1100 m) **PC**

Ectropothecium regulare (Brid.) A. Jaeger **Afr** (na) **NY**

Mittenothamnium reptans (Hedw.) Cardot **Pan** (850 m) **BOL**

HYPOPTERYGIACEAE

Hypopterygium tamarisci (Sw.) Brid. ex Müll. Hal. **Pan** (850 m) **BOL**

Lopidium struthiopteris (Brid.) M. Fleisch. **Pal** (450-850 m) **BOL**

LEUCOBRYACEAE

Campylopus arctocarpus subsp. *madecassus* (Besch.) J.-P. Frahm **Afr** (1450-1850 m) **BOL**

Campylopus arcuatus (Brid.) A. Jaeger **Afr** (1650-180 m) **BOL**

Campylopus cuspidatus subsp. *frahmii* Pócs **End** (na) **BOL**

Campylopus flaccidus Renaud & Cardot **Afr** (2000 m) **MO**

Campylopus flexuosus var. *flexuosus* (Hedw.) Brid. **Afr** (1650 m) **BOL**

Campylopus flexuosus var. *incacorralis* (Herz.) J.-P. Frahm **na** (na) **PC**

Campylopus introflexus (Hedw.) Brid. **Sco** (2050 m) **EGR**

Campylopus nivalis var. *nivalis* (Brid.) Brid. **Pan** (1250-1850 m) **BOL**

Campylopus robillardii Besch. **Afr** (1450 m) **PC**

Leucobryum boryanum Besch. **Emr** (na) **MO**

Leucobryum comorense Müll. Hal. **Emr** (900 m) **PC**

Leucobryum isleanum Besch. **Afr** (450-650 m) **BOL**

Leucobryum perrotii Renaud & Cardot **Afr** (900 m) **MO**

LEUCOMIACEAE

Leucomium strumosum (Hornsch.) Mitt. **Pan** (450-650 m) **BOL**

METEORACEAE

Aerobryopsis capensis (Müll. Hal.) M. Fleisch. **Afr** (450-1250 m) **BOL**

Floribundaria floribunda (Dozy & Molck.) M. Fleisch. **Afr** (450-650 m) **BOL**

Pilotrichella flexilis (Hedw.) Ångstr. **Af-am** (1050 m) **MO**

Pilotrichella mascarenica (Müll. Hal.) A. Jaeger **Afr** (1050 m) **MO**

Trachypodopsis serrulata var. *serrulata* (P. Beauv.) M. Fleisch. **Pan** (450-1850 m) **BOL**

NECKERACEAE

Alleniella ehrenbergii (Müll. Hal.) Enroth **Afr** (na) **PC**

Circulifolium exiguum (Bosch & Sande Lac.) S. Olsson, Enroth & D. Quandt **Pal** (450-650 m) **BOL**
Deslooveria usagara (Mitt.) Enroth **Afr** (450-850 m) **BOL**
Deslooveria variifolioides (De Sloover) Enroth **Afr** (450 m) **BOL**
Neckeropsis disticha (Hedw.) Kindb. **Pan** (450-850 m) **BOL**
Neckeropsis madecassa (Besch.) M. Fleisch. **Afr** (650 m) **BOL**
Orthostichella longinervis (Renauld & Cardot) B.H. Allen & Magill **Emr** (1050 m) **MO**
Orthostichella rigida (Müll.Hal.) B.H. Allen & Magill **Pan** (1900-2050 m) **NY**
Pinnatidendron piniforme (Brid.) Enroth **Afr** (na) **NY**
Porotrichum madagassum Kiaer ex Besch. **Afr** (450-650 m) **BOL**
Scabrellifolium elongatum (Welw. & Duby) Enroth **Afr** (450-850 m) **BOL**

