



## Disentangling the diversity and taxonomy of Hymenophyllaceae (Hymenophyllales, Polypodiidae) in the Mascarene archipelago, with ecological implications

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### Abstract

We here explore the diversity and ecology, and update the taxonomy of the fern family Hymenophyllaceae, which forms one of the most diverse and emblematic fern assemblages in rainforests of the Mascarene archipelago in western Indian Ocean. Since 1999, we extracted data from floras, literature, and field investigations conducted, and from an exhaustive examination of the collections at P, REU, and MAU. Our checklist recognizes 26 taxa involving 23 species, 2 local varieties and 1 new *forma*. We reconsider area of distribution in Mascarene Hymenophyllaceae and at least 3 species appear to be restricted to the archipelago. We discuss the updated taxonomy and discrimination of each taxon (including a new nomenclatural proposition for *Hymenophyllum tenellum* here renamed as *H. fumarioides*) and provide a dichotomous key. We present and discuss the ecology and elevational distribution of each species, in addition to the local endemism. Finally, we emphasize the importance of threatened lowland rainforests and of wet ravines in semi-dry forests, which host a high level of diversity in the context of local conservation of habitats.

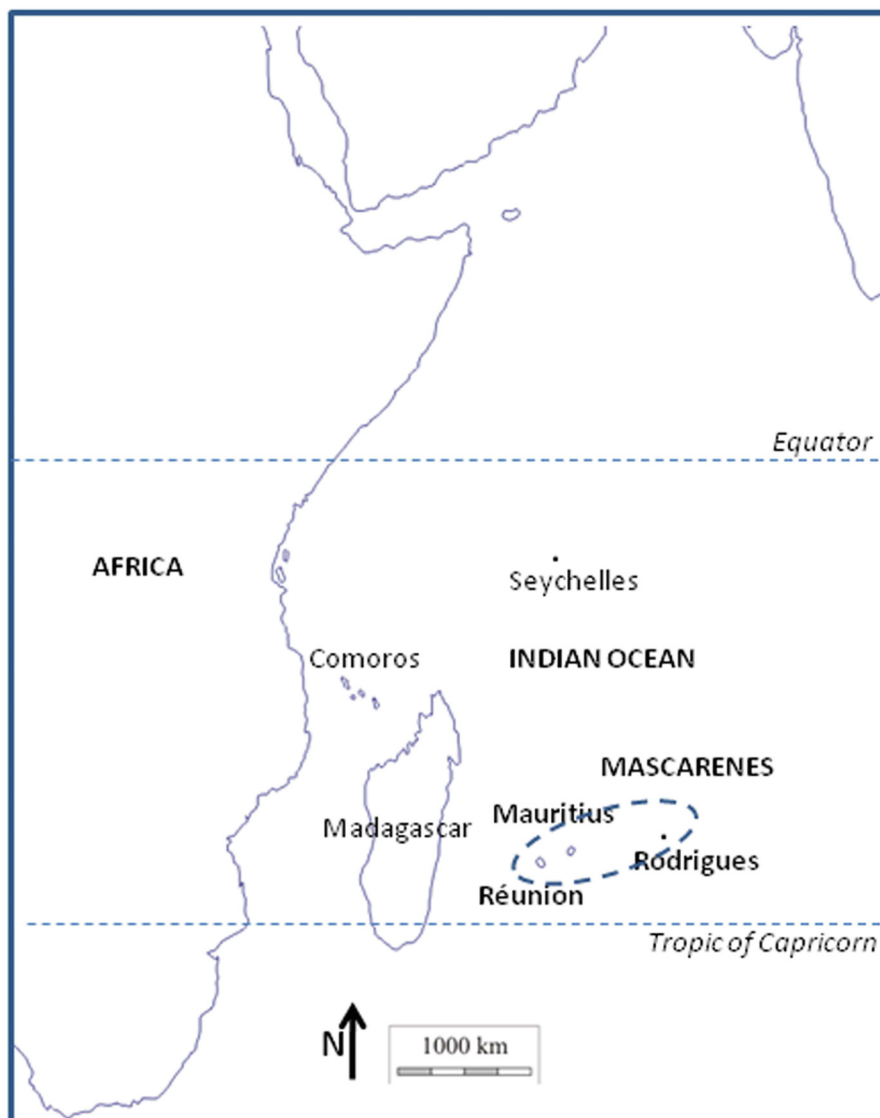
### Introduction

The Mascarenes or the Mascarene Archipelago are currently composed of three main islands (i.e., Reunion or La Réunion in French, Mauritius, and Rodrigues) in addition to numerous little atolls (e.g., Cargados Carajos), located in western Indian Ocean at least 665 km east of Madagascar for the closest island La Réunion (Fig. 1). These islands are of volcanic origin and connected to the Mascarene Plateau which is at least 35 Myrs old, and the current Mauritius, La Réunion, and Rodrigues would have emerged 8–10, 3–5, and 8–10 Myrs ago, respectively (McDougall *et al.* 1965; McDougall & Chamalaun 1969; Sheth *et al.* 2003). As oceanic volcanic islands, the local flora and fauna have originated by dispersal from neighboring islands and continents, and their relative isolation from continental landmasses and islands led to high levels of endemism (Thébaud *et al.* 2009), hence including the archipelago in a global biodiversity hotspot (Myers *et al.* 2000). The Mascarene Islands are, like many other volcanic archipelago and islands, natural laboratories for studying evolutionary processes, involving colonization and diversification events (Losos & Ricklefs 2009). Many studies on diverse lineages have been conducted and propose contrasting scenarios concerning the origins of Mascarenan organisms, indicating a complex global biogeographical history that involves, or not, ancient and currently submerged islands belonging to the Mascarene Plateau (e.g., Micheneau *et al.* 2008; Strijk *et al.* 2012; Bradler *et al.* 2015; Le Péchon *et al.* 2016; Hennequin *et al.* 2017). Although Madagascar and Africa have

often been suggested to have provided most of the Mascarenan diversity (as demonstrated for some lineages; e.g., Micheneau *et al.* 2008; Le Péchon *et al.* 2016), Asiatic and Pacific origins would also not be negligible (e.g., Bradler *et al.* 2015).

The Mascarenes host more than 1,200 native species of vascular plants, including 242 (20%) fern taxa of which at least 46 (19%) are endemic (Blanchard 2000). According to Hennequin *et al.* (2014), such local fern diversity originated from at least 197 colonization events of the current emerged islands (i.e., Mauritius, La Réunion and Rodrigues). In this context, we developed a project with the main objective to precisely investigate the origins and the diversification of ferns in the Mascarenes, as already initiated for some emblematic groups (e.g., genus *Ctenitis* (C.Chr.) C.Chr., Dryopteridaceae; Hennequin *et al.* 2017). Such a biogeographical approach requires accurate and updated taxonomy for local species (e.g., Duan *et al.* 2017 for *Ctenitis*). With at least 23 or 20 species, the Hymenophyllaceae or filmy ferns represent one of the most diverse fern families in the Mascarenes, after Dryopteridaceae (43 species), Pteridaceae (40 species), and with almost the same number of species as Polypodiaceae and Aspleniaceae (23 species for each family) (Tardieu-Blot 2008; Grangaud 2010; Hennequin *et al.* 2014). Ecologically, species of the Hymenophyllaceae are hygrophilous and thus restricted to very wet habitats, especially rainforests (Dubuisson *et al.* 2003). These ecological preferences, together with their diversity make filmy ferns a valuable model group for studying tropical rainforests in the Mascarenes, as well as habitats that are locally fragile and threatened by both anthropic activities and invasive exotic species (Strasberg *et al.* 2005).

In line with recent systematics studies in the Southwestern Indian Ocean region (Pynee *et al.* 2012; Dubuisson *et al.* 2013, 2014, 2016, 2017; Bauret *et al.* 2015; Saïd *et al.* 2017; Dubuisson & Hennequin 2018), this work aims 1) to assess species diversity, 2) to update the taxonomy of Hymenophyllaceae in the Mascarenes, and 3) to clarify the ecology and the elevational distribution for each taxon.



**FIGURE 1.** Location of the Mascarene Archipelago (or Mascarenes) in the western Indian Ocean (from Pynee *et al.* 2012).

## Materials and methods

The establishment of a complete checklist of Hymenophyllaceae in the Mascarene Archipelago, as undertaken for the Comores (Saïd *et al.* 2017), was conducted by combining three complementary approaches: (1) examination of floras and available databases, (2) examination of herbarium material from the Mascarenes housed at P, REU and MAU (acronyms follow Thiers 2018), and (3) field observations conducted on the three islands since 1999.

### *Floras, databases and herbaria*

Data were first extracted from floras and checklists that include information on ferns in the western Indian Ocean and neighbouring areas: Kuhn (1868), Baker (1877), Cordemoy (1891, 1895), Sim (1915), Bonaparte (1920b, 1923, 1925), Christensen (1920), Tardieu-Blot (1951, 1960, 1977, 2008), Schelpe (1966), Lorence (1976, 1978), Schelpe & Anthony (1986), Burrows (1990), Kornaš (1993, 1994), Beentje (2008), Roux (2009), Grangaud (2010), and Pynee *et al.* (2013). They were then compared to online databases Sonnerat (Paris herbarium P, <https://science.mnhn.fr/institution/mnhn/collection/p/item/search/form>), the Checklist of ferns and lycophytes of the world (<http://worldplants.webarchiv.kit.edu/ferns/>), the Index of the vascular flora of La Réunion (<http://flore.cbnm.org>), The Plant List (<http://www.theplantlist.org>), and the Catalogue of the Vascular Plants of Madagascar included in Tropicos (<http://www.tropicos.org/Project/Mada>). The data obtained from floras and databases were then updated according to recent taxonomy. This update was carried out via IPNI (<http://www.ipni.org>), Tropicos, Roux (2009), Grangaud (2010) and especially by following recent phylogenetic and taxonomic studies (Hennequin *et al.* 2003, 2010; Ebihara *et al.* 2006; Pynee *et al.* 2012; Dubuisson *et al.* 2013, 2014, 2016, 2017; Bauret *et al.* 2015; Ponce *et al.* 2017; Saïd *et al.* 2017; Dubuisson & Hennequin 2018). The aim of these taxonomic and nomenclatural investigations was to check and to obtain, for every potential distinct species, a valid and updated name. The taxonomic data were then checked on herbarium specimens stored at P, REU, and MAU in addition to types (if accessible) and recent fieldwork observations.

### *Ecology and elevational distribution*

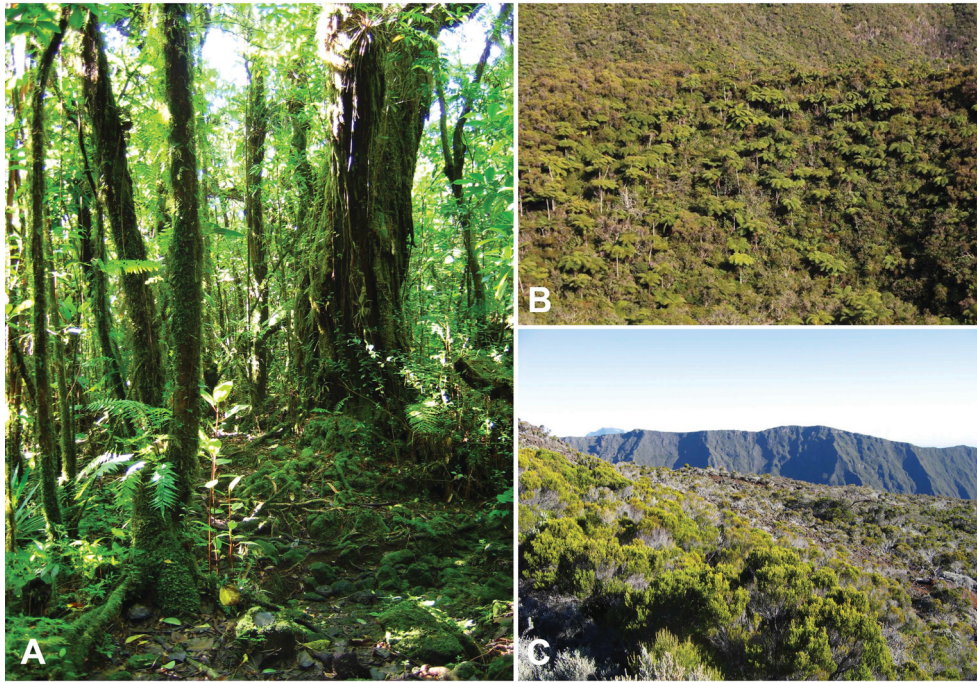
Using data extracted from our field observations on La Réunion and Mauritius, we explored the occurrence of Hymenophyllaceae species in the whole range of habitats and elevations. Specifically, occurrence data were obtained from 121 localities on La Réunion (83 on the eastern windward side, and 38 on the western leeward side), and 29 localities on Mauritius (all the localities are listed in Appendices 1 & 2, and are mapped in Appendices 3 & 4). Per locality, we reported all the species present by exploring a minimum surface of 100 m<sup>2</sup>. We selected more localities at low elevations on La Réunion in comparison to high elevations (above 1,000 m), resulting in an unbalanced sampling (see Appendix 1). Indeed, we intended to increase the observation effort at low elevations localities which have often been under-investigated. These are lowland forest remnants and wet ravines close to (peri)urban or anthropized zones and crops, both strongly modified by human activities and the presence of invasive species. The other plots at middle to high elevations were mostly located in protected areas (see Appendix 3), and we assumed that such selected plots and localities were enough to reflect the Hymenophyllaceae diversity at such elevations. Rodrigues hosts a single species restricted to a single wet ravine (Lorence 1976), explaining why this island was not investigated as thoroughly as La Réunion and Mauritius. We thus have for Rodrigues a single species occurrence and no additional data, and especially no elevational gradient.

On La Réunion, there are potentially three main forest habitats or ecosystems that can host the strongly hygrophilous Hymenophyllaceae (Cadet 1980; Blanchard 2000; Strasberg *et al.* 2005; Grangaud 2010):

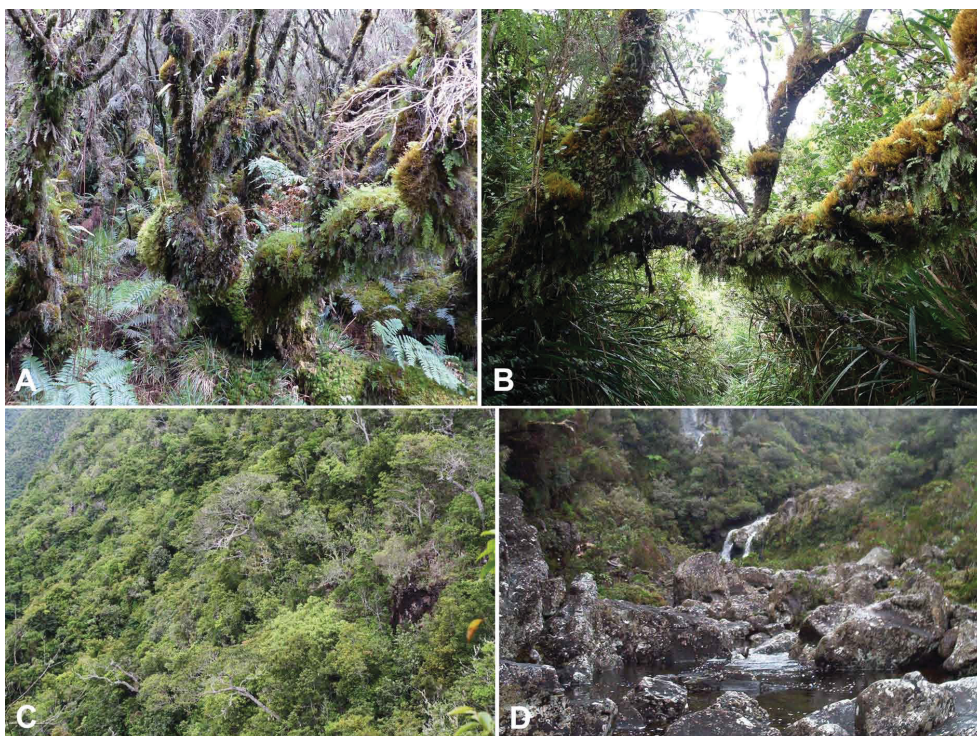
(1) The lowland rainforest (Fig. 2A) from sea level to 800 m on the eastern windward side (receiving rainfall from the trade-winds) and from 700 m to 1,100 m on the western leeward side (receiving less rainfall), dominated by Sapotaceae trees. A floristic sub-division can also be made at 650–700 m on the windward side (and 800–900 m on the leeward side) distinguishing a middle-elevation (foothills) rainforest from a strict lowland rainforest.

(2) The montane rainforest from 800 m to 1,900 m on the eastern windward side and from 1,100 m to 2,000 m on the western leeward side, dominated by Dombeyoideae trees (Malvaceae) with *Alsophila* spp. tree-ferns (Cyatheaceae) as emergent from the canopy (Fig. 2B), and locally hyperhumid habitats dominated by *Pandanus* spp. (Pandanaceae), locally named ‘Pandanaie’, or the ‘Avoune’ type vegetation with woody Ericaceae (e.g., endemic *Erica reunionensis* E.G.H.Oliv.) (Fig. 3A) or mostly above 1,500 m the ‘Tamarinaie’ forest dominated by the endemic *Acacia heterophylla* (Lam.) Willd. (Fabaceae) (Fig. 3B). Most of such habitats are currently included in the National Park of La Réunion.

(3) Ericoid thickets dominated by woody, more or less sclerophyllous Ericaceae from 1,900(2,000) m to the highest elevation (3,071 m) (Fig. 2C).



**FIGURE 2.** Wet Mascarenan ecosystems. A. Lowland windward rainforest dominated by Sapotaceae trees, showing the understory with numerous low epiphytic and terrestrial free-sporing plants (liverworts, mosses, ferns, lycopods and spikemosses) and a few herbaceous angiosperms (especially orchids) (La Réunion, ‘Mare Longue’ forest, ~450 m). B. Montane rainforest dominated by Dombeyoideae (Malvaceae) trees and *Alsophila* spp. tree-ferns (Cyatheaceae) as emergents from the canopy (La Réunion, ‘Cassé de Takamaka, Bébou’, 1,100–1,200 m). C. Montane ericoid thickets (La Réunion, ‘Enclos du Piton de la Fournaise’, ~2,200 m). (Photographs. A, C: C. Chaussidon; B: J.-M. Tamon).



**FIGURE 3.** Particular Mascarenan ecosystems. A. Hyperhumid montane ‘Avoune’ vegetation dominated by the endemic *Erica reunionensis* (Ericaceae), with most trunks and branches fully covered by epiphytes (liverworts, mosses, peat mosses, lycopods and ferns, especially here *Hymenophyllum capillare* and *H. inaequale*, and orchids) (La Réunion, ‘Pitons Mare à Boue’, ~1,600 m). B. Montane ‘Tamarinaie’ dominated by endemic *Acacia heterophylla* (Fabaceae), showing as for ‘Avoune’ tree-trunks and branches fully covered by epiphytes, including here *H. inaequale* (La Réunion, ‘Bélouve’, ~1,520 m). C. Remnant of leeward lowland semi-dry forest (La Réunion, ‘Ilet Solitude’, ~550 m). D. Typical wet ravines that host lithophytic Hymenophyllaceae on the wet and shaded rocks close to streams and waterfalls. (photographs. A: J.-Y. Dubuisson; B–C: J.-M. Tamon; D: A. Mercier).

On Mauritius, only 2% of the natural vegetation remains, and more or less preserved wet forest habitats are mostly present in the south in a few protected areas. Remnants of the lowland Sapotaceae rainforest are located more or less above 300 m, and especially above 500 m, theoretically up to the highest elevation (828 m), but they are often invaded at the lowest elevations by exotic Malagasy traveller's tree *Ravenala madagascariensis* Sonn. (Strelitziaceae) and many other exotic species (Fig. 4A). The lowest wet place susceptible to host Hymenophyllaceae is the forest located in 'Vallée de Ferney' from about 80 m elevation. Some particular habitats or ecosystems are observed in the rainiest places above 600–650 m. These are the Mauritian ericoid thicket with the endemic *Erica brachyphylla* (Benth.) E.G.H.Oliv. (Ericaceae), especially in 'Pétrin' locality (Fig. 4B), and above 700 m the hyperhumid marshlands and forest plots resembling La Réunion montane forests, especially at the 'Montagne Cocotte' locality (Blanchard 2000). We reported thus for all the diverse elevational plots and habitats/ecosystems detailed above the occurrence of the diverse Hymenophyllaceae taxa and their ecological preferences.



**FIGURE 4.** Mauritian ecosystems. A. Lowland Sapotaceae rainforest, here invaded by the exotic Malagasy traveller's trees *Ravenala madagascariensis* (Strelitziaceae) ('Vallée d'Osterlog' forest, ~260 m). B. 'Pétrin' locality showing particular habitat with thickets of the endemic *Erica brachyphylla* (Ericaceae) (~670 m) (photographs by J.-Y. Dubuisson).

## Results

Based on our extensive investigations, we recognise 23 species, two varieties, and one *forma nova* (as described below) of Hymenophyllaceae in the Mascarenes. These taxa are included in six different genera (following Ebihara *et al.* 2006). For comparison (see Table 1), former studies recognised 23 and 20 species, respectively (Tardieu-Blot 2008; Grangaud 2010). The most diverse genera in the archipelago are *Hymenophyllum* Sm. (Smith 1793: 418) (9 species and 1 *forma*) and *Crepidomanes* (C.Presl) C.Presl (Presl 1849: 258) (7 species and 2 varieties). *Didymoglossum* Desv. (Desvaux 1827: 330) and *Abrodictyum* C.Presl (Presl 1843: 20) are represented by 3 and 2 species respectively, and *Polyphlebium* Copel. (Copeland 1938: 55) and *Vandenboschia* Copel. (Copeland 1938: 51) are each represented by a single species. The taxonomy of all 26 recognized taxa is discussed below. However, the current presence of *H. balfourii* Baker (Baker 1891: 192), reported only in herbaria, awaits confirmation.

The distribution of these taxa is not homogeneous at the archipelago level (Table 2). All current 25 taxa occur on La Réunion, whereas Mauritius hosts 15 species. Rodrigues hosts a single species, *Didymoglossum cuspidatum* (Willd.) Ebihara & Dubuisson (Ebihara *et al.* 2006: 236), which is thus the only Hymenophyllaceae species occurring on all three main islands of the Mascarenes. Distribution and local richness also differ between La Réunion and Mauritius. On La Réunion, the highest diversity is 16 species per locality (as found at ‘Grand Etang’ at ~530 m) whereas on Mauritius, the diversity does not exceed 5 species per locality (as found at ‘Pétrin’ at ~670 m) (see Appendices 1 & 2).

