

## A SURVEY OF MARCHANTIALES FROM MADAGASCAR

**Catherine Reeb<sup>1\*</sup>, Lovanomenjanahary Marline<sup>2</sup>, Lucile Rabeau<sup>1</sup>, Ainazo Andriamanantena<sup>3</sup>, Roger Lala Andriamiarisoa<sup>4</sup>, Hery-Lisy Ranarijaona<sup>3</sup> & Tamás Pócs<sup>5</sup>**

<sup>1</sup>Institut de Systématique et Biodiversité, UMR7205, Sorbonne Université, Muséum National d'Histoire Naturelle, CNRS, EPHE. 57 rue Cuvier Case postale 39 France-75005 Paris; <sup>2</sup>Department of Biological Sciences, University of Cape Town, Private Bag X3, 7701 Rondebosch, South Africa; <sup>3</sup>Université de Mahajanga, Ecole Doctorale Ecosystèmes Naturels; <sup>4</sup>Missouri Botanical Garden P.O Box 3391 101 Antananarivo, Madagascar; <sup>5</sup>Department of Botany, Institute of Biology, Eszterházy Károly University, Eger, P.O. Box 43, H-3301; \*E-mail: [catherine.reeb@mnhn.fr](mailto:catherine.reeb@mnhn.fr)

**Abstract:** Based on the authors' recent collections and on older herbarium specimens (PC, TAN, EGR), the species of Marchantiidae (Marchantiopsida, Marchantiophyta) of Madagascar are reported with their description based on Malagasy specimens. A distribution map for each taxon is provided. Among the fifteen taxa identified, six are newly recorded for the island, including a new synonymy: *Asterella coronata* (Steph.) H.A.Mill = *Asterella bachmannii* (Steph.) S.W. Arnell. Most of Marchantiidae live in xeric areas (*Riccia* species, *Exormotheca pustulosa* Mitt.) or in exposed, only temporarily wet stations (*Plagiochasma*, *Asterella*). This preliminary study shows the evidence of under-prospection of such areas in Madagascar for bryophytes and the need of taxonomic work to clarify some genera (*Riccia*, *Asterella*, *Plagiochasma*) and to confirm the species hitherto reported.

**Keywords:** Madagascar, liverworts, Marchantiidae, distribution maps

## INTRODUCTION

Madagascar is considered a hotspot of biodiversity and many studies were already conducted upon ferns and angiosperms (Myers *et al.* 2000, Gautier and Goodman 2009). Bryologists have taken interest in bryophytes *sensu lato* (mosses, liverworts and hornworts) in Madagascar since the nineteenth century (Bescherelle 1880, 1891; Renauld and Cardot 1895; Dorr 1997, Marline *et al.* 2012).

Liverworts were early cited for the island but without references for the complex thalloids (Gottsche *et al.* 1844, Pearson 1891a, 1891b). Pearson (1893) cited the first thalloid species, *Marchantia viridula* Lehm., known today as *Marchantia globosa* Brid. ex Web. and present in Comores Islands (Bischler-Causse 1993) and La Réunion, but without description, specimens or locality information. In Stephani's work (Stephani 1891, 1892, 1893), the only Malagasy thalloid liverwort described is *Fimbriaria coronata* Steph., a synonym of *Asterella coronata* (Steph.) H.A.Mill.

The first detailed bryological studies on the Western Indian Ocean Islands focused on mosses (Renauld and Cardot 1895, Renauld 1897, 1909). So did Thériot (1920) who published six volumes on Malagasy mosses including *Sphagnum*, where only seven liverworts were just reported (*M. viridula* being always cited as the unique complex thalloid species). Despite historical collections from botanists who gathered plants in Madagascar in the first half of the twentieth century, no general studies on Malagasy liverworts were conducted at that time (Jovet-Ast 1948). Examining new collections and informations from collectors, Jovet-Ast (1948) cited *Targionia hypophylla*, *Riccia fluitans*, *Fimbriaria wilmsii* as present in Madagascar. During the second half of the twentieth century, several studies were conducted on leafy liverworts, new species were described and records were added for Madagascar in a continuous effort, but once again no thalloid liverworts (Tixier 1977, 1984, 1992; Pócs 1995, 2001, 2006; Pócs and Geissler 2002; Pócs and Schäfer-Verwimp 2006; Pócs *et al.* 2015, Pócs & Váňa 2015; Vanden Berghen 1981). The most recent check-list of bryophytes of Madagascar published in 2012 reported 1143 species and infraspecific taxa (Marline *et al.* 2012) including 14 Marchantiidae. Marchantiidae are thalloid liverworts represented all over the world by 372 species (Söderström *et al.* 2016). They are divided in four orders (Crandall-Stotler *et al.* 2009): Lunulariales (1-2 species), Marchantiales (340 species and 19 infraspecific taxa), Neohodgsoniales (1 species, restricted to New Zealand) and Sphaerocarpaceales (32) (Söderström *et al.* 2016, Wigginton 2009, Marline *et al.* 2012). According to our study, only Marchantiales occur in Madagascar.

The thallus of Marchantiales is dichotomously branched, sometimes occurring in rosettes or in isolated lobes forming more or less crowded mats on substratum. They are called “complex thalloid” liverworts, because their thallus is morphologically and functionally stratified. The photosynthetic zone is often restricted to the upper part of the thallus, with an epidermis usually interrupted by air pores, simple or bordered by a complex ring. Scales are often present on the ventral face and their characters are useful for identification. Gametangia of Marchantiales are often born on erect gametangiophores. The sporophytes hang down from female gametangiophores, except in the Ricciaceae family, where gametangia and sporophytes are embedded in the thallus. Marchantiales are often photophilous and they may tolerate high illumination and temperature variations (Bischler-Causse *et al.* 2005) being often the first colonizers of disturbed and open environments. They colonize rocks and soils, near watercourse, water-falls or seepages or in temporary flooding areas, alternating with long period of drought (*Riccia*, *Targionia*).

Thalloid liverworts, like *Marchantia* are locally called *Vahohombato*, *Vahohontany* (“stone tong”) or *Vohontany* (“earth blanket”). They are known to live in shady banks and crushed into mortar with other plants, are used to attract bees in new beehive (Boiteau *et al.* 1997). They may also be used in the process of huts construction (Boiteau *et al.* 1997).

This paper presents the description, distribution and ecological data of the species from the sub-class Marchantiales (Marchantiidae, Marchantiopsida, Marchantiophyta) encountered in Madagascar, based on the analysis of herbarium specimens and the authors’ recent collections. Six new records are proposed for Madagascar: *Asterella bachmannii* (Steph) S.W. Arnell, *Asterella marginata* (Nees) S.W. Arnell, *Exormotheca pustulosa* Mitt, *Riccia congoana* Steph, *Riccia atropurpurea* Sim, *Riccia stricta* (Lindenb.) Perold, including *Asterella coronata* (Steph.) Grolle proposed as a new synonym of the African *Asterella bachmannii* (Steph.) S.W. Arnell. One citation (*Riccia perssonii* S.A. Kahn) is not retained because no herbarium voucher is associated (Perold 1995b).

## **MATERIAL AND METHODS**

Examined material came from specimen collections from field trips in Madagascar and historical collections from herbaria including TAN, PC, MO and EGR, in Madagascar, such as those collected by Decary or Bosser (Dorr 1997). The geographical distribution of the species were assessed from available literature (*e.g.* Pócs and Geissler 2002) and recent collections.

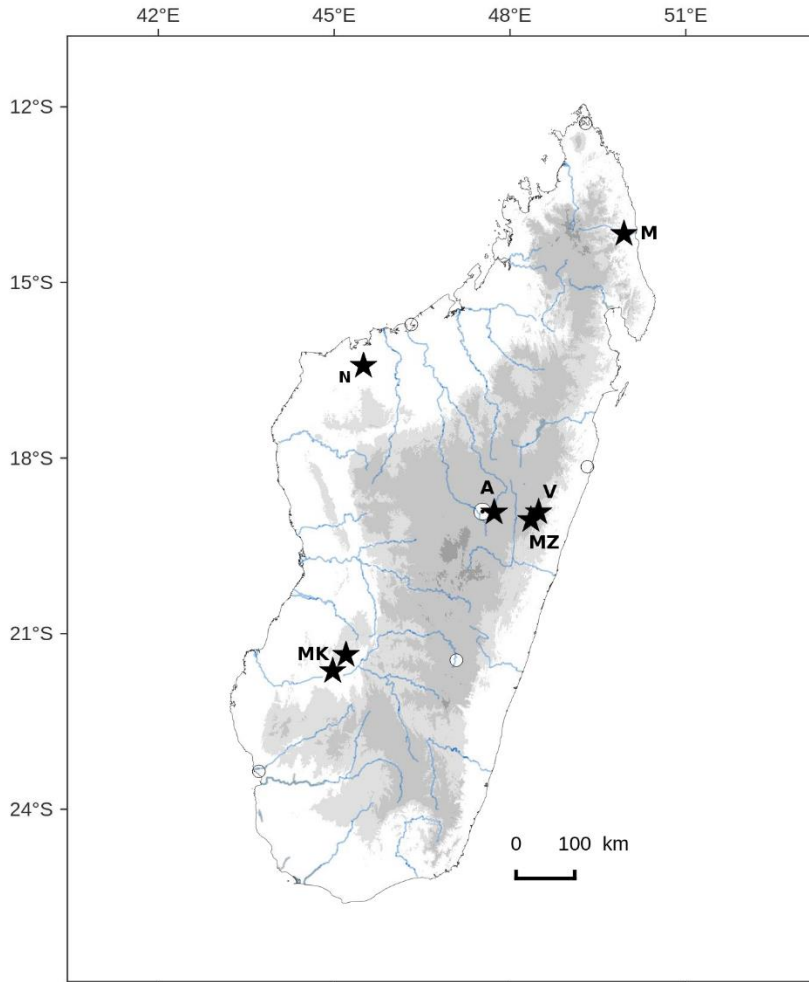
### **Recent investigated areas**

Between 2006 and 2014, several sites have been investigated in Madagascar for bryophytes. These areas are mostly located in the low and mid elevation evergreen humid forest (300-1500 m) (Moat and Smith 2007, Goodman 2009), except for the southern Makay Massif belonging to the dry West domain, in the dry deciduous forest area (Moat and Smith 2007, Goodman 2009). The sites are presented from North to South, each followed by the province and region in brackets (*Figure 1*).

The Makirovana Ambanjava complex (Antsiranana, Sava) was visited in April-May 2010 during a field trip organized by the Missouri Botanical Garden in the context of a conservation project driven by the local populations (M.B.G 2008). The total area covers 5200 ha and is covered by an evergreen low elevation humid forest on a gneiss-granite substratum. The steep elevational gradient is probably the reason of a high diversity (M.B.G 2008).

Namoroka National Park (Mahajanga, Soalala district) is located 50 km south of Soalala and was visited in October 2016. It is a typical Tsingy massif, characterized by ragged calcareous needles up to 100 meters high and dissected by a karstic network. The vegetation is a seasonal dry forest with a seven-months dry season.

Vohimana New Protected Area (Toamasina, Alaotra-Mangoro region) is located 150 km east from Antananarivo. The total area of 1635 is covered by a tropical submontane evergreen forest (790-1030 m). Bryophyte collections were conducted in July 2006, April 2010 and June-July 2012 together with a fern inventory (Reeb *et al.* 2012).



**Figure 1.** Map of recent missions in Madagascar, from North to South: M = Makirovana, N = Namoroka, V = Vohimana, MZ = Maromizaha, A = Angavokely, MK = Makay.

Maromizaha reserve (Toamasina, Alaotra-Mangoro region) is located 30 km west from Vohimana. It belongs to the same forest complex as Vohimana, 1880 ha covered by a mid-elevation evergreen forest (896-1213 m). The site was visited in July 2012.

Angavokely forest station (Antananarivo, Analamanga region) is located 36 km east from Antananarivo, and was visited in February 2011. It is in the central region (Perrier de la Bâthie 1921, Humbert and Cours Darne 1965) with dense evergreen seasonal forest (Faramalala 1995). Angavokely (1300-1787 m) although belongs to the Central High Plateau, is under influences of the eastern humid air. Its high elevation allows the presence of mountain vegetation types on the soil of intrusive gneiss-granitic rocks.

Makay massif (Tuléar, Astimo-Andrefana) was explored for bryophytes during the expedition "Makay Nature" in January 2011 (Wendenbaum 2011), June 2016, July 2017. Makay massif is located in the western part of Madagascar in subarid and dry series (Cornet 1974), west closed dry forest (Faramalala 1995, Moat and Smith 2007). It ranges from forests to impenetrable thickets, to bushland and low scrubs. Trees are largely deciduous apart from riparian elements along the rivers (Moat and Smith 2007). Vegetation is formed by many spiny and small-leaved species and the underlying vegetation is composed of succulents. Extending upon 14000 km<sup>2</sup>, the Makay is constituted by crumbly sandstone hills notched by deep canyons which give a ruiniform relief, especially eroded by the heavy rains from October to March (near 1000 mm/month). At the bottom of canyons, narrow gallery forests resist (or not!) to human pressures, especially by the grazing of the zebus and by bush fire. Exposed and sunny riverbanks, bordered by sandstone blocks are convenient for the settling of thalloid liverworts well adapted to dry areas with temporary inundations, such as *Riccia* or *Targionia*.

All of the collected specimens were deposited in "Herbier National du Parc Zoologique et Botanique de Tsimbazaza" (TAN, Antananarivo) with duplicates in "Muséum National d'Histoire Naturelle Paris herbarium" (PC, Paris) and at the Missouri Botanical Garden (MO). Species integrated in the distribution maps correspond to all specimens found in PC, TAN and the authors collection, and some specimen identified on the field but not collected: (1) Ambohitantely reserve, visited during the AETFAT field trip in April 2010 and the (2) Montagne d'Ambre, visited in August 2010.

### **Studied herbarium specimens**

Marchantiidae specimens from TAN, PC, MO and EGR were studied, including unreferenced and unidentified collections, even if sometimes annotated. Historical specimens were gathered by botanists who wandered across Madagascar collecting mainly angiosperms and ferns: Hildebrandt, the oldest (1879 and 1881), d'Alleizette (1906), Perrier de la Bathie (1921), Waterlot (1913-1914), Decary (1920-1940), Roger Heim (1934-1935), Bosser (1935-1962), Humbert (1960), Leandri (1952), Boiteau (1966-1968), Onraedt (1970-1974), Cremers (1973), Tixier (1975-1979). We could also study several untapped documents on Madagascar (specimens, micrographs etc.) gathered by S. Jovet-Ast (1914-2006), a specialist of the Ricciaceae family. Types (isotypes and syntypes) studied from PC herbarium are followed by "!".

### **Identification, descriptions and distribution maps**

Available literature on the African bryoflora (Arnell 1963, Perold 1999, Chuah-Petiot 2003, Jones 2004) and specific studies on Marchantiidae (Jovet-Ast 1955, Bischler-Causse 1978, Jovet-Ast 1989, Bischler-Causse 1993, Perold 1995a, b, c; Bischler-Causse *et al.* 2005, Long 2006, Fischer 2016) and herbarium specimens (from PC) were used as references for species identification.

For each species a short description of specimens is associated to a distribution map. For the complete description, we refer to the literature on African liverworts mentioned above. The measurements are given for the Malagasy specimens; if larger or smaller dimensions are found in the literature, they are reported in brackets. The barcode of PC specimens follows the abbreviation, when available. Spelling corrections of geographical names from original labels or additional geographic information may be added between squared brackets [ ]. When complete, dates were homogenized in "dd/mm/yyyy" format, in other cases the date from the original label was kept.

Distribution maps represent the known localities from all the studied specimens, and the comments about distribution are based on these maps.

## RESULTS

### Key of Malagasy Marchantiidae

- 1a** Thalli large (mostly > 1cm width), dark to yellowish green, translucent when humid, margins hirsute, ventral face with parallel and often curved lines of white rhizoids; air pores and air chambers absent; male receptacle on very short stalk (seems sessile).....***Dumortiera hirsuta***
- 1b** Thalli small to large, margins not hirsute, ventral face without parallel and curved lines of white rhizoids; air pores (see cross section) present; gametangia stalked or embedded.....**2**
- 2a** Dorsal epidermis in form of conical protuberances materializing the roof of air chambers, with a pore at apex of each protuberance.....***Exormotheca pustulosa***
- 2b** No dorsal conical protuberances, even if air chambers could be slightly elevated (see in cross section).....**3**
- 3a** Thalli small to medium, in partial or complete rosette or fan-like, air chambers in vertical channels or polygonal to rounded, sporophytes embedded.....**4**
- 3b** Thalli medium to large, not in rosette but in elongated lobe with dichotomous ramification; air pores compound or simple.....**10**
- 4a** Thalli iridescent, air chambers rounded to polygonal, in one layer; male gametangium marginal and disk shaped, sporophyte in apical cavities of the thallus, elaters and oil-bodies present.....***Cyathodium cavernarum***
- 4b** Thalli not iridescent; air chambers in vertical channels or large, polygonal in several layers (2-5), gametangia and sporophyte embedded in thallus but not apical; elaters and oil-bodies absent.....(***Riccia***) **5**
- 5a** Thalli less than 1 mm wide, cilia marginal and mixed with papilla on dorsal face.....***R. atromarginata* var. *jovet-astii***
- 5b** No cilia on the thalli.....**6**
- 6a** Thalli strap like, with rounded or polygonal air chambers, often aquatic or semi-aquatic, sporophyte bulging ventrally.....**7**
- 6b** Thalli not strap like, air chambers in vertically parallel channels, sporophyte not bulging or bulging dorsally.....**8**
- 7a** Apex rounded without groove often thickened into a bulge;



- spores with 5-6 complete alveoli on distal face.....***R. stricta***
- 7b** Narrow groove visible in apical part, apex narrow and emarginate, not thickened into a bulge; spores with 8-10 complete alveoli on distal face.....***R. cf. purpurascens***
- 8a** Thalli spongiose, becoming lacunose with age. No ventral scales or evanescent ones.....***R. cavernosa***
- 8b** Thalli not spongiose, at least half of each ventral scale black coloured .....**9**
- 9a** Large species, lobes up to 5 mm wide, green to blue-green, margin scalloped by conspicuous black ventral scales.....***R. congoana***
- 9b** Medium size species, glaucous green, ventral scales purple-black in basal part with a conspicuous white upper margin, clasping together when dry, forming two typical white lips.....***R. atropurpurea***
- 10a** Thalli rolled around itself when dry showing the completely purple-black and shiny ventral face; pores visible by naked eyes when wet; sporophyte apically and ventrally embedded in a mussel like black, clapping involucre .....***Targionia hypophylla***
- 10b** Thalli not showing a complete purple-black shiny ventral face; pores visible by naked eyes or not when wet; archegoniophore stalked and sporophyte hanging below archegoniophore lobes.....**11**
- 11a** Pores barrel shape, air chambers in one layer, filled with chlorophyllose filaments; gemma cups present; antheridiophores and archegoniophores raised on a long stalk .....(***Marchantia***) **12**
- 11b** Pores simple, air chambers empty in one to several layers; no gemma cups.....**13**
- 12a** Thalli 5-10 mm wide without dark median line; pores of 70-125(-200)  $\mu\text{m}$  diameter bordered by 7-8 rings of cells; antheridiophores of 10-14 mm diameter.....***Marchantia pappeana***
- 12b** Thalli 3-6(-7.5) mm wide generally with a conspicuous dark median line; pores 40-70(-100)  $\mu\text{m}$  diameter bordered by 5-6(-7) rings of cells; antheridiophores of 3-5(-8) mm diameter .....***Marchanta debilis***
- 13a** Archegoniophore arising apically, on stalk, female receptacle with rhizoid furrows, pseudoperianth present and splitting longitudinally into 8-16 slender segments.....(***Asterella***) **14**

- 13b** Archegoniophore not apically arising, on stalk, female receptacle without rhizoid furrows, pseudoperianth absent.....***Plagiochasma microcephalum* var. *microcephalum***  
**14a** Carpocephalum covered with papillae more than 200 µm high, generally two yellow pseudoperianths, ventral scales generally with one appendage.....***Asterella bachmannii***  
**14b** Carpocephalum with low papillae and generally 4 pseudoperianths, 1-2 appendages.....***Asterella marginata***

The species are presented in the alphabetical order within family. Synonyms and types are given by date of citation. Specimens are presented by geographic range, using the six official Malagasy provinces. Taxa recorded as new for Madagascar are followed by a “\*”. Types examined are followed by “!”.

#### AYTONIACEAE

In older publications, the family name is often written as "Aitoniaceae"; the genus *Aytonia*, is also found spelled by the variant: (1) *Aytonia* J.R. & G. Forst, *Char. Gen. Pl.*: 147 (1776); Lindb.: 291 (1898); Schiffn.: 30 (1983). **Type**: *A. rupestris*, (2) *Aitonia* J.R. & G. Forst, *Comm. Soc. Reg. Göttingen* 9: 46, 73 (1787), orth. var.

But as "Aitoniaceae" is an Angiosperm family (Aitoniaceae Harv. & Sond.), endemic of South-Africa, the correct name for this liverwort family is "Aytoniaceae" and *Aytonia* for the genus, basionym of *Plagiochasma*.

***Asterella bachmannii*\*** (Steph.) S.W. Arnell. *Hepat. S. Africa* 62. 1963. **Basionym**: *Fimbraria bachmannii* Steph. *Hedwigia* 33(1): 7 (1894). **Type**: SOUTH-AFRICA, Transvaal, s.d., *MacLea* s.n., exsiccata *Rehman* 3 (PC-PC 0736583! JE) (spelling var. *Fimbriaria*). **Synonym**: *Asterella coronata* (Steph.) H.A.Mill., *Phytologia* 47: 319 (1981) syn. nov. **Basionym**: *Fimbraria coronata* Steph. *Spec. Hep.* 6: 12 (1917). **Type**: MADAGASCAR, Vallée de la Mandraka, 15 août 1906, d'Alleizette 60 (PC-PC10155!), d'Alleizette 125 (PC-PC10156!). **Thallus** thick, clear and shiny green, with purple margin, only slightly undulated, 13–20 mm long and 2,5–4 mm wide. **Air**

**chambers** in several layers. Pores surrounded by 2 rings of 6–8 cells. **Ventral scales** in two ventral rows, triangular, pink, 1500–1650  $\mu\text{m}$  long, 500–600  $\mu\text{m}$  wide; appendage pink, lanceolate constricted at the basis, apex acute, 800–850  $\mu\text{m}$  long, 120–160  $\mu\text{m}$  large. Dioïcous. **Antheridia** in sessile cushions near apex of main branches, sometimes on lateral innovations. **Carpocephalum** papillose, with two yellow pseudoperianths. **Spores** yellow, translucent with crenulate margin, 90–120  $\mu\text{m}$  diameter and with 8 alveoli in the proximal face.