ORTHOTRICACEAE

Macromitrium fimbriatum (P. Beauv.) Schwägr. **Emr** (1450-1850 m) **BOL**
Macromitrium microstomum (Hook. & Grev.) Schwägr. **Pal** (1250 m) **PC**
Macromitrium orthostichum Nees ex Schwägr. **Pal** (1900-2100 m) **MO**
Macromitrium serpens (Bruch ex Hook. & Grev.) Brid. **Pal** (1250 m) **BOL**
Macromitrium subtortum (Hook. & Grev.) Schwägr. **Afr** (1250 m) **PC**
Macromitrium sulcatum var. *sulcatum* (Hook.) Brid. **Afr** (1250-850 m) **BOL**
Schlotheimia angulosa (P. Beauv.) Dixon **Afr** (1250-2050 m) **BOL**
Schlotheimia badiella Besch. **Emr** (1250-1650 m) **BOL**
Schlotheimia excorrigata Müll. Hal. ex Cardot **Afr** (1250 m) **PC**
Schlotheimia ferruginea (Bruch ex Hook. & Grev.) Brid. **Afr** (1450-2050 m) **BOL**
Schlotheimia fornicata Duby **Emr** (1850 m) **PC**
Schlotheimia microcarpa Schimp. ex Müll. Hal. & Geh. **Emr** (1450 m) **PC**
Schlotheimia percuspidata Müll. Hal. **Afr** (1650-2050 m) **BOL**
Schlotheimia squarrosa Brid. **Emr** (1850 m) **PC**

PHYLLOGONIACEAE

Phyllogonium viscosum (P. Beauv.) Mitt. **Pan** (1050 m) **MO**

PILOTRICHACEAE

Cyclodictyon aubertii (P. Beauv.) Kuntze **Emr** (450-650 m) **BOL**
Lepidopilum lastii Mitt. **Afr** (1050 m) **MO**
Thamniopsis utacamundiana (Mont.) W.R. Buck **Pan** (750-1050 m) **MO**

POLYTRICHACEAE

Pogonatum convolutum (Hedw.) P. Beauv. **Af-am** (750-800 m) **EGR**
Polytrichum subpilosum P. Beauv. **Afr** (800 m) **MO**

POTTIACEAE

Anoetangium madagassum Renauld & Paris **End** (na) **PC**

PTEROBRYACEAE

Orthorrhynchidium planifrons (Renauld & Paris) Renauld & Cardot **Afr** (850 m) **PC**
Orthostichopsis subimbricata (Hampe) Broth. **End** (na) **DUKE**

PYLAISIADELPHACEAE

Isopterygium intortum (P. Beauv.) A. Jaeger **Emr** (850 m) **PC**

RACOPIACEAE

Racopilum africanum Mitt. **Afr** (650 m) **PC**
Racopilum madagassum Renauld **Afr** (650-1050 m) **BOL**
Racopilum capense Müll. Hal. ex Broth. **Afr** (900 m) **MO**

RHACOCARPACEAE

Rhacocarpus purpurascens (Brid.) Paris **Pan** (2130 m) **MO**

RHIZOGONIACEAE

Pyrrhobryum spiniforme (Hedw.) Mitt. **Pan** (450-1050 m) **BOL**

RUTENBERGIACEAE

Rutenbergia limbata (Hampe) Besch. **End** (850-1650 m) **BOL**
Rutenbergia madagassa Geh. & Hampe **End** (1250-1650 m) **BOL**

SEMATOPHYLLACEAE

Acanthorrhynchium papillatum (Harv.) M. Fleisch. **Emr** (750 m) **MO**
Acroporium megasporum (Duby) M. Fleisch. **Af-am** (1050-2050 m) **BOL**
Brittonodoxa subpinnata (Brid.) W.R. Buck, P.E.A.S. Câmara & Carv.-Silva **Pan** (na) **MO**

Macrohymenium acidodon (Mont.) Dozy & Molk. **Afr** (1250-2050 m) **BOL**

Macrohymenium mitratum var. *strictum* (Bosch & Sande Lac.) B.C. Tan, T.J. Kop. & D.H. Norris. **Pal** (na) **NY**

Radulina borbonica (Bel.) W.R. Buck **Pal** (450-1050 m) **BOL**

Rhaphidorrhynchium rubricaule (Besch.) Broth. **Emr** (2050 m) **PC**

Sematophyllum crassiusculum (Brid.) Broth. **Emr** (250-650 m) **BOL**

Sematophyllum schimperii (Besch. ex Paris) Broth. **Afr** (1650 m) **PC**

Sematophyllum sinuosulum (Besch.) Broth. **Afr** (1250-1650 m) **BOL**

Taxithelium lindbergii (A. Jaeger) Renauld & Cardot **Pan** (850-1000 m) **MO**

Trichosteleum debettei var. *laevisetum* Cardot **End** (450-1650 m) **BOL**

Trichosteleum pervilleanum (Schimp. ex Müll. Hal. & Geh.) W.R. Buck **Afr** (250 m) **BOL**