Habitat distribution is also not homogeneous among Hymenophyllaceae taxa, as reported in Table 3 (with full data presented in Appendices 1 & 2). On La Réunion, Hymenophyllaceae were observed from nearly sea-level, here 18 m with *Didymoglossum cuspidatum*, to 2,400 m elevation, with *Hymenophyllum inaequale* (Poir.) Desv. (Desvaux 1827: 335). On Mauritius, Hymenophyllaceae were observed from 89 m (*D. lorencei* (Tardieu) Ebihara & Dubuisson (Ebihara *et al.* 2006: 236) and *Abrodictyum parviflorum* (Poir.) Bauret & Dubuisson (Dubuisson *et al.* 2017: 211)) to 735 m (*H. hirsutum* (L.) Sw. (Swartz 1800: 99)). The highest species diversity is reported in La Réunion lowland rainforests with a maximum of 21 taxa out of 25 (84%), and especially below 650 m because the foothills host 18 (72%) taxa only (Fig. 5). The highest diversity, however, is not observed at the lowest elevations near the sea-level, but between 450 m and 600 m on La Réunion with 19 taxa (76%). In addition, we observe only 15 (58%) and 8 (32%) taxa respectively below 300 m and 150 m. On Mauritius, the pattern is similar with a maximum of 10 taxa out of 15 (66.7%) close to 600 m. The diversity remains high in La Réunion montane rainforest with 15 taxa (60%) and a maximum of 12 taxa (48%) per locality (here at ‘Ilet Patience’ at 1,250 m). Above 1,500 m, the diversity decreases to reach 7 taxa (28%). Only 5 species (20%) remain at the tree-line (corresponding to the limit of the montane forest at ~1,900–2,000 m) and 3 (1.2%) in the ericoid thickets above 1,900 and up to 2,400 m. These are *Abrodictyum parviflorum*, *Hymenophyllum inaequale*, and *Polyphlebium diaphanum* (Kunth) Ebihara & Dubuisson (Ebihara *et al.* 2006: 240). In Mauritian ericoid thicket (‘Pétrin’, ~670 m) only 5 species are observed: *Abrodictyum parviflorum*, *A. tamarisciforme* (Jacq.) Ebihara & Dubuisson (Ebihara *et al.* 2006: 244), *Hymenophyllum digitatum* (Sw.) Fosberg (Fosberg & Sachet 1980: 1), *Crepidomanes minutum* (Blume) K.Iwats. (Iwatsuki 1985: 524) var. *mascarenense* Pynee & Dubuisson (Pynee *et al.* 2012: 28), and *H. hirsutum*. *Abrodictyum parviflorum* is also observed at all elevational transects performed in La Réunion. *Abrodictyum tamarisciforme* and *Hymenophyllum digitatum* are also observed in lowland and montane rainforests, whereas the last two species are restricted to lowland rainforests. In Mauritian hyperhumid montane-like forest above 700 m (‘Montagne Cocotte’), 3 species are observed: *A. parviflorum*, *H. hirsutum*, and *H. hygrometricum* (Poir.) Desv. (Desvaux 1827: 333), the latter being present in La Réunion lowland and montane forests. As such, these Mauritian taxa do not seem to be particularly specialized to a particular habitat, and are potentially present below 1,000 m at the archipelago level.

Hymenophyllaceae are *a priori* absent in semi-dry forests that theoretically characterize the low elevations in Mauritius and the lowland (below 700–800 m) on the leeward side in La Réunion (Fig. 3C). Yet, investigations in wet ravines in semi-dry forests especially on La Réunion (Fig. 3D) reveal an unexpected diversity of at least 8 taxa in such ravines from 300 m to 800(900) m, as lithophytes on shaded wet rocks. These species are also present at the same elevations in the rainforest on the windward side.

Of the 25 Mascarenan taxa, 22 (88%) are colonial epiphytes or lithophytes colonizing their substrates, one is a non-colonial individual epiphyte growing mostly on tree-fern trunks (*Abrodictyum tamarisciforme*), one is terrestrial (*A. parviflorum*), and one is hemi-epiphytic (*Vandenboschia gigantea* (Bory ex Willd.) Pic.Serm. (Pichi Sermolli 1968: 197)), first colonizing the forest floor, and secondly able to climb on tree-trunks (see Fig. 18 C–E).

**Table 1.** List of Hymenophyllaceae species recorded for the Mascarene archipelago and comparison with previous studies; all species in Tardieu-Blot (2008) were reported by her as belonging to *Trichomanes* or *Hymenophyllum*, following the traditional bi-generic classification of Hymenophyllaceae. X = reported.

Taxa	Present study	Tardieu-Blot (2008)	Grangaud (2010)
<i>Abrodictyum parviflorum</i> (Poir.) Bauret & Dubuisson (*)	X	X (as <i>Trichomanes meifolium</i> Bory ex. Willd)	X (as <i>Abrodictyum meifolium</i> (Bory ex. Willd) Ebihara & Dubuisson)
<i>Trichomanes parviflorum</i> Poir.		X (considered as a distinct species)	
<i>Abrodictyum tamarisciforme</i> (Jacq.) Ebihara & Dubuisson	X	X	X
<i>Crepidomanes bipunctatum</i> (Poir.) Copel.	X	X	X
<i>Crepidomanes bonapartei</i> (C.Chr.) J.P.Roux	X		X
<i>Crepidomanes fallax</i> (Christ) Ebihara & Dubuisson	X	X	X
<i>Crepidomanes frappieri</i> (Cordem.) J.P.Roux	X	X	
<i>Crepidomanes inopinatum</i> (Pic.Serm.) J.P.Roux	X	X	X
<i>Crepidomanes inopinatum</i> var. <i>tamonii</i> Y. Robert & Dubuisson	X		
<i>Crepidomanes melanotrichum</i>		X	
<i>Crepidomanes minutum</i> (Blume) K.Iwats.	X	X (as <i>Trichomanes mannii</i> Hook.)	X
<i>Crepidomanes minutum</i> var. <i>mascarenense</i> Pynee & Dubuisson	X		
<i>Crepidomanes trinerve</i> (Baker) Dubuisson & Ebihara	X		
<i>Didymoglossum barklyanum</i> (Baker) J.P.Roux	X	X	X
<i>Didymoglossum cuspidatum</i> (Willd.) Ebihara & Dubuisson	X	X	X
<i>Didymoglossum lorencei</i> (Tardieu) Ebihara & Dubuisson	X	X	X
<i>Hymenophyllum balfourii</i> Baker	X	X	
<i>Hymenophyllum capillare</i> Desv.	X	X	X
<i>Hymenophyllum capillare</i> f. <i>nanum</i> Hennequin & Dubuisson, f. nov.	X		
<i>Hymenophyllum digitatum</i> (Sw.) Fosberg	X	X (as <i>Trichomanes digitatum</i> Sw.)	X
<i>Hymenophyllum fumarioides</i> Willd.	X	X (as <i>Hymenophyllum tenellum</i> (Jacq.) Kuhn)	X (as <i>Hymenophyllum tenellum</i> (Jacq.) Kuhn)
<i>Hymenophyllum hirsutum</i> (L.) Sw.	X	X (as <i>H. ciliatum</i> (Sw.) Sw.)	X
<i>Hymenophyllum hygrometricum</i> (Por.) Desv.	X	X	X
<i>Hymenophyllum inaequale</i> (Poir.) Desv.	X	X (as <i>H. polyanthos</i> (Sw.) Sw.)	X
<i>Hymenophyllum peltatum</i> (Poir.) Desv.	X	X	X
<i>Hymenophyllum sibthorpioides</i> (Bory ex Willd.) Mett. ex Kuhn	X	X	X
<i>Polyphlebium diaphanum</i> (Kunth) Ebihara & Dubuisson	X	X (as <i>Trichomanes borbonicum</i> Bosch)	X (as <i>Polyphlebium borbonicum</i> (Bosch) Ebihara & Dubuisson)
<i>Vandenboschia gigantea</i> (Bory ex Willd.) Pic.Serm.	X	X	X

(\*) Includes *Abrodictyum meifolium* (Bory ex. Willd) Ebihara & Dubuisson according to Dubuisson *et al.* (2017).

**TABLE 2.** Distribution of Hymenophyllaceae species on the three main islands of the Mascarene Archipelago, in addition to other areas. X = present.

Taxa	La Réunion	Mauritius	Rodrigues	Madagascar	Comores	Seychelles	Tropical Africa	Tropical Asia and/or Pacific islands	Neotropics
<i>Abrodictyum parviflorum</i> (Poir.) Bauret & Dubuisson	X	X		X		X			
<i>Abrodictyum tamarisciforme</i> (Jacq.) Ebihara & Dubuisson	X	X		X					
<i>Crepidomanes bipunctatum</i> (Poir.) Copel.	X	X		X	X			X	
<i>Crepidomanes bonapartei</i> (C.Chr.) J.P.Roux	X	X		X					
<i>Crepidomanes fallax</i> (Christ) Ebihara & Dubuisson	X			X			X		
<i>Crepidomanes frappieri</i> (Cordem.) J.P.Roux	X			X			X		
<i>Crepidomanes inopinatum</i> (Pic. Serm.) J.P.Roux	X			X	X		X		
<i>Crepidomanes inopinatum</i> var. <i>tamonii</i> Y. Robert & Dubuisson	X	X							
<i>Crepidomanes minutum</i> (Blume) K.Iwats.	X			X			X	X	
<i>Crepidomanes minutum</i> var. <i>mascarenense</i> Pynee & Dubuisson	X	X		X	X	X			
<i>Crepidomanes trinerve</i> (Baker) Dubuisson & Ebihara	X	X		X	X				
<i>Didymoglossum barklyanum</i> (Baker) J.P.Roux	X	X							
<i>Didymoglossum cuspidatum</i> (Willd.) Ebihara & Dubuisson	X	X	X	X		X			
<i>Didymoglossum lorencei</i> (Tardieu) Ebihara & Dubuisson	X	X		X	X				

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**Table 2. (Continued)**

Taxa	La Réunion	Mauritius	Rodrigues	Madagascar	Comores	Seychelles	Tropical Africa	Tropical Asia and/or Pacific islands	Neotropics
<i>Hymenophyllum balfourii</i> Baker	(*)	(*)		X					
<i>Hymenophyllum capillare</i> Desv.	X			X	X				
<i>Hymenophyllum capillare</i> f. <i>nanum</i> Hennequin & Dubuisson, f. nov.	X			(***)	(***)		(***)		
<i>Hymenophyllum digitatum</i> (Sw.) Fosberg	X	X		X		X	X	X	
<i>Hymenophyllum fumarioides</i> Willd.	X	X							
<i>Hymenophyllum hirsutum</i> (L.) Sw.	X	X		X	X	X	X		X
<i>Hymenophyllum hygrometricum</i> (Por.) Desv.	X	X							
<i>Hymenophyllum inaequale</i> (Poir.) Desv.	X	X		X	X	X			
<i>Hymenophyllum peltatum</i> (Poir.) Desv.	X			X			X		X
<i>Hymenophyllum sibthorpioides</i> (Bory ex Willd.) Mett. ex Kuhn	X			X	X				
<i>Polyphlebium diaphanum</i> (Kunth) Ebihara & Dubuisson	X			X	X		X	X	X
<i>Vandenboschia gigantea</i> (Bory ex Willd.) Pic. Serm.	X	(**)		X	X		X		
Total taxa	25	15	1						

(\*) awaits rediscovery; (\*\*) reported in collection but not recently observed in the wild, (\*\*\*) to be confirmed.

## Discussion

### *Dichotomous key for Mascarenan Hymenophyllaceae*

The present key requires that fertile specimens (with sori) and rhizomes are available.

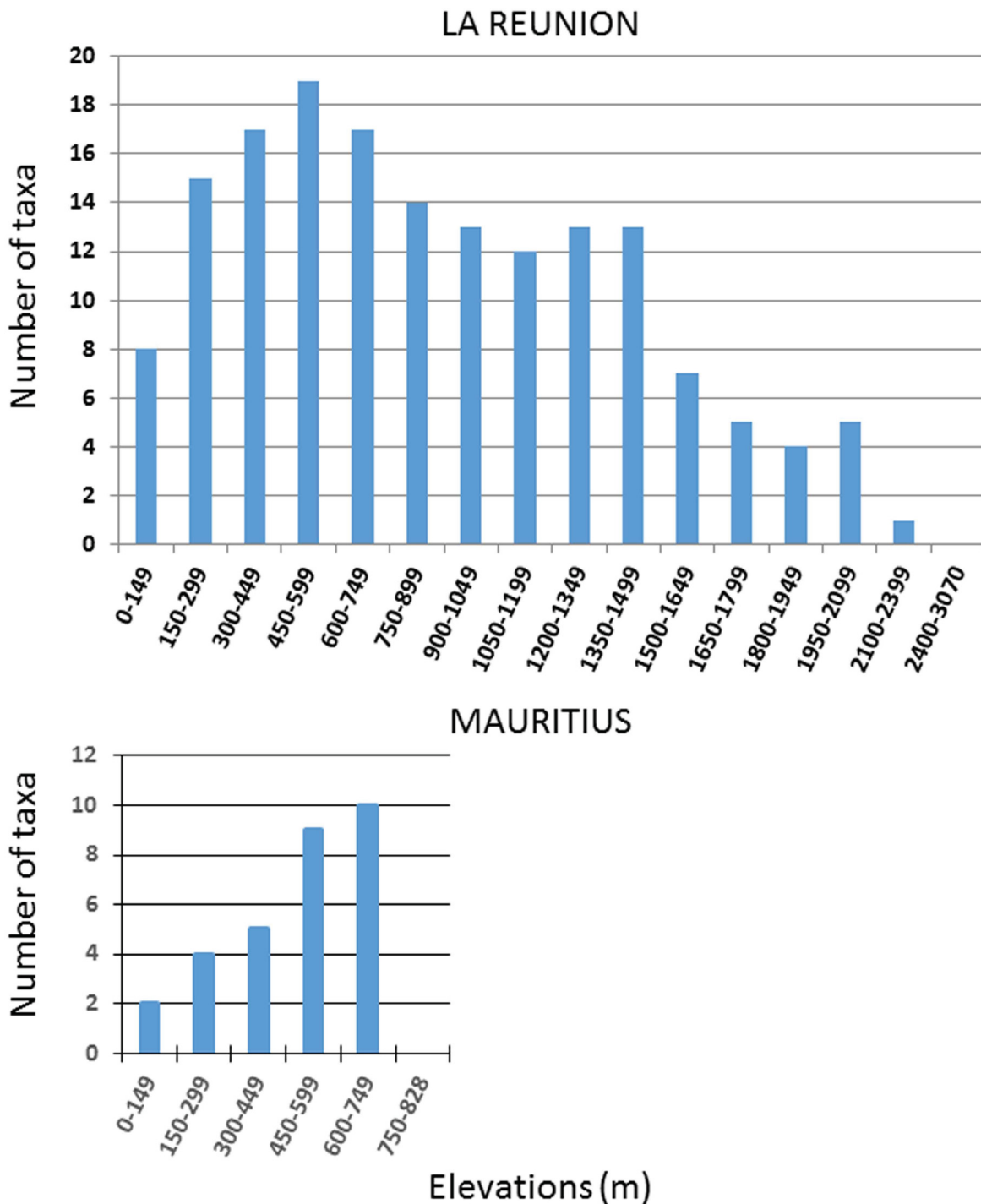
1. Sori with a developed base, usually tubular to campanulate ..... **10.**
- Sori without a developed tubular base ..... **2.**
2. Fronds at least pinnate, never flabellate or reniforme; sorus margins entire or toothed ..... **3.**
- Fronds flabellate to reniform, palmatisect or digitate; sorus margins always toothed ..... *Hymenophyllum sibthorpioides*
3. Sorus margins entire ..... **4.**
- Sorus margins toothed or seeming jagged ..... *Hymenophyllum fumarioides*
4. Fronds glabrous ..... **8.**
- Fronds hairy ..... **5.**
5. Stipes wingless; lamina hairs not pedunculated ..... **6.**

-	Stipes winged; lamina hairs pedunculated .....	<i>Hymenophyllum hirsutum</i>
6.	Fronds linear to narrowly oblong, fertile specimens dwarf (< 6cm) or large (up to 40 cm) .....	7.
-	Fronds deltoid to widely lanceolate, fertile specimens never dwarf .....	<i>Hymenophyllum hygrometricum</i>
7.	Fertile fronds usually less than 6 cm long .....	<i>Hymenophyllum capillare</i> f. <i>nanum</i>
-	Fertile fronds usually more than 10 cm long (up to 40 cm) .....	<i>Hymenophyllum capillare</i>
8.	Fronnd margins entire, not toothed or serrulate .....	9
-	Fronnd margins toothed or serrulate .....	<i>Hymenophyllum peltatum</i>
9.	Fertile fronds usually less than 4 cm long .....	<i>Hymenophyllum balfourii</i>
-	Fertile fronds usually more than 10 cm long, up to 30(–40) cm long .....	<i>Hymenophyllum inaequale</i>
10.	Rhizomes filiform and more or less lax, < 1 mm diam., rootless or with few, reduced roots; fertile fronds usually less than 20 cm long .....	13.
-	Rhizomes thick and stout, > 1 mm diam., usually with numerous, robust roots; fertile fronds usually longer than 20 cm long ..	11.
11.	Rhizomes short-creeping or erect, never branched; fronds usually in clumps .....	12.
-	Rhizomes long-creeping, usually branched; fronds widely separated .....	<i>Vandenboschia gigantea</i>
12.	Rhizomes short-creeping; fronds always plane; ultimate segments with lamina width exceeding 3 cells on both sides of the veins and with a distinct row of marginal cells .....	<i>Abrodictyum tamarisciforme</i>
-	Rhizomes erect; fronds plane or with a brush-like form; ultimate segments sub-capillary with a reduced lamina not exceeding 3 cells on both sides of the veins, and lacking a distinct row of marginal cells .....	<i>Abrodictyum parviflorum</i>
13.	Fronds digitate to highly divided .....	16.
-	Fronds entire to lobed .....	14.
14.	Laminae with false veins parallel to true veins .....	15.
-	Laminae without false veins .....	<i>Didymoglossum barklyanum</i>
15.	Fronds with marginal hairs; sori with brown margins .....	<i>Didymoglossum lorencei</i>
-	Fronds glabrous; sori without brown margins .....	<i>Didymoglossum cuspidatum</i>
16.	Laminae lacking more or less continuous submarginal false veins; sori lips variable but never triangular .....	17.
-	Laminae with more or less continuous submarginal false veins; sori lips triangular .....	<i>Crepidomanes bipunctatum</i>
17.	Fertile fronds usually less than 6 cm long, digitate or not .....	22.
-	Fertile fronds usually more than 6 cm long, never digitate .....	18.
18.	Rhizome trichomes short and not branched .....	19.
-	Rhizome trichomes long and branched .....	<i>Crepidomanes frappieri</i>
19.	Fronnd stipes and rachises not widely winged .....	20.
-	Fronnd stipes and rachises widely winged .....	<i>Crepidomanes fallax</i>
20.	Rhizomes rootless or bearing root-like shoots; sori campanulate more or less as long as wide, in any case less than twice longer than wide .....	<i>Crepidomanes inopinatum</i> var. <i>inopinatum</i>
-	Roots, if any, few and reduced; sori tubular longer than wide, often twice or more longer than wide .....	<i>Polyphlebium diaphanum</i>
22.	Fronnd margins glabrous .....	23.
-	Fronnd margins with solitary minute dark trichomes .....	<i>Hymenophyllum digitatum</i>
23.	Rhizome trichomes short and not branched .....	24.
-	Rhizome trichomes long and branched .....	<i>Crepidomanes frappieri</i>
24.	Fronds clearly stipitate, with stipe wingless or with a thin wing, and often, when dry, laminar folds parallel to veins .....	25.
-	Fronds sessile, or short stipitate with stipe wings broadened towards the apex, and always lacking, when dry, folds parallel to veins .....	<i>Crepidomanes bonapartei</i>
25.	Stipes with thin wings .....	27.
-	Stipes wingless .....	26.
26.	Fronds less than 2.5 cm long; stipe proliferation absent or exceptional; usually below 1,000 m .....	<i>Crepidomanes minutum</i> var. <i>mascarenense</i>
-	Fronnd up to 6 cm long; stipe proliferation frequent; usually above 1,000 m .....	<i>Crepidomanes minutum</i> var. <i>minutum</i>
27.	Sorus lips slightly dilated; folds parallel to veins absent to present; laminar cells with straight walls .....	<i>Crepidomanes inopinatum</i> var. <i>tamonii</i>
-	Sorus lips widely dilated to becoming slightly bilabiate; folds parallel to veins always present; laminar cells with wavy walls .....	<i>Crepidomanes trinerve</i>

### **Taxonomic treatment**

The present revision revealed that numerous type specimens of many studied species must actually be treated as syntypes following Art. 40 Note 1 of the ICN (Turland *et al.* 2018), even if particular specimens are often listed as holotypes and/or isotypes in recent floras and synopsis (e.g., Tardieu-Blot 2008; Roux 2009) in addition to some databases (e.g., JSTOR, Tropicos...), and as adopted in recent revisions for the region (Bauret *et al.* 2015; Dubuisson *et al.* 2016, 2017; Saïd *et al.* 2017; Ponce *et al.* 2017; Dubuisson & Hennequin 2018). This concerns more particularly the numerous ‘old’ species names, especially those described by Willdenow (1810) based on Bory de Saint-Vincent’s specimens, or by Poiret (1808) based on Petit-Thouars’ specimens. In order to precise the application of names, we selected lectotypes, as permitted by the ICN (Art. 9.11, 9.17), based on the thorough examination of specimens listed as types and of annotations on the sheets. For the taxa described by Willdenow, the link between the B original material used by Willdenow and the P original material including annotations by Bory is obvious. For the taxa described by Poiret, the reference to the Petit-Thouars’ collection (at P) is also obvious. The reference to Petit-Thouars’ material is

also clearly indicated for some taxa described by Desvaux, and specimens are clearly identified in collections. The taxa described by Swartz are mostly based on well-identified S specimens. Those described by Blume are based on its own collection principally stored at L, also involving well-identified specimens.



**FIGURE 5.** Distribution of Hymenophyllaceae species richness in relation to elevations, here on the windward side of La Réunion and on Mauritius (data are reported in Appendices 1 & 2). The range of each taxon is assumed to correspond to the range between the minimum and the maximum elevation at which they have been observed, even if the taxon has not been observed in all intermediate localities between such limits.

**TABLE 3.** Distribution of Hymenophyllaceae species in the diverse habitats in the Mascarene Archipelago (and on the windward side for La Réunion). X = present.