**Distribution:** Humid to sub-humid central zone, above 400 m (*Figure 73*). Occurs also in Africa (South-Africa, Zimbabwe, Malawi).

**Ecology:** on rocks or humid banks along rivers and open areas.

**Specimens examined:** ANTANANARIVO, Tsanisana [*Nanisana*], 01/1906, d'Alleizette (PC-PC0049107); bord de la Manankaza, [*Manankazo*] 130 km de la route de Majunga, *Bosser*, (PC); 04/1904, *Waterlot 138* (PC-PC0738492); Ambohimanga, 06/1914, *Waterlot 169* (PC-PC0738503), *Waterlot 167* (PC-PC0738501); Andramasina, 30 km SSE d'Antananarivo, *Leandri 3089* (PC); Andramasina, 1350 m, 25/05/1976, *Tixier H10020* (PC-PC0738874); Befotaka, Pic de Karafanga [*Farafangana*], 06/08/1926, *Decary s.n.* (PC-PC0738499); Vallée de la Mandraka, 1200 m, 24/02/1974, *Onraedt 74M2003* (PC-PC0738867); Vallée de la Mandraka, 23/10/2015, *Reeb & Solofo CR15M91*; Ambatoloama [*Ambatoloana*], PK64 route de Tamatave [*Toamasina*], 1250 m 18/05/1976, *Tixier H10019* (PC-PC0738873); MAHAJANGA, Bealanana, Mangindrano, forêt de moyenne d'altitude d'Antsihavo à 7 km de la commune rurale de Mangindrano, 14°14'37"S 49°00'34"E 1325 m, 02/12/2005. *R.L. Andriamiarisoa 660* (MO); FIANARANTSOA, Ranomafana National Park, Namorona river, alt 1080–1150 m, 26/07/2004, *S. & T. Pócs 04126/AR* (EGR, MO, PC-PC0738869, TAN); Ranomafana National Park, 3km from Vohiparara village, 24/07/2004, *T. Pócs & R. Ranaivojaona 04121/E* (EGR, MO, PC-PC0738870, TAN); Isalo National Park Malaso circuit on a sandstone block, 28/05/2016, *C. Reeb, L. Rabeau CR16M159* (PC, MO).

Observation of isotypes of *A. coronata* and comparison with specimens and description of *A. bachmannii* led to the conclusion that these species are identical (vegetative characters, spore

characters and dimensions). We propose the synonymy of *A. coronata* (Steph.) Grolle with *A. bachmannii* (Steph.) S.W. Arnell which is the accepted name of the species according art. 11 (priority rule ICN).

***Asterella marginata*\*** (Nees.) S.W.Arnell *Hepaticae of South Africa* 62. 1963. **Basionym:** *Fimbraria marginata* Nees. *Hortae Physicae Berolinenses* 44. 1820 **Type:** Capite b. spei, crescit iuxta viam in monte Leuwenstaart ad terram, leg. Bergius (BM) (spelling var. *Fimbriaria*). **Thallus** thick, undulate with purple margins (*Figure 2*), 20–23 mm long and 2,5–5 mm wide, sometimes with ventral innovations, some lobes cordate with overlapping apex after notches. Air chambers in several layers in cross section. **Pores** slightly elevated, surrounded by 2 rings of 5–6(–9) cells. **Ventral scales** in two lateral rows, triangular, red to purple, 1000–1500 µm long and 400–450 µm wide; appendages 1–2, lanceolate, pink, 450–700(–1200) µm long, 120–150 µm wide, not or slightly constricted at basis, few small papilla along the margin, apex acute with a single apical cell. Dioicous? **Antheridia** in sessile cushions on ventro-lateral innovations or at base of main branches. **Carpocephalum** rounded when young and slightly papillose due to air chambers, umbonate when mature with 3–4 (mostly 4) slanted pseudoperianths, palea up to 2 mm. **Spores** yellow-orange with a crenate margin, of 114–133(–140) µm diameter with 6 clear alveoli on the distal face and a net triradiate mark on the proximal face.

**Distribution:** Humid to sub-humid central zone, elevation more than 400 m (*Figure 73*). Occurs in South-Africa.

**Ecology:** on rocks or humid banks along rivers or trails.

**Specimens examined:** ANTANANARIVO, Entre Antananarivo et Befato [*Betafo*], juin 1894, *Caussèque* 345 (PC-PC0738875); Ambohimanga, 27/03/1921, *Decary s.n.* (PC-PC0738500, PC0738502, PC0738495, PC0738496, PC0738497); Imerina, montagne de Behenjy, 11/05/1921, *Decary s.n.* (PC-PC0738498); Pk 28 route du Sud, 03/1956, *Bosser* 9207 (PC-PC0738506), 09/1960, *Bosser* 14586 (PC-PC0738506); Iharanandriana, Pk 39 route du Sud, 05/1962, *Bosser* 15898 (PC-PC0738505); Nanisana, *Alleizette*, (PC); Andramasina, 30 km SSE d'Antananarivo, 1400-1500 m 17 février

1960, *Leandri 3101bis* (PC); Analabe, près d'Ambositra, *Onraedt 70M359* (PC); MAHAJANGA, Bealanana, Mangindrano, forêt de Bemafo, Ambohimirahavavay. Forêt dense humide, sempervirente. 29/11/2005 *R.L. Andriamiarisoa 621* (MO). TOAMASINA, Zahamena, 1H30 de Ranofotsy along river Ankotokotroka [*Ankotokotroka*] 1169 m, 17°36'39"S 48°40'21"E, *Reeb & Andriamanantena CR13Z65* (PC-PC0738872, TAN).



**Figure 2.** *Asterella marginata*, near Fianaransoa. Scale bar 1 cm.

**Excluded species:** *Asterella wilmsii* (Steph.) S.W. Arnell

*Asterella bachmannii* and *Asterella marginata* differ mostly by (1) larger dimensions for *A. marginata*, (2) number of pseudoperianths, regularly 2 for *A. bachmannii*, 4 for *A. marginata* and (3) the appendages, generally one constricted at basis in *A. bachmannii* and often 2 appendages not constricted at basis in *A. marginata* (this character is sometimes difficult to evaluate because of its variability within a single thallus).

*A. wilmsii* and the endemic species *Asterella coronata* (Steph.) Grolle are cited in Madagascar checklist (Wigginton 2009, Marline *et al.* 2012).

*A. bachmannii* and *A. marginata* can be easily confused (Vanden Berghen 1972, Perold 1999), but we found also that *A. wilmsii* is very close to *A. marginata*. This last species was retained for Malagasy specimens based on the ventral scales and appendages (2 not constricted, only one in *A. wilmsii*), carpocephalum characters and spore diameter (smaller than in *A. wilmsii* according Perold's description).

***Plagiochasma microcephalum*** (Steph.) Steph. var. ***microcephalum***. Bull. Herb. Boissier 6: 781, 1898. **Basionym:** *Aytonia microcephala* Steph. Botanisch Jaarboek 20: 301, 1895. **Type:** TANZANIA, Usambara, Holst C.H.E 392 (G-G00121196).

**Thallus** dark green when dry and yellow-green and dull with purple margin when re-hydrated, 10–25 mm long and 4–5 mm large. **Pores** simple, slightly elevated, surrounded by 2 rings of 5–7 cells. In cross section, epidermal pore simple and slightly elevated. **Ventral scales** in two rows, purple, with external hyaline cells and central purple cells, 720–1550  $\mu\text{m}$  long, up to 1000  $\mu\text{m}$  large; appendages 1(-2), rounded to triangular, mostly apiculate, of different sizes, generally slightly constricted or folded at basis, 5-7(-8) rows of cells in the width of the appendage, some external cells oblique and internal cells elongated trapezoidal to rectangular; few cells with persistent oil-bodies in the body of scale and appendage. Monoicous. Antheridial receptacles on the median part of the thallus. **Archegoniophores** rounded and pedunculate. Spores not seen. No asexual reproduction structures.

**Distribution:** to date, only found in Madagascar at elevation > 1000 m (Figure 74). *P. microcephalum* occurs from East-Africa to South-Africa and from Yemen to South-West India (Perold 1995a, Bischler 1978).

**Ecology:** it grows in patches on shaded and temporary hydrated rocks, naked or covered by compact layer of humus, even if may support a long dry season.

Bischler (1978) identified specimens of Onraedt 70m158 and Decary



*s.n.* This species is recognized by the characters of appendages especially by the presence of 1-2 rows of external cells in which oblique rectangular cells are always found. This is the main difference we found when compared with *Plagiochasma beccarianum* Steph., which seems to be close, when sterile. The shape of the antheridial receptacle differentiates also *Plagiochasma* species, but this character was not very clear on old collections. The examined Malagasy specimens have always apiculate appendages, a rare character according to Bischler (1978), but with a high variability in shape.

**Specimens examined:** ANTANANARIVO, Ambohimanga, 20 km d'Antananarivo, alt 1000 m, 06/01/1970, *Onraedt 70M158* (PC-PC0738865); Ambohimanga, 27/03/1921, *Decary s.n.* (PC-PC0738866); Andramasina, fév. 1958, *Decoings BD3069* (TAN); Andramasina 30 km SSE d'Antananarivo, 1400-1500 m 17/02/1960 *Leandri 3101bis* (PC). MAHAJANGA, bord de la Manankaza [*Manankazo*], 130 km de la route de Majunga [*Mahajanga*], 22/11/1951, *Bosser s.n.*

New fertile collections of Aytoniaceae are much needed in order to confirm the identity of these three species. *Asterella* has been studied both morphologically and molecularly with several sequences available on GenBank (Long 2001, 2005, 2006). Inclusion of Malagasy specimens in a molecular approach will be useful to delineate these species. In an upcoming study, DNA barcoding identification will be performed for Malagasy species.

## CYATHODIACEAE

***Cyathodium cavernarum*** Kunze, *Nov. Stirp. Pug.* 6: 18, 1834 (Lehmann 1834). **Type:** CUBA s. loc. 1824 Poeppig s.n. (holotype W, isotype, S. **Synonym:** *Cyathodium africanum* Mitt., *J. Proc. Linn. Soc. London* 22: 327 (1887). **Type:** TANZANIA, Usagara Mountains, J. Hannington s.n. (holotype, K).

*Cyathodium mexicanum* Steph. *Rev. Bryol.* 36: 139 (1909). *Cyathodium barodae* Chavan, *Bryologist* 11: 57 (1937). **Type:** INDIA Baroda state, Baroda, 1934-1935 Chavan s.n.

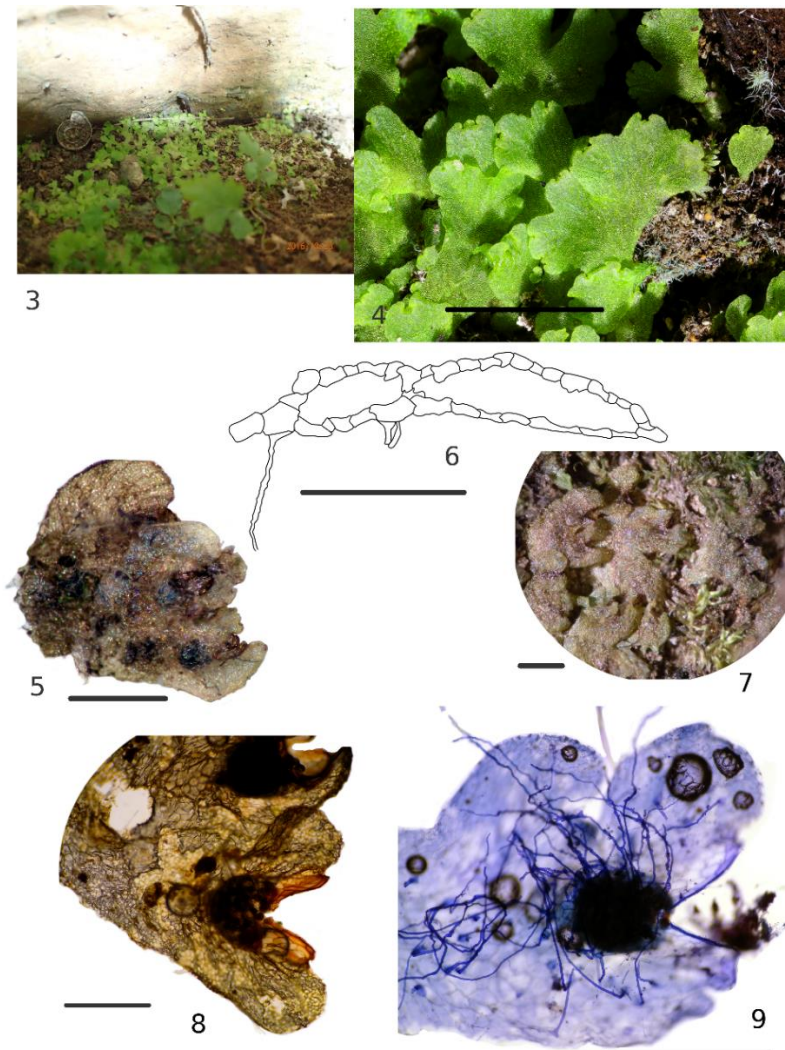
**Thallus** dichotomous, very thin, no mid-rib, rounded apex and lobes overlapping, iridescent in fresh (*Figures 3, 4*) and in dry herbarium specimens (*Figures 5, 7*), 1–3 mm wide. **Air chambers** slightly forming a network, in one row in cross section (*Figure 6*). **Pores** bordered by 2–3 circles of hyaline cells. **Ventral scales** inconspicuous or absent. Monoïcous. (Antheridia not seen): antheridal receptacle lateral terminal, cushion shaped or disk-shaped. **Archegonia** and capsules protected by an involucre globose to elliptic, without hairs but bearing few to numerous and irregular rhizoids (*Figures 8, 9*); mouth emarginate and flaring after a small narrowing border formed by a few rows of thickened cells appearing orange-brown (*Figure 8*). **Spores** brown 45–50(–83) µm with spinae 2–3(–4) µm long.

**Distribution:** found in Réserve speciale of Manongarivo and in the Namoroka tsingys (*Figure 75*). Occurs in India, Java, Africa and America.

**Ecology:** in Madagascar at the entrance of caves on naked and compact soils in a shady ambiance.

The specimens show all the characters of the species (Mitten 1887, Srivastava and Dixit 1996, Jones 1952, 2004). The involucre of the capsule is especially crowded with rhizoids, but without white erect whitish bristles typical for *Cyathodium aureonitens* Griff.





**Figures 3-9.** *Cyathodium cavernarum* Kunze. (3) General view on the field at the entrance of a cave, in Namoroka tsingy. (4) Close view of iridescent thalli. Photo: Gernordt Kunz. (5) Iridescent thallus in collection. (6) Cross section: only one layer of air chambers, and one cell thick epidermis. (7) Ventral face. (8) Details of the involucre with thickened cells at the opening of the mouth. (9) Bleach and blue treatment highlights rhizoids on the involucre (not spiny hairs like in *C. aureonitens* (Griff.) Mitt.), 9855/C. Scale bar 1 mm.

This tiny species cannot be missed because of its iridescence that is due to the position of the chloroplasts in the lens-shaped cells of the upper epidermis. This allows light to reflect and to refract through cells and air-chambers (Duckett and Ligrone 2006). Traditionally placed in the Targoniaceae family (Grolle 1995), the placement of the genus *Cyathodium* in the Cyathodiaceae family was confirmed by molecular and phylogenetic analysis (Boisselier-Dubayle *et al.* 2002; Duckett and Ligrone 2006).

Mitten (1887) gave a very short and incomplete description of *C. africanum* and claimed that it was very similar to the Indian *Cyathodium aureonitens* Griff., but he did not put the two names in synonymy. Nevertheless, Griffith (1849) draw a typical capsule with whitish bristles (p. 354) not present in *C. africanum*. It seems that a great confusion remained over time between *C. cavernarum* (= *C. africanum*) and *C. aureonitens* (Jones 1952, see Srivastava and Dixit 1996 p. 155), but Jones (1952) undoubtedly reported the two species in Africa.

In the more recent literature (Jones 1952, Jovet-Ast 1970, Vital 1974, Srivastava and Dixit 1996, Jones 2004, Bischler-Causse *et al.* 2005) *C. africanum* descriptions or illustrations are similar to those of *C. cavernarum* (Lehman 1834, Chavan 1937 under *C. barodae*) and Srivastava and Dixit (1996) proposed their synonymy in their revision of the genus. Vital (1974) and Jones (2004) observed the capsule of *C. cavernarum* crowded with rhizoids, like in Malagasy specimens (could they have been confused with the spiny whitish bristles observed in *C. aureonitens*?). We also examined all the African specimens from PC, reviewed by N. Salazar as *C. cavernarum* (Bischler-Causse *et al.* 2005) but primary identified as *C. africanum*. Jones (2004) followed the synonymy given by Srivastava and Dixit (1996) and considered *C. africanum* as a synonym of *Cyathodium cavernarum* Kunze. But Wigginton (2009) reinstated *C. africanum* waiting for clarification of the status of the *species*. *C. africanum* is also cited in the checklist of Madagascar (Marline *et al.* 2012). As in Söderström *et al.* (2016), only *C. cavernarum* is retained, we considered that it is the species found in Madagascar.

**Specimens examined:** ANTSIRANANA, réserve de Manongarivo, elev. 90-150 m, 13°54.9'S 48°27.8'E 23/07/1998, T. Pócs & A. Szabó

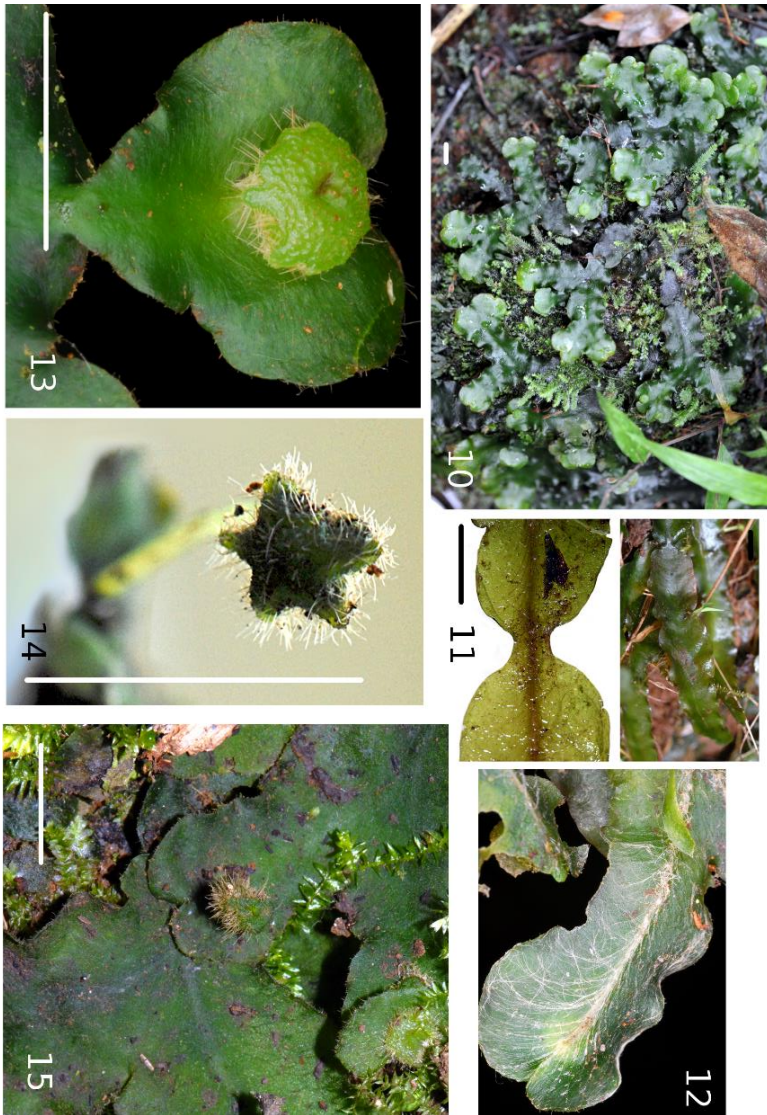
& *R. Ranaivojaona 9855/B* (EGR). MAHAJANGA, Tsingy de Namoroka on naked soil, very shady base of vertical walls in a cave opening 16°32'30S 45°18'39.9E *Reeb CR16M345*.

### DUMORTIERACEAE

***Dumortiera hirsuta*** (Sw.) Nees, *Nova Acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum* XII: 410, 1824. **Basionym:** *Marchantia hirsuta* Sw.: *Nova Genera et Species Plantarum seu Prodromus* 145, 1788. **Type:** JAMAICA, leg. *Swartz* s.n. (holotype S-B36649; isotype MW-Hb. Hoffm. 8497, UPS-BOT: B-039582). **Thallus** striped, rigid and fleshy, to 100 mm long and 20 mm wide, yellow-green to dark green, translucent to obscure (*Figures 10, 11, 15*) with dichotomous branching and apical reiterations, often preceded by a constriction of the thallus (*Figure 11*), dorsal face smooth, ventral face with an obvious central nerve, sometimes pink with long shiny rhizoids. **Pores** invisible on dorsal epiderm, absent also in cross section. **Ventral scales** discrete, whitish, their insertion forming a succession of incurved and parallel lines on each side of the central nerve (*Figure 12*). Dioicous or monoicous? **Antheridiophores** in disc shape receptacle, sessile or with a very short stalk. **Archegoniophores** often seen sessile with typical bristles on margin (*Figures 13, 14, 15*) before the stalk grows. **Spores** not seen. No gemmae or propagules.