SPHAGNACEAE

Sphagnum palustre L. **Af-am** (330-1100 m) **PC**

Sphagnum violascens Müll. Hal. **Pal** (na) **PC**

Sphagnum sp. **na** (1050-1450 m) **BOL**

STEREOPHYLLACEAE

Entodontopsis nitens (Mitt.) W.R. Buck & Ireland **Afr-am** (na) **MO**

THUIDIACEAE

Thuidium assimile (Mitt.) A. Jaeger **Pal** (650 m) **PC**

TRACHYPODACEAE

Trachypodopsis serrulata (P. Beauv.) M. Fleisch. **Pan** (1050 m) **MO**

Phytogeographic affinities of the bryophytes collected in the Parc National de Marojej

Eight major phytogeographic patterns were recognized for the bryophytes collected from the

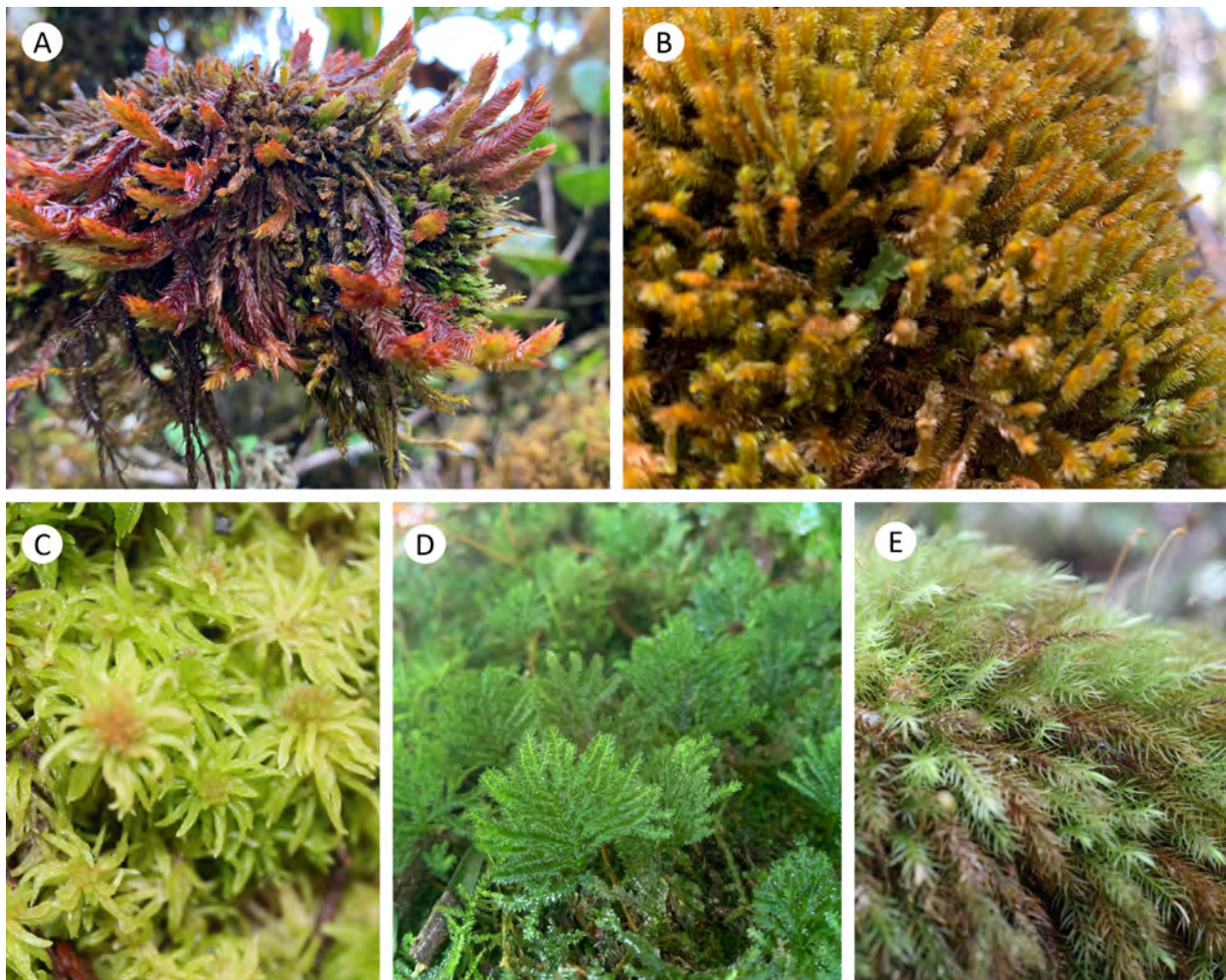


Figure 2. Common species of mosses and liverworts. **A)** *Pleurozia gigantea* (F. Weber) Lindb., **B)** *Herbertus dicranus* (Taylor ex Gottsche *et al.*) Trevis., **C)** *Sphagnum* sp., **D)** *Hypopterygium tamarisci* (Sw.) Brid. ex Müll. Hal, and **E)** *Pyrrhobryum spiniforme* (Hedw.) Mitt. (All photos by Lovanomenjanahary Marline.)