Taxa	Lowland rainforest (0–800 m)		Montane rainforest (800–1900 m)		Tree-line 1,900– 2,000 m	La Réunion ericoid thickets Above (1,900)2,000 m	Mauritian ericoid thickets (‘Pétrin’) 670 m	Mauritian hyperhumid montane-like forest (‘Mt Cocotte’) Above 670 m	La Réunion wet ravines in semi-dry forests 300–800 m
	0– 650 m	650– 800 m	800– 1500 m	1500–1900 m (‘Tamarinaie’)					
<i>Abrodictyum parviflorum</i> (Poir.) Bauret & Dubuisson.	X	X	X	X	X	X	X	X	
<i>Abrodictyum tamarisciforme</i> (Jacq.) Ebihara & Dubuisson	X	X	X				X		
<i>Crepidomanes bipunctatum</i> (Poir.) Copel.	X	X							
<i>Crepidomanes bonapartei</i> (C.Chr.) J.P.Roux	X								X
<i>Crepidomanes fallax</i> (Christ) Ebihara & Dubuisson	X								
<i>Crepidomanes frappieri</i> (Cordem.) J.P.Roux	X	X							X
<i>Crepidomanes inopinatum</i> (Pic. Serm.) J.P.Roux			X						
<i>Crepidomanes inopinatum</i> var. <i>tamonii</i> Y. Robert & Dubuisson	X								X
<i>Crepidomanes minutum</i> (Blume) K.Iwats.			X						
<i>Crepidomanes minutum</i> var. <i>mascarenense</i> Pynee & Dubuisson	X	X					X		
<i>Crepidomanes trinerve</i> (Baker) Dubuisson & Ebihara	X	X							X
<i>Didymoglossum barklyanum</i> (Baker) J.P.Roux	X	X							X
<i>Didymoglossum cuspidatum</i> (Willd.) Ebihara & Dubuisson	X	X	X						X
<i>Didymoglossum lorencei</i> (Tardieu) Ebihara & Dubuisson	X								X

...continued on next page

**TABLE 3.** (Continued)

Taxa	Lowland rainforest (0–800 m)		Montane rainforest (800–1900 m)		Tree-line	La Réunion ericoid thickets	Mauritian ericoid thickets (‘Pétrin’)	Mauritian hyperhumid montane-like forest (‘Mt Cocotte’)	La Réunion wet ravines in semi-dry forests
<i>Hymenophyllum capillare</i> Desv.	X	X	X	X	X				
<i>Hymenophyllum capillare</i> f. <i>nanum</i> Hennequin & Dubuisson, f. nov.		X	X	?					
<i>Hymenophyllum digitatum</i> (Sw.) Fosberg	X	X	X	X			X		
<i>Hymenophyllum fumarioides</i> Willd.	X	X	X						
<i>Hymenophyllum hirsutum</i> (L.) Sw.	X	X					X	X	
<i>Hymenophyllum hygrometricum</i> (Por.) Desv.	X	X	X	X				X	
<i>Hymenophyllum inaequale</i> (Poir.) Desv.	X	X	X	X	X	X			
<i>Hymenophyllum peltatum</i> (Poir.) Desv.			X	X	X				
<i>Hymenophyllum sibthorpioides</i> (Bory ex Willd.) Mett. ex Kuhn	X	X	X						X
<i>Polyphlebium diaphanum</i> (Kunth) Ebihara & Dubuisson	X	X	X	X	X	X			
<i>Vandenboschia gigantea</i> (Bory ex Willd.) Pic.Serm.	X	X	X						
Total taxa	21	18	15	7	5	3	5	3	8

**Family Hymenophyllaceae Mart. (von Martius 1835: 3)**

Genus *Abrodictyum* C.Presl (Presl 1843: 20)

**1. *Abrodictyum parviflorum* (Poir.) Bauret & Dubuisson (Dubuisson *et al.* 2017: 211), Fig. 6**

*Trichomanes parviflorum* Poir. (Poiret 1808: 83). Type:—MADAGASCAR. Without locality, without date, *L.-M.A. du Petit-Thouars s.n.* (lectotype P, P00482986!, here designated; isolectotype P, P00482987!).

= *Trichomanes lanceolatum* Poir. (Poiret 1808: 83). Type:—MADAGASCAR. Without locality, without date, *L.-M.A. du Petit-Thouars s.n.* (lectotype P, P00482989!, here designated; isolectotype P, P00482990!).

= *Trichomanes meifolium* Bory ex Willd. (Willdenow 1810: 509, 510). ≡ *Macroglena meifolia* (Bory ex Willd.) Copel. (Copeland 1938: 83). ≡ *Cephalomanes meifolium* (Bory ex Willd.) K.Iwats. (Iwatsuki 1984: 177). ≡ *Abrodictyum meifolium* (Bory ex Willd.) Ebihara & Dubuisson (Ebihara *et al.* 2006: 244). Type:—LA RÉUNION. ‘des bois très élevés à Bourbon’, without date, *J.B.G.M. Bory de St.-Vincent 125* (lectotype B, BW 20 201010!, here designated; isolectotype P, P00612303!).

= *Trichomanes longisetum* Bory ex Willd. (Willdenow 1810: 510, 511). Type:—LA RÉUNION. ‘Bois de Bourbon’, without date, *J.B.G.M. Bory de St.-Vincent 126* (lectotype B, BW 20 211010!, here designated; isolectotype P, P00064994!).

= *Trichomanes foeniculaceum* Bory ex Willd. (Willdenow 1810: 511). Type:—‘Les Iles de France et de Bourbon.’, without date, *J.B.G.M. Bory de St.-Vincent 127* (lectotype B, BW 20 212010!, here designated; isolectotype P, P00064992!).

Note—Re-examination of type specimens allowed here to correct and complete information concerning vouchers and locality for some taxa (*T. meifolium*, *T. longisetum* and *T. foeniculaceum*) compared to the most recent publications on the subject (Dubuisson *et al.* 2017; Dubuisson & Hennequin 2018).

Short description—Terrestrial or lithophytic, less often epiphytic; thick, short and erect rhizomes with robust roots and clustered erect fronds; fronds well stipitate, up to 40 cm long, quite variable, narrowly to widely lanceolate or elliptic, more rarely triangular, plane (Fig. 6C) or with a brush-like shape (Fig. 6B), tripinnate-pinnatifid, with linear (sub)capillary ultimate segments and a thin lamina not exceeding 3 rows of cells on both sides of the veins (Fig. 6D); sori numerous, paratactic, obconic to slightly campanulate, truncated or with a very slightly dilated mouth (Fig. 6D); receptacle short to long-exserted.

Global distribution—Western Indian Ocean (excl. Comores).

Current distribution in Mascarenes—La Réunion, Mauritius.

Ecology—Usually terrestrial in the understory of rainforests, occasionally lithophytic, more rarely epiphytic on the base of trunks, often near streams, from low to high elevations (90–2,200 m).

Representative specimens examined—MAURITIUS. Mt Cocotte, October 2010, *S. Hennequin et al.* 318 (MAU 0008184, P02432374, P02432375).

—LA RÉUNION. Without locality, without date, *L.-M.A. du Petit-Thouars s.n.* (P00064996); Hauts de St Denis, 1833, *Goudot s.n.* (P00612302); without locality, 1834, *Bernier 33* (P00064995, on the same sheet as the *A. meifolium* isotype); Brûlé de St Denis, 1886, *C. Keller s.n.* (P01526528); Forêt des Makes, May 1947, *J. Bosser 11152* (P01526536); Saint-Philippe, Forêt de Mare Longue, December 1967, *T. Cadet 1183* (P01526521); Forêt des Cabris, Plaine des Palmistes, November 1985, *K. Kramer et al.* 9363 (P01526512); Bébour, April 1999, *J.-Y. Dubuisson HR-1999-21* (P), *HR-1999-22* (P); Saint-Philippe, Forêt de Mare Longue, April 2002, *J.-Y. Dubuisson HR-2002-13* (P02433295, mix of plane [left] and brush-like [right] forms); Le Tremblet, April 2003, *J.-Y. Dubuisson HR 2003-2* (P, brush-like form), *HR 2003-2'* (P, plane form).

Note—This species was first named *A. meifolium* and is known under this name in the main floras (Tardieu-Blot 1951, 2008; Grangaud 2010). This name was traditionally used for the brush-like form while Tardieu-Blot treated the local plane forms as the supposedly distinct *Trichomanes parviflorum*. Dubuisson *et al.* (2017) demonstrated that *A. meifolium* and *T. parviflorum* belong to a single and highly polymorphic species, hence designating the new combination *A. parviflorum* as the valid species according to nomenclatural rules.



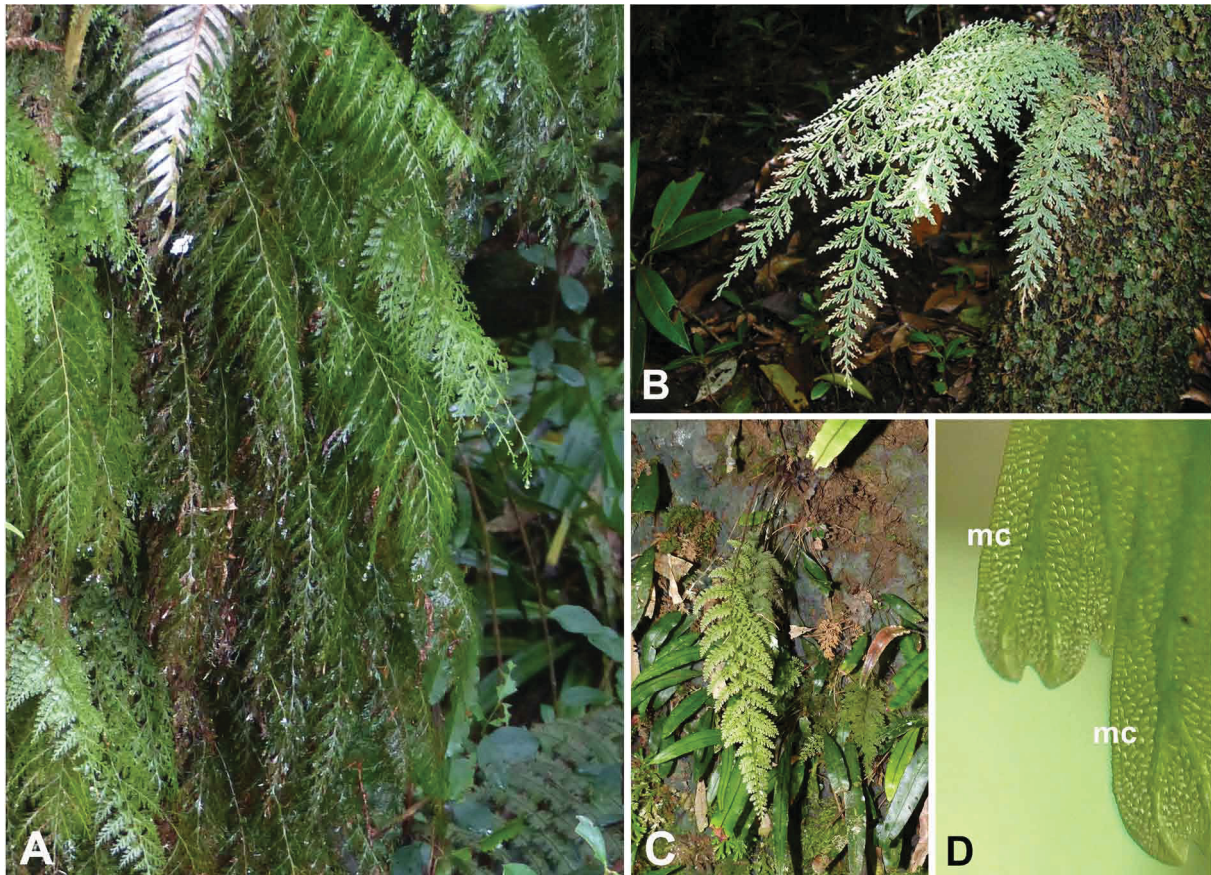
**FIGURE 6.** *Abrodictyum parviflorum* (Poir.) Bauret & Dubuisson. A. typical habit, here as terrestrial (La Réunion, ‘Mare Longue’). B. Brush-like ‘*meifolium*’ form (La Réunion, ‘Grand Etang’). C. Plane ‘*parviflorum*’ form (La Réunion, ‘Grand Etang’). D. Detail of subcapillary ultimate segments and sori (photographs. A: C. Chaussidon; B, D: L. Bauret; C: J.-Y. Dubuisson).

## 2. *Abrodictyum tamarisciforme* (Jacq.) Ebihara & Dubuisson (Ebihara *et al.* 2006: 244), Fig. 7

*Trichomanes tamarisciforme* Jacq. (von Jacquin 1791[1789]: 285). Type:—LA RÉUNION. ‘Sponte crescit in insula Borboniae’, without date, without collector (holotype von Jacquin (1789): pl. 21, fig. 2). Note: The LINN specimen (LINN-HS1641-10) collected in La Réunion strongly resembles the illustration provided by von Jacquin, hence suggesting it could correspond to the original observed material.

= *Trichomanes stylosum* Poir. (Poiret 1808: 82). ≡ *Selenodesmium stylosum* (Poir.) Copel. (Copeland 1938: 81). ≡ *Abrodictyum stylosum* (Poir.) J.P.Roux (Roux 2009: 38). Type:—MADAGASCAR. Without locality, without date, *L.-M.A. du Petit-Thouars s.n.* (lectotype P, P00482618!, here designated; isolectotype P, P00482633!).

= *Trichomanes achilleifolium* Bory ex Willd. (Willdenow 1810: 512), as ‘*achilleaefolium*’. Type:—“Ile de France & de Bourbon”, without date, *J.B.G.M. Bory de St.-Vincent s.n.* (lectotype B, BW 20 214010!, here designated; isolectotype P, P00477829!).



**FIGURE 7.** *Abrodictyum tamarisciforme* (Jacq.) Ebihara & Dubuisson. A. A dense population of many individuals covering a trunk (La Réunion, ‘Grand Etang’). B. Single individual as epiphytic on a tree-fern trunk, which is also covered here by *Didymoglossum cuspidatum* (La Réunion, ‘Mare Longue’). C. Lithophytic individual, the little individual at the bottom right is *A. parviflorum* (Poir.) Bauret & Dubuisson (La Réunion, ‘Grand Etang’). D. Detail of segments with typical distinct marginal row of cells (mc) (photographs. A, C: J.-Y. Dubuisson; B: C. Chaussidon; D: L. Bauret).

Short description—Epiphytic, more rarely lithophytic ferns. Rhizomes short-creeping, with robust roots and clustered erect fronds, becoming more or less pendant in epiphytic specimens; fronds well stipitate, up to 50 cm long, usually lanceolate, less often oblong or ovate, appearing often falciform because of a curved rachis, usually bi-pinnate-pinnatifid, less often tri-pinnate-pinnatifid, and linear ultimate segments with usually 4(5) rows of lamina cells on both sides of the veins including a clearly distinct margin (Fig. 7D); sori numerous, paratactic, obconic, usually truncated or with a slightly dilated mouth; receptacle short to relatively long-exserted (up to 1 cm long).

Global distribution—Madagascar and Mascarenes.

Current distribution in Mascarenes—La Réunion, Mauritius.

Ecology—Usually epiphytic, often on tree-fern trunks (*Alsophila* spp.), less often lithophytic (especially on Mauritius), in the understory of rainforests, from low to middle elevations (250–1,700 m), more abundant in montane forests.

Specimens examined—MAURITIUS. Without locality, without date, *without collector* (P01381686); without locality, without date, *without collector* (P01381687); without locality, without date, *P. Commerson s.n.* (P01485626); Pétrin, area above Black River Gorges, October 1974, *Barclay 3329* (MAU); Bar Le Duc, inside private hunting zone, December 2012, *K. Pynee et al. s.n.* (MAU 0009261); Grand Bassin, Gouly Père Nature Reserve, October 2015, *Gungadurdoss et al. s.n.* (MAU 0019238); Pétrin, State Land Raoul, next to road to Grand Bassin, February 2016, *K. Pynee et al. s.n.* (MAU 0019004, MAU 0019005); Brise Fer, Next Conservation Management Area, February 2016, *K. Pynee et al. s.n.* (MAU 0011485).

—LA RÉUNION. Plaine des Fougères, 1850, *M. Boivin s.n.* (P01430194); without locality, before 1857, *P. Commerson 1480* (P00674943); without locality, without date, *J.M.C. Richard 298* (P01430186); Cilaos, November 1973, *F. Badré 907* (P01596683); Takamaka, May 1974, *J. Bosser 22047* (P01596685); Takamaka, May 1976, *J. Bosser 22241* (P01596679); Saint Philippe, Forêt de Mare Longue, April 1999, *J.-Y. Dubuisson HR-1999-11* (P); Saint Philippe, Forêt de Mare Longue, April 2002, *J.-Y. Dubuisson HR-2002-15* (P02433297).

Note—Dubuisson *et al.* (2017) reported a clearly distinct lamina margin (Fig. 7D) that allows distinguishing the species from other *Abrodictyum* in the western Indian Ocean.

Genus *Crepidomanes* (C.Presl) C.Presl (Presl 1849: 258)

### 3. *Crepidomanes bipunctatum* (Poir.) Copel. (Copeland 1938: 59), Fig. 8A–C

*Trichomanes bipunctatum* Poir. (Poiret 1808: 69). ≡ *Didymoglossum bipunctatum* (Poir.) E.Fourn. (Fournier 1873: 263). Type:—MADAGASCAR. ‘De Madagascar’, without date, *L.-M.A. du Petit-Thouars s.n.* (lectotype P, P00482602!, here designated; isolectotypes P, P00477821!, P00477823!).

= *Hymenophyllum filicula* Bory ex Willd. (Willdenow 1810: 528). ≡ *Trichomanes filicula* (Bory ex Willd.) Bory (Bory 1829: 283). ≡ *Taschneria filicula* (Bory ex Willd.) C.Presl (Presl 1851: 618). Type:—‘In insula Mauriti, Borbonia’, without date, *J.B.G.M. Bory de St.-Vincent s.n.* (lectotype B, BW 20 233010!, here designated; isolectotype P, P00477824!).

= *Trichomanes bilabiatum* Nees & Blume (von Blume & Nees 1823: 123, 124). ≡ *Crepidomanes bilabiatum* (Nees & Blume) Copel. (Copeland 1938: 59). Type:—JAVA. Without locality, without date, without collector (holotype *Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur.* (1823): Plate XIII, Fig. 2).

Short description—Epiphytic or less often lithophytic; long-creeping filiform rhizomes, rootless and densely covered by dense black trichomes, bearing widely separated pending fronds; fronds with fully winged stipes, up to 12 cm long, lanceolate to ovate, less often triangular, pinnate-pinnatifid to bi-pinnate-pinnatifid with false veins more or less continuous, parallel to the margin and not connected to true veins (Fig. 8B); sori numerous, paratactic, with obconic to campanulate base and triangular lips (Fig. 8C); receptacle usually covered by the lips.

Global distribution—Western Indian Ocean to Pacific Ocean.

Current distribution in Mascarenes—La Réunion, Mauritius.

Ecology—Epiphytic on tree-trunks, less often lithophytic, in lowland rainforests (50–850 m).

Representative specimens examined—MAURITIUS. Rambouillet, April 2011, *K. Pynee s.n.* (MAU 0008203); Tamarind Falls, May 2011, *K. Pynee et al. s.n.* (MAU 0008262); Trou aux Cerfs, July 2015, *K. Pynee et al. s.n.* (MAU 0008301); Bar Le Duc, August 2011, *K. Pynee et al. s.n.* (MAU 0008303); Brise Fer CMA, October 2010, *S. Hennequin et al. 346* (MAU 0009477); Macabé, October 2010, *S. Hennequin et al. 343* (MAU 0017487).

—LA RÉUNION. Mare Longue, April 1999, *J.-Y. Dubuisson HR-1999-3* (P); Mare Longue, March 2005, *T. Janssen et al. 2693* (P00590808).

Note—This species is distinguishable from other *Crepidomanes* species in the archipelago by the combination of the more-or-less continuous false-veins parallel to the margins, and the typical triangular sorus lips.

### 4. *Crepidomanes bonapartei* (C.Chr.) J.P.Roux (Roux 2009: 39), Fig. 8D, E

*Trichomanes bonapartei* C.Chr. (Christensen 1920: 14, 15), as ‘*bonapartii*’. ≡ *Gonocormus bonapartei* (C.Chr.) Copel. (Copeland 1938: 101). Type:—MADAGASCAR. ‘Région floristique du Centre. Massif de Manongarivo.’, without date, *H. Perrier de la Bâthie 7745* (holotype P, P00466425!).

Short description—Epiphytic or lithophytic; long-creeping filiform rhizomes, rootless and densely covered by dense black trichomes, bearing widely separated pending fronds; fronds sessile or with short stipes with wide wings broaden towards the apex, up to 4 cm long, lobed to mostly pinnatifid, rarely flabellate, never with laminar folds parallel to veins; sori few, paratactic, obconic to campanulate with a very slightly dilated mouth (Fig. 8E); receptacle mostly included, sometimes exerted.





**FIGURE 8.** A. *Crepidomanes bipunctatum* (Poir.) Copel., as epiphyte on a tree-trunk (Mauritius, ‘Bar le Duc’). B. *C. bipunctatum*, detail of segments with false veins parallel to the margins (fv). C. *C. bipunctatum*, sori (s) with triangular lips. D. *C. bonapartei* (C.Chr.) J.P.Roux, as lithophyte on wet rock (La Réunion, ‘Grand Etang’). E. *C. bonapartei*, detail of subsessile or short-stipitate fronds and one sorus (photographs: A: J.-Y. Dubuisson; B–C: L. Bauret; D–E: E. Grangaud).

Global distribution—Madagascar and Mascarenes.

Current distribution in Mascarenes—La Réunion, Mauritius (see note below).

Ecology—Epiphytic or lithophytic on shady wet rocks, mostly near streams, in lowland rainforests and wet ravines (150–650 m), and also one reported population in a wet ravine of the La Réunion western side in semi-dry forest remnants.

Specimens examined—MAURITIUS. Tamarind Falls, March 1975, *D. Lorence 1134* (MAU 0012282).

—LA RÉUNION. Mare Longue, April 1999, *J.-Y. Dubuisson HR1999-5’* (P); Mare Longue, April 2003, *J.-Y. Dubuisson HR2003-7* (P).

Note—As reported by Dubuisson *et al.* (2013), this dwarf species can be confused in the field and in collections with *C. minutum* (Blume) K.Iwats. and *C. trinerve* (Baker) Dubuisson & Ebihara (Dubuisson *et al.* 2013: 187), both taxa presented below. Contrary to these two species, *C. bonapartei* has sessile fronds or short winged stipes, and never displays laminar folds parallel to veins. The species is known in Mauritius from a single herbarium specimen (see above), pending new observations on the island.

**5. *Crepidomanes fallax*** (Christ) Ebihara & Dubuisson (Ebihara *et al.* 2006: 238), Fig. 9A, B

*Trichomanes fallax* Christ (Christ 1909a: 24, 25). = *Vandenboschia fallax* (Christ) Copel. (Copeland 1938: 52). Type:—DEMOCRATIC REPUBLIC OF CONGO. Route de Zobia à Buta, 10 May 1907, *F. Seret 863* (holotype BR, BR00000080543331; isotype P, P00064997!).

*Trichomanes latilobum* Bonap. (Chevalier 1920: 755), *nom. nud.* Intended type:—‘Côte d’Ivoire-Bassin du Haut-Nuon, pays des Dyolas, entre Sempleu et Ganhoué’, without date, *A. Chevalier 21140* (not located).