**Distribution:** humid and sub-humid forests from Center to North (Montagne d'Ambre) (*Figure 74*). *D. hirsuta* has an oceanic subcosmopolitan distribution (Perold 1993, Bischler 1998).

**Ecology:** in shady humid environment.



**Figures 10-15.** *Dumortiera hirsuta* (Sw.) Nees. (10) Specimen along a streambed with typical undulate margins. Zahamena, January 2014. (11) Branch showing constriction at the base. Réserve de Vohimana, 2010. (12) White ventral scales in parallel curved lines and central nerve. Vohimana, April 2010. Photo: Ehoarn Bidault. (13) (14) Archegoniophores. Vohimana, April 2010. (15) Mature archegoniophore on a mat thallus, Montagne d'Ambre, August 2010. Scale bar 1cm.



Most specimens are fertile. The species shows some variability with: (1) rigid, olive green thallus with long branches, especially in the Vohimana reserve where it is found creeping among Poaceae at the bottom of a waterfall or (2) deep green, more flexible thallus is observed in shady stations, on rocks, always around waterfalls or permanent water seepages. We suspect that this species could be more widespread in Madagascar, in the humid to sub-humid areas, especially near riverine forest, streams and waterfalls.

*D. hirsuta* was cited for the first time for Madagascar by Marline *et al.* (2012), after the Bryolat field trip in the Marojejy National Park in 2009. It seems to be present in each humid forest we visited. We found also numerous specimens of *D. hirsuta* in the historical collections. *D. hirsuta* was known for Mauritius since the nineteenth century (Gottsche *et al.* 1844), and this is an example of a thalloid liverwort being under-studied in Madagascar, unidentified plants being kept in herbarium since a long time.

**Specimen examined:** ANTANANARIVO, Anjozorobe 01/02/1959, *Bosser* 12648, (TAN); Cascade d'Ankitsoko, 24/09/1934, *Heim* 1367a (PC-PC0738507); s.l., 1934-1935, *Heim* 1101a (PC-PC0738518); Vallée de la Mandraka, 23/10/2015, *Reeb & Solofo* CR15M94; ANTSIRANANA, Marojejy National Park, elev. 690 m, 14°26'07.8S 49°45'49.9E, 27/11/2009, *Ah-Peng* 349; Anjangoveratra, forêt du Makirovana, elev. 508 m, 14°10'17.4S 49°57'07.5E, 07/05/2010, *Reeb* CR302, (TAN, PC-PC0738892); Massif du Makirovana, 22/08/2010, *Reeb* CR322, (TAN, PC-PC). FIANARANTSOA, Sud Betsileo, Ankafina [=Tsarafady], März 1881, Hildebrandt *s.n.* (PC-PC0738893); Ihosy, près de Ranotsara, 01/12/1963, *Bosser* 17768 (TAN, PC); Parc National de Ranomafana, near Ambodiamontana, valley Namorona, 25/07/2004, *S. & T. Pócs* 04118/J (EGR); TOAMASINA, Ambavaniasy, réserve de Vohimana, elev. 849 m, 18°55'43.6S 48°29'56.6E, 15/04/2010, *Reeb, Andriamanantena & Bidault* CRAE93, (PC-PC0738888, TAN); Ambavaniasy, réserve de Vohimana elev. 789 m, 18°55'12.7S 48°30'57.9E, 13/04/2010, *Reeb, Andriamanantena & Bidault* CRAE7, (TAN, PC-PC0738889); Zahamena, 1h30 de Ranofotsy, le long de l'Ankrokotroka, 1169m, 17°36'39.0S 48°40'21E, 04/01/2014, *Reeb & Andriamanantena* CR13Z93 (PC-PC0768890), CR13Z85 (PC-

PC0768891). It was also observed in Ambohitantely forest and in Montagne d'Ambre National Park, above 400 m.

### EXORMOTHECACEAE

***Exormotheca pustulosa***\* Mitt. *Nat. Hist. Azores or Western Islands* 326, 1870 **Type:** MADEIRA, Pico de Barcellos, leg. *Johnson* (holotype, NY). **Synonym:** *Exormotheca africana* Steph. *Spec. Hep.* 6: 18, 1917. **Thallus** compact and bifurcate in two ligulate lobes, small, < 1cm long, (*Figure 16*), dorsal surface irregular due to air chamber elevation with pores, margin recurved when dry, scales covering the dorsal margin. **Air chambers** conspicuous, elevated up to 320 µm in cross section (*Figure 17*). **Ventral scales** conspicuous, purple-black, covering flanks (*Figure 18*), exceeding the margin, especially near apical zone; scales not present on the central zone of the ventral face. Monoicous or dioicous? **Antheridia** sunken in the thallus, prolonged by a protruding neck, emerging between air chambers and around the same height. **Archegoniophores** in a central cushion. **Spores** not seen.

**Distribution:** one collection in South Central area. Occurs in the Atlantic islands (St. Helena, Madeira, Azores), Mediterranean areas (Portugal, South of France, Italy, Spain), Arab Peninsula, widespread in tropical and South Africa, Comores and La Réunion (Bischler, 1976, Perold 1999) and was found finally in Mexico (Bischler *et al.* 2005).

This is the first record of the species for Madagascar. It is not surprising to find it in the semi-arid region of the island (*Figure 75*). New collections are needed in order to enlarge its known distribution and ecology in the country.

The unique specimen of *E. pustulosa* is more than fifty years old, and it was not easy to get clear and clean cross sections. However, this noteworthy liverwort is easy to recognize to the naked eyes by (1) the conically juxtaposed air chambers, (2) the lateral scales, and (3) the organization of reproductive structures.

**Specimen examined:** FIANARANTSOA, Ihosy, sur terre humide, Janv. 1962, *Bosser 15376* (PC-PC0715993, TAN).

## MARCHANTIACEAE

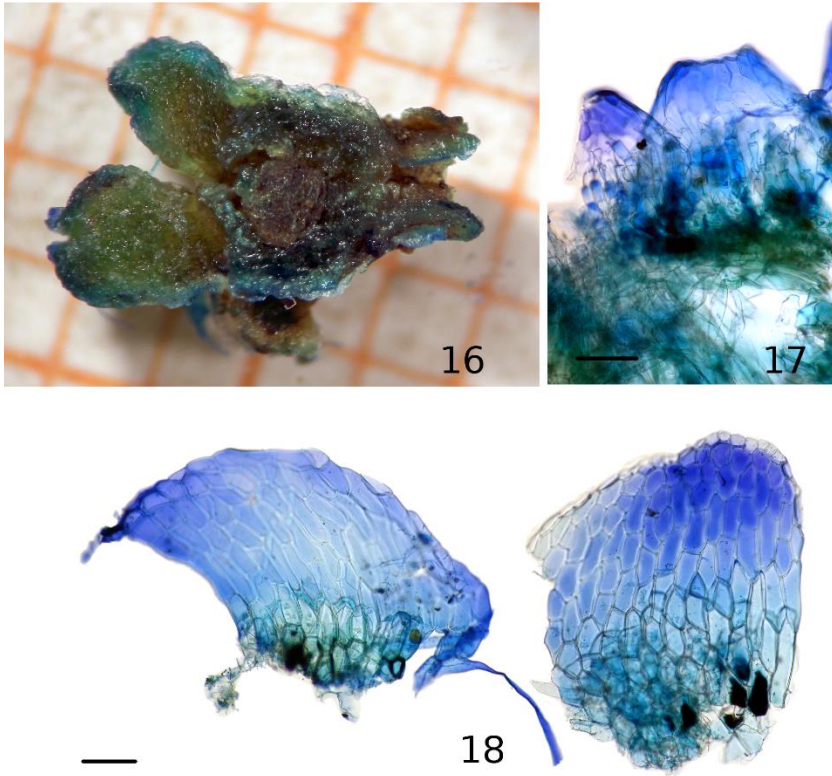
***Marchantia debilis*** K.I.Goebel, Organographie der Pflanzen. Ed. 2 2(1): 901. 1915

**Type:** CAMEROON, Urwaldgebiet von Bipindi, Zenker, *Flora von Kamerun exs.* 1339 (BM!, BR, E, F, G!, GOET, M, S, isotypes).

**Synonym:** *M. chevalieri* Steph. ex Bonner, Candollea14: 103 (1953).

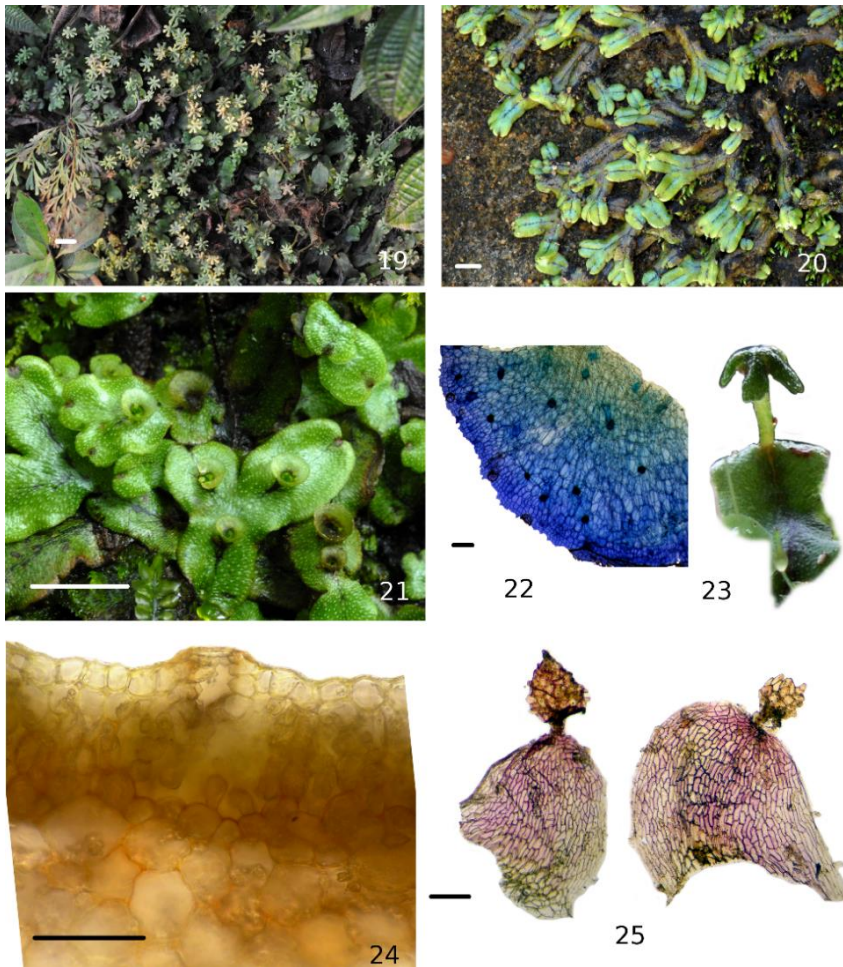
**Type:** IVORY COAST, Haute Côte d'Ivoire, pays Dijola, environs de Ona, 4-1909, *Chevalier s.n.* (G, PC). **Thallus** dichotomous, elongated, bright green with a narrow median black line, often interrupted, margin recurved on fresh specimen, hyaline sometimes coloured with purple, entire, undulate to crisped; thallus small to medium sized 20–30 mm long, each axis 3–6(–7.5) mm wide (*Figures 19, 20*). **Air pores** visible, 40–70(–100)  $\mu\text{m}$  diameter bordered by 5–6(–7) rings of cells, 2–3 above epidermis, and 2–3 projecting into the cavity (*Figure 24*). **Ventral scales** in 4 rows, not extending more than 30–50 % of thallus width, purple at least in median portion, 1210–1950  $\mu\text{m}$  long, 830–910  $\mu\text{m}$  wide, oil cells scattered; appendage ovate to orbicular, purple, (300–) 450–550  $\mu\text{m}$  long, bordered by unicellular teeth, oil-bodies absent (*Figure 25*). **Cupules** shortly ciliate, cilia 1–2 cells long (*Figures 21, 22*). Dioicous. **Antheridiophore** at apex of axis, stalk 13–15 mm long, with a single band of air cavities, receptacle 3–5(–8) mm diameter with (4–) 7–10 rays generally asymmetric. **Archegoniophore** at apex of axis, stalk 6–9 mm long, with a single band of air cavities, receptacle (3–)4–5 mm diameter, deeply divided to the 0.5–0.8 of the receptacle diameter into (5–)7–10 lobes, generally symmetric (*Figures 19, 23*). Lobes broadened and/or truncate at apex. Sporophyte not seen on Malagasy specimens.

**Distribution:** widely distributed from South to North, not in dryer areas (*Figure 76*). Occurs in continental Africa.



**Figures 16-18.** *Exormotheca pustulosa* Mitten. (16) Close view of a re-hydrated thallus. (17) Elevated air chamber: chlorophyllose filaments rise to more than half the high of the pore. (18) Ventral scales, *Bosser* 15376. Coloration with bleached (20 %), rinsed and diluted methylen blue. Scale bar 100  $\mu$ m.





**Figures 19-25.** *Marchantia debilis* K.I.Goebel. (19) Population of *M. debilis*, with archegoniophores. Andasibe, Vakona Lodge, October 2015. Scale bar 1cm. (20) Closer view showing the typical black central line. Massif du Makay. Scale bar 5 mm. (21) Vegetative propropagules in cupules. Vohimana, 2010. Scale bar 5 mm. (22) Lamina of the cupule: margin shortly ciliate, cilia less than 2 cells, *Cremers* 2685. Coloration with bleached (20 %), rinses and diluted methylen blue. (23) Archegoniophore, receptacle deeply divided. Vohimana reserve, July 2006. (24) Cross section of the thallus. Scale bar 100  $\mu$ m. (25) Ventral scales, with relatively small appendages compared to the scale body. Scale bar 100  $\mu$ m.

**Selected specimens examined:** ANTANANARIVO, 54 km route de Moramanga, Anosibe, 15/09/1653, *Bosser 6411* (PC-PC0738843); Ambohipotsy, 18/06/1880, *Wildebrandti 4234* (PC-PC0738836); 10/1913, *Waterlot 13* (PC-PC0738835), 14 (PC-PC0738833); Fort Voyron, 15/01/1921, *Decary s.n.* (PC-PC0738816); Mandraka Pk 69, forêt de la Mandraka, au sol, alt 1000 m, 18/07/1972, *Cremers 2259*; Anjozobé [*Anjozorobe*], 22/08/1977, *Tixier s.n.* (PC-PC0738840); Ambatomirahavavy, Lemurs Parc, 18°57'04.8S 47°21'25.72E, 1280m, 20/10/2015, *Reeb CR15M61*; Ampefy, chutes de la Lily, 19°01'54.2S 46°41'03.4E, 1156 m, 19/10/2015, *Reeb, Riza & Albert CR15M51*. ANTSIRANANA, Sud d'Ambanja, sur rocher, 13°42'18.01S 48°27'6.93E, 13/08/1973, *Cremers 2455* (TAN); Sud Est d'Ambilobe, forêt d'Anjahana, 28/08/1973, *Cremers 2685*, (PC-PC0167105, TAN); Ambilobe, 26/07/1939, *Decary s.n.* (PC-PC0738844); Analavelona, Andriamiarisoa *ACR1131* (MBG); Diego-Suarez, Ambilobe, bords de la Mahavavy, s.d., *Waterlot 121* (PC-PC0738849); Diego-Suarez, Les Roussettes [Mt. Ambre], 06/11/1975, *Tixier 7474* (PC-PC0738838), 7667 (PC-PC0738846); Nossi-Bé, mai 1879, *Hildebrandt 4233* (PC-PC0738851); Parc national du Marojejy, Mandena, Andampibe valley, 22/03/1990, *Pócs 90110/J* (PC-PC0738839); Réserve spéciale de Manongarivo. Evergreen riverine forest along Ambakatra river, alt 90-150 m, 13°54.9'S 48°27.8'E, 23/07/1998, *T. Pócs, A Szabó & R. Ranaivojaona 9855/C* (EGR); Tsaratanana RNI. River Andilambe. Low elevation humid forest savoka on granite, 17/11/2001, *Chris Birkinshaw 1110* (MO); Sava, Andapa, Doany, Andranomilolo forêt dense humide de moyenne altitude située à environ 13 km à l'Ouest du village d'Andranopositra. 14°20'32"S 49°19'05"E 1438 m, 13/11/2006, *D. Ravelonarivo et al. 2048* (MO). FIANARANTSOA, [Atsimo-Atsanana], Vondrozo, Parc de Farafanga [*Farafangana*], 04/09/1926, *Decary s.n.* (PC-PC0738850); Fort-Carnot, vallée de la Sandrananta, *Decary s.n.* (PC-PC0738847); Affluent du Haut Sascelava [*Sahasinka*], 14/09/1934, *Heim 1424a* (PC-PC0738536); vallée du Sakalena, 14/06/1939, *Decary s.n.* (PC-PC0738810) and 15/06/1939, *Decary s.n.* (PC-PC0738853); Près de Fort Carnot, *Heim s.n.* (PC-PC0738513); MAHAJANGA, Pk 274 RN4, rivière Antetezana, *Boiteau 1004* (PC-PC0738845); Vohitany (canton de Gogogogo), fev. 1962,

*Bosser 15416* (PC-PC0738852); Tsingy de Namoroka, on rocks along Namoroka river, under shady mangoo trees 16°24'00S 45°17'22E, 21/10/2016 *Reeb CR16M308* TOAMASINA, Alaotra-Mangoro, Ambavaniasy, réserve de Vohimana, falaise entre pont de pierre et tunnel désaffecté, elev. 789 m, 18°55'13.1S 48°30'57.1E, 13/04/2010, *Reeb, Andriamanantena & Bidault CRAE10* (PC, TAN); réserve de Vohimana, sur sentier botanique, elev. 789 m, 18°55'12.7S 48°30'57.9E, 13/04/2010, *Reeb, Andriamanantena & Bidault CRAE9*, (PC, TAN); réserve de Vohimana, talus sur la rive gauche de la rivière Vohimana, elev. 798 m, 18°55'25.6S 48°30'41.5E, 15/04/2010, *Reeb, Andriamanantena & Bidault CRAE146, CRAE 150bis, CRAE151bis* (PC, TAN); Réserve de Vohimana, 771 m, 18°55'15.2S 48°30'56.1E, 10/07/2006 *Reeb MH4* (PC-PC0738877), *Reeb MH6* (PC-PC0738876); Zahamena, Andriamiarisoa *ACR108* (MBG); vallée de l'Anony, 05/08/1921, *Decary s.n.* (PC-PC0738837, PC0738841); Andasibe, Vakona Lodge, 18°53'20.5S 48°25'54.6E 979 m, 24/10/2015, *Reeb CR15M99*. TOLIARA, Atsimo-Andrefana, Massif du Makay, camp 1, falaise sur la rivière Androsy, elev. 259 m, 21°36'02.1S 45°06'40.8E, *Reeb CR119* (PC-PC0738855, TAN); Massif du Makay, camp 1, au pied de la cascade de la rivière Androsy, elev. 274 m, 21°35'36.5S 45°06'39.8E, 12/01/2011, *Reeb CR1121* (PC-PC0738854, TAN); Massif du Makay, camp 1, petit vallon affluent de l'Androsy, elev. 259 m, 21°36'13S 45°06'39.1E, 10/01/2011, *Reeb CR1111* (PC-PC0738856), *CR1116* (PC-PC0738857, TAN); Massif du Makay, camp 2, le long de la rivière d'Ambotorabatorano, elev. 303 m, 21°34'04.9S 45°04'33.7E, *Reeb CR11132* (PC-PC0738858, TAN); Massif du Makay, camp 2, remontée rivière Ambotorabatorano, 21°36'00S 45°06'41E, 15/01/2011, *Reeb CR1166* (PC-PC0738859, TAN); Massif du Makay, camp 4, rivière Ankolitsiky, elev.1901 m, 21°37'46.5S 45°00'18.5E, 22/01/2011, *Reeb CR11107* (PC-PC0738861, TAN), *Reeb CR11109* (PC-PC0738883, TAN), *CR11111* (PC-PC0738862, TAN); Massif du Makay, camp 4, cascade en surplomb, elev. 221 m, 21°37'30.6S 45°00'26.7E, 23/01/2011, *Reeb CR11116* (PC-PC0738860, TAN); Massif du Makay, camp 4, petit canon rive gauche de l'Ankolitsiky, elev. 224 m, 21°37'31.1S 45°00'25.5E, 23/01/2011, *Reeb CR11112bis* (PC, TAN); Fort-Dauphin, vallée de Mandrara,

01/08/1926, *Decary* s.n. (PC-PC0738842); Ihosy, 20/10/1940, *Decary* s.n. (PC-PC0738834).

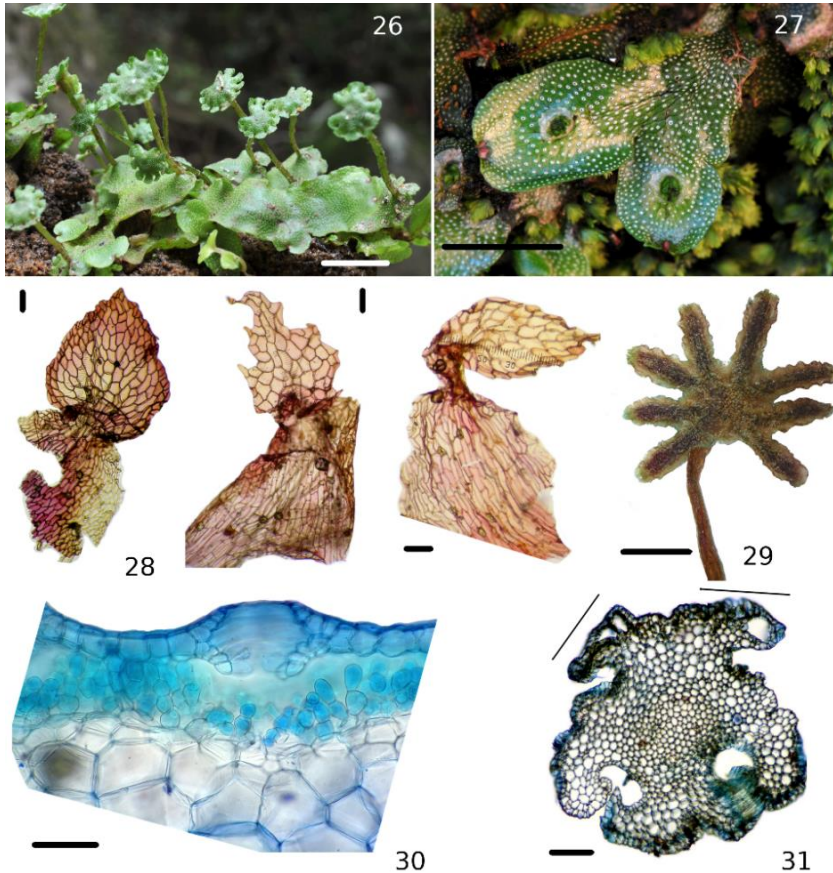
***Marchantia pappeana*** Lehm. Novarum et minus cognitarum stirpium, pugillus X: 21 (1857); Bischl.: 76 (1993); Perold: 197 (1995c).