Parc National de Marojejy (Table 1): endemic to the Malagasy Region (sub-endemic) (13%); endemic to Madagascar (11%); African (40%); Paleotropical (10.7%); Panropical (10.7%); African-American (6.8%); African-Asian (< 1%); and Cosmopolitan (2.3%).

Discussion

The present work enriches working knowledge on the bryophyte flora of the Parc National de Marojejy. This checklist reports 364 species and infraspecific taxa, including 40 (11%) that are endemic to Madagascar. This is a much higher number as compared to other massifs, such as Manongarivo, where Pócs and Geissler (2002) reported 176 species and infraspecific taxa from the massif, with a similarity of 42%, 30%, and 17% respectively, for families, genera, and species from Marojejy. However, the percentage of endemic taxa found at Manongarivo was much higher compared to Marojejy (18% vs. 11%). The most dominant families in the Parc National de Marojejy are Lejeuneaceae (liverwort) and Dicranaceae (moss), which are globally diverse on island massifs in the southwestern Indian Ocean (Pócs & Geissler, 2002; Ah-Peng *et al.*, 2012).

Compared to other spore dispersed plant groups such as pteridophytes, which includes 239 recorded species on Marojejy (Rakotonrainibe, 2000), the species richness of bryophytes is higher. However, the level of endemism is much higher for pteridophytes (43%). Although these two groups are both dispersed by spores (transported by wind), their dispersal capacities are different: bryophytes have a smaller spore size that allows them to have a wider dispersal range (Zanten & Pócs, 1981).

The most recent checklist of bryophytes from Madagascar reports 766 species of moss, 443 species of liverworts and 5 species of hornworts (Marline *et al.*, 2022b). In this paper, liverworts (212 species and infraspecific taxa) are more diverse than mosses (152 species and infraspecific taxa), which is the case on other Old World islands with undisturbed rainforests (Aranda *et al.*, 2014). Bryophytes listed in this paper are mostly based on the work of Marline *et al.* (2020), which focused on the epiphytic microhabitat where liverworts are generally more diverse than mosses (Cornelissen & Gradstein, 1990; Gradstein *et al.*, 2001; Acebey *et al.*, 2003; Monica *et al.*, 2022). Further work on the ground-dwelling, epiphyllous, lignicolous microhabitats and the unknown canopy community is needed to better understand the true diversity of Marojejy's bryoflora.

Summary conclusion

We present a non-exhaustive list of the bryophytes of the Parc National de Marojejy. To date, 364 species and infraspecific taxa (29% of bryophyte species of Madagascar) are reported from the Marojejy Massif. Liverworts are the most diverse comprising 22 families, 59 genera, and 212 species and infraspecific taxa. Moss comprises 30 families, 65 genera and 152 species and infraspecific taxa. The recorded species are mostly African with a large number of endemics to Madagascar and to the Malagasy region (sub-endemic), illustrating the uniqueness of these species' assemblages on the Marojejy Massif. This annotated list illustrates mainly the epiphytic community, it will be greatly completed by further studies on the ground-dwelling, epiphyllous, rupicolous and canopy communities. Much work is needed to complete our knowledge of the bryophyte flora of Madagascar. Identification and monitoring tools need to be developed to accelerate the knowledge of this poorly known flora.

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References

- Acebey, A., Gradstein, S. R. & Krömer, T. 2003. Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. *Journal of Tropical Ecology*, 19 (1): 9-18.
- Ah-Peng, C., Chuah-Petiot, M., Descamps-Julien, B., Bardat, J., Stamenoff, P. & Strasberg, D. 2007.