Short description—Epiphytic or lithophytic; long-creeping filiform rhizomes, rootless and densely covered by dense black trichomes, bearing widely separated pending fronds; fronds well stipitate with widely winged stipe and rachis (Fig. 9B), up to 10(–15) cm long, narrowly elliptic to lanceolate, less often oblong, pinnatifid to pinnate-pinnatifid; sori few to numerous, paratactic, as long as to longer than wide, campanulate with a slightly dilated mouth; receptacle short to long-exserted.

Global distribution—Central Africa to western Indian Ocean.

Current distribution in Mascarenes—La Réunion.

Ecology—Lithophytic on shady wet rocks, mostly near streams (on La Réunion, elsewhere noted mostly epiphytic), in lowland rainforests and wet ravines (300–550 m).

Specimens examined—LA RÉUNION. Rivière des Marsouins, September 1979, *T. Cadet 4426* (P01526283, P01526284, P01526285).

Note—This species is more or less widespread (but rare) in wet tropical Africa and Madagascar, and is quite rare on the Mascarenes, only present in a few localities (especially ravines) on the eastern side of La Réunion. It can easily be distinguished from other Mascarenan *Crepidomanes* by its widely winged stipe and rachis (Fig. 9B).

**6. *Crepidomanes frappieri*** (Cordem.) J.P.Roux (Roux 2001: 45), Fig. 9C–F

*Trichomanes frappieri* Cordem. (Cordemoy 1895: 32, 33). Type:—LA RÉUNION. Brûlé de St. Denis, 1891, *Bédier s.n.* (neotype P, P00477825!), designated by Pichi Sermolli (1983: 130, 131).

= *Trichomanes ramitrichum* Faden (Faden 1977: 5). = *Vandenboschia ramitricha* (Faden) Pic.Serm. (Pichi Sermolli 1983: 251). Type:—KENYA. ‘Kericho District, South West Man Forest, along the Kiptiget (Chepkoiisi) River’, 12 June 1972, *R.B. Faden & J. Grumbley 72/338* (holotype EA, EA000002578!; isotypes BR, BR0000008051899!, FI, FI003167!, K, K000435647!).

Short description—Epiphytic or lithophytic; long-creeping filiform rhizomes, rootless and densely covered by long, black and branched trichomes (Fig. 9E), bearing widely separated pending fronds; fronds conspicuously stipitate with wingless stipes, up to 15 cm long (usually less than 10 cm in La Réunion), elliptic to lanceolate, usually pinnate-pinnatifid, with sometimes, when dry, folds parallel to veins; sori few to numerous, paratactic, cylindrical to campanulate with a slightly dilated mouth to clearly developed lips, receptacle long-exserted and with sporangia often protruding outside the indusium (Fig. 9F).

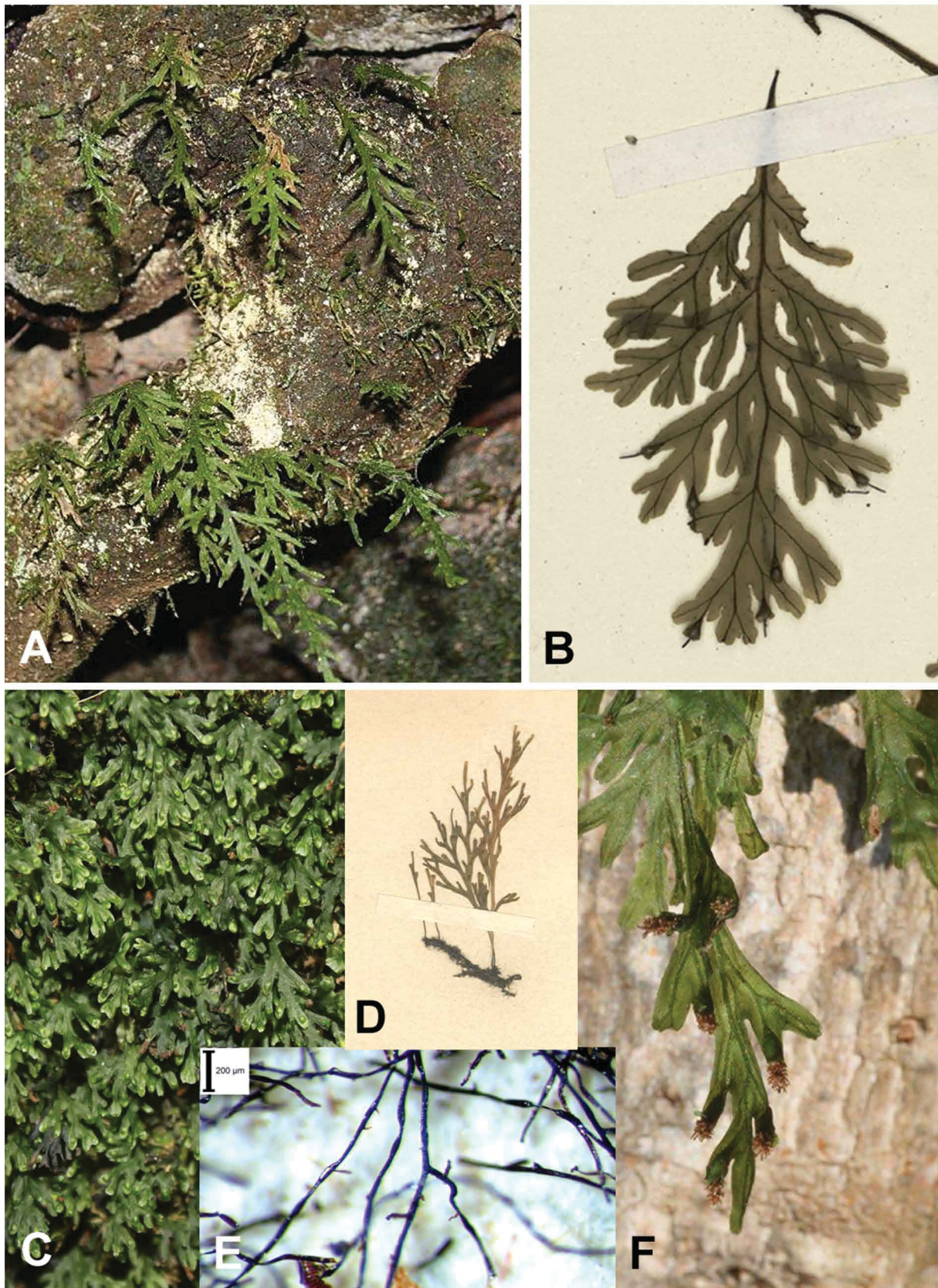
Global distribution—Central Africa to western Indian Ocean.

Current distribution in Mascarenes—La Réunion.

Ecology—Epiphytic and more often lithophytic on shaded, wet rocks on La Réunion, in rainforests and wet ravines on the eastern side at low elevations (50–1,000 m), and also in wet ravines of the western side in semi-dry forest remnants. Outside of La Réunion, and especially in continental Africa, the species seems to occur at higher elevations, from submontane forests up to 2,000 m (Kornaś 1994).

Specimens examined—LA RÉUNION. Bras Panon, 2010, *Y. Robert 1290* (private collection); Les Canots, September 2009, *J.-M. Tamon 456* (private collection); Grand Bassin, November 2012, *J.-M. Tamon 910* (private collection); Ravine les Orangers, June 2016, *J.-M. Tamon 1300* (private collection).

Note—From its gross frond shape, this species can be confused with *C. inopinatum* (Pic.Serm.) J.P.Roux (Roux 2001: 45), but it exhibits long branched trichomes on the rhizome (Fig. 9E), which are not observed in any other *Crepidomanes* species on the archipelago. *Crepidomanes frappieri* shares this feature with the Malagasy *C. longilabiatum* (Bonaparte 1925: 13, 14) J.P.Roux (Roux 2009: 40), hence defining the section *Cladotrichoma* Dubuisson & Rouhan (Dubuisson *et al.* 2013: 186).



**FIGURE 9.** A. *Crepidomanes fallax* (Christ) Ebihara & Dubuisson, as lithophyte on wet rock (La Réunion, ‘Rivière des Marsouins’). B. *C. fallax*, habit (from Madagascar, F. Rakotonrainibe 6467, P00248564). C. *C. frappieri* (Cordem.) J.P.Roux, covering a rock in a wet ravine (La Réunion, ‘Ravine Rivière Ste Anne’). D. *C. frappieri*, habit, type specimen (Bédier s.n., P00477825). E. *C. frappieri*, detail of long branched rhizome trichomes. F. *C. frappieri*, detail of sori (photographs. A, C & F: J.-M. Tamon).

**7. *Crepidomanes inopinatum*** (Pic.Serm.) J.P.Roux (Roux 2001: 45) var. *inopinatum*, Fig. 10A

*Vandenboschia inopinata* Pic.Serm. (Pichi Sermolli 1983: 245, 246). ≡ *Trichomanes inopinatum* (Pic.Serm.) J.E.Burrows (Burrows 1990: 93). Type:—‘Zaire, dorsale ad ovest del Lago Kivu, montagne di Shamulamba’, 24 October 1953, *R.E.G. Pichi Sermolli 4455* (holotype FI, FI-PS 19455; isotypes K, K000435648!; BR, BR0000008054661!).

= *Trichomanes pyxidiferum* L. (Linné 1753: 1098) f. *majus* Taton (Taton 1946: 34) Type:—DEMOCRATIC REPUBLIC OF CONGO. Ruwenzori, 14 May 1914, *J.C.C. Bequaert 4245* (lectotype BR, BR0000008054494!, here designated); Ruwenzori, 13 May 1914, *J.C.C. Bequaert 4231* (paralectotype BR, BR0000013204853!); Ruwenzori, 15 May 1914, *J.C.C. Bequaert s.n.* (paralectotype BR, BR0000013204877!); Ruwenzori, 15 May 1914, *J.C.C. Bequaert s.n.* (paralectotype BR, BR0000013204860!).

Short description—Epiphytic or lithophytic; long-creeping filiform rhizomes, rootless and densely covered by dense black trichomes, bearing widely separated pending fronds; fronds conspicuously stipitate, with wing on the upper part of the stipe (or with full winged stipes if short), up to 10(–15) cm long, lanceolate to ovate, pinnate-pinnatifid to bipinnate-pinnatifid with sometimes, when dry, folds parallel to veins; sori numerous, paratactic, mostly as long as wide, obconic to campanulate with a slightly dilated mouth; receptacle short to long-exserted.

Global distribution—Central Africa to western Indian Ocean.

Current distribution in Mascarenes—La Réunion.

Ecology—Epiphytic on tree-trunks, or lithophytic on wet rocks usually near streams, in montane rainforests (1,200–1,500 m on La Réunion; up to 2,500 m in continental Africa).

Specimens examined—LA RÉUNION. Without locality, 1832, *J.N. Bréon s.n.* (P01522393); Without locality, May 1847, *A.C.J. Bernier 907* (P01522402); Without locality, 1892, *E.J. de Cordemoy 133bis* (P00477827); Without locality, 1895, *H.J. de Cordemoy s.n.* (P01522401); Bélouve, May 2002, *E. Grangaud 978*; Bébou, March 2003, *E. Grangaud 1184*; Bois Sans Souci, April 2003; *E. Grangaud 1285*. Note: The Grangaud’s specimens are available in the private collection of the collector.

Note—*Crepidomanes inopinatum* var. *inopinatum* can easily be confused with *Polyphlebium diaphanum*, better known locally as *P. borbonicum* (Bosch) Ebihara & Dubuisson (Ebihara *et al.* 2006: 240), which exhibits a similar gross morphology and can grow sympatrically (see Fig. 18A). But as already reported by Dubuisson *et al.* (2013), *C. inopinatum* shows campanulate sori which are as long as wide, never significantly longer than wide (see Fig. 10B), whereas *P. diaphanum* has clearly cylindrical sori that are always longer than wide and often up to twice as long as wide (see Fig. 18B).

**8. *Crepidomanes inopinatum*** (Pic.Serm.) J.P.Roux var. *tamonii* Y. Robert & Dubuisson (Dubuisson *et al.* 2014: 165, 166), Fig. 10B

Type:—LA RÉUNION. La Possession, ravine de la Grande Chaloupe, August 2006, *Y. Robert 913* (holotype P, P02433924!; isotype REU!)

Short description—Similar to the typical variety but usually lithophytic with dwarf fronds up to 4 cm long and often when dry, folds parallel to veins.

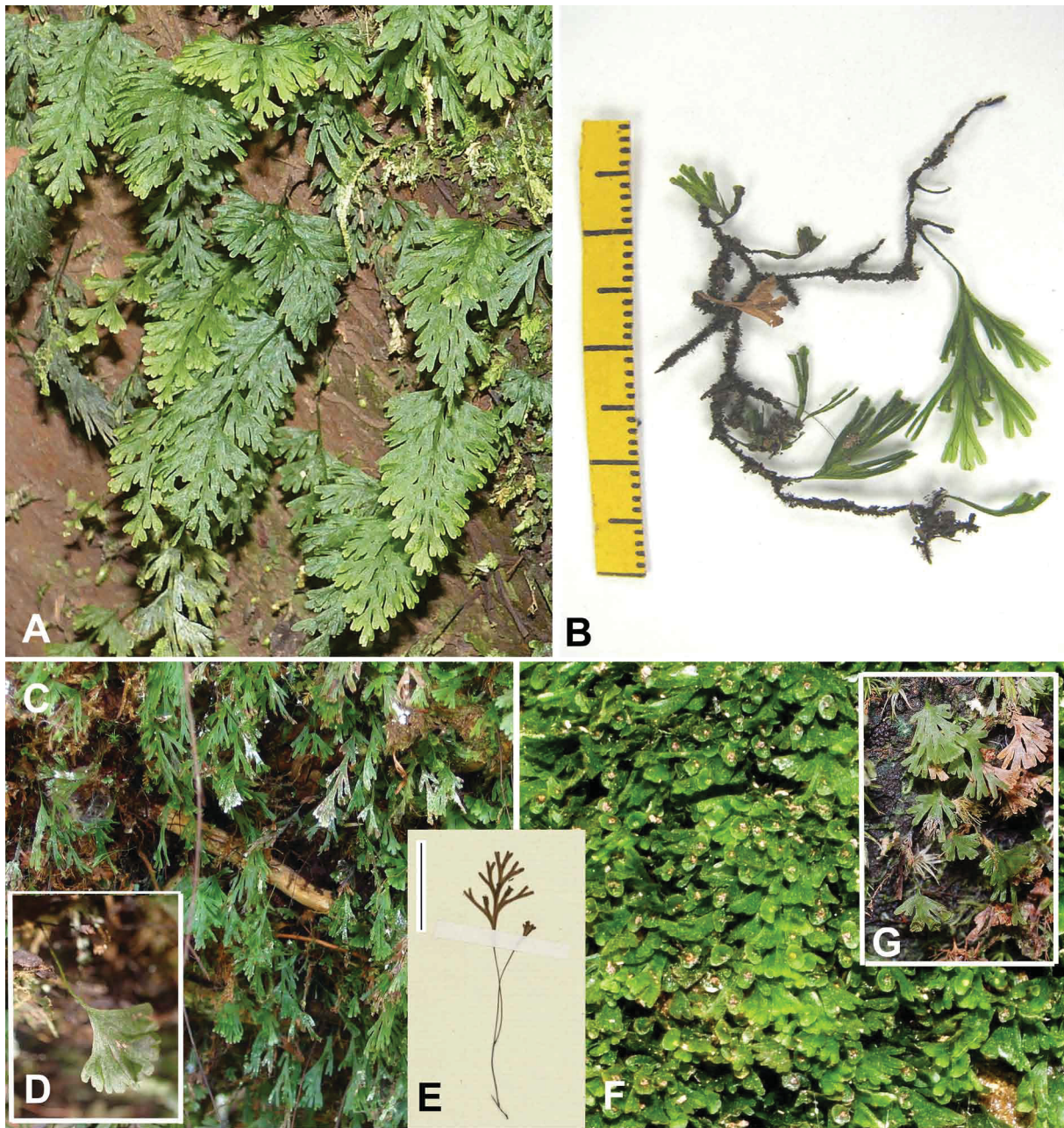
Global distribution—La Réunion, one population reported in Mauritius.

Ecology—Lithophytic on wet and shaded rocks in wet ravines of the western side in semi-dry forest remnants, in addition to a few populations in locally-called ‘végétation de fond de cirque’ in north-eastern side (‘Rivière du Mât’ or ‘Mare à Poule d’eau’), at low elevations (150–900 m).

Specimens examined—MAURITIUS. Curepipe, Trou aux cerfs, October 2015, *Pynee et al. s.n.* (MAU 0017487, MAU 0017488).

—LA RÉUNION. Vallée de la Grande Chaloupe, La Montagne, October 1972, *T. Cadet 3810* (REU08464); Ravine des Avirons, August 2005, *E. Grangaud 1688-1*; Sentier du Petit Louis, Grand Bassin, June 2006, *Y. Robert 885*; Tampon, sentier Piton Petit Louis vers Grand-Bassin, June 2006, *Y. Robert s.n.*; Sainte Marie, ravine Kiwi, July 2006, *Y. Robert 890*; Bras Panon, berges de la rivière du Mât, July 2009, *Y. Robert 1298*; Salazie, mare à Poule d’eau, August 2009, *Y. Robert 1317*; Saint Louis, les Canots, January 2014, *Y. Robert 1655*; Saint Leu, ravine du Trou, December 2005, *Tamon & Fontaine s.n.*; Sainte Marie, falaise du Cap Soldat, October 2007, *Tamon s.n.*; La Possession, Ilet Solitude, december 2007, *Tamon s.n.*; La Possession, Sentier de Dos d’Ane vers Deux bras, March 2010, *Tamon s.n.* Note: Except *T. Cadet 3810* available in REU, the holotype available at P and the Mauritian specimens, all other examined specimens are available in respective private collections of E. Grangaud, Y. Robert and J.-M. Tamon (La Réunion).

Note—As Dubuisson *et al.* (2013, 2014) have shown, this dwarf variety can easily be confused with *C. trinerve*, found in equivalent lowland habitats, especially when specimens show laminar folds parallel to veins. Subtle differences concern the sori, which exhibit a slightly dilated mouth vs. a well dilated bilabiate mouth for *C. trinerve* (see Fig. 11B), and laminar cells, which have straight walls vs. undulated wavy walls for *C. trinerve* (see Figs 2 and 3 in Dubuisson *et al.* 2013). A population was observed in Mauritius for the first time in 2015 (see above).



**FIGURE 10.** A. *Crepidomanes inopinatum* (Pic.Serm.) J.P.Roux var. *inopinatum*, as lithophyte (La Réunion, ‘Petite Plaine’). B. *C. inopinatum* var. *tamonii* Y.Robert & Dubuisson, habit (Y. Robert 913, P02433924). C. *C. minutum* (Blume) K.Iwats. var. *minutum*, as epiphyte (La Réunion, ‘Bébour’). D. *C. minutum* var. *minutum*, frond with long terete wingless stipe. E. *C. minutum* var. *minutum*, showing stipe proliferation, scale = 1 cm (from Madagascar, F. Rakotondrainibe 3698, P00085267). F. *C. minutum* var. *mascarenense* Pynee & Dubuisson, as epiphyte (La Réunion, ‘Grand Etang’). G. *C. minutum* var. *mascarenense*, detail of fronds with short stipes. (photographs. A: J.-Y. Dubuisson; C–D: C. Chaussidon; F–G: E. Grangaud).

**9. *Crepidomanes minutum* (Blume) K.Iwats. (Iwatsuki 1985: 524) var. *minutum*, Fig. 10C–E**

*Trichomanes minutum* Blume (von Blume 1828: 223). ≡ *Gonocormus minutus* (Blume) Bosch (van den Bosch 1861a: 7–8, pl. 3). Type:—  
 JAVA. Without locality, without date, C.L. Blume s.n. (lectotype L, L0544607!, specimen A, here designated). Note: also designated as type of *T. parvulum* Blume, non Poir. (1808).

- = *Trichomanes proliferum* Blume (von Blume 1828: 224). ≡ *Gonocormus prolifer* (Blume) Prantl (Prantl 1875: 51). Type:—JAVA. Without locality, without date, *C.L. Blume s.n.* (lectotype L, L0052391!, here designated; isolectotype L, L0544607!, specimen B).
- = *Trichomanes saxifragoides* C.Presl. (Presl 1843: 39). ≡ *Gonocormus saxifragoides* (C.Presl.) Bosch (van den Bosch 1861a: 9). Type:—PHILIPPINES. Luzon, without date, *H. Cuming 256* (lectotype K, K000375720!, inadvertently designated by Tindale (1963); isolectotypes L, L0537118!, P, P00624459!).
- = *Trichomanes palmatum* C.Presl. (Presl 1843: 39, 40). Type:—PHILIPPINES. Luzon, without date, *H. Cuming 209* (holotype L?; isotype P, P00624461!).
- = *Trichomanes mannii* Hook. (Hooker & Baker 1868: 75, 76). ≡ *Gonocormus mannii* (Hook.) G.Kunkel (Kunkel 1963: 212). ≡ *Crepidomanes mannii* (Hook.) J.P. Roux (Roux 2000: 155). Type:—EQUATORIAL GUINEA. ‘Fernando Po’, before 1861, *G. Mann s.n.* (syntype K?; isosyntype GH, GH00022249!).
- = *Trichomanes lepervanchei* Cordem. (Cordemoy 1891: 14). Type:—LA RÉUNION. Plaine des fougères, without date, *M. Lepervanche-Mezière 7* (lectotype P, P02141627!, here designated; isolectotype P, P02141628!). Note. Cordemoy has not precisely designated the type among all the Lepervanche’s collected Hymenophyllaceae specimens. Such gathering (*M. Lepervanche-Mezière 7*) can nevertheless be *a posteriori* designated, as we did here, because it is the sole plant from the Lepervanche’s collection that can be attributed to the present species.
- = *Trichomanes matthewii* Christ (Christ 1909b: 56). ≡ *Gonocormus matthewii* (Christ) Ching (Ching 1959: 177). Type:—CHINA. Kuang-toung: North river, Mong-si-hai, 11 December 1907, *C.G. Matthew 26* (holotype P, P00623412!, isotype K, K001090162!). Note: in the introduction of his article including the description of *T. matthewii*, Christ (1909b) clearly mentioned that all the specimens are housed at the Muséum national d’Histoire naturelle, i.e. the Paris Herbarium (P). This allows treating the specimen at P as the holotype.
- = *Trichomanes musolense* Brause ex Brause & Hieron. (Brause & Hieronymus 1915: 377, 378). Type:—EQUATORIAL GUINEA. ‘Westafrika: Fernando Poo, Musola oberhalb San Carlos (Westküste)’, November 1911, *J. Mildbraed et al. 7057* (syntypes B, BW 20 0105426!, BW 20 0105427!; isosyntype P, P00482619!).
- = *Trichomanes ruwenzoriense* Taton (Taton 1946: 31, pl. 3, figs K, L), as ‘*ruwenzoriensis*’. ≡ *Gonocormus ruwenzoriensis* (Taton) Pic. Serm. (Pichi Sermolli 1968: 175). ≡ *Crepidomanes ruwenzoriense* (Taton) J.P. Roux (Roux 2009: 40). Type:—DEMOCRATIC REPUBLIC OF CONGO. ‘Secteur des lacs Edouard et Kivu: Ruwenzori, Lamia’, before 1920, *J.C.C. Bequaert s.n.* (holotype BR, BR0000008054166!).
- = *Gonocormus australis* Ching (Ching 1959: 163). Type:—CHINA. Hainan, without date, *E. Smith 1397* (holotype BM, BM001044300!).