**Type:** SOUTH AFRICA, 'In Prom. B.S. leg. *Pappe*', ex herb. Lehmann (RO, holo.?, G ex herb. Univ. di Roma). **Synonyms:** *M. planiloba* Steph. Bot. Jahrb. Syst. 8: 90 (1886); Steph.,: 181-182 '153-154' (1886b). **Type:** SÃO TOMÉ, Cachoeira do Rio Manuel Jorge, circa S. Nicolau, 800 m, 1885, *Moller* 32 (G). *M. planiloba* Steph. var. *walteri* Burgeff: Genet. Stud. Marchantia: 276 (1943). **Type:** TANZANIA, 'Nderema in Ost-Usambara, etwa 1000 m, leg. H. Walter. *M. wilmsii* Steph.: 126 (1892). **Type:** SOUTH-AFRICA, Transvaal, McLea in Rehmann Hep. austro-afr. Exs. 1 (PC, BM, G, NY, S). *M. parviloba* Steph.: Bot. Jahrb. Syst. 20: 305 (1895). **Type:** UGANDA, Runssoro, um 2800 m, 10 Juli 1891, *Stuhlmann* 2368a (G, BM). *M. winkleri* Steph. in Bonner Candollea 14: 112 (1953). **Type:** CAMEROON, *Winkler* 270 (G). *M. stephanii* Vanden Berghen: Bull. Jard. Bot. Etat. 24: 50 (1954). **Type:** TANZANIA, Usambara, *Holst* 692 (FH, G). *M. flavescens* Steph. in Bonner Candollea 14: 107 (1953). **Type:** GUINÉE ÉQUATORIALE, det. Fernando Póo, 1911 *Mildbraed* 6275 (G).

**Thallus** dichotomous, green without median dark line (*Figures* 26, 27), ventral face green or purple, medium size, 25–65 mm long, each axis 5–10 mm large; margins entirely purple or not. **Pores** well visible (*Figure* 27), relatively large 70–125(–200) µm diameter bordered by 7-8 rings of cells, 3–4 above epidermis, 3-4(–5) projecting in air-cavities (*Figure* 30). **Ventral scales** in 4 rows not extending more than 50 % of the thallus width, often purple, 800–1400 µm long, oil bodies scattered; appendages rounded, orbicular or broadly triangular, 450–750 µm long, 330–550 µm wide, bordered by an irregularly toothed margin with one-celled teeth or regular margin (*Figure* 28). **Cupules** with cilia 2-3(– 6) cells long. Dioicous. **Antheridiophores** at apex of axis, stalk 22–25 mm long, in cross section with 2 bands of air cavities, receptacle (5–)10–13(–14) mm diameter, palmate and divided in into (6–)7–9 rays more or less asymmetric (*Figure* 29). **Archegoniophores** at apex of the axis, stalk



10–20 mm long, in cross section with two bands of air cavities (*Figure 31*), receptacle (5–)6–7(–11) mm diameter divided up to the quarter of the receptacle diameter into (8–)10–12 flat lobes (*Figure 26*). **Spores** 17–35  $\mu\text{m}$ .



**Figures 26-31.** *Marchantia pappeana* Lehm. (26) Fertile population, with archegoniophores. Zahamena January 2014. Scale bar 1 cm. (27) Close view of a thallus showing the large pores easily visible by eyes, no central black line. Massif du Makay. Scale bar 1cm. (28) Ventral scales, *Cremers* 1987 and *Bosser* 13282. Scale bar 100  $\mu\text{m}$ . (29) Antheridiophore. Scale bar 1cm. (30) Cross section of the thallus. Coloration with bleached (20 %), rinses and diluted methylen blue. Scale bar 100  $\mu\text{m}$ . (31) Cross section of the stalk of an archegoniophore showing 2 opposite bands of air chambers (black lines). Scale bar 100  $\mu\text{m}$ .

**Distribution:** widely distributed from South to North, not in dryer areas (*Figure 77*). Widely distributed in tropical Africa.

**Ecology:** on edges of water (waterfalls, rivers with slow current, ponds), terrestrial banks in shaded or open and exposed areas, on damp soils or rocks, sometimes flooded.

Bischler (1993), distinguished two subspecies of *M. pappeana*, *M. pappeana* subsp. *pappeana* and *M. pappeana* subsp. *robusta*, but only the former is found in Africa including Madagascar. In the African flora of Jones (2004) only the species *M. pappeana* is cited, we retained that choice.

**Selected specimens specimen examined:** ANTANANARIVO, 22/04/1906, *Alleizette 7bis* (PC-PC0738822); Tsimbazaza, tourbière de Tsimbazaza, sur terre, elev. 1250 m, 06/08/1972, *Cremers 2409* (PC-PC0738825, TAN), *Cremers 2417* (TAN); elev. 1100 m, 09/10/1927, *Decary s.n.* (PC-PC0738793); centre route du Sud Pk 210, rochers humides et ombragés, 01/12/1951, *Bosser 1254* (TAN); Pk 28 route du Sud, paroi rocheuse humide et ombragée, 01/09/1957, *Bosser 12232* (PC-PC0738832, TAN); Behenjy face Est 36 km Sud d'Antananarivo, elev. 1400 m, 07/09/1972, *Cremers 2325* (PC-PC0738827, TAN); Manjakatempo, 16/08/1934, *Heim s.n.* (PC-PC0738524); Manjakatempo, 25/05/1951 *Benoist 1076* (PC-PC0738796), *Benoist 1076* (PC-PC0738808); Imerina, Janv. 1881, leg. *Wildebranti 4235* (PC-PC0738792); Mandraka Pk 69, forêt de la Mandraka, au sol, alt 1000 m, 18/07/1972, *Cremers 2257* (PC-PC0738828, TAN), *Cremers 2258* (PC-PC0738831, TAN), *Cremers 2259* (PC-PC0738830, TAN); Mandraka, août 1906, *d'Alleizette 84* (PC-PC0738821); cascade de la Mandraka, 16/08/1953, *Bosser 6028* (PC-PC0738788); Mandraka, fev. 1953, *Bosser 5028* (PC-PC0738804); forêt de la Mandraka, elev. 800 m, 31/03/1972, *Cremers 1987* (PC-PC0738826, TAN); forêt de la Mandraka, talus ombragé humide, 01/09/1959, *Bosser 13282* (TAN); Mandraka, Gilles, (PC); Tananarive, Ambohimanga, bouquetau, juin 1914, *Waterlot 167* (PC-PC0738801), *169* (PC-PC0738798); MAHAJANGA, Bealana, Mangindrano, forêt de moyenne altitude d'Antsahivo sur rocher au bord de la rivière 02/12/2005 *R.L.Andriamiarisoa 662* (MO-66223240). ANTSIRANANA, entre Vohémar et Ambilobe, 29/07/1939, *Decary s.n.* (PC-PC0738809); entre Vohémar et

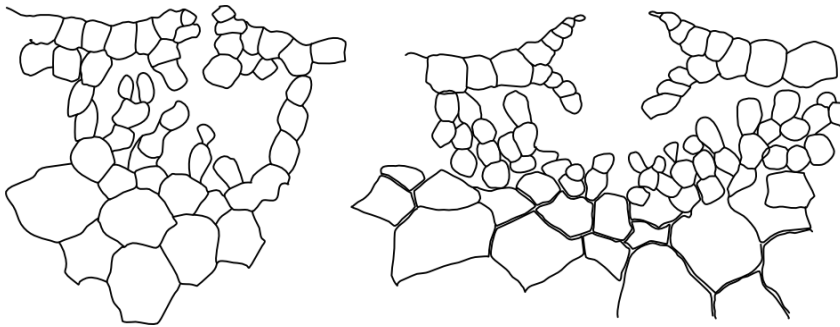
Ambilobe, 30/07/1939, *Decary s.n.* (PC-PC0738807); Marojejy, roche humide le long de la rivière Manantenina, elev. 600-700 m, 12/02/1989, *Miller & Lowry 4009* (TAN); massif du Betsomanga, Antongondriha, vallée inférieure de l'Androranga, 17-20/11/1950, leg. *Humbert & Capuron* (PC-PC0738818); Nord d'Anosibe, 17/02/1930, *Decary s.n.* (PC-PC078814); Tsaratiteraka (Tsianovoha), *Heim 1350a*, (PC-PC07738511); Diego-Suarez, Joffreville, domaine de Fontenay, 28/08/2010, *Reeb CR2010M* (PC); FIANARANTSOA, [Ranomafana], vallée du Namorona, 22/11/1938, *Decary s.n.* (PC-PC0738794); Ambatomboay, Octobre 1934, *Heim s.n.* (PC); Andrambovato, 27/04/1979 *Tixier 12391* (PC-PC0738824), *12393* (PC-PC0738823); Farafanga, Befotaka, 16/08/1926, *Decary s.n.* (PC-PC0738815); Fianarantsoa-Masongary Pk 28, chutes de Ranomafana, sur rochers en sous-bois, elev. 1165 m, 01/05/1972, *Cremers 2097* (TAN); parc national de Ranomafana, Along the N side of main road at the head the big waterfalls of Namorona river. Alt 1080-1150 m, 21°14.70-86'S 47°23.82'E, 29/07/2004, S. & T. Pócs 04126/AO, 04126/AN, 04126/AZ (EGR). Forêt de Saharevo, 01/09/1934, *Heim s.n.* (PC-PC0738529); Forêt de Saharevo, 02/09/1934, *Heim s.n.* (PC-PC0738531); Station forestière d'Andrambovato, elev. 1030 m, 01/11/1956, *Decoings 1848* (TAN); Vallée du Sakalena, 13/06/1939, *Decary s.n.* (PC-PC0738787); TOAMASINA, sud de Moramanga, entre Sandrangato et Anosibe, 3-7/11/1952, *Leandri 1572* (PC-PC0738806), *1600C*, *1603bis* (PC-PC0738799); 54 km route de Moramanga, Anosibe, 15/09/1953, *Bosser 6410* (PC-PC0738786); Ambatovavy, Bamafo river, Andriamiarisoa *ACR635*, *ACR662* (MBG); Ambohimangakely, *Decary s.n.* (PC); Analamazaotra, en forêt, 15/04/1939, *Decary s.n.* (PC-PC0738789); Imerimandroso, 0207/1921, *Decary s.n.* (PC-PC0738812); Nord d'Anosibe, 18/02/1930, *Decary s.n.* (PC-PC078803); Périnet, talus humide en forêt, *Boiteau 0228* (PC); près d'Ambositra, *Decary*, (PC); Forêt de Périnet, 9/11/1951, *Benoist 1822* (PC-PC0738800, PC0738805); Forêt de Périnet, elev. 900-1000 m, 02/10/1971, *Cremers 1928* (PC-PC0738829, TAN); station forestière de Périnet, 13/05/1966, *Boiteau 216* (PC-PC0738797), *228* (PC-PC0738790); Sud de Moramanga, entre Sandrangato et Anosibe, alt 800-1100 m; Alaotra-Manongarivo, Réserve de

Vohimana, 771 m, 18°55'15.2S 48°30'56.1E, Reeb MH1 (PC-PC078878); Andasibe, Vakona Lodge, 18°53'20.5S 48°25'54.6E, 956 m, 24/10/2015, Reeb CR15M100; Zahamena, 1H30 de Ranofotsy, le long de la rivière Ankotrokotroka, 1169 m, 17°36'39S 48°40'21E Reeb & Andriamanantena CR13Z82 (PC-PC0738879), CR13Z74 (PC-PC0738880), CR13Z82 (PC-PC0738881); Maroantsetra, 20/10/1920, Decary s.n. (PC-PC0738817); TOLIARA, col de Tapia, 29/12/1976, Tixier 10071 (PC-PC0738813), 10079 (PC-PC0738811); Massif du Makay, cascade rivière Androsy, elev. 274 m, 21°35'36.5S 45°06'39.8E, 12/01/2011, Reeb CR1120 (PC-PC0738882, TAN); Massif du Makay, au pied marécage tourbeux, elev. 295 m, 21°34'17.7S 45°04'32.6E, 15/01/2011, Reeb CR1153 (PC-PC0738864, TAN); Midongy du Sud, 23/06/1926, Decary s.n. (PC-PC0738802).

It appears that in African historical collections, *M. debilis* and *M. pappeana* were often identified as several species listed now as synonyms (Bischler 1993, Grolle 1995). They were sometimes misidentified and often confused (Bischler 1993, Jones 2004). Several specimens were identified as *Marchantia globosa* Brid. ex Web. which is only encountered in Comores, Mauritius and Réunion islands (Bischler 1993).

The examined Malagasy specimens of *Marchantia* are all related to *M. debilis* or *M. pappeana*. The two species can be separated on by: (1) size, width of the thallus and diameter of the receptacle of the antheridiophore, (2) diameter of the pores (Figure 32), (3) size of the appendage of ventral scales (always smaller in *M. debilis*), (4) absence of median dark line in *M. pappeana*, ciliation of the cupules (shorter in *M. debilis*). The number of rings around the pores and cells projecting above epidermis and in air cavities appears variable but if associated with the pore diameter, the two species are distinct. If the plants are fertile, the number of bands of air-cavities in gametangiophores can also distinguish the species (one in *M. debilis*, two in *M. pappeana*). The diameter of spores overlaps and cannot be a diagnosis character. The two species are often in mixed populations (see Cremers 2259).





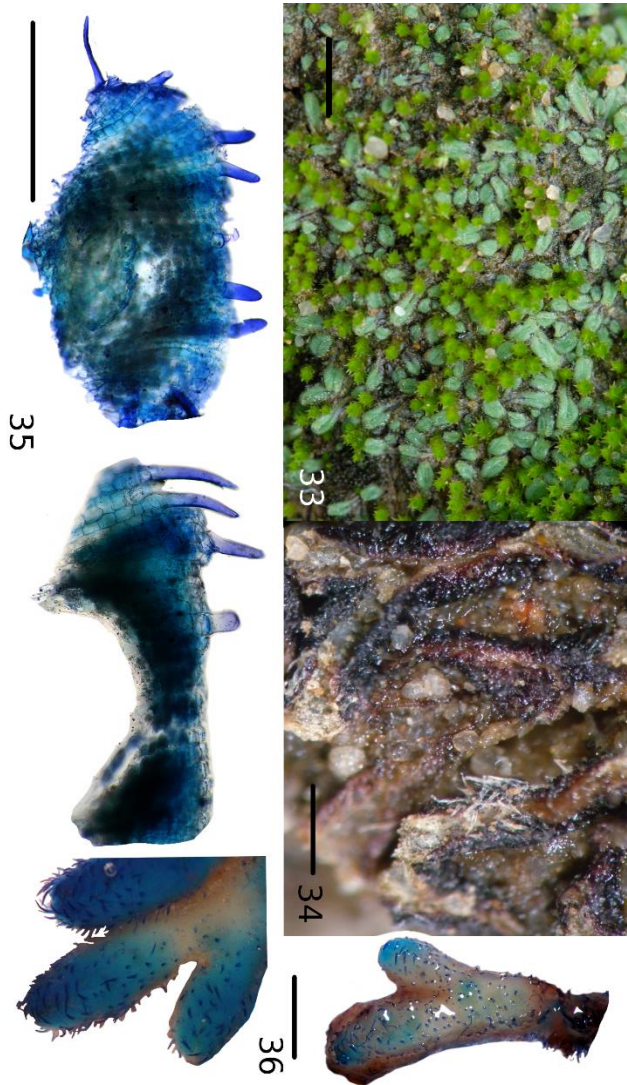
**Figure 32.** Comparison of the pores in cross section of (left) *Marchantia debilis*, Cremers 2455 and (right) *Marchantia pappeana*, Reeb CR1153.

## RICCIACEAE

***Riccia atromarginata* Levier var. *jovet-astii*** Rauh & Buchloh  
*Revue Bryologique et Lichénologique* 30: 77. 1961.

**Type:** MADAGASCAR Gneis-Hügel bei Fianarantsoa (Madag. Centr.)  
December 1959 N° 1900 leg. W. Rauh (isotype PC-PC0103703!).

**Thalli** in incomplete or partial rosettes, lobes linear to ovate, very narrow but deep central groove, apex emarginate; glaucous-green to bright green with dark purple flanks (*Figure 33*), small, less than 10 mm long, lobes 0.5–1 mm wide (*Figure 34*); in cross section as wide as thick, without bulging lobes, margin rounded, dorsal epithelium unistratose, cells globose, assimilation tissue in vertical columns of 6–8 isodiametric cells; marginal cilia curved and interlocking on dorsal face, in several rows, sometimes sparsely covering the dorsal face (*Figures 35, 36*), cilia smooth (80–) 150–250(–300)  $\mu\text{m}$  long. **Ventral scales** not reaching the margin of the thallus, purple or hyaline in part. Dioicous. **Antheridia** with prominent hyaline neck (not seen on Malagasy specimens). **Archegonia** with purple necks (not seen on Malagasy specimens). Several sporophytes per lobes (up to 3), slightly bulging on dorsal face. **Spores** massively black in mass, brown when alone, globular and irregularly triangular or polygonal with rounded angles, not winged, 68(–92)  $\mu\text{m}$  diameter; ornamentation similar on both faces, 10–12 rounded alveoli in diameter, separated by thick edges.



**Figures 33-36.** *Riccia atromarginata* Levier var. *jovet-astii* Rauh & Buchloh. (33) On the field in the Makay Massif, Reeb CR11104. Scale bar 1 cm. (34) Dry specimen showing the black-red flanks, Bosser 15420. Scale bar 1 mm. (35) Cross section of thallus, Onraedt 70M02. Scale bar 500  $\mu$ m. (36) Lobes with paler margins after coloration, but allowing observation of ciliae and dorsal papillae in good conditions, Onraedt 70M02. Coloration with bleached (20 %), rinses and diluted methylen blue. Scale bar 1 mm.

**Distribution:** three localities, one in Tsimbazaza park, Southern, dry and lowland areas (*Figure 79*). Occurs in European Mediterranean countries, North Africa, Arabic peninsula and Socotra.

*R. atromarginata* var. *jovet-astii* is recognized by: (1) the small size of the thallus, (2) the marginal cilia and the dorsal cilia-papilla, (3) the low and inconspicuous purple scales, (4) the distal face of spore with thickened walls.

Ciliate *Riccia* are rather problematic taxa, with taxonomy not fully resolved. Grolle (1995) retained *R. atromarginata* var. *jovet-astii* and *Riccia trichocarpa* Howe for Madagascar. Kürschner (2000) reported it from several localities in Yemen. In the recent check-list (Marline *et al.* 2012), the only ciliate *Riccia* cited is *Riccia crinita* Taylor. As stated by Jovet-Ast (1986), *R. crinita* is an Australian species that she considered with doubt as synonym for *R. trichocarpa*. Grolle (1995) considered *R. trichocarpa* as a critical taxon, based on Jovet-Ast's remarks. Then, Perold (1999) recognized *R. trichocarpa* for South-Africa, but did not mention at all *R. crinita*! However, the ciliate Malagasy specimens cannot be *R. trichocarpa* or *R. crinita*, because of their very small size, the shorter cilia and smaller spores without wing.

This variety was described from one collection from Fianarantsoa (Rauh and Buchloh 1961) then Jovet-Ast (1955, 1989) discussed the "*atromarginata*" complex, including this variety. The distinction between cilia and papilla is not evident, dorsal papilla are described as finger-like and shorter (182–190  $\mu\text{m}$ ) than cilia (up to 430  $\mu\text{m}$ ), which are also slightly curved. We found that papilla could also be small cilia, and we could not find real distinction between the two in literature.

The examination of the type specimens shows a morphological similarity between *R. atromarginata* and *R. atromarginata* var. *jovet-astii*. The latter is a little bit smaller and its spores bear thicker cell walls between alveoli (as noticed by Jovet-Ast 1989); we did not find that spores have pillar (thickness) at angles of the alveoli as described and illustrated in Rauh and Buchloh (1961).

**Specimens examined:** ANTANANARIVO, Tsimbazaza, 1200 m, 14/01/1970, *Onraedt 70MO2* (PC-PC738909); TOLIARA, Sud PK 434

Route Amboasary-Ft.Dauphin [Amboasary], fév 1962, *Bosser 15420*, (PC-PC0738908, PC0716004); Massif du Makay, camp 3, sur rochers, elev. 176 m, S 21°40'14.6 E 44°59'22, 20/01/2011, *Reeb CR1192* (PC-PC0738910, TAN), *Reeb CR1197* (PC-PC0738911, TAN).

**Supplementary material examined** *Riccia atromarginata* Levier **Type:** SICILIA Villa Belmonte prope Panormum, 25 Dec 1888, *Dr. H.Ross s.n.* (PC-PC0103704!).