- Bryophyte diversity and distribution along an altitudinal gradient on a lava flow in La Réunion. *Diversity and Distributions*, 13 (5): 654-662.
- Ah-Peng, C., Wilding, N., Kluge, J., Descamps-Julien, B., Bardat, J., Chuah-Petiot, M., Strasberg, D. & Hedderson, T. A. J. 2012.** Bryophyte diversity and range size distribution along two altitudinal gradients: Continent vs. island. *Acta Oecologica*, 42: 58-65.
- Ah-Peng, C., Cardoso, A. W., Flores, O., West, A., Wilding, N., Strasberg, D. & Hedderson, T. A. 2017.** The role of epiphytic bryophytes in interception, storage, and the regulated release of atmospheric moisture in a tropical montane cloud forest. *Journal of Hydrology*, 548: 665-673.
- Aranda, S. C., Gabriel, R., Borges P. A. V., Santos A. M. C., de Azevedo E. B., Patiño, J., Hortal, J. & Lobo, J. M. 2014.** Geographical, temporal and environmental determinants of bryophyte species richness in the Macaronesian Islands. *PLoS ONE*, 9 (7): e101786.
- Brinda, J. C. & Atwood, J. J. (eds.) 2023.** The Bryophyte Nomenclator. Retrieved April 27, 2023 from <http://www.bryonames.org/>
- Cornelissen, J. H. C. & Gradstein, S. R. 1990.** On the occurrence of bryophytes and macrolichens in different lowland rainforest types at Mabura Hill, Guyana. *Tropical Bryology*, 3: 29-35.
- Crandall-Stotler, B., Stotler, R. E. & Long, D. G. 2009.** Phylogeny and classification of the Marchantiophyta. *Edinburgh Journal of Botany*, 66 (1): 155-198.
- Gabriel, R., Coelho, M. M. C., Henriques, D. S. G., Borges, P.A.V., Elias, R.B., Kluge, J. & Ah-Peng, C. 2014.** Long-term monitoring across elevational gradients to assess ecological hypothesis: A description of standardized sampling methods in oceanic islands and first results. *Arquipelago-Life and Marine Sciences*, 31: 45-67.
- Garreau, J.-M. & Manantsara, A. 2003.** The protected-area complex of the Parc National de Marojejy and Réserve Spéciale d'Anjanaharibe Sud. In *The natural history of Madagascar*, eds. S. M. Goodman & J. P. Benstead, pp. 1451-1458. The University of Chicago Press, Chicago.
- GBIF.org (March 2023).** GBIF Occurrence Download <https://doi.org/10.15468/dl.pcgqs3>
- Goffinet, B., Buck, W. R. & Shaw, A. J. 2009.** Morphology and classification of the Bryophyta. In *Bryophytes biology*, eds. B. Goffinet & A. J. Shaw, pp. 55-138. Cambridge University Press, Cambridge, United Kingdom.
- Goodman, S. M. 2000.** Description of the Parc National de Marojejy, Madagascar, and the 1996 biological inventory of the reserve. In A floral and faunal inventory of the Parc National de Marojejy, Madagascar: With reference to elevation variation, ed. S. M. Goodman. *Fieldiana: Zoology*, new series, 97: 1-18.
- Gradstein, S. R., Griffin, D., Morales, M. I. & Nadkarni, N. M. 2001.** Diversity and habitat of mosses and liverworts in the cloud forest on Monteverde, Costa Rica. *Caldasia*, 23 (1): 203-212.
- Gradstein S. R. & Reeb C. 2022.** The genus *Plagiochila* (Dumort.) Dumort. (Marchantiophyta) in Madagascar. *Cryptogamie, Bryologie* 43 (5): 65-106.
- Grolle, R. 1974.** Eine neue *Taxilejeunea* aus Madagascar und Réunion. *Journal of Bryology*, 8: 93-96.
- Grolle, R. 1984.** Miscellanea Hepaticologica 221-230. *Journal of the Hattori Botanical Laboratory*, 55: 501-511.
- Grolle, R. 1985.** Zur Kenntnis der Lebermoosgattung *Otolejeunea*. *Haussnechtia* 2: 45-56.
- Jones, E. W. 1992.** African Hepatics XLII. *Radula marojezica* E.W. Jones, a new species from Madagascar. *Journal of Bryology*, 17: 307-311.
- La Farge, C. 2002a.** *Leucoloma* II: A revision of *Leucoloma* series *Holomitrioidea* (Dicranaceae). *Bryologist*, 105: 591-605.
- La Farge, C. 2002b.** *Leucoloma* III: A species synopsis: typification, synonymy and excluded names. *Bryologist*, 105: 606-624.
- Madagascar Catalogue. 2023.** Catalogue of the plants of Madagascar. Missouri Botanical Garden, St. Louis & Antananarivo. [<https://tropicos.org/Project/Madagascar>]
- Marline, L. 2018.** Diversity and biogeography of Madagascan bryophytes with an analysis of taxic and functional diversity along an elevational gradient in Marojejy National Park. PhD Thesis, Department of Biological Sciences, University of Cape Town, Cape Town.
- Marline, L., Andriamiarisoa, R. L., Bardat, J., Chuah-Petiot, M., Hedderson, T. A. J., Reeb, C., Strasberg, D., Wilding, N. & Ah-Peng, C. 2012.** Checklist of the bryophytes of Madagascar. *Cryptogamie Bryologie*, 33 (3): 199-255.
- Marline, L., Ah-Peng, C. & Hedderson, T. A. J. 2020.** Epiphytic bryophyte diversity and range distributions along an elevational gradient in Marojejy, Madagascar. *Biotropica*, 52 (5): 616-626.
- Marline, L., Ah-Peng, C. & Hedderson, T. A. J. 2022a.** Bryophyte diversity, endemism, and phytogeography. In *The new natural history of Madagascar*, ed. S. M. Goodman, pp. 510-520. Princeton University Press, Princeton.
- Marline, L., Ah-Peng, C. & Hedderson, T. A. J. 2022b.** Checklist of the bryophytes of Madagascar. In *The new natural history of Madagascar*, ed. S. M. Goodman, pp. 521-537. Princeton University Press, Princeton.
- Messmer, M., Rakotomalaza, P. J. & Gautier, L. 2000.** Structure and floristic composition of the vegetation of the Parc National de Marojejy, Madagascar. In A floral and faunal inventory of the Parc National de Marojejy, Madagascar: With reference to elevational variation, ed. S. M. Goodman. *Fieldiana: Zoology*, new series, 97: 41-104.
- Monica, B. B., Gradstein, S. R., Guiérot, L., Léon-Yanez, L., Bendix, J. & Bader, M. Y. 2022.** Diversity patterns of epiphytic bryophytes across spatial scales: Species-rich crowns and beta-diverse trunks. *Biotropica*, 54: 893-905.