Short description—Epiphytic or lithophytic; long-creeping filiform rhizomes, rootless and densely covered by dense black trichomes, bearing widely separated pending fronds; fronds with usually long terete wingless stipes (Fig. 10D) often bearing buds that can provide new fronds (called stipe proliferation; Fig. 10E), up to 6 cm long, but more often less than 4 cm long, flabellate, palmatisect to digitate, less often pinnatifid, with sometimes, when dry, folds parallel to veins; sori few, paratactic, tubular to funnellform with a slightly dilated mouth; receptacle usually included to slightly exerted.

Global distribution—From central Africa to the Pacific islands (and Hawaiï).

Current distribution in Mascarenes—La Réunion.

Ecology—Usually epiphytic in the Mascarenes (reported as mostly lithophytic in Asia) on tree-trunks in montane rainforests (950–1,600 m in western Indian Ocean, up to 2,000 m in Africa and Asia).

Specimen examined—LA RÉUNION. Without locality, 1892, *H.J. de Cordemoy 133* (P01627289); Bébou, May 2005, *E. Grangaud 1679* (collector’s private collection).

Note—*Crepidomanes minutum* var. *minutum* is usually observed as a rare epiphyte in montane rainforests, explaining its absence on Mauritius where such habitats are lacking, and specimens exhibit the typical stipe proliferation which is the synapomorphy of the section *Gonocormus* (Bosch) K.Iwats. (Iwatsuki 1984: 174; see Ebihara *et al.* 2006) (Fig. 10E). As showed by Pynee *et al.* (2012) and Dubuisson *et al.* (2013) and as developed below, the lowland populations in the western Indian Ocean define a distinct variety characterized by smaller individuals and rarity of proliferation. In the western Indian Ocean, *C. minutum* var. *minutum* is considered as a dwarf species with laminae that rarely exceed 3 cm in length. But in continental Africa, ‘giant’ specimens with fronds that can exceed 6 cm (with bi-pinnatifid laminae up to 4–5 cm long) are not rare, especially at high elevations (up to 2,000 m), as illustrated by the specimens identified under the synonym *C. ruwenzoriense* (see Kornaś 1994).

**10. *Crepidomanes minutum*** (Blume) K.Iwats. var. *mascaenense* Pynee & Dubuisson (Pynee *et al.* 2012: 28), as '*mascaenensis*', Fig. 10F, G.

Type:—MAURITIUS. Mt. Lagrave, 18 January 1974, *D. Lorence s.n.* (holotype MAU, MAU 0009282!).

Short description—As the typical variety but displaying dwarf fronds (up to 2.5 cm), mostly flabellate or digitate, and usually no stipe proliferation.

Global distribution—Western Indian Ocean.

Current distribution in Mascarenes—La Réunion, Mauritius.

Ecology—Epiphytic on tree-trunks in lowland rainforests (50–850 m).

Specimens examined.—MAURITIUS. Osterlog Valley, October 2010, *Hennequin et al.* 340 (P02432434); Macabé, October 2010, *Hennequin et al.* 370 (MAU 0008233, P02432404); Pétrin, June 2016, *K. Pynee et al. s.n.* (MAU 0017503); Without locality, without date, *L. Barclay s.n.* (MAU 0009281).

—LA RÉUNION. Le Tremblet, April 2003, *J.-Y. Dubuisson HR-2003-5* (P); *J.-Y. Dubuisson HR-2003-6* (P); Basse Vallée-Vallée heureuse, May 2005, *J.-Y. Dubuisson HR-2005-6* (P).

Note—Originally considered as endemic to the Mascarenes, the lowland populations with dwarf specimens lacking proliferation designating the var. *mascaenense* are actually observed on all the islands of the western Indian Ocean with lowland rainforests (including the Seychelles and Comores). This reinforces the hypothesis that such populations are lowland ecotypes of a species more often observed in montane rainforests.

**11. *Crepidomanes trinerve*** (Baker) Dubuisson & Ebihara (Dubuisson *et al.* 2013: 187), Fig. 11

*Trichomanes trinerve* Baker (1877: 465). Type:—MAURITIUS. Without locality, without date, *H. Barkly and A.M. Barkly s.n.* (holotype K, K000228373!).

= *Trichomanes ambongoense* Bonap. (Bonaparte 1920a: 13, 14). Type:—MADAGASCAR. 'Ambongo', without date, *H. Perrier de la Bâthie 7501* (lectotype P, P00466414!; isolectotype P, P00466408!, designated by Dubuisson *et al.* 2013); *H. Perrier de la Bâthie 7769* (paralectotype P, P00466412!, P00466413!); *H. Perrier de la Bâthie 7770* (paralectotype P, P00466410 !, P00466411!); *H. Perrier de la Bâthie 7771* (paralectotype P, P00466409!, P00482601!).

= *Trichomanes angustilaciniatum* Bonap. (Bonaparte 1925: 11, 12). Type:—MADAGASCAR. 'Massif d'Andringitra', April 1921, *H. Perrier de la Bâthie 13756* (lectotype P, P00482604!, here designated; isolectotype P, P00482603!).



**FIGURE 11.** *Crepidomanes trinerve* (Baker) Dubuisson & Ebihara. A. As lithophyte in a wet ravine of the western side of La Réunion ('Les Canots'; photograph by J.-M. Tamon). B. Habit (from Comores, *F. Rakotonrainibe 6651*, P00310478; modified from Dubuisson *et al.* 2013).

Short description—Lithophytic, less often epiphytic; long-creeping filiform rhizomes, rootless and densely covered by dense black trichomes, bearing widely separated pending fronds; fronds with slightly winged stipes, up to 3.5(–5) cm long, flabellate to obovate, palmatisect to digitate, less often pinnatifid, with always, when dry, folds parallel to veins; sori few, paratactic, campanulate with a well dilated mouth; receptacle usually included to slightly exerted.

Global distribution—Western Indian Ocean (incl. Comores; excl. Seychelles).

Current distribution in Mascarenes—La Réunion, Mauritius.

Ecology—Usually lithophytic on shaded, wet rocks in lowland rainforests at low elevations (500–800 m) and one population reported in a wet ravine on the western side of La Réunion in remnants of semi-dry forest. Because of the easy confusion with the other dwarf *Crepidomanes* species, additional field investigations are required to assess the distribution of this species in the Mascarenes.

Specimens examined—MAURITIUS. Montagne du Corps de Garde, November 1973, *M.J.E. Coode 4103* (MAU 0012276); Rivière des Galets, *D. Lorence 1483* (MAU 0012277); Montagne des Deux Mamelles, January 1972, *D. Lorence s.n.* (MAU 0012278); Tamarind Falls, March 1975, *D. Lorence 1133* (MAU 0012279); Vacoas, 1867, *C. Meller s.n.* (MAU 0012280); Without locality, without date, *sine collector* (MAU 0012281).

—LA RÉUNION. Les Canots, September 2009, *J.-M. Tamon 113* (private collection).

Note—As reported in Dubuisson *et al.* (2013) and Saïd *et al.* (2017), *Crepidomanes trinerve* is often confused with *C. minutum*, the first being even considered as a synonym of *C. minutum* by Roux (2009). Both taxa are nevertheless clearly distinct based on the stipe, which is terete and wingless in *C. minutum* (see Fig. 10C–G) and slightly but always winged in *C. trinerve*, in addition to some sorus features (Dubuisson *et al.* 2013). *Crepidomanes trinerve* was initially considered absent on La Réunion and the La Réunion specimens of *C. trinerve* were considered to be *C. inopinatum* var. *tamonii* (Dubuisson *et al.* 2014). However, *C. trinerve* specimens were finally and recently discovered and clearly identified on La Réunion at ‘Les Canots’ locality. The species is known on Mauritius from the type and a few herbarium specimens (see Dubuisson *et al.* 2013).

Genus *Didymoglossum* Desv. (Desvaux 1827: 330)

**13. *Didymoglossum barklyanum* (Baker) J.P.Roux (Roux 2009: 41), Fig. 12A**

*Trichomanes barklyanum* Baker (Baker 1867: 338, t. 8, fig. F), as ‘*barklyanum*’. Type:—MAURITIUS. ‘Tamari cascade’, without date, *H. Barkly & A.M. Barkly s.n.* (holotype K, K000228376!; isotype P, P00477822!). Note: in the introduction of his article including the description of *T. barklyanum*, Baker (1867) clearly mentioned that all the specimens are housed in the Kew collections (K). This allows treating the specimen at K as the holotype.



**FIGURE 12.** A. *Didymoglossum barklyanum* (Baker) J.P.Roux, as lithophyte (Mauritius, ‘Vallée d’Osterlog’). B. *D. lorencei* (Tardieu) Ebihara & Dubuisson, as lithophyte (La Réunion, ‘Grand Etang’). C. *D. lorencei*, detail of frond with marginal trichomes (photographs. A–C: J.-Y. Dubuisson; D: J.-M. Tamon).



Short description—Epiphytic or lithophytic; long-creeping filiform rhizomes, rootless and densely covered by dense black trichomes, bearing widely separated pending fronds; fronds sub-sessile or with short stipes, up to 1.5 cm long, narrowly ovate to oblong, entire with entire to mostly sinuate margins, with pinnate venation, lacking false veins, hairy with dark, not pedonculated, and usually paired trichomes on the margin; a single terminal sorus per fertile frond, cylindrical to narrowly campanulate with lips usually parallel and with brown margins; receptacle usually covered by the lips.

Global distribution—Endemic to the Mascarenes.

Current distribution in Mascarenes—La Réunion, Mauritius.

Ecology—Epiphytic on tree-trunks or lithophytic on shaded, wet rocks in lowland rainforests, with a few populations on shaded, wet rocks in wet ravines of the western side of La Réunion in remnants of semi-dry forests (50–700 m).

Specimens examined—MAURITIUS. Valley Cascade, March 1975, *D. Lorence 1174* (MAU); Vallée d'Osterlog, October 2010, *S. Hennequin et al. 367* (MAU, P02432431).

—LA RÉUNION. Brûlé de Takamaka, October 2010, *S. Hennequin et al. 308* (P02432361).

Note—This species was initially considered endemic to Mauritius (Roux 2009), but has recently been confirmed on La Réunion (Grangaud 2010). But because of its minute size and possible confusion in the field with similar *Didymoglossum* species, its potential presence outside Mascarenes, and especially in Madagascar, awaits confirmation. Its distinction is nevertheless easy, because it is the only *Didymoglossum* species in the western Indian Ocean that does not display false veins parallel to true veins.

### 15. *Didymoglossum cuspidatum* (Willd.) Ebihara & Dubuisson (Ebihara *et al.* 2006: 236), Fig. 13

*Trichomanes cuspidatum* Willd. (Willdenow 1810: 499). ≡ *Microgonium cuspidatum* (Willd.) C.Presl (Presl 1843: 20). Type:—MAURITIUS. 'Grandes forêts des Iles de France', without date, *J.B.G.M. Bory de Saint-Vincent s.n.* (lectotype B, BW 20 205010!, here designated; isolectotype P, P00612305!).

= *Trichomanes bojeri* Hook. & Grev. (Hooker & Greville 1829: pl. 155). Type:—'In sylvis umbrosis, ad arborum truncos, in Insula Mauritiis', without date, *D. Bojer s.n.* (holotype K, K000435677!).

Short description—Epiphytic or lithophytic; long-creeping filiform rhizomes, rootless and densely covered by dense black trichomes, bearing widely separated pending fronds; fronds sub-sessile or well stipitate, up to 6 cm long, usually less than 3–4 cm long, quite variable and highly polymorphic, glabrous, entire with entire to mostly sinuate margins, to slightly lobed, sub-circular to narrowly deltoid to lanceolate, sometimes linear, with palmate venation, false veins parallel to true veins in addition to a continuous sub-marginal false vein (Fig. 13E); 1–10 sori per fertile frond, cylindrical to narrowly campanulate with a slightly dilated mouth and usually immersed in apical distinct lobes when numerous; receptacle short to long-exserted.

Global distribution—Western Indian Ocean (excl. Comores).

Current distribution in Mascarenes—La Réunion, Mauritius, Rodrigues.

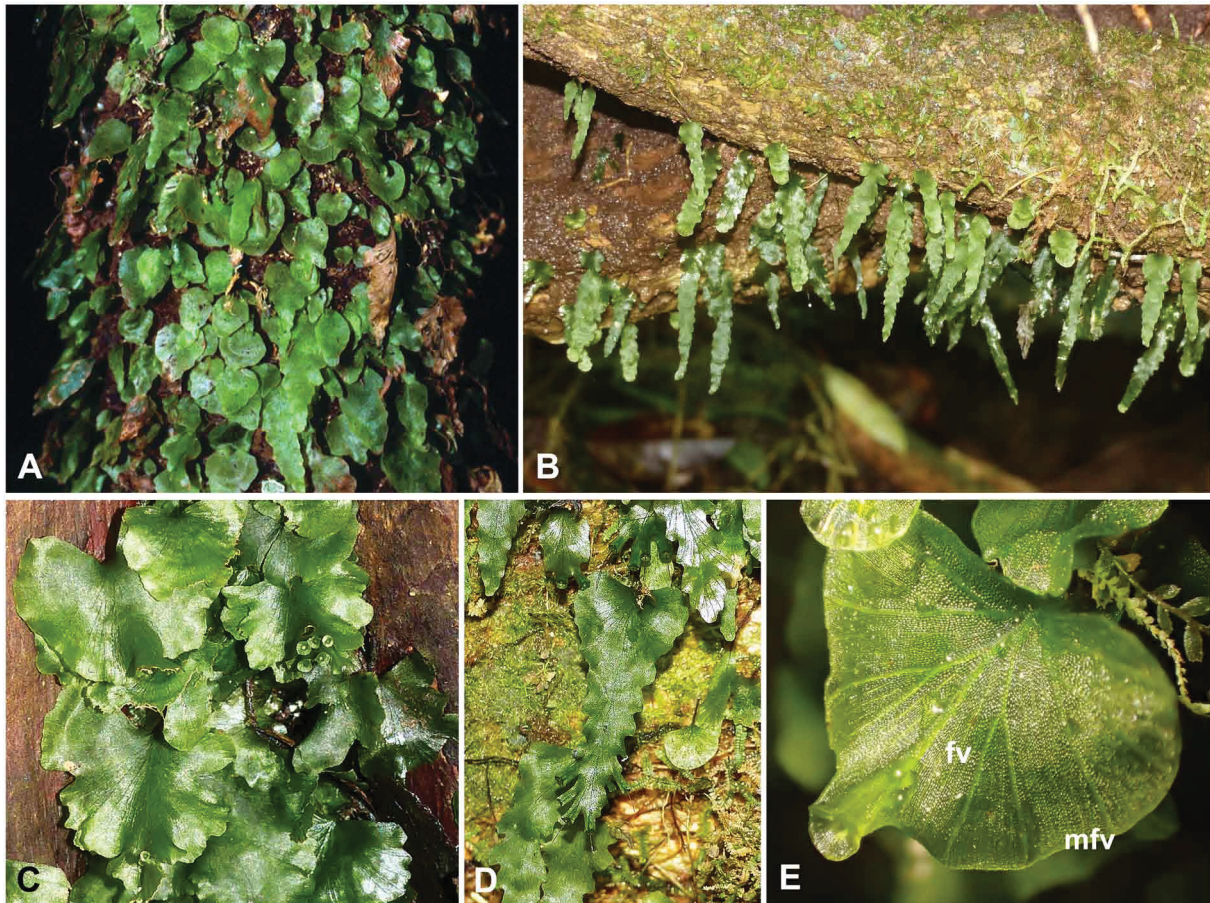
Ecology—Opportunistic, epiphytic and lithophytic on various substrates in the understory of rainforests and in wet ravines from low to middle elevations (0–1,300 m). The species is usually abundant in lowland rainforests, but is rarer and mostly located in wet ravines in montane rainforests. This is the single Hymenophyllaceae species present on Rodrigues, in a single wet ravine.

Specimens examined—'Ile de Mascareigne', without locality, 1831, *C. Bélanger s.n.* (P00612306).

—MAURITIUS. Bel Ombre, October 2010, *S. Hennequin et al. 383* (MAU 0008184, P02432448); Fayence Mt., December 2007, *K. Pynee et al. s.n.* (MAU 0008189); Rambouillet, April 2011, *K. Pynee s.n.* (MAU 0008209); Alma Hill, September 2012, *K. Pynee et al. s.n.* (MAU 0008224); Bar Le Duc, August 2011, *K. Pynee et al. s.n.* (MAU 0009100); Trou aux Cerfs, October 2015, *K. Pynee et al. s.n.* (MAU 0011483); Mare Longue, October 2010, *S. Hennequin et al. 361* (MAU 0011513, P02432425).

—LA RÉUNION. Without locality, without date, *J.M.C. Richard 122* (P00065001); Ilet Alcide, November 2004, *F. Rakotonrainibe et al. 6897* (P00411902).

Note—This widespread species is readily distinguished from the other *Didymoglossum* species in Mascarenes by its glabrous fronds. Its distinctiveness outside the Mascarenes is discussed in Saïd *et al.* (2017).



**FIGURE 13.** *Didymoglossum cuspidatum* (Willd.) Ebihara & Dubuisson. A. Typical sub-circular, and lanceolate to deltoid sterile forms as usually observed (La Réunion, ‘Mare Longue’). B. Linear sterile forms (La Réunion, ‘Grand Etang’). C. Ovate to lanceolate fertile fronds with apical sori (La Réunion, ‘Forêt de Bon Accueil, Les Makes’). D. Narrowly lanceolate fertile frond with apical sori (La Réunion, ‘Grand Etang’). E. Small sub-circular/ovate fertile frond with a single sorus, showing sub-marginal false vein (mfv) and false veins parallel to true veins (fv) (photographs. A–D: J.-Y. Dubuisson; E: L. Bauret).

**14. *Didymoglossum lorencei*** (Tardieu) Ebihara & Dubuisson (Ebihara *et al.* 2006: 236), Fig. 12B–D

*Trichomanes lorencei* Tardieu (Tardieu-Blot 1977: 147, pl. 1, t. 7–13). Type:—MAURITIUS. Valley Cascade, March 1975, *D. Lorence* 1175 (holotype P, P00477828!).

Short description—Epiphytic or lithophytic; long-creeping filiform rhizomes, rootless and densely covered by dense black trichomes, bearing widely separated pending fronds; fronds sessile to sub-sessile, up to 1.5 cm long, oblong to obovate, entire with entire to undulate margins, with palmate venation and false veins parallel to true veins, hairy with dark, not pedonculated trichomes on lamina margins (Fig. 12D); a single terminal sorus per fertile frond, cylindrical with lips usually parallel and with brown margins; receptacle usually covered by the lips..

Global distribution—Western Indian Ocean (excl. Seychelles).

Current distribution in Mascarenes—La Réunion, Mauritius.

Ecology—Epiphytic on tree-trunks or lithophytic on shaded, wet rocks in lowland rainforests (150–550 m) and also one reported population in a wet ravine of the western side of La Réunion in remnants of semi-dry forest.

Specimens examined—MAURITIUS. Vallée de Ferney, October 2010, *S. Hennequin et al.* 400 (MAU, P02432468)

—LA RÉUNION. Brûlé de Takamaka, June 2006, *E. Grangaud 1752* (P01627307), October 2010, *S. Hennequin et al.* 309 (P02432362).

Note—This rare dwarf species can be confused in the wild with *D. barklyanum*, but clearly shows false veins parallel to true veins, absent in the latter species.

Genus *Hymenophyllum* Sm. (Smith 1793: 418)

Subgenus *Hymenophyllum*

**15. *Hymenophyllum fumarioides*** Bory ex Willd. (Willdenow 1810: 526), Fig. 14A, B

≡ *Mecodium fumarioides* (Bory ex Willd.) Copel. (Copeland 1938: 22). Type:—MAURITIUS. ‘Grands bois à l’île de France’, without date, *J.B.G.M. Bory de Saint-Vincent 119*, (lectotype B, BW 20 229010!, here designated; isolectotype P, P00547028!).

= *Trichomanes inaequale* Poir. var. β Poir. (Poiret 1808: 75). Type:—MADAGASCAR? Without locality, without date, *L.-M.A. du Petit-Thouars s.n.* (lectotype P, P00483518!, here designated). Note: the Malagasy origin is doubtful (as discussed below).

= *Hymenophyllum ricciiifolium* Bory ex Willd. (Willdenow 1810: 531), as ‘*ricciaefolium*’. Type:—LA REUNION. ‘Les grands bois à Bourbon’, without date, *J.B.G.M. Bory de St.-Vincent 118* (lectotype B, BW 20 236020!, here designated; isolectotype P, P00477837!).

= *Sphaerocionium tenellum* (Jacq.) C.Presl (Presl 1843: 34), based on *Adiantum tenellum* Jacq. (von Jacquin 1789: 287, pl. 21, fig. 3).  
≡ *Hymenophyllum tenellum* (Jacq.) Kuhn (Kuhn 1868: 42), *nom. illeg.*, non D.Don (Don 1825: 12) ≡ *Meringium tenellum* (Jacq.) Copel. (Copeland 1938: 42). Type:—LA REUNION. ‘Crescit in insula Borboniae’, without date, *without collector* (holotype von Jacquin (1789): pl. 21, fig. 3).

Note: Tardieu-Blot (2008) added *H. emersum* Baker (Hooker & Baker 1868: 451) as a synonym. But the type of this species (*Thwaites s.n.*, K001090270!) is from Sri Lanka and clearly a distinct species (even if the Mauritian syntype -K000435618!- is clearly a *H. fumarioides*), hence we excluded this taxon from the synonym list.

Short description—Epiphytic; long-creeping filiform rhizomes, bearing sparsely distributed roots and reddish-brown trichomes, and widely separated pending fronds; fronds glabrous, with undulated winged, glabrous stipes and rachises, up to 15 cm long, elliptic to ovate, pinnate-pinnatifid to bi-pinnate-pinnatifid, with curled/undulated lamina in the wild; sori numerous, paratactic, usually at the frond apices, bilabiate with a small base and with irregularly toothed, seeming jagged, margins; receptacle slightly exerted at maturity (Fig. 14B).

General distribution—Mascarenes, its presence in Madagascar is doubtful.

Current distribution in Mascarenes—La Réunion, Mauritius.

Ecology—Epiphytic on tree-trunks in lowland and montane rainforests (250–1,400 m).

Representative specimens examined—MAURITIUS. Plateau de Mare Longue, October 2010, S. Hennequin *et al.* 359 (MAU 0011495, P02432423).