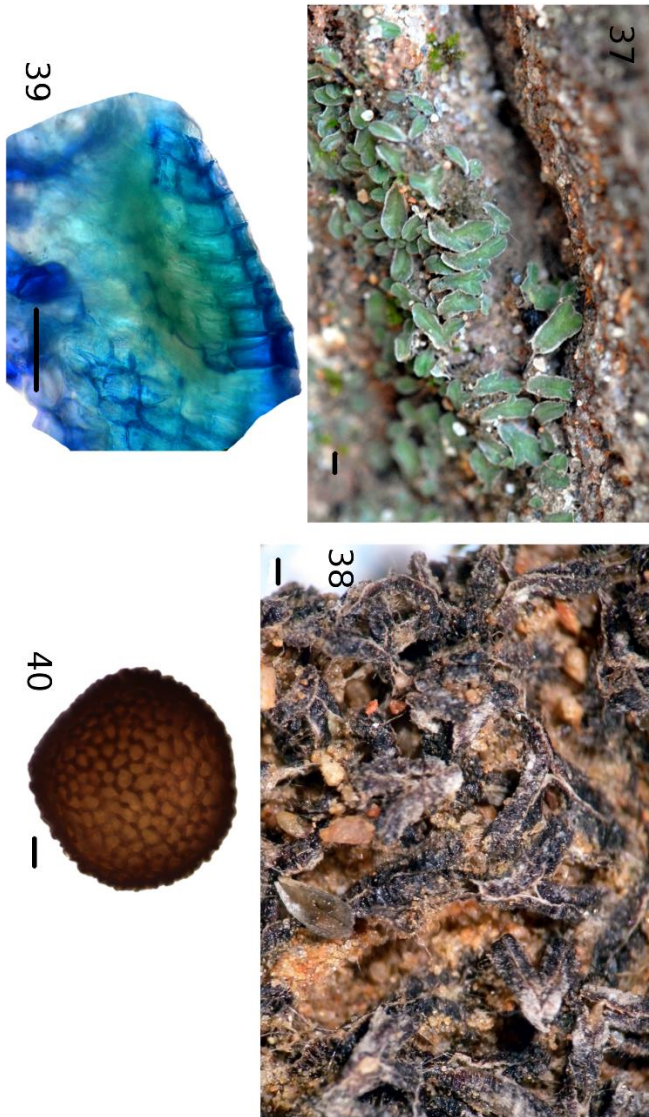
***Riccia atropurpurea*\*** Sim. *Trans. Roy. Soc. S. Afr.* 15: 11. 1926.

**Type:** SOUTH AFRICA, Natal, Edendale Falls, *Sim 8112* (lectotype, PRE-CH1023). **Thalli** in incomplete rosettes up to 20 mm across, glaucous green with a white margin, lobes with a deep central furrow (*Figure 37*), 5-8(-10) mm long, often a smaller branch bifurcating below apex; when dry, margins clasp together dorsally, hiding the dorsal face, then covered by the ventral scales; in cross section, assimilation tissues in parallel lines with narrow air-chambers; epidermal cells soon collapsing, with thickened cell walls (*Figure 39*). **Ventral scales** obvious, black and bright, the white margin forming two lips rising upon the central part of the thallus (*Figure 38*). **Spores** 70-90 µm (*Figure 40*).

**Distribution:** from North to South, in a discontinuous distribution (*Figure 81*). Occurs in Sub-Saharan Africa.

**Ecology:** very common on exposed banks of the canyons in the Makay Massif, on temporary humid sandstone plates.

The species is easily recognizable by (1) the dorsally collapsing flanks, (2) the hyalin-white line bordering margins and (3) the thickened cell walls of the epidermis.



**Figures 37-40.** *Riccia atropurpurea* Sim. (37) On the field, humid thalli showing thin, white margins. Makay Massif, 2011. Scale bar 1 mm. (38) Dry thalli, dorsal faces claspings and white margins forming two lips. Scale bar 1 mm. (39) Cross section showing collapsed epidermal cells with thickened cell walls. Scale bar 100  $\mu$ m. (40) Spore, distal face. Scale bar 10  $\mu$ m.



**Selected specimens examined:** ANTANANARIVO, 24/12/1923, *Decary s.n* (PC-PC0738906); Tsimbazaza, chemin du jardin botanique, sol minéral, 14/03/1970, *Onraedt* (TAN); Tsimbazaza, Déc. 1960, *Bosser 14797* (PC-PC0715996, TAN); TOLIARA, 10 km avant Betroka, rocher temporairement humide, Fév. 1963, *Bosser 16908* (PC-PC0715985, PC0715997, TAN); Route de Betroka PK 65-66, Fév. 1963, *Bosser 16909* (PC-PC0715995); Forêt d'Anjahana, au sud-est d'Ambilobe, 28/08/1973, *Cremers 2687-a* (PC-PC0715986); Massif du Makay, camp 2, rive droite Ambotorabatorano, elev. 295 m, 21°34'13S 45°04'32.3E, 15/01/2011, *Reeb CR1159* (PC-PC0738895, TAN), *Reeb CR1160* (PC-PC0738896, TAN); Massif du Makay, camp 2, vallon à gauche en remontant la rivière Ambotorabatorano, 16/01/2011, *Reeb CR1173* (PC-PC0738897, TAN); Massif du Makay, camp 3 remontée de l'Ankolitsiky, gros bloc, 18/01/2011, *Reeb CR1176* (PC-PC0738898, TAN), *CR1183* (PC-PC0738896, TAN); Massif du Makay, camp 3 forêt d'Ambalamanga, sur terre, elev. 153 m, 21°40'29.3S 44°59'36.3E, 19/01/2011, *Reeb CR1186*, (PC-PC0738899, TAN), *CR1187* (PC-PC0738900, TAN), *CR1189* (PC-PC0738901, TAN); Massif du Makay, camp 3, sur rocher, elev. 176 m, 21°40'14.6S 44°59'22E, 20/01/2011, *Reeb CR1191bis* (PC-PC0738902, TAN), *CR1193* (PC-PC0738903, TAN); Massif du Makay, camp 3, rocher sur sable, elev. 176 m, 21°40'14.6S 44°59'22E, 20/01/2011, *Reeb CR11102*, *CR11105*; Massif du Makay, camp 4, falaise, elev. 214 m, 21°37'25.2S 45°00'05.0E, 23/01/2011, *Reeb CR11118*, *CR11119*, *CR11121*.

***Riccia cavernosa*** Hoffm. *Deutschland Flora* 2: 95. 1796.

**Synonym:** *Ricciella rautanenii* Steph. Bulletin de l'Herbier Boissier 3: 374. 1895. **Type:** Africa occidentalis in agro Herera propre Usab in albeo fluminis Tsoacahub as terram. leg. M. Rautanen.

**Thallus** often in regular rosettes up to 30 mm wide (*Figure 41*), bright green to yellowish green, lobes up to 3.5(-4) mm wide, 10 mm long, becoming spongy and lacunose with age (disintegration of upper epidermis) (*Figures 41, 42, 43*). **Ventral scales** absent or evanescent. Monoicous. **Antheridia** and **archegones** sunk in the thallus. **Sporophyte** protruding somewhat ventrally, even if visible dorsally, numerous, crowded. **Spores** reddish brown to black,

triangular-globular, winged, (60-)64-90(-120)  $\mu\text{m}$  with a network of few ridges forming sometimes complete alveoli, proximal face with a conspicuous triradiate mark (*Figures 44, 45, 46*).

**Distribution:** central and southern areas, 0-1200 m in a discontinuous distribution (*Figure 81*). Cosmopolitan species.

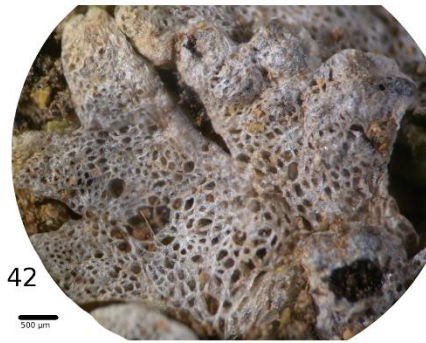
**Ecology:** *R. cavernosa* is a hygrophilous species occurring on fresh muddy soils close to rivers.

This species is easily recognizable by the spongy and lacunose thallus, mostly in rosettes. *R. crystallina* too has this spongy habit and may be confused. The two species were thoroughly compared by Jovet-Ast (1964, 1966, 1986) and Perold (1995b, 1999). They may be confused, but the latter one has not been identified for Madagascar. The main differences being on spore ornamentation (complete alveoli in *R. crystallina*) and size, smaller for *R. crystallina* even if they overlap (60-86.5  $\mu\text{m}$  for *R. crystallina*; 60-120  $\mu\text{m}$  for *R. cavernosa*).

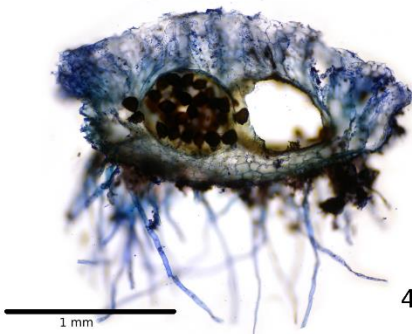
**Specimens examined:** ANTANANARIVO, environs de Tananarive, PK22 route d'Arivonimamo bord de ruisseau, nov. 1960, *Bosser 14698* (PC -PC0716016); environs de Tananarive, PK23 route d'Arivonimamo terre mouillée bord de rivière, nov. 1957, *Bosser 12299* (PC-PC0716018); mbatomirahavavy, Lemurs Parc, 18°57'04.8S 47°21'25.2E, 1266 m, 20/10/2015, *Reeb CR15M66* FIANARANTSOA, chutes de l'Ikopa, sables humides bord de rivière, alt. 1200 m, août 1955, *Bosser 8316* (PC -PC0716015); TOAMASINA, Ambohijanahary, W. lac Aloatra terre humide en bord de ruisseau, juin 1955, *Bosser 8144* (PC -PC0716017); au bord du Fiarenana [*Fiherenana*], à Sakaraha, sur terre sablonneuse ombragée champ cultivé, alt. 380 m, 01/07/1971 *Onraedt 71M5500* (PC-PC0716018); au bord du Fiherenana, près de Miary, sur limon exondé du fleuve, alt. ca. 200 m, 30/06/1971, *Onraedt 71M5527* (PC-PC0716021); TOLIARA, bord de l'Onilahy, près de Ambohimahavelona, sur limon exondé au bord du fleuve, alt. ca. 30 m, 29/09/1971, *Onraedt 71M5501* (PC-PC0716020); Manombo, côte sud-est, sur argile à nu par le retrait des eaux, bush à l'ombre des arbres, alt. 20 m, 26/06/1971 [1972 on original label], *Onraedt 71M5502* (PC-PC0716022).



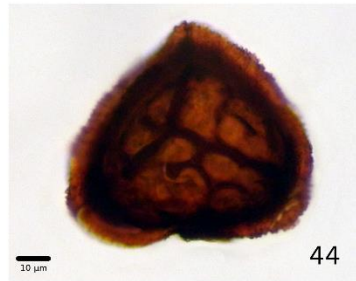
41



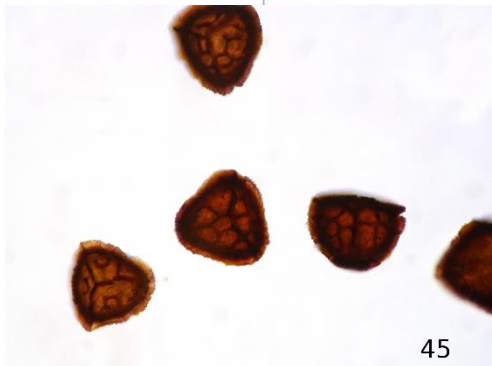
42



43



44



45



46

**Figures 41-46.** *Riccia cavernosa* Hoffm.. (41) Rosette with lacunose areas. Antananarivo, Lemurs Parc, 2015. Scale bar 1 mm. (42) Detail of a lacunose area, *Bosser* 14698. Scale bar 500 µm. (43) Cross section of a thallus with an embedded sporophyte and large, ill-defined air-chambers. Scale bar 1 mm. (45) Spores. (44) (46) proximal faces of spores, *Bosser* 14698. Scale bar 10 µm.



***Riccia congoana***\* Steph. *Bull. Herb. Boissier* 6: 328, 1898.

**Type:** CONGO, Fr. Equatorial Africa, Forêts de Ceseles, *Voz M. de F.*, s.n. (holotype, G-00067873).

**Synonyms:** *Riccia rhodesiae* S.W.Arnell. *Bot. Not.* 105: 313, 1952.

**Type:** ZIMBABWE (S. Rhod.), Victoria Falls, on soil near Trolley Junction, 11/11/1951 S.W.Arnell 1291 p.p., (holotype, S-B45273; BOL; PRE). *Riccia berriei* E.W.Jones. *Trans. Brit. Bryol. Soc.* 3: 224,

1957. **Type:** NIGERIA, St Anne's Churchyard, Kudeti, Ibadan, *Berrie 1956*. *Riccia nigrosquamata* E.W.Jones. *Trans. Brit. Bryol. Soc.* 3: 222,

1957. **Type:** TANZANIA Tanganyika, Lighthouse Island, Dar-es-Salaam Harbour, *Jones 699* (BM, holotype). *Riccia aegyptiaca*

S.W.Arnell. *Bot. Not.* 116: 9, 1963. **Type:** EGYPT, Gebl. Elba Dist., Wadi Aideib, 21/01/1962 M. Kassas s.n. (holotype, S-B43872;

isotype, CAI). *Riccia limbatoides* O.H.Volk. *Vegetatio* 55: 58, 1984.

**Type:** NAMIBIA, Grootfontein, Farm Gaikos, *Volk 00747* (M, PRE).

**Thalli** light to dark, green to bluish-green, in dense overlaying patches, generally in partial rosettes, large, 25–30 mm across; often bifurcated in two tongue-like branches, black scales forming a narrow scalloped border (*Figures 47, 48*), lobes (–2)–3–5 mm large, reticulate when young, degenerating in old age, with a narrow furrow all along the thallus, sometimes bifurcating near the apical zone, on larger or older thallus. In cross section, flanks very obliques, margin overhanging (*Figure 49*); dorsal epiderm unistratose, soon collapsing, assimilation tissue nearly half of the thallus thickness (*Figure 49*). **Ventral scales** black and conspicuous, shiny, adherent to the flanks and not easily removable (*Figures 47, 50*). Monoicous. **Antheridia** along the furrow, projecting. No sporophytes seen.

**Distribution:** southern areas in open and dry lands at low elevation (*Figure 79*). Occurs in Africa.

**Ecology:** in semi-shaded position, at the bottom of bushes, on shaded sandstone or muddy banks.

*R. congoana* seems to be quite common in the Makay massif, and a few specimens have been found in the same type of environment in Toliara province (*Figure 79*); it is often close to *R. atropurpurea* stations, but always in a more shaded area.



**Figures 47-50.** *Riccia congoana* Steph. (47) (48) On the field in the Makay massif, Reeb CR11103. Scale bar 1 mm. (49) Cross section of a thallus, Reeb CR1172. Scale bar 1 mm. (50) Ventral faces with scalloped margins, Reeb CR11103. Scale bar 1 mm.

This species is recognized by (1) its large size, *R. congoana* is the largest *Riccia* in Madagascar; morphologically close species are *R. angolensis* Steph. and *R. okahandjana* S.W. Arnell (not cited for Madagascar), which are smaller, (2) the scalloped margin drawn by the scales and (3) the overhanging margins. Flanks of close species rise more vertically with no overhanging margins. It is necessary to collect fertile specimen of *R. congoana* to confirm vegetative characters.

**Specimens examined:** TOLIARA, RN11 piste forestière d'Imonty, *Keranden 1544* (PC-PC0715991, TAN); Tombeaux des rois Mahafaly à 45 km Sud d'Ampany, Mars 1964, *Bosser 17811* (PC-PC0715994, TAN); Antanimora (S.O) déc 1959, *Bosser 13364* (PC-PC0738907); Massif du Makay, après piste aéroport Berohorofo, bord de lavaka, S 21°37'22 E 45°09'67.2, 09/01/2011, *Reeb CR111, CR111 bis*; Massif du Makay, camp 2, rive droite Ambotoraborano, elev. 295 m, S 21°34'13 E 45°04'32.3, 15/01/2011, *Reeb CR1158, CR1162*; Massif du Makay, camp 2, premier vallon à gauche en remontant la rivière Ambotoraborano, elev. 329 m, S 21°34'03.5 E 45°04'28.8, 16/01/2011, *Reeb CR1172, CR1174, CR1180*; Massif du Makay, camp 3, forêt d'Ambalamanga sur terre, elev. 153 m, S 21°40'29.3 E 44°59'36.3, 19/01/2011, *Reeb CR1188*; Massif du Makay, camp 3 forêt d'Ambalamanga, triangle de terre, elev. 153 m, S 21°40'29.3' E 44°59'36.6, 19/01/2011, *Reeb CR1189*; Massif du Makay, camp 3, sur rochers, elev. 176 m, S 21°40'14.6 E 44°59'22, 20/01/2011, *Reeb CR1195*; Massif du Makay, camp 3, sur rochers, elev. 176 m, S 21°40'14.6 E 44°59'22, 20/01/2011, *Reeb CR1198, CR11103* (PC-PC0738905, TAN).

***Riccia cf. purpurascens*** Lehm. & Lindenb. *Linnaea* 4: 371. 1829. **Type:** Cape crescit humi in sylvula quercina ad latus boreale et ad radicem montis Tafelberg. Ecklon in Herb. L. **Thallus** in small ribbons, overlapping in dense populations (*Figure 51*), light green, margins undulated or straight; branches narrow, up to 5 mm long and 2 mm wide, apex narrowed and emarginate (*Figure 52*); dorsal epidermis areolate, groove narrow and distinct in the apical region, slightly enlarging after. In cross section, thallus concavo-convex to plano-convex with flanks oblique in older parts (*Figure 54*),

assimilation tissue occupying most of the height of the thallus. **Air chambers** more or less visible, in cross section in 2–3 layers. **Ventral scales** hyaline, towards apex. Dioicous. **Sporophyte** bulging ventrally (*Figure 53*). **Spores** light brown to orange, semi-translucent, 70–80 µm diameter, with 8–10 complete or reticulated alveoli on distal face (*Figure 55*). Triradiate mark on proximal face with incomplete alveoli.

**Distribution:** two localities, Tsimbazaza and Makirovana (*Figure 80*). South-Africa.

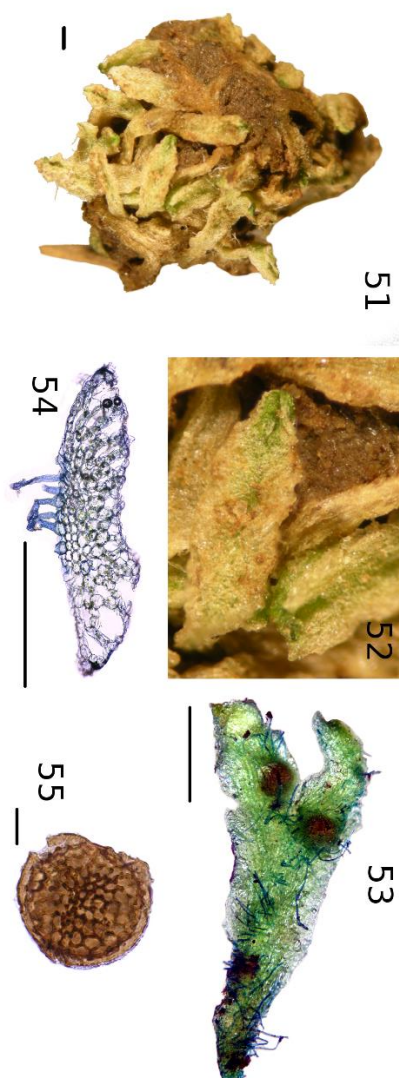
**Ecology:** Malagasy specimens are located in humid areas (Tsimbazaza park in Central plateau, and Makirovana in eastern humid forest), on naked and humid soil.

**Specimens examined:** ANTANANARIVO, Antananarivo, sur terre près des serres du parc de Tsimbazaza, elev. 1250 m, 06/08/1973, *Cremers 2418* (PC-PC0715987); ANTSIRANANA, Makirovana, Ambodimanga au pied de Makirovana, elev. 41 m, 14°11'13.6"S 49°59'09.2"E, 03/05/2010, *Reeb CR203* (PC).

In Malagasy specimens identified as *R. purpurascens*, although the number of alveoli on spore distal face is higher than in the type, and we could not observed the ventral tubercles. But all other characters match the description, especially the narrowed apex, the deep groove in apical region and the keeled ventral face.

The *Riccia fluitans* L. complex is very problematic (Schuster 1987, Jovet-Ast 1986, Manju *et al.* 2012) and its status for Africa has been lengthily discussed by Perold (1990, 1999). According to Perold (1990), a clarification of the *R. fluitans* complex is much needed. We follow Perold's treatment, and two species are considered to be present in Madagascar, *R. stricta* and *R. purpurascens*. *R. purpurascens* was considered as endemic from the Cape province and we do not exclude that *R. cf. purpurascens* could be another variation in the *fluitans* complex.

The distinction between *R. stricta* and *R. purpurascens* are: (1) groove marked in *R. purpurascens*, and sporophyte ventral with a straight collar. (2) in *R. stricta*, sporophyte emerges to the dorsal face by an oblique collar, straight in *R. purpurascens*. (3) spore ornamentations.



**Figures 51-55.** *Riccia purpurascens* Lehm. & Lindenb.. (51) Rehydrated thalli, Makirovana, Reeb CR203. Scale bar 1 mm (52) Details, Reeb CR203 (53) Ventral face. Scale bar 1 mm. (54) Cross section. Scale bar 500 µm. (55) Spore, distal face. Scale bar 10 µm.