- Morris, J. L., Puttick, M. N., Clark, J. W., Edwards, D., Kenrick, P., Pressel, S., Wellman, C. H., Yang, Z., Schneider, H. & Donoghue, P. C. J. 2018.** The timescale of early land plant evolution. *Proceedings of the National Academy of Sciences of the USA*, 115: E2274-E2283.
- Pócs, T. 2021.** The African species of *Drepanolejeunea vesiculosa* group with description of *Drepanolejeunea vanderpoortenii* spec. nova (Jungermanniopsida) from Madagascar. *Acta Botanica Hungarica*, 63 (1-2): 195-212.
- Pócs, T. & Geissler, P. 2002.** The bryophytes collected in the Réserve Spéciale de Manongarivo, Madagascar. Dans *Inventaire floristique et faunistique de la Réserve Spéciale de Manongarivo (NW Madagascar)*, eds. L. Gautier & S. M. Goodman. *Boissiera*, 59: 41-76.
- Pócs, T. & Váňa, J. 2015.** East African Bryophytes XXX. New liverwort and hornwort records. *Acta Biologica Plantarum Agriensis*, 3: 3-21.
- Pócs, T. & Schäfer-Verwimp, A. 2006.** East African Bryophytes, XXIII. Three new species of *Diplasiolejeunea* (Lejeuneaceae, Jungermanniopsida) from Madagascar *Cryptogamie, Bryologie*, 27 (4): 439-452.
- Rakotondrainibe, F. 2000.** Pteridophyte diversity patterns along an elevation gradient in the Parc National de Marojejy. In *A floral and faunal inventory of the Parc National de Marojejy, Madagascar: With reference to elevational variation.* ed. S. M. Goodman. *Fieldiana: Zoology, new series*, 97: 19-40.
- Tahinarivony, J. A. 2023.** Typologie des habitats en fonction du gradient altitudinal : Cas du Parc National de Marojejy. In *A floral and faunal inventory of the Parc National de Marojejy: Altitudinal gradient and temporal variation*, eds. S. M. Goodman & M. J. Raheirilalao. *Malagasy Nature*, 17: 102-135.
- Thiers, B. 2010** - (and continuously updated). Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/ih/>.
- Tropicos.org.** Missouri Botanical Garden. 28 Mar 2023 <<https://tropicos.org>>
- Zanten, B. O. V. & Pócs, T. 1981.** Distribution and dispersal of bryophytes. *Advances in Bryology*, 1: 479-562.