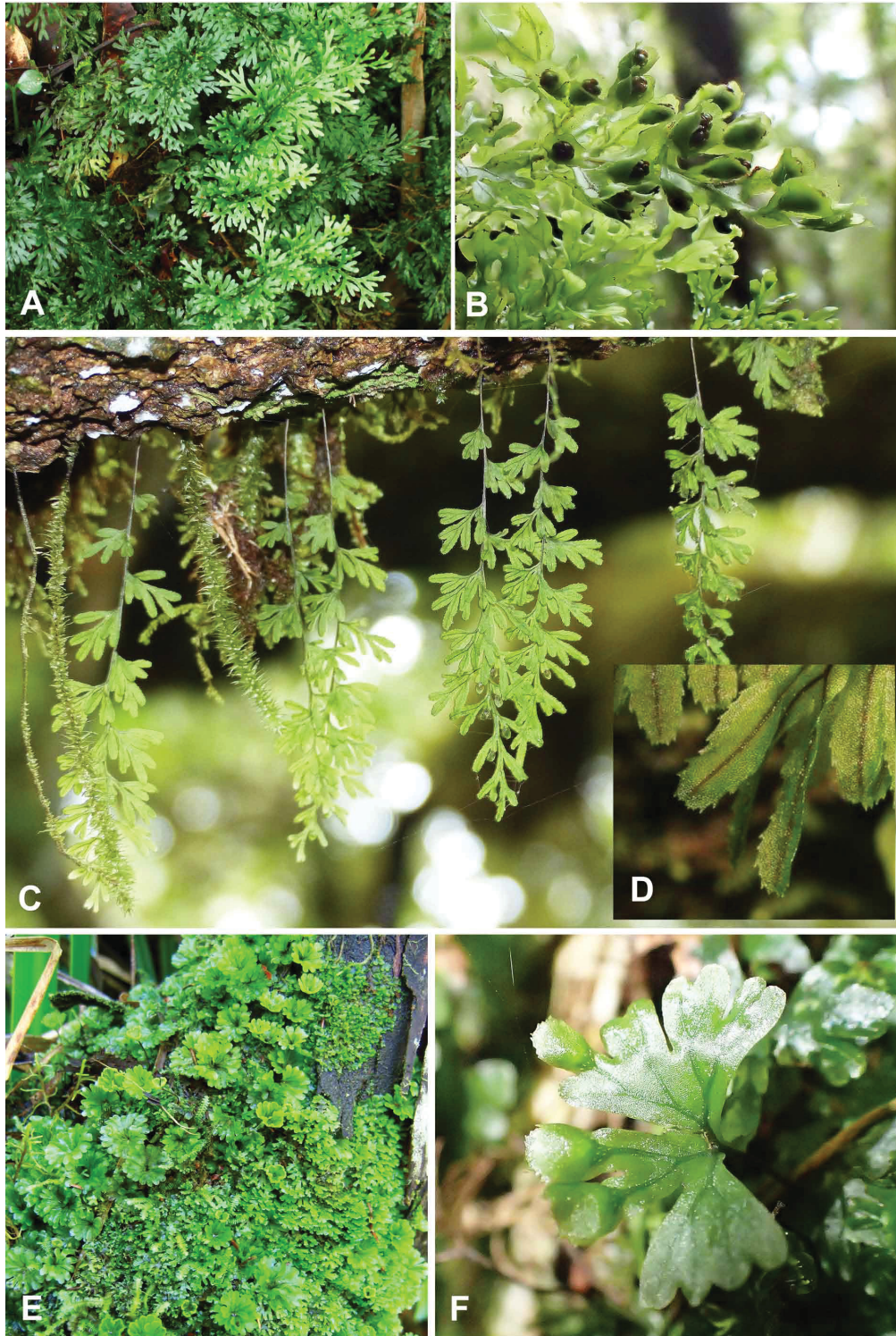
—LA RÉUNION. Saint Philippe, May 1957, *J. Bosser 12152* (P01305955); Forêt de Mare Longue, September 1968, *T. Cadet 1633bis* (P01305829, specimen A, mix with *H. hygrometricum* (Poir.) Desv.), *T. Cadet 1634* (P01305852); Basse Vallée, April 1999, *J.-Y. Dubuisson HR-1999-15* (P); Bébou, April 1999, *J.-Y. Dubuisson HR-1999-27* (P); Mare Longue, November 2004, *F. Rakotondrainibe et al. 6899* (P00411900).

Note—This species is known in principal floras (Tardieu-Blot 1951, 2008; Grangaud 2010) as *Hymenophyllum tenellum* (Jacq.) Kuhn, but Grangaud noted that the name was likely illegitimate and suggested *H. ricciiifolium* Bory ex Willd as the valid name. *Hymenophyllum tenellum* is a combination based on *Adiantum tenellum* Jacq. (Kuhn 1868), and actually firstly named *Sphaerocionium tenellum* (Jacq.) C.Presl (Presl 1843), but the name *Hymenophyllum tenellum* had already been proposed before by Don (1825) to designate a clearly distinct Asiatic species (type: *Hamilton & Wallich s.n.*; BM001044318). *Hymenophyllum tenellum* (Jacq.) Kuhn and its homotypic synonyms are therefore illegitimate. The synonym *Hymenophyllum ricciiifolium* described by Willdenow (1810) appears *a priori* as a good candidate. But as demonstrated by Said *et al.* (2017), *H. fumarioides* Bory ex Willd. has been used to describe the same species and this name was proposed before *H. ricciiifolium* by the same author. We thus here propose *H. fumarioides* as the valid name for specimens formerly identified and named *H. tenellum*. And we can note here that Cadet (1980) had already used *H. fumarioides* for naming the taxon.

The species is recognized by its small to medium-size elliptic to ovate, pinnate-pinnatifid to bi-pinnate-pinnatifid curled fronds combined with sori with mostly irregularly toothed, seemingly jagged, margins. Except for the closely related *H. sibthorpioides* (Bory ex Willd.) Mett. ex Kuhn (Kuhn 1868: 41) which has dwarf flabellate to reniform fronds, the sori of the other Mascarenan *Hymenophyllum* species always show conspicuously entire, and neither toothed nor jagged, margins.

The species has not been observed by us neither in the Malagasy collections we have studied, nor in the wild in Madagascar. The Malagasy origin of the type of the synonym *Trichomanes inaequale* Poir. var. β Poir. thus appears doubtful and is likely erroneous. Some Malagasy collections (e.g., *F. Rakotondrainibe et al. 6981*, P00411775, or *F. Rakotondrainibe 3032*, P00067129) have been identified as *H. tenellum*, but such specimens, even if they seem

slightly crisped, have sori with entire margins, and overall and sorus shapes that do not fit with typical *H. tenellum*. In addition to margin differences, the sori of *H. fumarioides* are not or only slightly immersed into the lamina, ovate, and usually longer than wide, and with a small base, whereas the sori of Malagasy specimens are clearly immersed into the lamina, (sub)circular and often shorter than wide, with no small base but two basal veinlets. These features suggest a relationship to subgenus *Mecodium*, and likely to the local species *H. capense* Schrad. (Schrader 1818: 919). We therefore propose here that *H. fumarioides* is endemic to the Mascarenes.



**FIGURE 14.** A. *Hymenophyllum fumarioides* Bory ex. Willd, as epiphyte (La Réunion, ‘Mare Longue’). B. *H. fumarioides*, detail of curled/cripsed segments and sori with toothed margins. C. *H. peltatum* (Poir.) Desv., as epiphyte (La Réunion, ‘Pitons Mare à Boue’). D. *H. peltatum*, detail of toothed/serrulate laminar margins. E. *H. sibthorpioides* (Bory ex Willd.) Mett. ex Kuhn, as epiphytic (La Réunion, ‘Vallée Heureuse’). F. *H. sibthorpioides*, fertile frond and sori with toothed margins (photographs. A, E: C. Chaussidon; B, F: L. Bauret; C: J.-Y. Dubuisson; D: J.-M. Tamon).

**16. *Hymenophyllum peltatum* (Poir.) Desv. (Desvaux 1827: 333), Fig. 14C, D**

*Trichomanes peltatum* Poir. (Poiret 1808: 76), non Baker (Baker 1867: 336, 337, t. 8, fig. C) ≡ *Meringium peltatum* (Poir.) Copel. (Copeland 1938: 98). Type:—MAURITIUS. ‘Ile de France’, without date, *J.B.G.M. Bory de St.-Vincent s.n.* in herb. Du Petit-Thouars (lectotype P, P00789570!, inadvertently designated by Tindale (1963); isolectotype LE, LE00007981!).

= *Hymenophyllum unilaterale* Bory ex Willd. (Willdenow 1810: 522). Type:—LA RÉUNION. ‘Rochers humides à 1000 toises Bourbon’, without date, *J.B.G.M. Bory de St.-Vincent s.n.* (lectotype B, BW 20 225010!, here designated; isolectotypes FI, FI003711!, P, P00477834!). Note: It is highly possible that these specimens collected by Bory and here considered by Willdenow are part of the same gathering as those considered by Poiret for *Trichomanes peltatum* (see above), as it seems to be indicated in a label on the sheet of the LE00007981 specimen. Accordingly, this name would be illegitimate.

= *Hymenophyllum menziesii* C.Presl (Presl 1843: 51). ≡ *Hymenophyllum peltatum* (Poir.) Desv. var. *menziesii* (C.Presl) C.Ch. (Christensen 1940: 6). Type:—ARGENTINA. Isla de los Estados, ‘Habitat in Staatenland’, before 1842, *A. Menzies s.n.* (holotype E, E00215323!).

= *Hymenophyllum uncinatum* Sim (Sim 1915: 81). Type:—SOUTH-AFRICA. ‘Tafelberg, XII 1891’, *T. Kässer 1007* (holotype PRE, PRE0085675!; isotype PRE, PRE0592122!).

Short description—Epiphytic or lithophytic; long-creeping filiform rhizomes, bearing sparsely distributed roots and rare reddish-brown trichomes, and widely separated pending fronds; fronds glabrous, with narrowly winged stipes and rachises, up to 20 cm long, sometimes longer but mostly less than 15 cm long, narrowly lanceolate to oblong, sometimes linear, pinnate-pinnatifid, with toothed margins (Fig. 14D); numerous sori, paratactic, usually on the acroscopic most-proximal pinnules, bilabiate with a small base and with entire (not toothed) margins; receptacle included.

General distribution—Tropical and subtropical Africa, western Indian Ocean, subantarctic islands (Crozet, Kerguelen, Marion, Prince Edward), Tristan da Cunha, Andes from Venezuela to southern South-America (Patagonia and neighboring islands). The precise distribution in neotropics is detailed in Kessler & Smith (2017).

Current distribution in Mascarenes—La Réunion.

Ecology—Epiphytic on tree-trunks or lithophytic on wet rocks in montane rainforests and at high elevations up to the treeline (1,350–1,900 m).

Representative specimens examined—LA RÉUNION. Without locality, without date, *Maire s.n.* (P01324708); Cilaos, February 1969, *T. Cadet 2044* (P01324711); Notre Dame de la Paix, June 2006, *E. Grangaud 1756* (P01324717).

Note—This species is more widespread in temperate wet regions at low elevations, explaining why it is observed at high elevations in the tropics in ‘temperate’ or ‘fresh’ ecosystems. It can easily be confused with the sub-cosmopolitan *H. tunbrigense* (L.) Sm. (Smith 1794: pl. 162), absent in the Mascarenes and with a questionable presence on Madagascar. It differs by the sorus margin, which is entire in *H. peltatum* and toothed in *H. tunbrigense*. The accurate distribution of *H. peltatum* remains to be assessed, as molecular studies have shown that the La Réunion specimens do not group with neither Australasian specimens (Hennequin *et al.* 2010; del Rio *et al.* 2017) nor with South American ones (Larsen *et al.* 2013).

**17. *Hymenophyllum sibthorpioides* (Bory ex Willd.) Mett. ex Kuhn (Kuhn 1868: 41), Fig. 14E, F**

*Trichomanes sibthorpioides* Bory ex Willd. (Willdenow 1810: 498). Type:—‘Les grands bois de Bourbon’, without date, *J.B.G.M. Bory de St.-Vincent s.n.* (lectotype B, BW 20 204010!, here designated; isolectotype P, P00612300!). Note: the P sheet actually indicates ‘Ile de France’ as the locality collect, which is the former name for Mauritius, and not La Réunion (formerly named Bourbon).

= *Trichomanes adianthinum* Bory (Bory 1833: 78). Type:—LA RÉUNION or MAURITIUS. Without locality, without date, *C. Bélanger s.n.* (lectotype P, P00477836!, here designated; isolectotype P, P00630420!).

= *Trichomanes thouarsianum* C.Presl (Presl 1843: 40). Type:—‘Habitat in insula Borbonia’, without date, *L.-M.A. du Petit-Thouars s.n.* (not located). Note: this name is tentatively placed here in synonymy, as the sorus margin is not described as toothed but entire.

= *Hymenophyllum palmatum* Bosch (van den Bosch 1859: 385), based on *Trichomanes flabellatum* Bory (Bory 1833: 77), non Bory ex Desv. (Desvaux 1827: 325). Type:—‘Ile de Mascareigne’, without date, *J.B.G.M. Bory de St.-Vincent s.n.* (lectotype P, P00065012!, here designated; isolectotype K, K000435612!, here designated according to note of M. Tindale on the sheet). Note: The P00065012 specimen collected by Bory in ‘Ile de Mascareigne’ (former name for La Réunion) named on the sheet *T. flabellatum* as a new species, and secondarily identified on the sheet as *H. palmatum* by van den Bosch, is very likely to be part of the original material (we designated it here as lectotype). The K specimen, annotated as “part of the type collection” by M. Tindale would thus become an isolectotype.

Note: *Trichomanes flabellatum* Bory ex Desv. (Desvaux 1827: 325), *nom. nud.*, non Bosch (van den Bosch 1859: 353) is often cited as synonym. Desvaux cites as type *T. flabellula* d’Urv. (Dumont d’Urville 1826: 597). But *Trichomanes flabellula* d’Urv. is a species

described by Dumont d'Urville for 'les îles Malouines' (Falklands). *Hymenophyllum sibthorpioides* is not present in the southern Atlantic region, hence explaining that we excluded this taxon for this treatment.

*Trichomanes parvulum* Poir. (Poiret 1808: 64), non Copel. (Copeland 1933: 145) is also often listed as synonym of *H. sibthorpioides*, but this synonymy is questionable. The original description actually does not allow clearly supporting the synonymy either to *H. sibthorpioides* or to the distinct *Crepidomanes minutum*, and the not-well preserved P type specimens (*L.-M.A. du Petit-Thouars s.n.*; holotype P, P00065014!; isotype P, P00065015!) could also belong to the latter species. As such this taxon could be treated as a *nomem dubium*, and pending additional investigations on such specimens, we propose thus to exclude it from the list.

Short description—Epiphytic; long-creeping filiform rhizomes, bearing sparsely distributed roots and long reddish-brown trichomes, and widely separated fronds; fronds glabrous, with wingless terete stipes, up to 4 cm long, slightly curled in the wild, flabellate to reniform, palmatisect with dichotomous venation; few sori, paratactic, bilabiate with a small base and with toothed margins; receptacle slightly exerted at maturity (Fig. 14).

Global distribution—Western Indian Ocean, East and South Africa.

Current distribution in Mascarenes—La Réunion, Mauritius (see below)

Ecology—Epiphytic on tree-trunks in lowland to montane rainforests (100–1,500 m), and also one population in a wet ravine of the western side of La Réunion in remaining semi-dry forest.

Specimens examined—MAURITIUS. Tamatave, October 1978, *D. Lorence 2006* (MAU).

—LA RÉUNION. Without locality, without date, *M. Lepervanche 6* (P00065013); without locality, without date, *J.B.G.M. Bory de St. Vincent s.n.* (P00065012); Mare à Poule d'eau, 1835, *Bernier s.n.* (P00612301).

Note—This species is distinguishable by the combination of flabellate to reniform fronds and bilabiate sori with toothed margins. However, sterile specimens can be confused with sterile specimens of flabellate forms of *Crepidomanes minutum*, suggesting potential problems with the type specimens of supposed synonyms (see above). The species appears currently absent from Mauritius. Apart from the type of the species apparently collected in 'Ile de France' (an old name of Mauritius) and the specimen *D. Lorence 2006* collected in 1978, the other MAU herbarium specimens are actually *C. minutum* var. *mascarenense* or *C. trinerve* (see Dubuisson *et al.* 2013). Thus, the species appears not have been observed since 1978 on Mauritius and its current presence on the island awaits confirmation.

### Subgenus *Sphaerocionium*

#### 18. *Hymenophyllum capillare* Desv. (Desvaux 1827: 333), Fig. 15A, B

≡ *Sphaerocionium capillare* (Desv.) Copel. (Copeland 1938: 33). Type:—LA REUNION. 'Pend aux arbres dans les forets humides Ile Bourbon', without date, *without collector* (lectotype P, P00065016!, here designated). Note: The reference both in the protologue and on the sheet to 'Tristan da Cunha' (label handwritten by Desvaux in the left bottom corner) and to '*Trich. hirsutum* Du Pet.-Th.' (handwritten by Thouars) supports the type status of the specimen here selected as lectotype. However, considering the handwritten label by J.M.C. Richard (Director of the Botanical Garden in La Réunion from 1831) on the left of the plant, the origin of the plant might be ambiguous, as the plant is here said from 'Bourbon' (La Réunion). In fact, as detailed by Christensen (1940) and, later supported by Morton (1973), the annotation by Desvaux mentioning 'Insula Tristan da Cunha' is erroneous because *H. capillare* does not occur on this island. Thus, the Bourbon annotation makes sense even if it seems to have been later crossed out on the sheet.

= *Hymenophyllum pendulum* Bory (Bory 1834: 81, 82, pl. 8, fig. 2). ≡ *Sphaerocionium pendulum* (Bory) C.Presl (Presl 1843: 34). Type:—'Des forêts de Mascareigne', an X [1801–1802], *J.B.G.M. Bory de St. Vincent s.n.* (lectotype P, P00477830!, here designated in accordance with the lectotypification proposed by R. Pichi-Sermolli directly on the sheet). Note: the lectotypification is supported by the strong resemblance between the illustration in Bory (1834) and the Bory's specimen.

Short description—Epiphytic; long-creeping filiform rhizomes, bearing sparsely distributed roots and long reddish-brown trichomes, and widely separated pending fronds; fronds with usually wingless stipes and rachises, up to 40 cm long, linear to narrowly oblong, bi-pinnate-pinnatifid, less often tripinnate, densely hairy with reddish-brown, stellate, non-pedunculated trichomes on rachises, veins, on both sides of laminae and margins; numerous sori, paratactic, bilabiate without a developed base nor lateral veinlets, but with hairy margins; receptacle short and included.

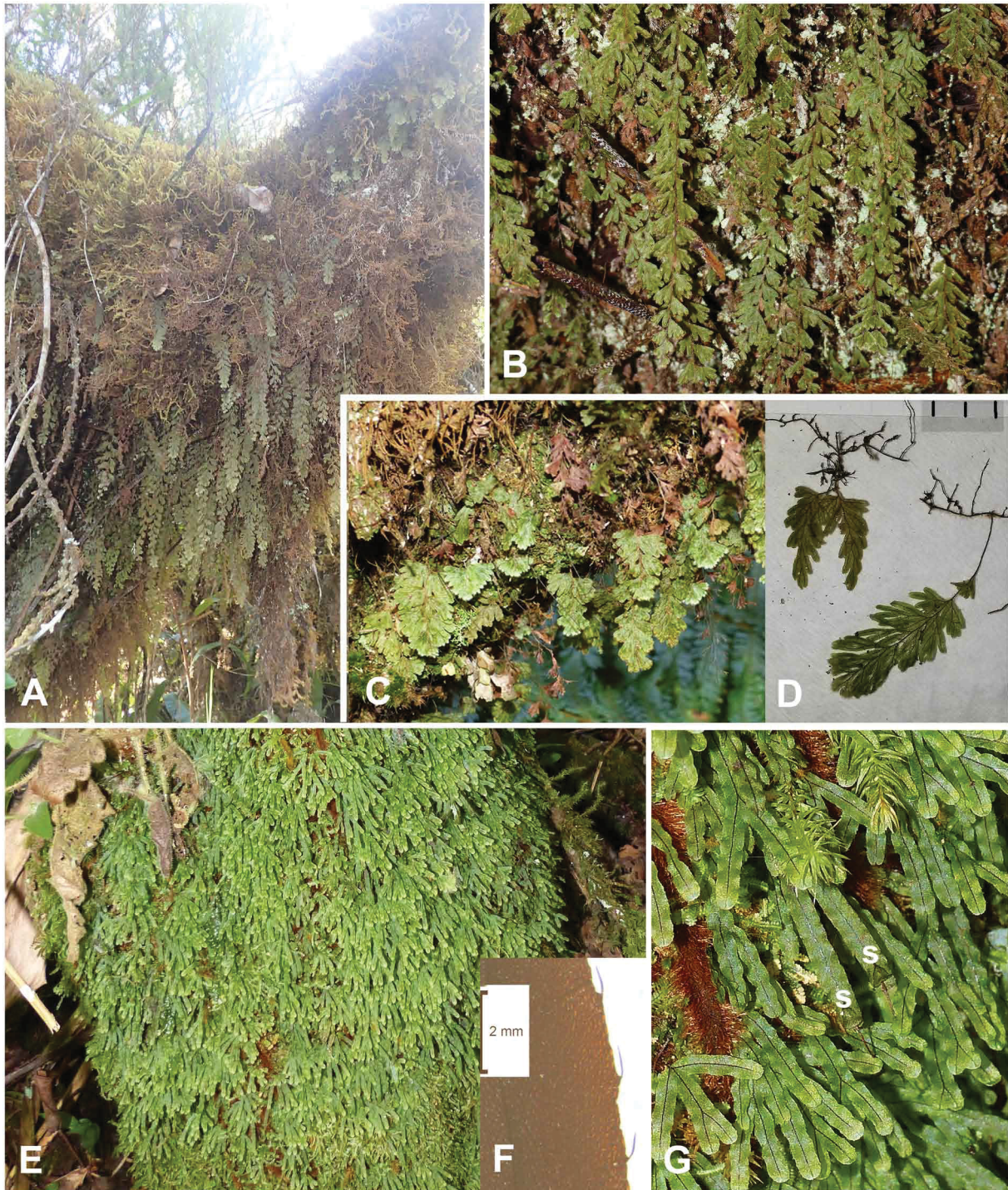
Global distribution—Central Africa to western Indian Ocean.

Current distribution in Mascarenes—La Réunion.

Ecology—Epiphytic on tree-trunks in lowland to montane rainforests up to the tree-line (400–2,000 m).

Representative specimens examined—LA RÉUNION. Without locality, without date, *J.B.G.M. Bory de St. Vincent s.n.* (P00477830); GR de la Roche écrite, January 2002, *Pignal et al. 1951* (P00239563); Bébou, without date, *T. Cadet 540bis* (P01328009); Montagne Saint Denis, September 1968, *T. Cadet 1511* (P01328014); Plaine des Chicots, November 1970, *T. Cadet 2892* (P01328020).