***Riccia stricta***\* (Lindenb.) Perold. *Bothalia* 20: 197. 1990.

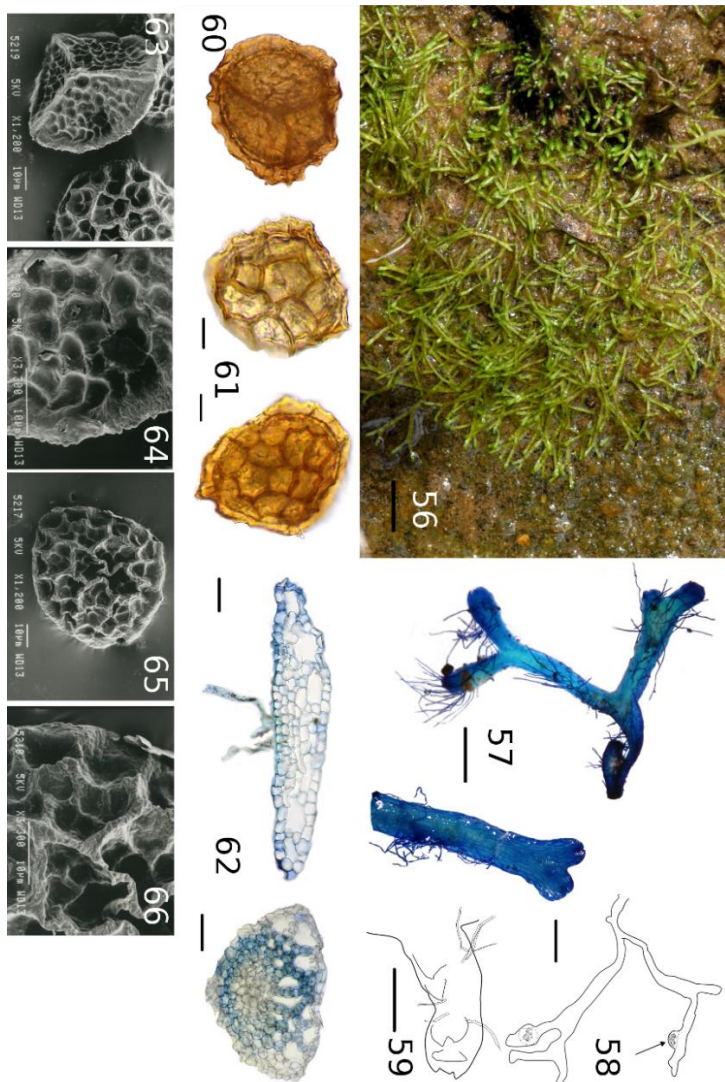
**Type:** SOUTH-AFRICA, Cape, Philipstown, ad arborum truncos, Ecklon s.n. (BM) **Basionyme:** *Riccia fluitans* var. *stricta* Gottsche *et al.* *Synopsis Hepaticarium* 4: 610. 1846. **Thallus** strap like, green, branches furcate (*Figure 56*), up to 20 mm long, less than 1.2 mm wide, apex rounded and often thickened to bulbous, often slightly tapering and narrower than following segment (*Figures 56, 57*); distinct areolation materializing limits of air chambers visible or not on the dorsal face, often at the apical segment (*Figures 57, 62*). **Ventral scales** present at the apical zone, not protruding, single rounded to triangular, often divided but remaining joined at basis (*Figure 59*). Monoicous. Sexual reproduction very frequent, gametangia not seen. **Sporophyte** protruding on ventral face (*Figure 58*). **Spores** orange–brown to light brown, semi-translucent (not opaque), triangular globular, wing obvious 4–8  $\mu\text{m}$  wide, (50–)60–80  $\mu\text{m}$  diameter; 5–6 complete alveoli in distal face; triradiate mark obvious on proximal face, each facet with 6–10 alveoli complete or not; (*Figures 60, 61, 63–66*).

**Distribution:** from North to South, 0–1200 m (*Figure 80*). Occurs in Sub-Saharan Africa (Perold 1999), India (Manju *et al.* 2012) and probably also in North America (Schuster 1992).

**Ecology:** in freshwater, running or stagnant, or on banks, close to the river for terrestrial form.

Since 1836 this species has been considered as a variety of *R. fluitans*, *R. fluitans* var. *stricta* (Lindenberg 1836). Jones (1957) observed that the spores of African's specimens are different from the European ones. Perold (1990) proposed a new combination *R. stricta* (Lindenb.) Perold. This species appears also to be close to *R. stenophylla* Spr. (Schuster 1992). She argued that all the African collections of the difficult and very variable group of *R. fluitans* that she studied were indeed *R. stricta*. We have found in Jovet-Ast's archive documents of her study of Onraedt 14M2023 (*Figure 16 H–K*) that the spores by SEM show the same ornamentation as described by Perold (1990).





**Figures 56-66.** *Riccia stricta* (Lindenb.) Perold. (56) On the field along the banks of a small stream, Makay Massif, Reeb CR1144. Scale bar 1 cm. (57) Thallus ventral (left) and dorsal (right) face. Coloration with bleached (20 %), rinses and diluted methylen blue. (58) Bulging sporophyte in lateral view. (59) Ventral view with scales. Scale bars 1 mm. (60) Spore proximal face. (61) Spore distal face. Optical microscopy, scale bars 10 μm. (62) Cross section old branch (left), terminal branch (right). Coloration with bleached (20 %), rinses and diluted methylen blue. (63) (64) Spore proximal face. (65) (66) Spore distal face, *Onraedt* 14M2023, scanning electronic microscopy by Mme Jovet-Ast, 1994.

The main characters that differentiate the two species are: (1) apex narrowed in *R. stricta*; (2) frequent presence of sporophyte in *R. stricta* compared to *R. fluitans*. These species appear to be also close to *R. stenophylla* Spr. (Schuster 1992), but the *R. stricta* spore ornamentation shows large, very thick and deep walled alveoli and is different from both those of *R. fluitans* and *R. stenophylla*.

**Specimen examined:** ANTANANARIVO, Antananarivo, sur la terre près des serres du parc de Tsimbazaza, elev. 1250 m, 06/08/1973, *Cremers 2409* (PC-PC0738825, PC0715990, TAN); *Cremers 2415* (PC); Antananarivo, Tourbière de Tsimbazaza, 1250 m, 06/08/1973, *Cremers 2417* (TAN); route d'Antsirabe, 11 km environ d'Antananarivo, rizières après la récolte, 14/07/1951, *Benoist* (PC); Antananarivo, Jard. Bot. de Tsimbazaza, elev. 1400 m, 28/02/1974, *Onraedt 14M2023*, (PC-PC0715988); In montibus Ankaratra 1877, *M. Borgen 110* (PC-PC0715999); Environs d'Antananarivo, PK 22 route d'Antananarivo, Sept. 1959, *Bosser 13262* (PC-PC0715992, TAN); ANTSIRANANA, forêt d'Anjahana, au sud-est d'Ambilobe, dans le lit du fleuve Antsiatsia, 28/08/1973, *Cremers 2686* (PC). FIANARANTSOA, Forêts de Ranomafana, 60km au Nord de Fianarantsoa, elev. 900 m, 16/08/1971, *Onraedt 71M5045* (PC-PC0715989); Andringitra, Mts near Ambalavao, elev. 1012 m, 21°56'S 45°65'E, 20/09/1994, *S. Orbán 9459/B* (EGR, PC-PC0716003); Fianarantsoa, Parc National de Ranomafana, S. slope of Mt. Vatolampy, elev. 1015 m, 21°15.37'S 47°24.76E 29/07/2004, *S. & T. Pócs 04127/C* (EGR, PC-PC00716001); Ranomafana National Park 1km W from Ambatolahy, elev. 1015 m, 21°15' 19"S 47°24'48"E, 27/09/1994, *S. Orbán 9466/C* (EGR, PC-PC0716002). TOAMASINA, Pays des Antsianaka [*Antsihanaka*], leg. Perrot 1890 (PC-PC0715898); Pays des Antsianaka [*Antsihanaka*], Mars 1891 leg. *Perrot* (PC-PC0716000); route de Tamatave [Toamasina], 11 km est de Manjakandriana (Ambatoloana), elev. 1300 m, 09/1962, *Bosser 16201* (PC). TOLIARA, au bord du Fiherenana, près de Miary, elev. 200 m, 30/06/1971, *Onraedt 71M5526* (PC); Makay, le long de la rivière Ambotorabatorano, sur grès 21°34'04.9S 45°04'33.7E 303m 01/04/2011 *CR1144* (TAN-PC).

**Species to be confirmed:** *Riccia perssonii* S.A. Kahn is cited for Madagascar (Marline *et al.* 2012), and was first identified by Perold

(1995b), but without any specimen reference. The spores of this heterothallic species are in tetrads, which is a rare character state in *Riccia*. But we could not see or collect specimens of this species.

## TARGIONIACEAE

***Targionia hypophylla*** L. *Species Plantarum* 2: 1136. 1753.

**Type:** 'Italia, Hispania, Constantinopoli' + citation (syn.); Dill.: 532. Lichen No. 9, tab. 78, fig. 9. (1741) (OXF, syn.); (H-SOL, isosytype) [according to Isov. (1970) and quoted by Grolle (1976)].

**Synonymes:** *Targionia michelii* Corda. *Naturalientausch* 12: 649. 1829. **Type:** Italy, leg. Sieber. *Targionia mexicana* Lehm. & Lindenb. *Nov. Stirp. Pug.* 4: 27-28. 1832. **Type:** Mexico, leg. Schiede. *Targionia capensis* Huebener. *Hep. Germ.* 17. 1834. *Targionia bifurca* Nees & Mont. *Ann. Sci. Nat., Bot., ser. 2*, 9: 40 & 113. 1838. **Type:** Chile, 'prope Quillota', leg. Brotero. *Targionia convoluta* Lindenb. & Gott. *Syn. Hep.* 576. 1846. **Type:** Mexico, ad Chinantla, leg. Liebman.

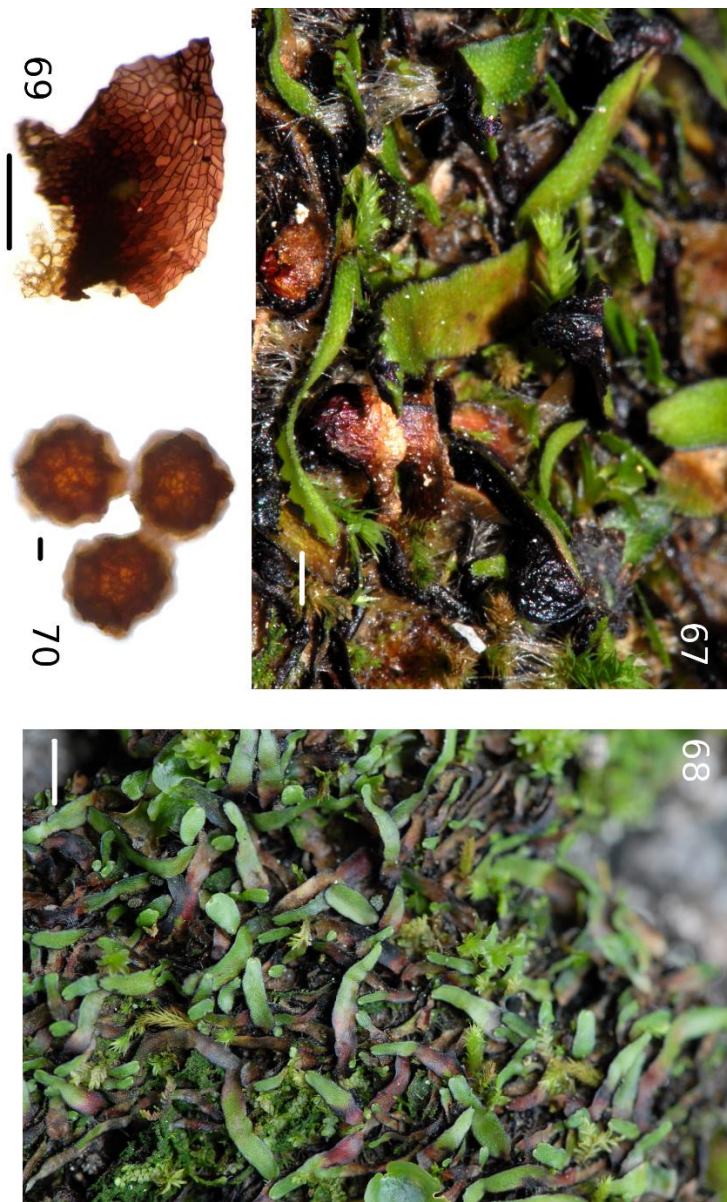
**Thalli** in crowded patches of strap-like and simple branches (not in rosettes) (*Figures 67, 68*), cordate when young up to 3mm wide, fleshy to leathery, dark green, without groove, margin often purple; when dry, the margins are inrolled letting the ventral scales cover all the thallus. **Air pores** visible. **Ventral scales** in two rows reaching the margins, shiny purple-black (*Figures 67, 69*). Dioicous or autoicous. **Antheridia** terminal or lateral on branches which arise ventrally. **Archegonia** in ventral position just below the apex of the branches, protected by a black shiny involucre, opening by a longitudinal and central fissure. **Sporophyte** sub-sessile with globose capsules. "When dry the apical portion of thalli bearing the sporophytes bends upward away from the substratum and the valves of the involucre gape apart like a mussel" (Jones 2004). **Spores** light brown to reddish brown, 44-64(-77)  $\mu\text{m}$ ; distal face with alveoli limited by thick walls, bottom of the alveolus covered by smaller and thinner reticulation (*Figure 70*).

**Distribution:** known from around Antananarivo and in central plateau (*Figure 78*). Sub-cosmolitan.

**Ecology:** on temporary humid banks, or compact banks. All the specimens examined were assigned to *T. hypophylla*, although

another species, *Targionia lorbeeriana* Müll.Frib. was cited for Africa (Arnell 1963). This last species is a triploid of *T. hypophylla* (Zamora *et al.* 1990). After examining numerous South African specimens and the type specimen of *T. lorbeeriana*, Perold stated that all the studied African collections were *T. hypophylla*. The distinction of the two species can be done on thallus and cells dimensions and on spore ornamentation (Jovet-Ast and Zigliara 1966). Malagasy specimens match the *T. hypophylla* description.

**Specimen examined:** ANTANANARIVO, Tananarive, 03/1914, talus, *Waterlot 94* (PC- PC0716010), *Waterlot 97* (PC- PC0716009); Andramasina (Ambatolampy), vestige de forêt d'altitude, 1300 m, déc. 1958, *Bosser 12324* (PC-PC0716008); Fort-Voyron, 19/01/1921, *Decary s.n.* (PC- PC0716011); Antananarivo, 13/02/1921, *Decary s.n.* (PC-PC0716013, PC0716014); Forêt d'Angavokely, alt 1603 m, S 18°55'24.9 E 47°44'21.7, 02/02/2011, *Reeb & Andriamiarisoa CR11185* (PC, TAN). FIANARANTSOA, Ankafotra (Ambafiandrohana) 1700 m, 16/02/1938, *Decary s.n.* (PC-PC0716012).



**Figures 67-70.** *Targionia hypophylla* L. (67) Population, showing the mussel-like ventral valvae enclosing the sporophyte. Scale bar 1 mm. (68) Scale bar 5 mm (69) Scale bar 500  $\mu$ m. (70) Scale bar 10  $\mu$ m. Angavokely, Reeb & Andriamiarisoa, CR111855.



## CONCLUSIONS

Six new records of Marchantiidae are proposed for Madagascar: *Asterella bachmanii* (Steph.) S.W.Arnell. (as synonym of *A. coronata* Steph.), *Asterella marginata* (Nees) S.W.Arnell, *Exormotheca pustulosa* Mitt., *Riccia congoana* Steph., *Riccia atropurpurea* Sim. and *Riccia stricta* (Lindenb.) Perold. Two cited species are not recognized here: (1) *Asterella wilmsii*, which is probably misidentified and assigned here to *A. marginata*, (2) *Riccia perssonii*, which was not seen in the collections and with no voucher references (Perold 1995).

No endemic Marchantiidae were discovered in Madagascar, and the synonymy of *A. coronata* could be seen as a confirmation of the relatively low level of endemism of bryophytes lineages and the need of further revisions including molecular studies (Vanderpoorten *et al.* 2010). We make the assumption that new records or new species could be discovered in the genus *Riccia*, where several specimens could not be identified using the available literature. One can notice that the *Lunularia* genus common in East Africa has not been cited before for Madagascar and was not recorded in the studied collections.

Morphological observations highlight the necessity of extensive studies to clarify or confirm the status of several taxa in order to assess their whole variability. An integrative approach combining molecular analysis and morphometry etc. should be one way to evaluate species delimitations in Malagasy and African related taxa. Although taxonomic work was achieved for Eurasian and American species, similar studies on African *Asterella* are awaiting (Long 2006). The same effort must be done for *Riccia*, especially for the *fluitans* group to clarify species. Some species are known only by a few specimens and collection effort in potentially favorable environments and seasons has to be conducted to enlarge the knowledge; this is the case of *Cyathodium africanum*, *Targionia hypophylla* and *Plagiochasma microcephalum*.

In our study, fifteen species of Marchantiidae are reported for Madagascar; fifteen species are also known for La Réunion, 230 times smaller than Madagascar (Ah-Peng and Bardat 2005). If we



refer to the largest genus, *Riccia* (Ricciaceae), four species are cited for La Réunion, sixty-six for South Africa (Wigginton 2009) compared to only six (seven, if *Riccia perssonii* could be confirmed) species known in Madagascar. It is reasonable to hypothesize that Madagascar is understudied, especially for the complex thalloid species.

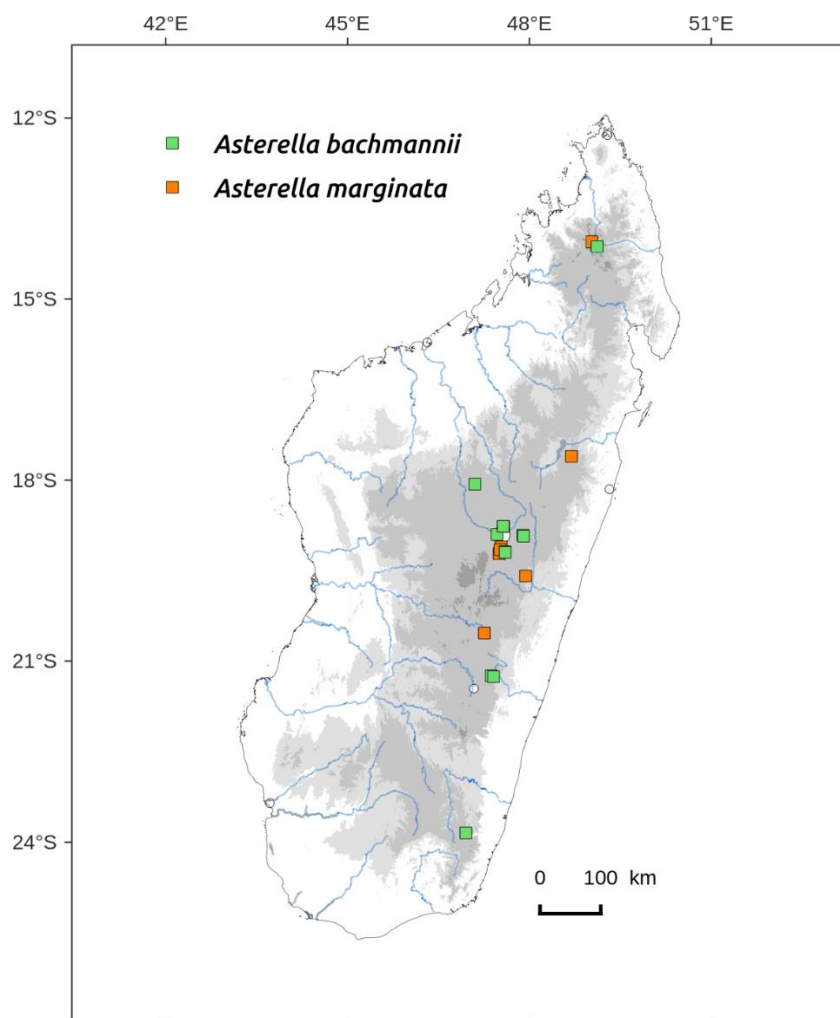
During our recent field trips in Madagascar, it seemed difficult to see Marchantiidae in *a priori* favourable environments (road banks, high plateau steppes etc.), except in the Makay Massif where abundant Ricciaceae were found. We suggest that these plants living in open areas are probably under a great fire pressure mainly due to the practice of traditional *tavy* (slush and burn) culture (Figures 71, 72). Some species are known to be fire resistant and to appear as primitive colonizer after fire (Esposito *et al.* 1999). But repeated fire has not the same effect than occasional ones, and in numerous places the soil is bare, missing bryophytes on a degraded laterite substratum repeatedly burn. Further exploration of stations cited by former collectors or of favourable stations could test that hypothesis. Experimentation on thalloid liverworts resistance to fire could also help to understand their strategies and adaptations in such context.

### **Participation of the different authors**

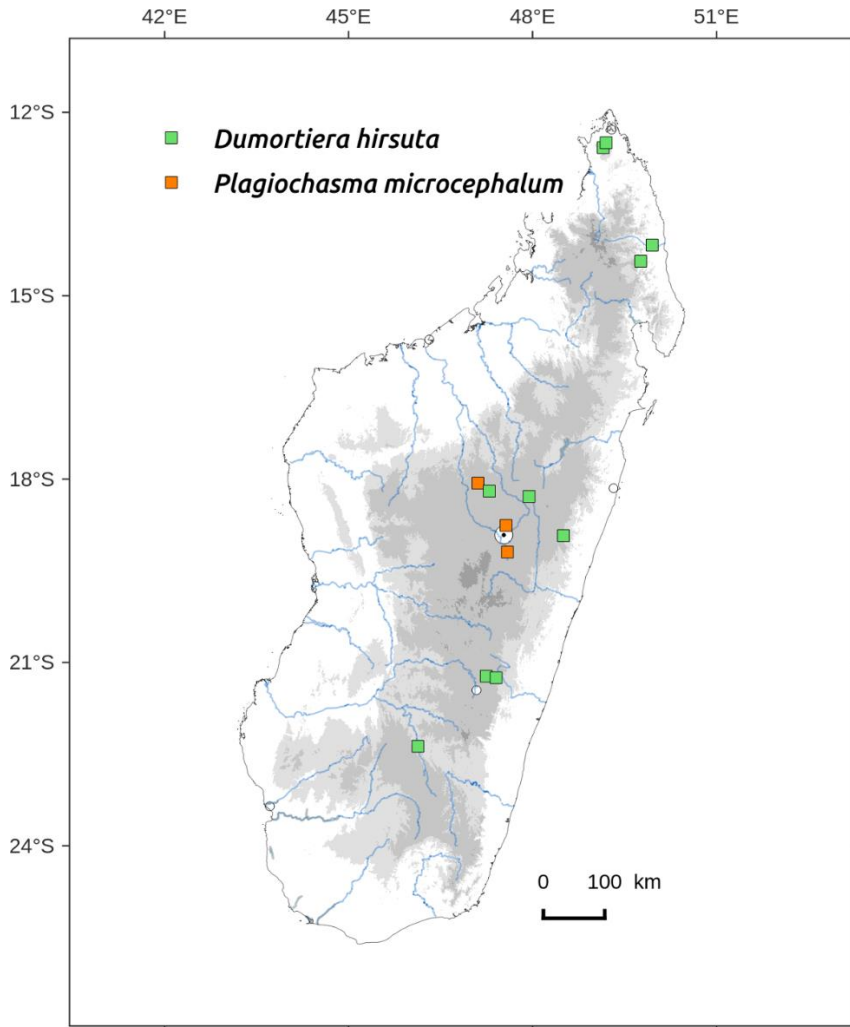
Catherine Reeb collected plants in Madagascar, identified and described specimens, wrote and illustrated the paper. Lovanomenjanahary Marline collected specimens in Madagascar and contributed to the writing of the whole publication. Lucile Rabeau collected plants in Madagascar and contributed to the writing on the Ricciaceae. Ainazo Andriamanantena collected plants in Madagascar, gathered historical references, identified and described specimens; this study was initiated in the context of her master thesis in 2010. Roger Lala Andriamiarisoa organized Angavokely fieldtrip, collected specimens all around Madagascar and provided drawings. Hery-Lisy Ranarijaona, supervised the project and reviewed the publication for Malagasy vegetation. Tamás Pócs collected specimens and gave his expertise and corrections for the publication.