Note—*Hymenophyllum capillare*, at least the typical form, is easily distinguished from other Mascarenan hairy *Sphaerocionium* species by its linear to narrowly oblong fronds with wingless stipes (vs. winged for *H. hirsutum*) and rachises (vs. winged for both *H. hirsutum* and *H. hygrometricum*, at least at its upper part for the latter species).



**FIGURE 15.** A. *Hymenophyllum capillare* Desv., typical form, as epiphyte (La Réunion, ‘Forêt de Bon Accueil, Les Makes’). B. *H. capillare*, typical form, detail of fronds. C. *H. capillare* f. *nanum* Hennequin & Dubuisson, *f. nov.*, as epiphyte (La Réunion, ‘Pitons Mare à Boue’). D. *H. capillare* f. *nanum*, habit, type individual, scale = 0.5 cm (La Réunion, ‘Forêt de Bon Accueil, Les Makes’, J.-Y. Dubuisson & L. Bauret HR 2016-10, P). E. *H. digitatum* (Sw.) Forsberg, as epiphyte (La Réunion, ‘Forêt de Bon Accueil, Les Makes’). F. *H. digitatum*, detail of laminar margin showing minute dark trichomes. G. *H. digitatum*, detail of fronds and sori with tubular bases (s) (photographs. A–B: L. Bauret; C–G: J.-Y. Dubuisson).

**19. *Hymenophyllum capillare* Desv. f. *nanum* Hennequin & Dubuisson, f. nov., Fig. 15C, D**

Similar to typical *Hymenophyllum capillare* but with fertile fronds dwarfed, up to 6 cm long (generally less than 4 cm long), with rachis often partly to fully winged (vs. always wingless for the typical form, or only in its upper part).

Type:—LA RÉUNION. Forêt de Bon Accueil, 17 April 2016, *J.-Y. Dubuisson & L. Bauret HR 2016-10* (holotype P, P00915544!).

Global distribution—Discovered in the wild on La Réunion in 2016, and represented at P by a few additional specimens from the island. Further studies are needed at other localities (Mauritius, Madagascar and tropical Africa) to assess the distribution of this dwarf form outside of the island.

Specimens examined—LA RÉUNION. Mare Longue, April 2016, *L. Bauret 191* (P); Plaine des Palmistes, June 1957, *J. Bosser 11600* (P01328012); Mare Longue, October 1972, *T. Cadet 3841* (P01328011).

Note:—In the literature (e.g., Tardieu-Blot 1951, 2008; Kornaš 1993), the range of fertile frond length for typical *H. capillare* varies from (6–)7 cm to 40 cm long. We discovered on La Réunion in 2016 colonies of dwarf specimens with fertile fronds from 2.5 cm to 6 cm long, which were firstly suggested to belong to a new distinct species, especially by displaying in many cases winged rachis (vs. wingless in *H. capillare*). The sterile fronds of juvenile *H. capillare* are actually similar with rachis more or less winged. Such atypical colonies seem to correspond to dwarf mature forms keeping a juvenile morphology (progenesis), and personal unpublished molecular data confirm their inclusion in *H. capillare*. Because this dwarfed form is found in sympatry in the same localities as the typical form, we decide here to propose a *forma nova* instead of a new variety, the latter one being rather used for designating distinct populations (e.g., as applied here for *C. inopinatum* var. *tamonii* and *C. minutum* var. *mascarenense*). Ellison *et al.* (2014) strongly argued for the abandon of infrageneric taxa as varieties and forma in modern taxonomy in the context of stabilization of names. We support this point of view but keep here this new forma for the following reasons. The dwarf forms are morphologically clearly distinct from the typical specimens and we still have to check if they occur in all populations within the whole distribution of the species or are only restricted to some local populations and/or may be related/adapted to some micro-habitats. If their presence appears actually normal and widespread, such dwarf forms would have to be finally integrated into the whole variability of a single taxon. If they represent particular, not frequent and likely local cases, their distinction could provide useful information in a context of conservation. For now, this form remains a hypothesis.

**20. *Hymenophyllum digitatum* (Sw.) Fosberg (Fosberg & Sachet 1980: 1), Fig. 15E–G**

*Trichomanes digitatum* Sw. (Swartz 1806: 370). ≡ *Gonocormus digitatus* (Sw.) Prantl (Prantl 1875: 51). ≡ *Microtrichomanes digitatum* (Sw.) Copel. (Copeland 1938: 36). ≡ *Crepidomanes digitatum* (Sw.) K.Iwats. (Iwatsuki 1984: 175). Type:—‘Habitat in Ins. Franciae et Borboniae’, without date, *without collector s.n.* (holotype S?, not located). Note: a potential type is kept at P, *L.-M.A. du Petit-Thouars s.n.* (P00064999!).

= *Trichomanes digitatum* Poir. (Poiret 1808: 70), *nom. illeg.* Type:—MADAGASCAR. ‘Ile de Madagascar’, without date, *L.-M.A. du Petit-Thouars s.n.* (lectotype P, P00612304!, here designated)

= *Trichomanes lanceum* Willd. (Willdenow 1810: 500). ≡ *Trichomanes loreum* Bory (Bory 1833: 79), *nom. illeg.* Type:—LA REUNION. ‘Ile de Bourbon’, without date, *J.B.G.M. Bory de St.-Vincent s.n.* (lectotype B, BW 20 208010!, here designated; isolectotype P, P04022563!). Note: Bory (1833: 78) proposed to rename *T. lanceum* as *T. loreum* because he considered that the concerned species does not exhibit significant lanceolate fronds and that his name was the first he has chosen before the Willdenow’s publication. However such proposition is not valid, and the Willdenow’s name, based on the same type specimen, keeps the priority and validity.

= *Trichomanes piliferum* Alderw. (van Alderwerelt van Rosenburgh 1922: 225). Type:—JAVA. Buitenzorg, Mt. Salak, November 1920, *van den Brink 4116* (not located).

= *Trichomanes taeniatum* Copel. (Copeland 1932: 6, pl. 2). ≡ *Microtrichomanes taeniatum* (Copel.) Copel. (Copeland 1938: 37). Type:—TAHITI. Pare, Fautaua, 13 May 1930, *M.L. Grant 3561* (holotype US, US00134628!).

= *Trichomanes digitatum* Sw. var. *uluguruense* Reimers (Reimers 1933: 912). Type:—TANZANIA. ‘Uluguru-Gebirge: NW., Bondua’, 25 November 1932, *H.J. Schlieben 3028* (holotype B, BW 20 0104376!; isotype B, BW 20 0104375!, BR, BR0000013204945!, BR0000013204952!).

= *Hymenophyllum alternatum* Fosberg (Fosberg 1950: 135), based on *Trichomanes dichotomum* Kunze (Kunze 1847: 302, *nom. nud.*; 1848: 285), *nom. illeg.* ≡ *Gonocormus dichotomus* (Kunze) Prantl (Prantl 1875: 51). ≡ *Microtrichomanes dichotomum* (Kunze) Copel. (Copeland 1938: 36). Type:—JAVA. Salak, November 1843, *H. Zöllinger 1707* (type P, P00624455!).

Note: Tardieu-Blot (1951) also cites *Trichomanes blumei* Hassk. as a synonym, but despite information provided by Tropicos and IPNI, we did not succeed in finding any publication from Hasskarl including the description of the species. The only study we found on ferns by Hasskarl (published in 1856-1857) concerns Gleicheniaceae and tree-ferns from Java (Hasskarl 1856).



Short description—Epiphytic; long-creeping filiform rhizomes, bearing sparsely distributed roots and long reddish-brown trichomes, and widely separated pending fronds; fronds with filiform wingless stipes, up to 5 cm long, palmate to mostly digitate, bearing marginal isolated minute black hairs (Fig. 15F), quite rare to absent on old leaves / specimens; sori few, terminal on most-apical segments, with a well-developed campanulate part, two lateral veinlets and a dilated bilabiate mouth; receptacle included to exerted at full maturity (Fig. 15G).

Global distribution—East tropical Africa to Pacific Islands.

Current distribution in Mascarenes—La Réunion, Mauritius (quite rare on the island).

Ecology—Usually epiphytic on the Mascarenes (reported as mostly lithophytic in Asia) on tree-trunks in lowland to montane rainforests (400–1,700 m).

Representative specimens examined—MAURITIUS. Without locality, without date, *F.W. Sieber s.n.* (P04022565); Brise Fer, December 2012, *K. Pynee et al. s.n.* (MAU 0009345); Rivière du Poste, March 2012, *K. Pynee et al. s.n.* (MAU 0011494); Mt Cocotte, October 2012, *K. Pynee et al. s.n.* (MAU 0011914); Plaine Paul, January 2013, *K. Pynee et al. s.n.* (MAU 0012600); Pétrin, February 2016, *K. Pynee et al. s.n.* (MAU 0017695).

—LA RÉUNION. Without locality, 1831, *C. Bélanger s.n.* (P0422564); Plaine des Palmistes, July 1875, *M.G. de L'Isle 354* (P00065000); Roche écrite, April 2005, *T. Janssen et al. 2750* (P00590831).

Note—*Hymenophyllum digitatum* is the only *Hymenophyllum* species on the Mascarenes and in the western Indian Ocean that has sori with a developed campanulate part (Fig. 15G), a feature that usually characterizes trichomanoids. This explains that most of the described related species were first placed in *Trichomanes* and that the Mascarenan species is named *T. digitatum* in Tardieu-Blot (1951, 2008). The taxonomic position of this species and relatives has actually been questionable and discussed for a long time. Copeland (1938) included these species in his genus *Microtrichomanes* (Mett.) Copel., based on *Microtrichomanes* Mett. (Mettenius 1864: 413, 414), considering such a genus as intermediate between *Hymenophyllum* and traditional *Trichomanes* (currently trichomanoids). The species actually combines *Trichomanes*-like sori and *Hymenophyllum*-like gross habit. Ebihara *et al.* (2004) nevertheless clearly demonstrated that most *Microtrichomanes* species, including traditional *T. digitatum*, belong to *Hymenophyllum* and more specifically to subgenus *Sphaerocionium*. Except for the sorus shape, *Microtrichomanes* taxa share with the other species of *Sphaerocionium* a laminar marginal indumentum, even if reduced.

## 21. *Hymenophyllum hirsutum* (L.) Sw. (Swartz 1800: 99), Fig. 16A–C

*Trichomanes hirsutum* L. (Linné 1753: 1098). ≡ *Sphaerocionium hirsutum* (L.) C.Presl (Presl 1843: 34). Type:—based on Plumier (see Cremers & Aupic 2008), 'Plum. fil. 73, t.50, f.B; Pet. fil. 105, t.15, f.5. Habitat in America' (lectotype: *Traité des fougères de l'Amérique* (1705), t. 50, fig. B, designated by Morton 1947); Plumier in herbier Tournefort 5315-1 (epitype P-TRF, P00322153!, designated by Cremers & Aupic 2008).

= *Trichomanes ciliatum* Sw. (Swartz 1788: 136). ≡ *Hymenophyllum ciliatum* (Sw.) Sw. (Swartz 1800: 100). ≡ *Sphaerocionium ciliatum* (Sw.) C.Presl (Presl 1843: 34). Type:—JAMAICA. Without locality, without date, *O. Swartz s.n.* (lectotype S, S-R-2960!, inadvertently designated by Proctor (1985); isolectotypes B, BW 20 222010!, LD, LD1773824!). Note: The combination *Hymenophyllum ciliatum* (Sw.) Fosberg, coined by Fosberg (in Fosberg & Sachet 1980: 1) and listed as such in some floras and databases, is illegitimate. Fosberg noted he had not found such a combination but he thus omitted the earlier work by Swartz, published in 1800.

= *Hymenophyllum arbuscula* Desv. (Desvaux 1827: 332). Type:—LA REUNION. 'Habitat in Borbonia', without date, *without collector* (lectotype P, P00477831!, here designated).

= *Hymenophyllum ciliatum* (Sw.) Sw. var. *imbricatum* Bonap. (Bonaparte 1923: 200). Type:—GABON. 'Pays Itsogho. Vallée de la Waka. Entre Moubenu et Dizoma.', October 1916, *G. Le Testu 2160* (holotype P, P00483495!; isotype P, P00483494!).

= *Hymenophyllum boryanum* Willd. (Willdenow 1810: 518, 519). ≡ *Hymenophyllum ciliatum* (Sw.) Sw. var. *boryanum* (Willd.) Mett. ex Kuhn (Kuhn 1868: 39). Type:—LA REUNION. 'Bourbon', without date, *J.B.G.M. Bory de St.- Vincent s.n.* (lectotype B, BW 20 240010!, here designated; isolectotype P, P00477832!).

Note: *Hymenophyllum ciliatum* (Sw.) Sw. var. *majus* Tardieu (Tardieu-Blot 1951: 14) was previously listed as additional synonym (Saïd *et al.* 2017) but our re-examination of specimens (P01315030, P00483494) seems to indicate that they rather belong to the distinct Malagasy *H. poolii* Baker (Baker 1876: 415) or eventually are hybrids between *H. hirsutum* and *H. poolii* (as also suggested by F. Rakotondrainibe, comm. pers.), hence explaining that we excluded this taxon for this treatment.

Short description—Epiphytic; long-creeping filiform rhizomes, bearing sparsely distributed roots and long reddish-brown trichomes, and widely separated pending fronds; fronds with winged stipes and rachises (Fig. 16B), up to 13 cm long, lanceolate to triangular, pinnate-pinnatifid to bipinnate-pinnatifid, densely hairy with light reddish-brown, stellate, pedonculated trichomes on rachises, veins and margins; numerous sori, round, paratactic, bilabiate without a developed base nor lateral veinlets and with hairy margins; receptacle short and included (Fig. 16C).



**FIGURE 16.** A. *Hymenophyllum hirsutum* (L.) Sw., as epiphyte (La Réunion, ‘Grand Etang’). B. *H. hirsutum*, detail of a frond showing the hairy winged stipe. C. *H. hirsutum*, detail of bilabiate hairy sori. D. *H. hygrometricum* (Poir.) Desv., as epiphyte (La Réunion, ‘Bébour’). E. *H. hygrometricum*, wet fronds become greener as shown here (photographs: A: J.-Y. Dubuisson; B–C: L. Bauret; D–E: C. Chaussidon).

Global distribution—Western Indian Ocean, tropical Africa, Neotropics.

Current distribution in Mascarenes—La Réunion, Mauritius.

Ecology—Epiphytic on tree-trunks in lowland rainforests (150–1,000 m).

Representative specimens examined—MAURITIUS. Pigeon Wood, September 2009, *K. Pynee et al. s.n.* (MAU 0011517); Pétrin, February 2016, *K. Pynee et al. s.n.* (MAU 0019002); Mt Cocotte, October 2010, *S. Hennequin et al. 323* (MAU 0022461, P02432384).

—LA RÉUNION. Mare Longue, April 2002, *J.-Y. Dubuisson HR 2002-16* (P0243298).

Note—This species is easily distinguished from the other hairy Mascarenan *Hymenophyllum* species by its fully winged stipes.

**22. *Hymenophyllum hygrometricum* (Poir.) Desv. (Desvaux 1827: 333), Fig. 16D, E**

*Trichomanes hygrometricum* Poir. (Poiret 1808: 79). ≡ *Sphaerocionium hygrometricum* (Poir.) Copel. (Copeland 1938: 31). Type:—‘Habitat in Madagascaria’, without date, *L.-M.A. du Petit-Thouars s.n.* (lectotype P, P00483511!, here designated; isolectotype P, P00483512!). Note: the species would be absent in Madagascar and endemic to the Mascarenes, the locality indicated by Poiret in his protologue and indeed corresponding to the P00483512 specimen would be therefore erroneous.

= *Hymenophyllum elasticum* Bory ex Willd. (Willdenow 1810: 520). ≡ *Sphaerocionium elasticum* (Willd.) C.Presl (Presl 1843: 34, t. 4, fig. 13). Type:—‘A Bourbon et l’île de France’, without date, *J.B.G.M. Bory de St.-Vincent s.n.* (lectotype B, BW 20 244010!, here designated; isolectotype P, P00477833!).

= *Hymenophyllum flavo-aureum* Bory (Bory 1834: 84). ≡ *Hymenophyllum hygrometricum* (Poir.) Desv. var. *flavo-aurea* (Bory) Mett. ex Kuhn (Kuhn 1868: 40). Type:—‘Mascareigne’, without date, *C. Bélanger s.n.* (not located).

Short description—Epiphytic; long-creeping thin rhizomes, bearing sparsely distributed roots and very abundant long reddish-brown trichomes, and widely separated pending fronds; fronds with wingless stipes and rachises narrowly winged at their upper part, up to 30 cm long, sometimes longer, deltoid to widely lanceolate, bi-pinnate-pinnatifid to tri-pinnate-pinnatifid, densely hairy with reddish-brown, stellate, non-pedunculated trichomes on rachises, veins and margins; numerous sori, paratactic, bilabiate without a developed base nor lateral veinlets, and with hairy margins; receptacle short and included.

Global distribution—Mascarenes, presence in Madagascar doubtful, presence in Seychelles awaits confirmation.

Current distribution in Mascarenes—La Réunion, Mauritius (rare on the island).

Ecology—Epiphytic on tree-trunks in lowland and montane rainforests (50–1,700 m).

Representative specimens examined—MAURITIUS. Brise Fer, December 2012, *K. Pynee et al. s.n.* (MAU 0009343); Mt Cocotte, March 2011, *K. Pynee et al. s.n.* (MAU 0019005); Mt Cocotte, March 2008, *K. Pynee et al. s.n.* (MAU).

—LA RÉUNION. Ste Agathe, July 1875, *M.G. de L’Isle 375* (P01330237); Bébour, April 1956, *J. Bosser 9565* (P01330245); Télélave, February 1962, *T. Cadet 13bis* (P01330241); Mare Longue, December 1967, *T. Cadet 1198* (P01330236), September 1968, *T. Cadet 1633* (P01330235).

Note—This robust species is readily distinguished from the other hairy species in the region by its overall shape (mostly deltoid to widely lanceolate vs. oblong to linear for *H. capillare*), and frond size, type of trichomes, and stipe wings (large fronds, not pedunculated trichomes, and wingless stipes vs. small fronds, pedunculated trichomes and winged stipes for *H. hirsutum*).

The type is cited from Madagascar, according to a little note on the original sheet. But except for this type specimen, the species has actually never been observed in the wild in Madagascar and is absent in Malagasy collections, as far as we are aware. We thus consider that the type locality is erroneous and according to the current distribution, that the type specimen would likely have been collected in the Mascarenes. Specimens resembling *H. hygrometricum* have been observed and collected in the Seychelles (B. Senterre, pers. comm.), but they could also belong to the Malagasy species *H. ivohibense* Tardieu (Tardieu-Blot 1941: 90, 91) that shows the same gross habit, but differs in having stipes winged at their upper part and pedunculated laminar trichomes. Additional investigations are thus needed to confirm the presence of *H. hygrometricum* outside of the Mascarenes.

Subgenus *Mecodium*

**23. *Hymenophyllum balfourii* Baker (Baker 1891: 192), Fig. 17A**

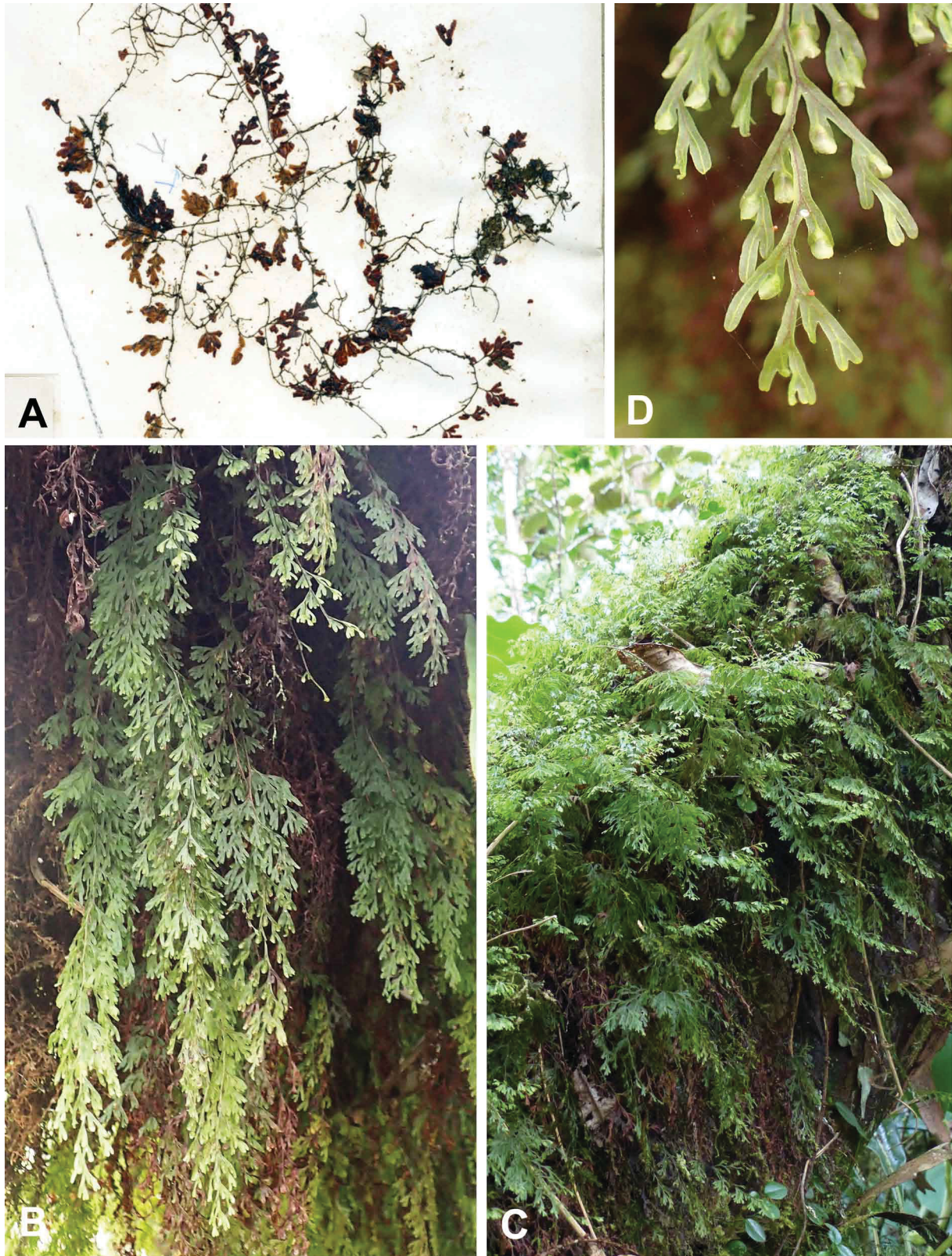
Type:—LA RÉUNION. Without locality, before 1875, *I.B. Balfour s.n.* (holotype K, K000435603!).