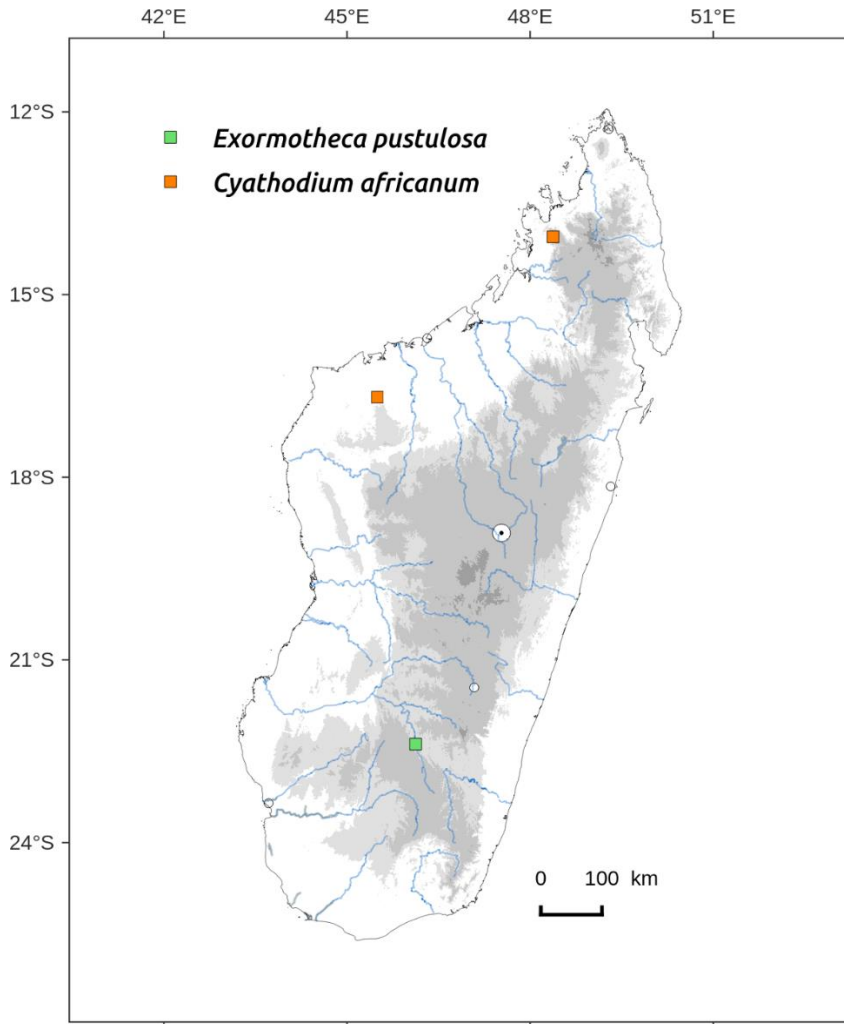
**Figures 71-72.** Fire and deforestation. (71) In Zahamena National Parc, 2015. Details of the soil show the potential impact on bryophytes. (72) In the Makay massif, 2011, on a river bank, a very favorable station for *Marchantia* and *Riccia*.



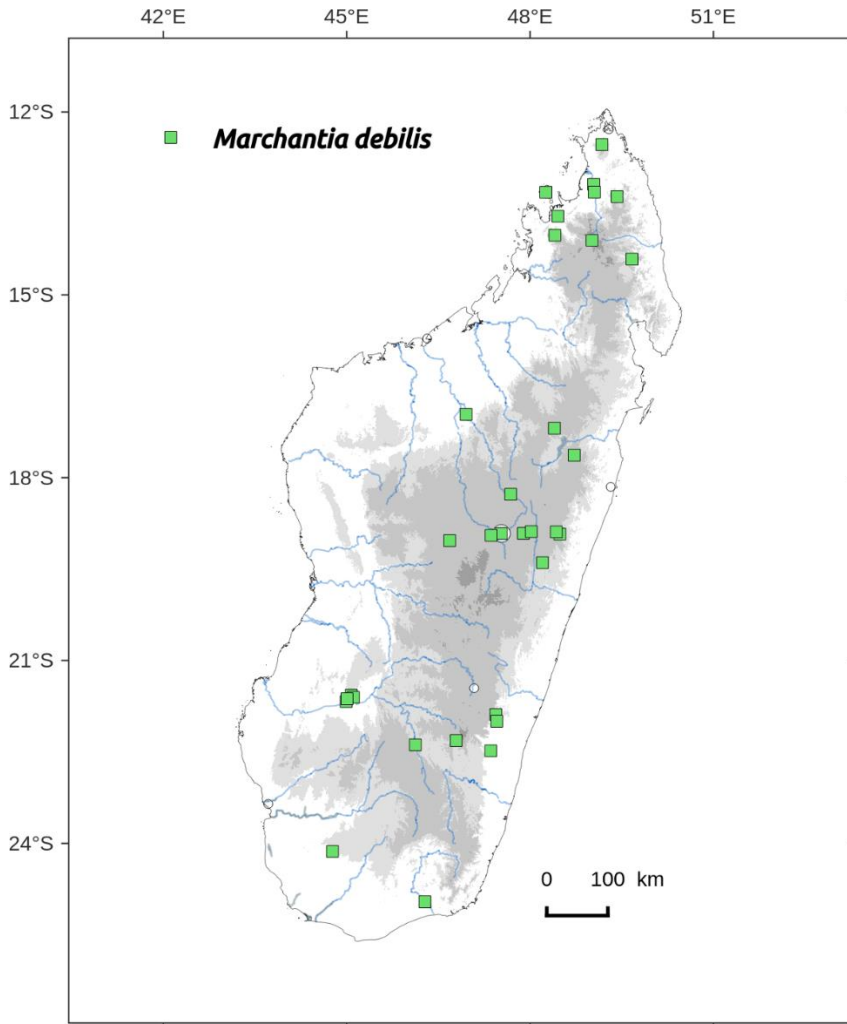
**Figure 73.** Distribution map of *Asterella bachmannii* and *Asterella marginata* in Madagascar, based on the specimens studied from EGR, PC and TAN herbarium and the authors' collections.



**Figure 74.** Distribution map of *Dumortiera hirsuta* and *Plagiochasma microcephalum* in Madagascar, based on the specimens studied from EGR, PC and TAN herbarium and the authors' collections.

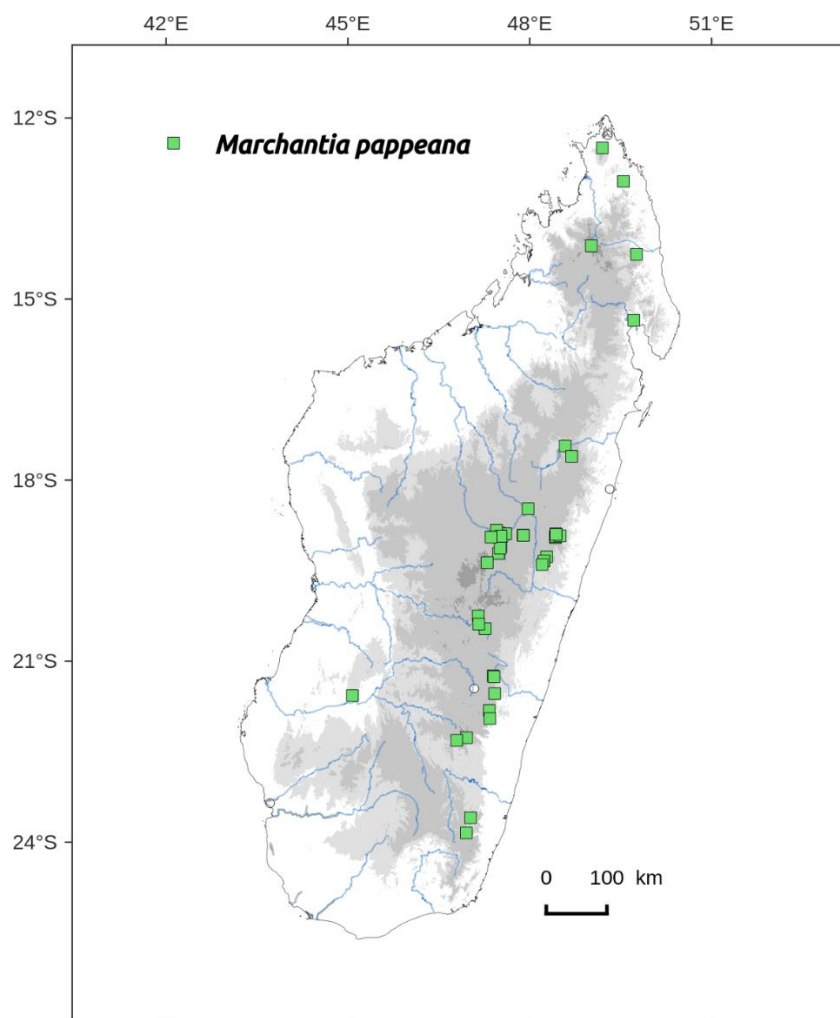


**Figure 75.** Distribution map of *Exormotheca pustulosa* and *Cyathodium africanum* in Madagascar, based on the specimens studied from EGR, PC and TAN herbarium and the authors' collections.

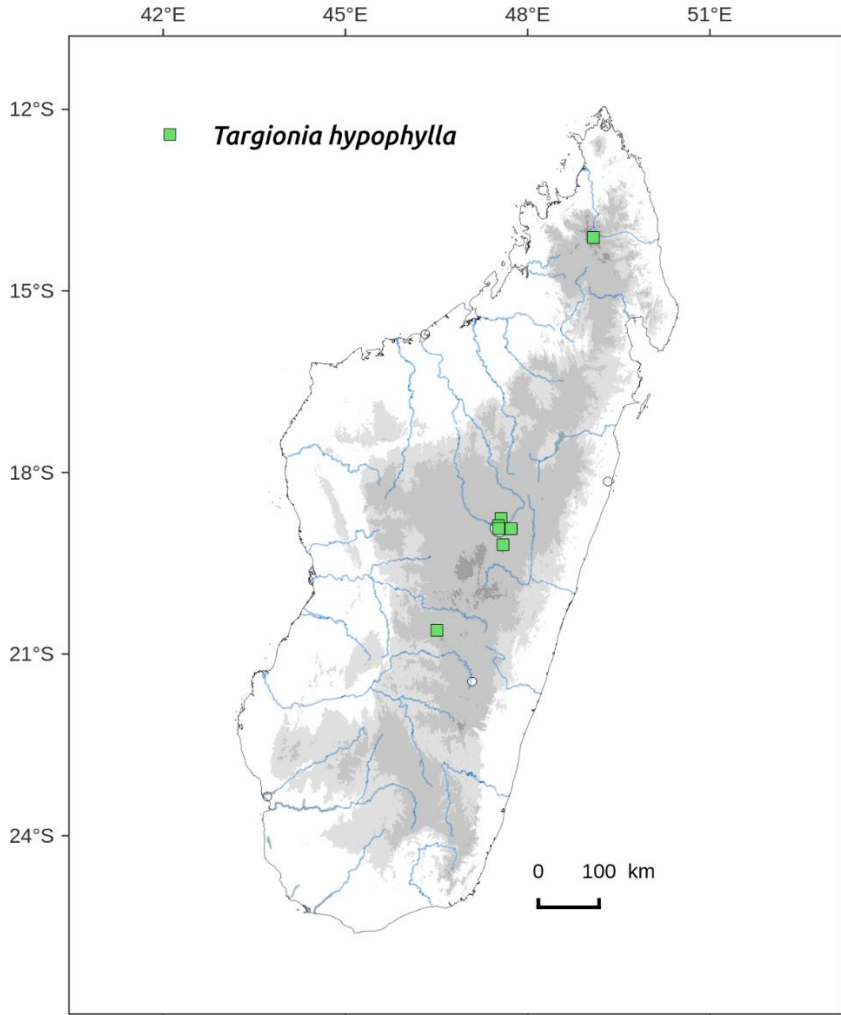


**Figure 76.** Distribution map of *Marchantia debilis* in Madagascar, based on the specimens studied from EGR, PC and TAN herbarium and the authors' collections.

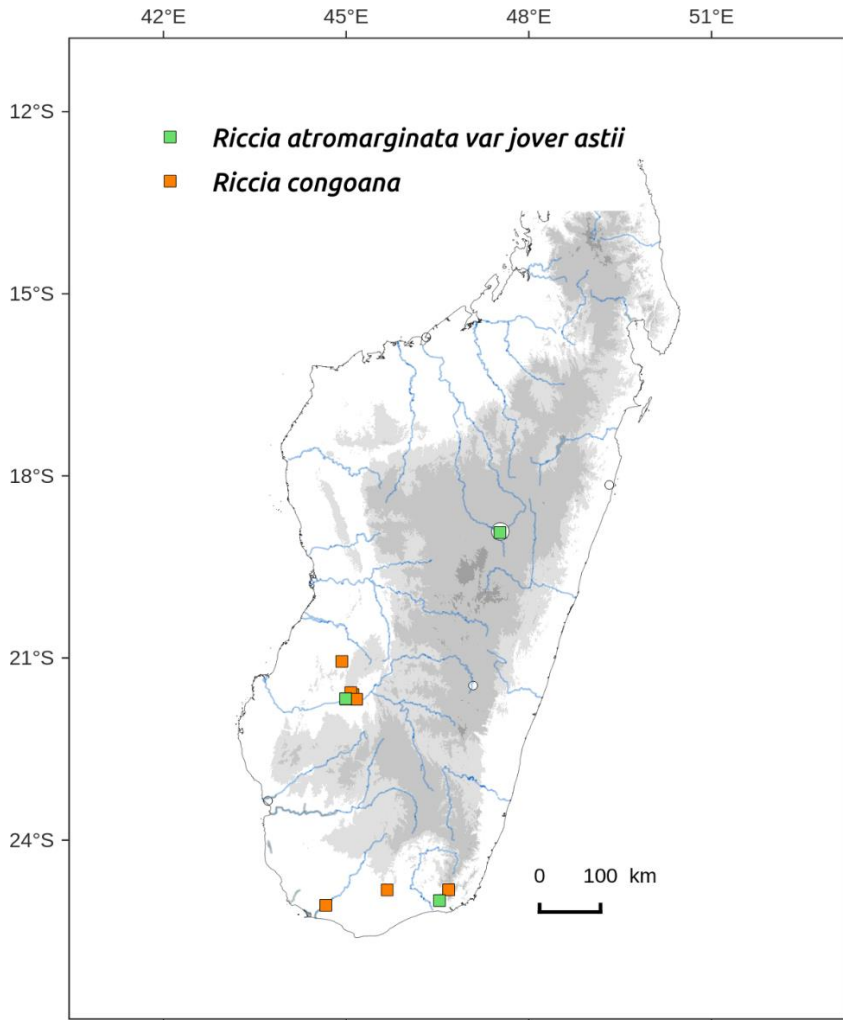




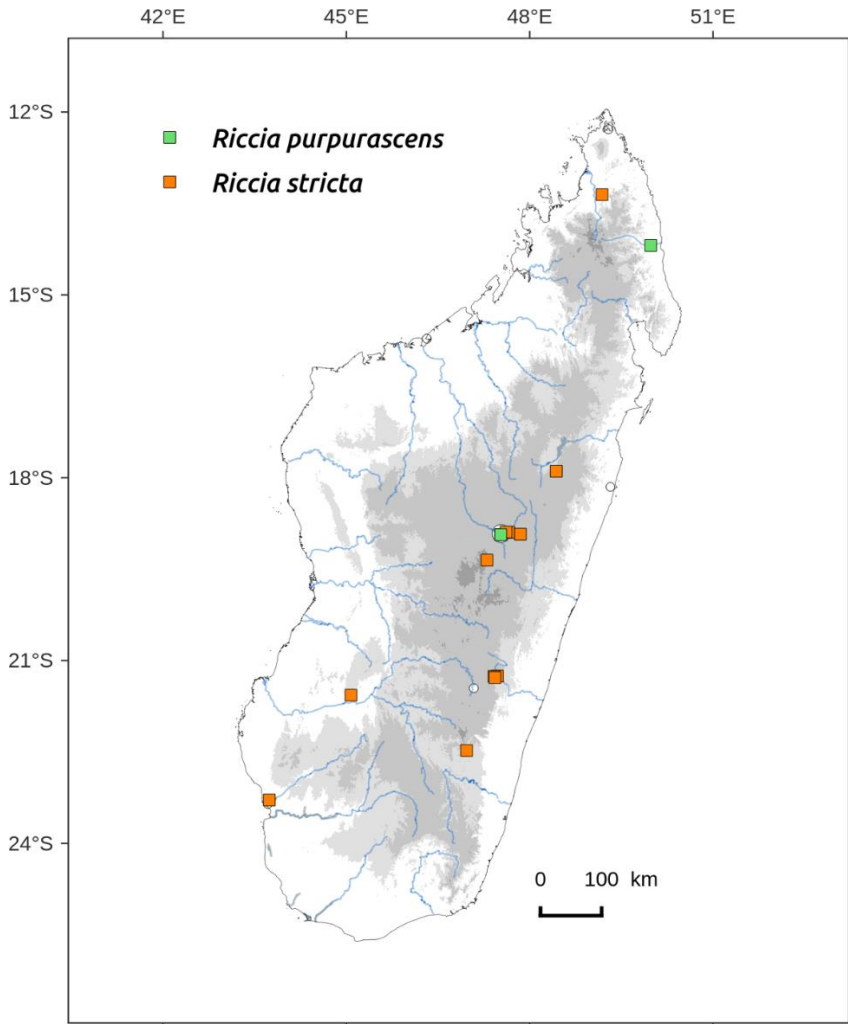
**Figure 77.** Distribution map of *Marchantia pappeana* in Madagascar, based on the specimens studied from EGR, PC and TAN herbarium and the authors' collections.



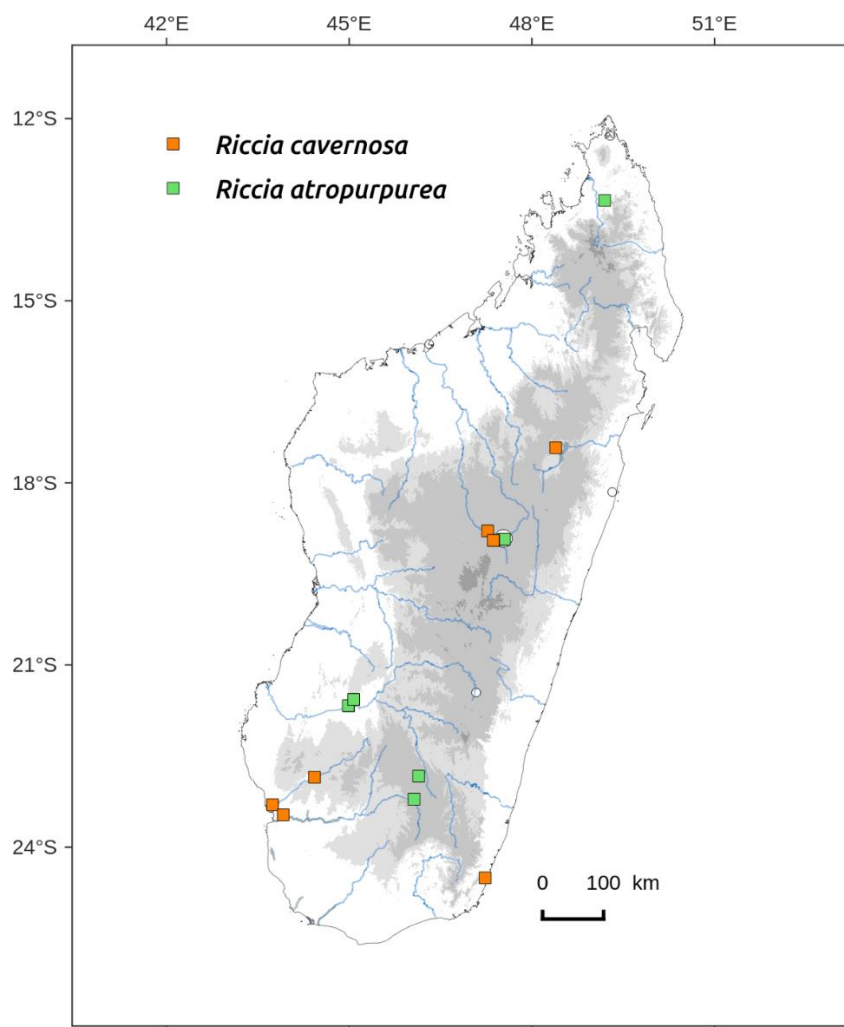
**Figure 78.** Distribution map of *Targionia hypophylla* in Madagascar, based on the specimens studied from EGR, PC and TAN herbarium and the authors' collections.



**Figure 79.** Distribution map of *Riccia atromarginata var. jover astii* and *Riccia congoana* in Madagascar, based on the specimens studied from EGR, PC and TAN herbarium and the authors' collections.



**Figure 80.** Distribution map of *Riccia purpurascens* and *Riccia stricta* in Madagascar, based on the specimens studied from EGR, PC and TAN herbarium and the authors' collections.



**Figure 81.** Distribution map of *Riccia cavernosa* and *Riccia atropurpurea* in Madagascar, based on the specimens studied from EGR, PC and TAN herbarium and the authors' collections.



**Figure 82.** Artistic representation of thalloid bryophytes taxa from Madagascar. Marchantiales (complex thalloid): A = *Marchantia pappeana*, B = *Symphyogyna podophylla*, (simple thalloid) C = *Riccia* sp. Pallaviciniaceae D = *Dumortiera hirsuta*, recently reported for Madagascar (Andriamiarisoa *et al.*, 2017). E = Anthocerotophyta. Drawings made by Roger Lala Andriamiarisoa.



**Acknowledgments** – The authors wish to thank: TAN herbarium, EGR herbarium and PC herbarium for the facilities for studying specimens. Madagascar National Park who provided authorizations to collect bryophytes in numerous areas: Vohimana, Maromizaha (GERP/SG/OUT/12/0020), Angavokely (N°030/11/MEF/SG/DGF/DCB. SAP/SCB 31/01/2011), Makay (N°360/10/MEF/SG/DGF/DCB.SAP/ SLRSE 28/12/2010), Makirovana (MBG collection authorization), Zahamena (N°275/13/MEF/SG/DGF/ DCB.SAP:SCB 14/11/2013). ONG “L’Homme et l’Environnement” who allowed Vohimana prospections. “Association Timarcha”, Campus Jussieu, UMPC, Paris, France who supported and funded 2006 and 2012 fieldtrips and collection. Thanks to the GERP and Pr. Jonah RATSIMBAZAFY for facilitating our visit of Maromizaha reserve. MBG (Missouri Botanical Garden) and Chris Birkenshaw who organized in the Makirovana fieldtrip, and Angavokely fieldtrip. Naturevolution and Evrard Wendenbaum for organizing the Makay fieldtrip and invited some of the authors to this adventure.

Thanks to PARRUR funding (PArtenariat et Recherche dans le secteur RURal) of the french IRD in Madagascar to give a grant for Zahamena field trip, to the co-author Andriamanantena.

Thanks to all the Malagasy people who helped the success of the different fieldtrips (carriers, cooks, drivers...), especially LeSabotsy in Ambavaniasy, réserve de Vohimana. Thanks to David Long for advices on *Asterella*.

## REFERENCES

- AH-PENG, C. & BARDAT, J. (2005). Check list of the Bryophytes of Réunion Island (France). *Tropical Bryology* **26**: 89–118. <https://doi.org/10.11646/bde.26.1.14>
- ANDRIAMIARISOA, R., CALLAGHAN, D. A. & REEB, C. (2017). in: ELLIS, L.T. *et al.*: New national and regional bryophyte records, 53. *Journal of Bryology*. **39**(4): 379–380. <https://doi.org/10.1080/03736687.2017.1384204>
- ARNELL, S. (1963). *Hepaticae of South Africa*. Swedish Natural Science Research Council, Stockholm. 411 pp.
- BESCHERELLE, E. (1880). Florule bryologique de l’île de Nossi-Bé. *Revue Bryologique* **7**: 1–14.
- BESCHERELLE, E. (1891). Selectio novorum muscorum. *Journal de botanique* (Morot) **5**(9): 142–148.
- BISCHLER, H. (1976). Exormotheca pustulosa Mitten. Distribution, écologie, caryotype, spores, parois sporales, germinations. *Revue Bryologique et Lichénologique* **42**: 769–783.
- BISCHLER, H. (1978). Plagiochasma Lehm. & Lindenb. II. Les taxa européens et africains. *Revue Bryologique et Lichénologique* **44**: 223–230.
- BISCHLER, H. (1993). Marchantia L. The European and African taxa. *Bryophytorum Bibliotheca* **45**: 1–129.
- BISCHLER, H. (1998). Systematics and evolution of the genera of Marchantiales. *Bryophytorum Bibliotheca* **51**: 1–152 + 24 plates.
- BISCHLER-CAUSSE, H., GRADSTEIN, S.R., JOVET-AST, S., LONG, D.G. & SALAZAR ALLEN, N. (2005). Marchantiidae. *Flora Neotropica Monograph* **97**: 1–267.
- BOISSELIER-DUBAYLE, M.-C., LAMBOURDIÈRE, J. & BISCHLER, H. (2002). Molecular phylogenies support multiple morphological reductions in the liverwort

- subclass Marchantiidae (Bryophyta). *Molecular Phylogenetics and Evolution* **24**: 66–77.
- BOITEAU, P., BOITEAU, M. & ALLORGE-BOITEAU, L. (1997). *Index des noms scientifiques avec leurs équivalents malgaches*. Ed Alzieu, Grenoble, France. (non-paginated)
- CHUAH-PETIOT, M. (2003). *Mosses, liverworts and hornworts from Kenya*. Nairobi, 273 pp.
- CORNET, A. (1974). *Essai de cartographie bioclimatique à Madagascar*. Orstom Publishers, Paris, 28 pp.
- CORNET, A. & GUILLAUMET, J. (1976). Divisions floristiques et étages de végétation à Madagascar. *Cahiers de l'Orstom, Série Biologie* **9**: 35–42.
- CRANDALL-STOTLER, B., CRANDALL-STOTLER, R. & LONG, D. (2009). Phylogeny and classification of the Marchantiophyta. *Edinburgh Journal of Botany* **66**: 155–198. <https://doi.org/10.1017/S0960428609005393>
- DOLCH, R. (2009). *Andasibe (Périnet), les efforts actuellement entrepris sont-ils suffisants pour protéger la nature du hot-spot de biodiversité à Madagascar?* In: GOODMAN, S. (ed.): *Paysages naturels et biodiversité de Madagascar*. Publications scientifiques du Muséum, Paris, pp. 547–557.
- DORR, L. (1997). *Plant Collectors in Madagascar and the Comoro Islands*. The Trustees Royal Botanical Garden Kew, 524 pp.
- DUCKETT, J. & LIGRONE, R. (2006). *Cyathodium* Kunze (Cyathodiaceae: Marchantiales), a tropical liverwort genus and family new to Europe, in Southern Italy. *Journal of Bryology* **25**: 88–96. <https://doi.org/10.1179/174328206X105353>
- ESPOSITO, A., MAZZOLENI S. & STRUMIA, S. (1999). Post-fire bryophyte dynamics in Mediterranean vegetation. *Journal of Vegetation Science* **10**: 261–268. <https://doi.org/10.2307/3237147>
- FARAMALALA, M. (1995). *Formations végétales et domaine forestier national de Madagascar. 1 : 1.000.000 color map*. Direction des Eaux et Forêts (DEF), centre National de Recherches sur l'Environnement (CNRE) et Foiben-Taontsarin-tanin'i Madagascar (FTM).
- GAUTIER, L. & GOODMAN, S. (2009). *Introduction à la flore*. In: GOODMAN, S. (ed.): *Paysages naturels et biodiversité de Madagascar*. Muséum National d'Histoire Naturelle, Publications scientifiques du Muséum, Paris, pp. 103–139.
- GOODMAN, S. (2009). *Paysages naturels et biodiversité de Madagascar*. Muséum National d'Histoire Naturelle, Publications scientifiques du Muséum, Paris, 694 pp.
- GOTTSCHKE, C.M., LINDENBERG, J.B. & NEES VON ESENBECK, C. (1844). *Synopsis Hepaticarum: coniunctis studiis scripserunt et edi curaverunt*. Hamburgi: Meissnerianis, 834 pp.
- GROLLE, R. (1995). The Hepaticae and Anthocerotae of the East African Islands, An annotated catalogue. *Bryophytorum Bibliotheca* **48**: 1–178.
- GRIFFITH, W. (1849). *Icones Plantarum Asiaticarum on the Higher Cryptogamous Plants* (part 2) Calcutta, 192 pp.
- HUMBERT, H. & COURS-DAME, G. (1965). Carte internationale du tapis végétal et des conditions écologiques. 3 coupures à 1/1000000 de Madagascar. *Travaux de section Scientifique et Technique de l'Institut Français de Pondichery*, hors-série 6.
- JONES, E.W. (1952). African hepatics. I. The genus *Cyathodium* in Africa. *Transactions of the British Bryological Society* **2**(1): 55–61.

- JONES, E.W. (1957). African Hepatics. XIII. The Ricciaceae in Tropical Africa. *Transactions of the British Bryological Society* **3**(2): 208–227.
- JONES, E.W. & PÓCS, T. (1987). African Hepatics. XXXVI. Three new species of Colura. *Journal of Bryology* **14**: 495–501.
- JOVET-AST, S. (1948). Les hépatiques de Madagascar. *Mémoires de l'institut scientifique de Madagascar. Série B.* **1**: 39–42.
- JOVET-AST, S. (1955). Riccia atromarginata Lev. et sa variété glabra Lev. au Maroc. *Revue bryologique et lichénologique* **24**: 240–247.
- JOVET-AST, S. (1964). Riccia crystallina L. emend Raddi et Riccia cavernosa Hoffm. emend Raddi. (Note préliminaire). *Revue bryologique et lichénologique* **33**: 459–483.
- JOVET-AST, S. (1966). Riccia crystallina L. emend Raddi et Riccia cavernosa Hoffm. emend Raddi. *Revue bryologique et lichénologique* **34**: 82–90.
- JOVET-AST, S. (1970). Cyathodium africanum Mitt. au Yémen et en Afrique. *Revue bryologique et lichénologique* **37**(1) 57–62.
- JOVET-AST, S. (1986). Les Riccia de la région méditerranéenne. *Cryptogamie Bryologie Lichénologie* **7**(3): 287–430.
- JOVET-AST, S. (1989). Un complexe de taxons dans le genre Riccia. *Cryptogamie Bryologie Lichénologie* **10**: 95–117.
- JOVET-AST, S. & ZIGLIARA, M. (1966). La paroi des spores de Targionia lorbeeriana et de Targionia hypophylla: sa valeur taxinomique. *Revue bryologique et lichénologique* **34**: 816–821.
- KÜRSCHNER, H. (2000). Bryophyte flora of the Arabian Peninsula and Socotra. *Bryophytorum Bibliotheca* **55**: 1–130.
- LINDENBERG, J. (1838). *Monographie der Riccieen 84 (1836)*. Natur-geschichte der europäischen Lebermoose, 440 pp.
- LONG, D.G. (2006). Revision of the genus Asterella P. Beauv. in Eurasia. *Bryophytorum Bibliotheca* **63**: 1–299.
- LONG, D.G. (2005). Studies on the genus Asterella (Aytoniaceae) VI: infrageneric classification in Asterella. *Journal of the Hattori Botanical Laboratory* **97**: 249–261.
- LONG, D.G. (2001 [2000]). Studies on the genus Asterella (Aytoniaceae). V. Miscellaneous notes on Asiatic Asterella. *Lindbergia* **26**: 43–45.
- M.B.G. (2008). *Complexe forestier Makirovana-Tsihomanaomby*. Rapport de Présentation du site.
- MANJU, C.N., RAJESH, K.P. & PRAKASHKUMAR, R. (2012). On the identity of Riccia fluitans (Ricciaceae: Marchantiophyta) in India. *Acta Biologica Plantarum Agriensis* **2**: 115–124.
- MARLINE, L., ANDRIAMIARISOA, R., BARDAT J., CHUAH-PETIOT, M., HEDDERSON, T., REEB, C., STRASBERG, D., WILDING, N. & AH-PENG, C. (2012). Checklist of the bryophytes of Madagascar. *Cryptogamie Bryologie* **3**: 199–255.  
<https://doi.org/10.7872/cryb.v33.iss3.2012.199>
- MITTEN, W. (1887). The Mosses and Hepaticae collected in Central Africa by the late right Rev. James Hannington, Bishop of Mombasa F.L.S, F.G.S. & c. with some others including those gathered by Mr H.H. Johnson on Kilimanjaro. *Journal of the Linnean Society* **32**: 298–327.
- MOAT, J. & SMITH, P. (eds.) (2007). *Atlas of the Vegetation of Madagascar*. Kew Publishing, 124 pp.

- MYERS, N., MITTERMEIER, R.A., MITTERMEIER, C.G., GUSTAVO, A.B., DA FONSECA, G. & KENT, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–858. <https://doi.org/10.1038/35002501>
- PEARSON, W. (1891a). Frullaniae madagascarienses precipue e collectione Borgeni. *Forhandling i Videnskabs-selskabet i Christiania* **2**: 1–9.
- PEARSON, W. (1891b). Lejeuneae madagascarienses precipue e collectione Borgeni. *Forhandling i Videnskabs-selskabet i Christiania* **8**: 1–9.
- PEARSON, W. (1893). Hepaticae Madagascariensis. Notes on a collection made by Rev. Borgchgreivink and Rev. Dahle; 1877-1882. *Forhandling i Videnskabs-selskabet i Christiania* **14**: 1–11.
- PEROLD, S.M. (1999). *Flora of Southern Africa, Hepatophyta*. Part 1: *Marchantiopsida, Fascicle 1: Marchantiidae*. In: LEISTNER, O.A. (ed.): National Botanical Institute Pretoria. 252 pp.
- PEROLD, S.M. (1990). Studies in the genus *Riccia* (Marchantiales) from Southern Africa. 19. Two new species: *R. pulveracea*, section *Pilifer* [sic], and *R. bicolorata*, section *Riccia*, group 'Squamatae'. *Bothalia* **20**: 185–190.
- PEROLD, S.M. (1993). Studies in Marchantiales (Hepaticae) from Southern Africa. 1. The genus *Dumortiera* and *D. hirsuta*; the genus *Lunularia* and *L. cruciata*. *Bothalia* **23**: 49–57.
- PEROLD, S.M. (1995a). Studies in Marchantiales (Hepaticae) from Southern Africa. 8. The genus *Plagiochasma*, Aytoniaceae. *Bothalia* **25**(1): 13–29.
- PEROLD, S.M. (1995b). A survey of the Ricciaceae of tropical Africa. *Fragmenta Floristica et Geobotanica* **40**: 53–91.
- PEROLD, S. (1995c). Studies in Marchantiales (Hepaticae) from Southern Africa. 9. The genus *Marchantia* and its five local species. *Bothalia* **25**: 183–204.
- PERRIER DE LA BATHIE, H. (1921). La végétation malgache. *Annales de l'Institut botanico-géologique colonial de Marseille* **3**(9): 1–226.
- PÓCS, T. (1995). East African Bryophytes, XIV. Hepaticae from the Indian Ocean Islands. *Fragmenta Floristica et Geobotanica* **40**: 251–277.
- PÓCS, T. (2001). East African Bryophytes, XVI. New taxa of Lejeuneoideae (Lejeuneaceae) collected in Manongarivo Special Reserve, NW Madagascar. *Candollea* **56**: 69–78.
- PÓCS, T. (2006). East African Bryophytes, XXI. Two new species of *Telaranea*, sect. *Tenuifoliae* and records on *Amazoopsis* from the Indian Ocean Islands. *Acta Botanica Hungarica* **48**: (1-2): 105–124. <https://doi.org/10.1556/ABot.48.2006.1-2.14>
- PÓCS, T. & GEISLER, P. (2002). *The bryophytes collected in the Réserve Spéciale de Manongarivo, Madagascar*. In: GAUTIER, L. & GOODMAN, S.M. (eds.): Inventaire floristique et faunistique de la Réserve Spéciale de Manongarivo (NW Madagascar). *Boissiera* **59**: 41–76.
- PÓCS, T., MÜLLER F. & SHEVOCK, R. (2015). Additions to the liverwort and hornwort flora of São Tomé and Príncipe II, with *Neurolejeunea*, a genus new to Africa. *Herzogia* **28**: 50–69. <https://doi.org/10.13158/heia.28.1.2015.50>
- 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.
- PÓCS, T. & VÁÑA, J. (2015). East African Bryophytes XXX. New liverwort and hornwort records. *Acta Biologica Plantarum Agriensis* **3**: 3–21.

- RAUH, W. & BUCHLOH, G. (1961). *Riccia atromarginata* Levier var. *jovet-astii* var. nov. *Revue bryologique lichénologique* **30**: 74–79.
- REEB, C., RANARIJAONA H.L. & DUBUISSON, J.-Y. (2012). Ecological survey of the Lycophytes and Ferns of the Vohimana Reserve, Madagascar. *Plant Ecology and Evolution* **145**: 410–418. <http://dx.doi.org/10.5091/plevevo.2012.516>
- RENAULD, F. (1897). *Prodrome de la flore bryologique de Madagascar, des Mascareignes et des Comores*. Monaco: Impr., de Monaco, 316 pp.
- RENAULD, F. (1909). *Essai sur les Leucoloma de Madagascar et supplément au prodrome de la flore bryologique de Madagascar des Mascareignes et des Comores*. In: *Mémoires et documents*, Par Ordre de S. A. S. le Prince Albert V Prince Souverain de Monaco.
- RENAULD, F. & CARDOT, J. (1895). CH. 39: *Histoire naturelle des plantes mousses*. In: ALFRED ET GUILLAUME GRANDIDIER (eds.): *Histoire physique, naturelle et politique de Madagascar*: v. 39.
- SCHUSTER, R. M. (1987). Studies on Metzgeriales. I. North American Aneuraceae. *Journal of the Hattori Botanical Laboratory* **62**: 299–329.
- SCHUSTER, R. M. (1992). *The Hepaticae and Anthocerotae of North America*, Vol. VI. Field Museum of Natural History, Chicago.
- SÖDERSTRÖM, L, HAGBORG, A., VON KONRAT, M., BARTHOLOMEW-BEGAN, S., BELL, D., BRISCOE, L., BROWN, E., CARGILL, D.C., DA COSTA, D.P., CRANDALL-STOTLER, B.J., COOPER, E., DAUPHIN, G., ENGEL, J., FELDBERG, K., GLENNY, D., GRADSTEIN, S.R., HE, X., HENTSCHEL, J., ILKIU-BORGES, A.L., KATAGIRI, T., KONSTANTINOVA, N.A., LARRAÍN, J., LONG, D., NEBEL, M., PÓCS, T., PUCHE, F., REINER-DREHWALD, E., RENNER, M., SASS-GYARMATI, A., SCHÄFER-VERWIMP, A., SEGARRA-MORAGUES, J., STOTLER, R.E., SUKKHARAK, P., THIERS, B., URIBE, J., VÁÑA, J, WIGGINTON, M., ZHANG, L., & ZHU, R-L. (2016). World checklist of hornworts and liverworts. *PhytoKeys* **59**: 1–828. <http://dx.doi.org/10.3897/phytokeys.59.6261>
- SRIVASTAVA, S. & DIXIT, R. (1996). The genus *Cyathodium* Kunze. *Journal of the Hattori Botanical Laboratory*. **80**: 149–215.
- STEPHANI, F. (1891). Hepaticae Africanae. *Hedwigia* **30**: 201–261.
- STEPHANI, F. (1892). Hepaticae Africanae. *Hedwigia* **31**: 165–174.
- STEPHANI, F. (1893). Hepaticae Africana. *Hedwigia* **32**: 10–29.
- THÉRIOT, M. (1920). *Contribution à la flore bryologique de Madagascar*. Le Havre : Imprimerie Micaux frères, 191 pp.
- TIXIER, P. (1977). Espèces nouvelles malgaches du genre *Diplasiolejeunea* (Spruce) Schiffn. (Hepaticae). *Lindbergia* **4**: 117–125.
- TIXIER, P. (1984). Bryophytes de la région malgache (révision bibliographique depuis 1950). *Bulletin Trimestriel de l'association pour l'Avancement de la Recherche Scientifique concernant Madagascar et le Région Malgache* **17**: 22–36.
- TIXIER, P. (1992). Deux espèces nouvelles malgaches du genre *Calymperopsis* (Musci). *Bryologist* **95**: 284–286.
- VANDEN BERGHEN, C. (1972). *Hépatiques et Anthocérotes*. In: Cercle Hydrobiologique de Bruxelles (ed.), *Résultats scientifiques. Exploration hydrobiologique du bassin du lac Bangweolo et du Luapula* **8**: 1–202.
- VANDEN BERGHEN, C. (1981). Le genre *Plagiochila* (Dum.) Dum. (Hepaticae) à Madagascar et aux Mascareignes, principalement d'après les récoltes de M. Onraedt. *Bulletin du Jardin botanique National de Belgique* **51**(1-2): 41–103.
- VANDERPOORTEN, A., GRADSTEIN, S.R., CARINE, M.A. & DEVOS, N. (2010). The ghosts of

- Gondwana and Laurasia in modern liverwort distributions. *Biological Reviews* **85**: 471–487. <http://dx.doi.org/10.1111/j.1469-185X.2009.00111.x>
- WENDENBAUM, E M. (2011). *Makay, à la découverte du dernier Eden*. La Martinière, 173 pp.
- WHITE, F. (2002). Vegetation Map of Africa. [Carte de Vegetation de l'Afrique]. UNESCO / AETFAT / UNSO.
- WIGGINTON, M.J. (ed.), (2004). E.W. Jones's *liverwort and hornwort Flora of West Africa*. Scripta Botanica Belgica, National Botanic Garden of Belgium, 444 pp.
- WIGGINTON, M.J. (2009). Checklist and distribution of the liverworts and hornworts of sub-Saharan Africa, including the East African Islands. *Tropical Bryology Research Reports* **8**: 1–116.
- ZAMORA, P.G., ROS, R.M. & GUERRA, J. (1990). Taxonomía numérica en Targionia L. (Hepática). *Anales del Jardín Botánico de Madrid* **46**: 393–404.

(submitted: 12.11.2017, accepted: 02.02.2018)