Short description—Lithophytic or epiphytic; long-creeping filiform rhizomes, bearing sparsely distributed roots and reddish-brown trichomes, and widely separated pending fronds; fronds glabrous, subsessile or with very short filiform stipes, up to 4 cm long, often less than 3 cm long, deltoid to ovate, digitate to pinnatifid, sometimes pinnate-pinnatifid with dichotomously dissected pinnae; sori few, on apical-most segments, bilabiate without a developed base but two lateral veinlets; receptacle filiform and included.

Global distribution—Madagascar and potentially in Mascarenes.

Current distribution in Mascarenes—The species awaits rediscovery on both La Réunion and Mauritius.

Ecology—Epiphytic on tree-trunks or lithophytic on wet rocks in montane rainforest usually at high elevations in Madagascar. Because of the lack of recent records in Mascarenes, we cannot define elevational range for the archipelago.



**FIGURE 17.** A. *Hymenophyllum balfourii* Baker, holotype (La Réunion, *I.B. Balfour s.n.*, K000435603). B. *H. inaequale* (Poir.) Desv., as epiphyte, narrowly lanceolate form (La Réunion, ‘Mare Longue’). C. *H. inaequale*, widely lanceolate to ovate form (La Réunion, ‘Forêt de Bon Accueil, Les Makes’). D. *H. inaequale*, detail of glabrous segments and sori (photographs: B. L. Bauret; C–D: J.-Y. Dubuisson).

Specimens examined—MAURITIUS. Without locality, 1864, *P.B. Ayres s.n.* (K000435602); Deux Mamelles, December 1972, *D. Lorence s.n.* (MAU 15023); Mount Lagrave, April 1974, *D. Lorence 780* (MAU 16362).

Note—According to unpublished molecular data from a Mauritian Lorence’s specimen, *H. balfourii* could be a dwarf form of *H. inaequale* (Poir.) Desv. (Desvaux 1827: 335). The species was discovered and described on La

Réunion at the end of the 19th century, and collected three times on Mauritius: the first time in 1864 with a specimen (*P.B. Ayres s.n.*, K000435602) present on the same sheet as the La Réunion type by Baker, the second time on ‘Deux Mamelles’ mountain in 1972 (*D. Lorence s.n.*, MAU 15023), and the third time on the Mount Lagrave in 1974 (*D. Lorence 780*, MAU 16362). The species has never been observed again on La Réunion since the original description, and its current presence on Mauritius awaits confirmation. The species could be thus considered as currently extinct on La Réunion or may be present but only at inaccessible sites at high elevations. On Mauritius, the species was observed in 1972 and 1974 as an epiphyte on respectively a tree and an *Alsophila* trunk in a degraded forest invaded by exotic species, as noted on the sheets. In the absence of precise location data, we have no guaranty that both populations still exist; in addition, the species has not been observed elsewhere since these last observations more than 40 years ago. Finally, in the P collections the species is only known by recent Malagasy specimens, but more investigations are required to confirm the affinity between these Malagasy specimens and the Mascarene ones. The potential rediscovery of the species can therefore be expected on both Mascarene islands.

#### 24. *Hymenophyllum inaequale* (Poir.) Desv. (Desvaux 1827: 335), Fig. 17B–D

*Trichomanes inaequale* Poir. (Poiret 1808: 74, 75). ≡ *Mecodium inaequale* (Desv.) Copel. (Copeland 1938: 96). Type:—‘île de Madagascar’, without date, *L.-M.A du Petit-Thouars s.n.* (lectotype P, P00483501!, here designated; paralectotype P, P00483502!, 2 fronds only, annotated ‘C’, bottom right corner).

= *Hymenophyllum gracile* Bory ex Willd. (Willdenow 1810: 527). ≡ *Sphaeroconium gracile* (Bory) C.Presl (Presl 1843: 35). Type:—MAURITIUS. ‘De l’île de France’, without date, *J.B.G.M. Bory de St.-Vincent 120* (lectotype B, BW 20 231010!, here designated; isolectotype P, P00477835!).

Short description—Epiphytic; long-creeping filiform rhizomes, bearing sparsely distributed roots and reddish-brown trichomes, and widely separated pending fronds; fronds stipitate, with stipes fully winged or winged only in their upper part and the wing usually thin (up to 2–3 cells wide), rarely wingless, and rachises fully winged, up to 30(–40) cm long, glabrous, quite variable in shape, triangular to lanceolate, or widely ovate, bipinnate-pinnatifid to often tripinnate-pinnatifid; numerous sori, paratactic, bilabiate without a developed base but two lateral veinlets; receptacle included, sometimes slightly exerted (Fig. 17D).

Global distribution—Western Indian Ocean, presence in tropical Africa (according to Kornaš 1984) awaits confirmation.

Current distribution in Mascarenes—La Réunion, Mauritius.

Ecology—Epiphytic on tree-trunks from lowland rainforests to high elevations (100–2,400 m).

Representative specimens examined—MAURITIUS. Gaulettes Serrées, May 2007, *K. Pynee et al. s.n.* (MAU 0008222); Alma Hill, October 2012, *K. Pynee et al. s.n.* (MAU 0008230); Tamarind Falls, May 2011, *K. Pynee et al. s.n.* (MAU 0008244); Bar Le Duc, August 2011, *K. Pynee et al. s.n.* (MAU 0009261); Curepipe Point, February 2013, *K. Pynee et al. s.n.* (MAU 0011917); Macabé, October 2010, *S. Hennequin et al. 338* (MAU 0014814, P02432402). —LA RÉUNION. Bélouve, April 1956, *J. Bosser 9563* (P01305963); Mare Longue, April 2016, *L. Bauret 187, 186, 190* (P); Vallée Heureuse, April 2016, *L. Bauret 197* (P); Ravine Pont Rouge, April 2016, *L. Bauret 192* (P); Pandanaie de la Plaine des Palmistes, April 2016, *L. Bauret 198* (P); Ravine des Grègues, April 2016, *L. Bauret 194* (P).

Note—*Hymenophyllum inaequale* can be easily confused with similar *Mecodium* species, and especially the specimens often classified under *H. polyanthos* (Sw.) Sw. (Swartz 1800: 102). However, molecular phylogenetic results indicate that *H. inaequale* is distinct from Tanzanian *H. kuhni* C.Chr. (Christensen 1905: 363) and paleotropical *H. “polyanthos”* (including *H. capense*) and all these species are also distinct from true neotropical *H. polyanthos* (Hennequin *et al.* 2003, 2010). Furthermore, *H. inaequale*, especially on La Réunion, presents a high level of polymorphism in laminar shape. At low elevations and in shady places, we often observe specimens showing quite long and pending narrowly lanceolate, plane fronds with highly acute to attenuate apices and pinnae often linear and clearly distinct and not overlapping (Fig. 17B). By contrast, at high elevations and in sunny places, specimens are smaller, with fronds more widely lanceolate or ovate, often with obtuse to rounded apices and apical pinnae often overlapping, and laminae sometimes slightly curled (Fig. 17C). Such differences could suggest the existence of at least two distinct species: *H. inaequale* and *H. kuhni* or *H. capense*, the latter both potentially present in the region (as discussed by Saïd *et al.* 2017). However, personal unpublished molecular data and presence of all the intermediate forms in the wild clearly indicate that *H. inaequale* is the single, large, highly polymorphic *Mecodium* species currently present in the archipelago.

**25. *Polyphlebium diaphanum* (Kunth) Ebihara & Dubuisson (Ebihara *et al.* 2006: 240), Fig. 18A, B**

- Trichomanes diaphanum* Kunth (Humboldt *et al.* 1815 [1816]: 25). ≡ *Vandenboschia diaphana* (Kunth) Copel. (Copeland 1938: 53). Type:—VENEZUELA. ‘Temperatis Provinciae Venezuelae’, without date, *A. Humboldt & A. Bonpland s.n.* (lectotype P, P00669210!, here designated; isoelectotype B, BW 20 0086870!, here designated, following the R. G. Stolze’s annotation of isotype on the sheet).
- = *Trichomanes borbonicum* Bosch (van den Bosch 1861b: 158, 159). ≡ *Vandenboschia borbonica* (Bosch) G.Kunkel (Kunkel 1963: 213). ≡ *Crepidomanes borbonicum* (Bosch) J.P.Roux (Roux 2001: 45). ≡ *Polyphlebium borbonicum* (Bosch) Ebihara & Dubuisson (Ebihara *et al.* 2006: 240). Type:—LA REUNION. ‘Hab. Ins. Borboniae’, without date, *L.H. Boivin 908* (lectotype B, BW 20 0103881!, designated by Schelpe & Anthony (1986: 76); isoelectotype P, P00065006!, here designated).
- = *Trichomanes brasiliense* Desv. (Desvaux 1827: 328, t. 7, f. 4). Type:—BRAZIL. ‘Habitat in Brasilia’, without date, *without collector* (lectotype P, P00624517!, here designated).
- = *Trichomanes eximium* Kunze ex Sturm (Sturm 1859: 271, Pl. 18, Fig. 2). Type:—VENEZUELA? Without locality, without date, *Moritz 148* (not located). Note: The type is reported in Kunze (1847: 350), and has not been observed, but the Fig. 2 (in Pl. 18) in Sturm (1859) shows clearly a *P. diaphanum*, hence we accept here the synonymy.
- = *Trichomanes debile* Bosch (van den Bosch 1861b: 154). ≡ *Trichomanes pyxidiferum* var. *debile* (Bosch) Sodiro (Sodiro 1890: 290). Type:—VENEZUELA. Carabobo, 1846, *Funck & Schlim 596* (isotype BR, BR0000006988135!, BR0000006987466!, BR0000006988128!, BR0000006987794!).
- = *Trichomanes hymenophylloides* Bosch (van den Bosch 1863: 209), *nom. nov.* for *Trichomanes leptophyllum* Bosch (van den Bosch 1858: 363), *nom. illeg.*, non A.Cunn. (Cunningham 1836: 368). ≡ *Vandenboschia hymenophylloides* (Bosch) Copel. (Copeland 1938: 53). ≡ *Polyphlebium hymenophylloides* (Bosch) Ebihara & Dubuisson (Ebihara *et al.* 2006: 240). Type:—SAINT VINCENT. Without locality, without date, *L. Guilding s.n.* (type GH, GH00022242!). Note: *Trichomanes leptophyllum sensu* Bosch actually corresponds to the illustration of *Trichomanes pyxidiferum* by Hooker & Greville (1831: pl. 206) based on specimens collected by L. Guilding in Saint Vincent Island and thus considered by van den Bosch as a distinct species, as discussed and confirmed later by Slosson (1915) (see also Ponce *et al.* 2017).
- = *Trichomanes tranninense* Fée (Fée 1869: 187, t. 69, f. 1). Type:—BRAZIL. Rio de Janeiro, Macaé, 19 May 1868, *A. Glaziou 2251* (holotype P, P00624521!; isotype BR0000013094973!).
- = *Trichomanes goetzei* Hieron. (Hieronymus 1900: 339). Type:—TANZANIA. Uluguru Gebirge, 22 November 1898, *W. Goetze 194* (holotype B, BW 20 0093147!; isotype BM).
- = *Trichomanes eximium* Kunze ex Sturm var. *crispulum* Rosenst. (Rosenstock 1924: 89). Type:—BRAZIL. Rio de Janeiro, Organ mountains, Est, August 1915, *P. von Luetzelburg 6196* (lectotype US, US00512793!, designated by Lellinger (1977: 732); isoelectotype M).
- = *Trichomanes pyxidiferum* L. var. *organense* Rosenst. (Rosenstock 1924: 89). Type:—BRAZIL. Rio de Janeiro, Serra dos Orgaos, 1910, *P. von Luetzelburg 92* (lectotype S, S06-1221!, here designated; isoelectotypes M; NY, NY 00144725!); BRAZIL. Rio de Janeiro, Serra dos Orgaos, 1910, *P. von Luetzelburg 93* (remaining syntype M).
- = *Trichomanes pyxidiferum* L. f. *gracile* Rosenst. (Rosenstock 1924: 90). Type:—BRAZIL. Rio de Janeiro, Corcovado, 1910, *P. von Luetzelburg 262* (lectotype NY, NY 00144726!, here designated; isoelectotype M).

Short description—Epiphytic or lithophytic; long-creeping filiform rhizomes, bearing sparsely distributed roots and reddish-brown trichomes, and widely separated pending fronds; fronds stipitate, up to 17 cm long, more often less than 10 cm long, deltoid to ovate, pinnate-pinnatifid to bipinnate-pinnatifid, without false veins or folds; sori numerous, paratactic, twice or more longer than wide, cylindrical with slightly dilated mouth (Fig. 18B); receptacle short to long-exserted.

Global distribution—Pantropical (see note).

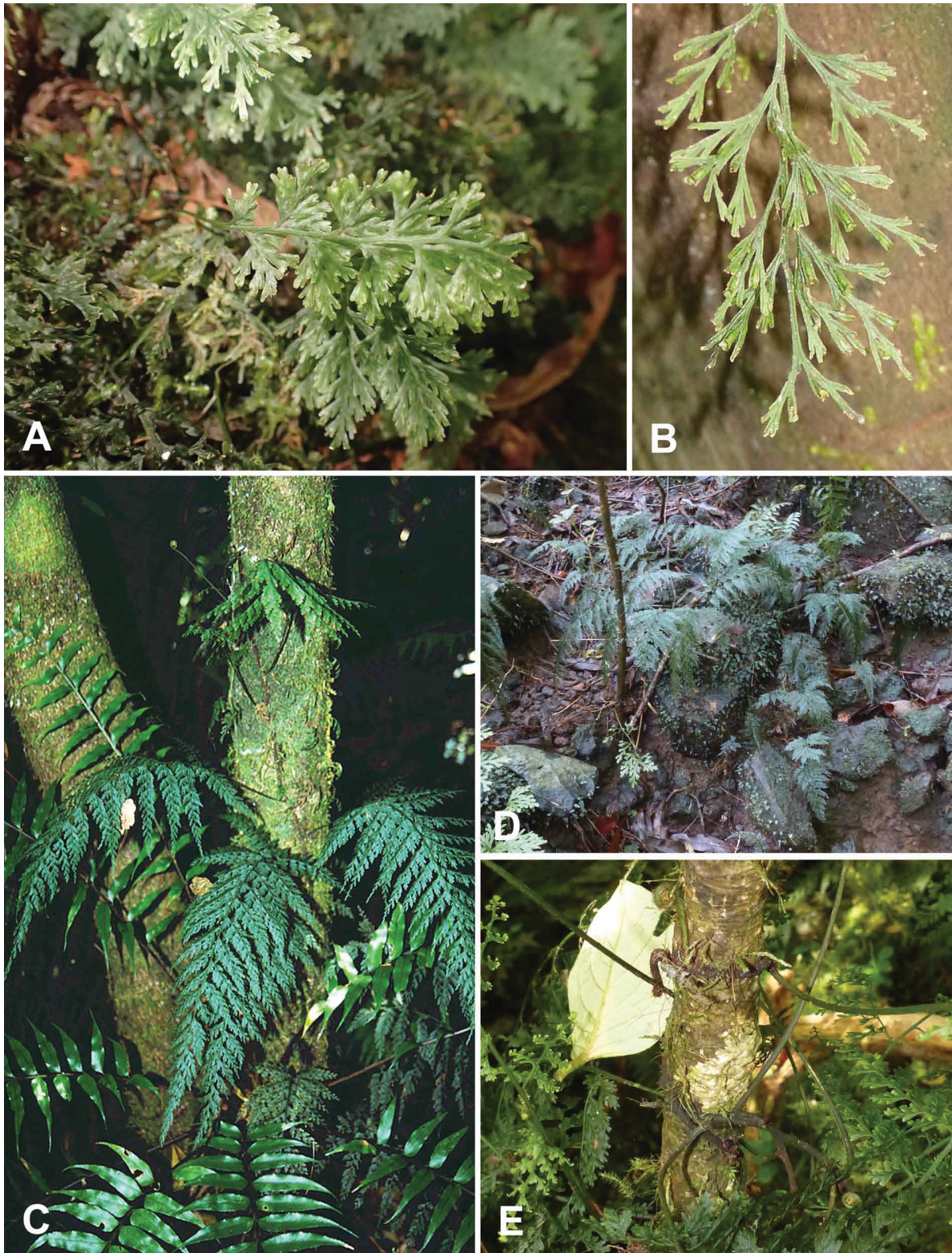
Current distribution in Mascarenes—La Réunion.

Ecology—Epiphytic on tree-trunks or lithophytic on wet rocks in lowland to montane rainforests and high elevations (550–2,100 m).

Specimens examined—LA RÉUNION. Without locality, without date, *J.M.C. Richard s.n.* (P01330947); Bélouve, October 1882, *sine collector* (P01330933); Bébou, March 1969, *T. Cadet 2099* (P01330937); Cirque de Takamaka, January 1972, *T. Cadet 3395* (P01330939); Petite Plaine des Palmistes, January 1973, *T. Cadet 4004* (P01330941); Bébou, April 1999, *J.-Y. Dubuisson HR-1999-22* (P), *HR-1999-31* (P).

Note—In local floras (e.g. Tardieu-Blot 1951, 2008; Grangaud 2010), this species is named *P. borbonicum* and considered as such to be restricted to tropical Africa and the western Indian Ocean. Ebihara *et al.* (2009) suggested that *P. borbonicum* should be included into a pantropical complex associating populations from the Pacific and neotropics. Ponce *et al.* (2017) clearly showed that the La Réunion specimens are phylogenetically imbedded into a robust clade

with neotropical *P. diaphanum* (and *P. hymenophylloides* considered as synonym). Furthermore, there is no clear morphological character that could allow precisely distinguishing all the specimens belonging to *P. borbonicum*, *P. diaphanum*, and *P. hymenophylloides*. We thus adopt here the taxonomic treatment of Ponce *et al.* (2017) considering *P. diaphanum* as a widespread pantropical species including *P. borbonicum*.



**FIGURE 18.** A. *Polyphlebium diaphanum* (Kunth) Ebihara & Dubuisson, as epiphyte (La Réunion, ‘Forêt de Bon Accueil, Les Makes’). B. *P. diaphanum*, detail of a frond and sori. C. *Vandemboschia gigantea* (Bory ex Willd.) Pic.Serm., climbing on a tree trunk (La Réunion, ‘Mare Longue’). D. *V. gigantea*, terrestrial parts (La Réunion, ‘Grand Etang’). E. *V. gigantea*, detail of a long-creeping climbing rhizome (photographs. A: L. Bauret; B–E: J.-Y. Dubuisson).

Genus *Vandenboschia* Copel. (Copeland 1938: 51)

**26. *Vandenboschia gigantea* (Bory ex Willd.) Pic.Serm. (Pichi Sermolli 1968: 197), Fig. 18C–E**

*Trichomanes giganteum* Bory ex Willd. (Willdenow 1810: 514, 515). ≡ *Trichomanes radicans* Sw. (Swartz 1800: 97) var. *gigantea* (Bory ex Willd.) Mett. ex Kuhn (Kuhn 1868: 36). Type:—‘Ile Mascareigne’, without date, *J.B.G.M. Bory de St.-Vincent 122* (lectotype B, BW 20 216010!, here designated; isolectotype P, P00477826!).

Short description—Terrestrial and climbing; long-creeping thick rhizomes with robust roots (especially on terrestrial parts), bearing widely separated erect to pending fronds; fronds stipitate, up to 60 cm long, lanceolate to ovate, bipinnate-pinnatifid to tripinnate-pinnatifid or more divided; numerous sori, paratactic, cylindrical to obconic with truncated mouth; receptacle short to long-exserted.

Global distribution—Comores, Madagascar, La Réunion.

Current distribution in Mascarenes—La Réunion.

Ecology—Hemiepiphytic in lowland to montane rainforests (450–1,500 m). The plant first colonizes a wide surface of soil in the understory (Fig. 18D), and then is able to secondarily climb onto tree-trunks (as also detailed in Dubuisson *et al.* 2003).

Specimens examined—MAURITIUS. Without locality, without date, *sine collector* (MAU 2079); without locality, without date, *sine collector* (P01526230); without locality, without date, *sine collector* (P01526238); without locality, without date (likely 19th century), *C. Meller s.n.* (MAU 2080); without locality, 1868, *C. Meller s.n.* (P01526229).

—LA RÉUNION. Without locality, 1848, *M. Boivin s.n.* (P01430213); Bébour, August 1971, (collected by M. Sauvage) *R. Hébant 121* (P); Takamaka, July 1991, *D. Lorence 6946* (MAU 22068); Forêt de Mare Longue, April 2002, *J.-Y. Dubuisson HR 2002-14* (P02433296).

Note—This species is known only from a few old specimens (from the 19<sup>th</sup> century) in the Mauritian collections, but has not recently been observed on Mauritius, and hence we decided not to report it from the island.

***Taxonomic synthesis***

We here confirm the recent list of Hymenophyllaceae for the Mascarenes proposed by Granguaud (2010) which was actually based on our observations. To this, we add two new species for La Réunion (*Crepidomanes frappieri* recently rediscovered, and *C. trinerve*), two new varieties (*C. inopinatum* var. *tamonii*, *C. minutum* var. *mascarenense*) and one new forma (*Hymenophyllum capillare* f. *nanum*). Before its rediscovery and re-identification in 2010 by Y. Robert, *C. frappieri* was considered as absent or extinct on La Réunion. It is currently known on the island from at least 15 populations. It had likely been confused with other small *Crepidomanes* species and our data highlight the importance of constant and exhaustive investigations in the wild, especially in lowland wet ravines (as discussed below). Investigations on synonyms of *H. sibthorpioides* (see taxonomic treatment) revealed possible confusion with *C. minutum* (as also suggested B. Senterre, pers. comm.). Additional work will be needed on both taxa, which could lead to nomenclatural changes. For example, if *Trichomanes parvulum* Poir., usually treated as a synonym of *H. sibthorpioides*, is shown to be *C. minutum*, then *T. parvulum* would be the valid name of the latter species and would have to be combined under *Crepidomanes*. Furthermore, we update the nomenclature of *Abrodictyum meifolium* renamed here *A. parviflorum* according to Dubuisson *et al.* (2017), *Polyphlebium borbonicum* renamed here *P. diaphanum* according to Ponce *et al.* (2017), and of *H. tenellum* renamed here *H. fumarioides* as a new treatment.

***Hymenophyllaceae endemism and ecology on the Mascarenes***

Before this study, a single species was considered to be endemic to the archipelago (*Didymoglossum barklyanum*). We demonstrate here that we can add two further species: *H. hygrometricum* and *H. fumarioides*. The presence of these two species outside of the Mascarenes, and especially in Madagascar, as reported in floras and/or herbaria, appears not to be verified and thus likely erroneous. The confirmation of endemism for the variety *C. inopinatum* var. *tamonii* and for the forma *H. capillare* f. *nanum*, needs additional investigations in the wild, especially in Madagascar. *Crepidomanes minutum* var. *mascarenense*, initially considered as endemic to the Mascarenes, is actually present on all the islands of the western Indian Ocean hosting Hymenophyllaceae (except Rodrigues). In addition, similar (but not related) dwarf forms with rare frond proliferation (and named “*saxifragoides*”) are frequently observed in Asia and the Pacific (Nitta *et al.* 2011).

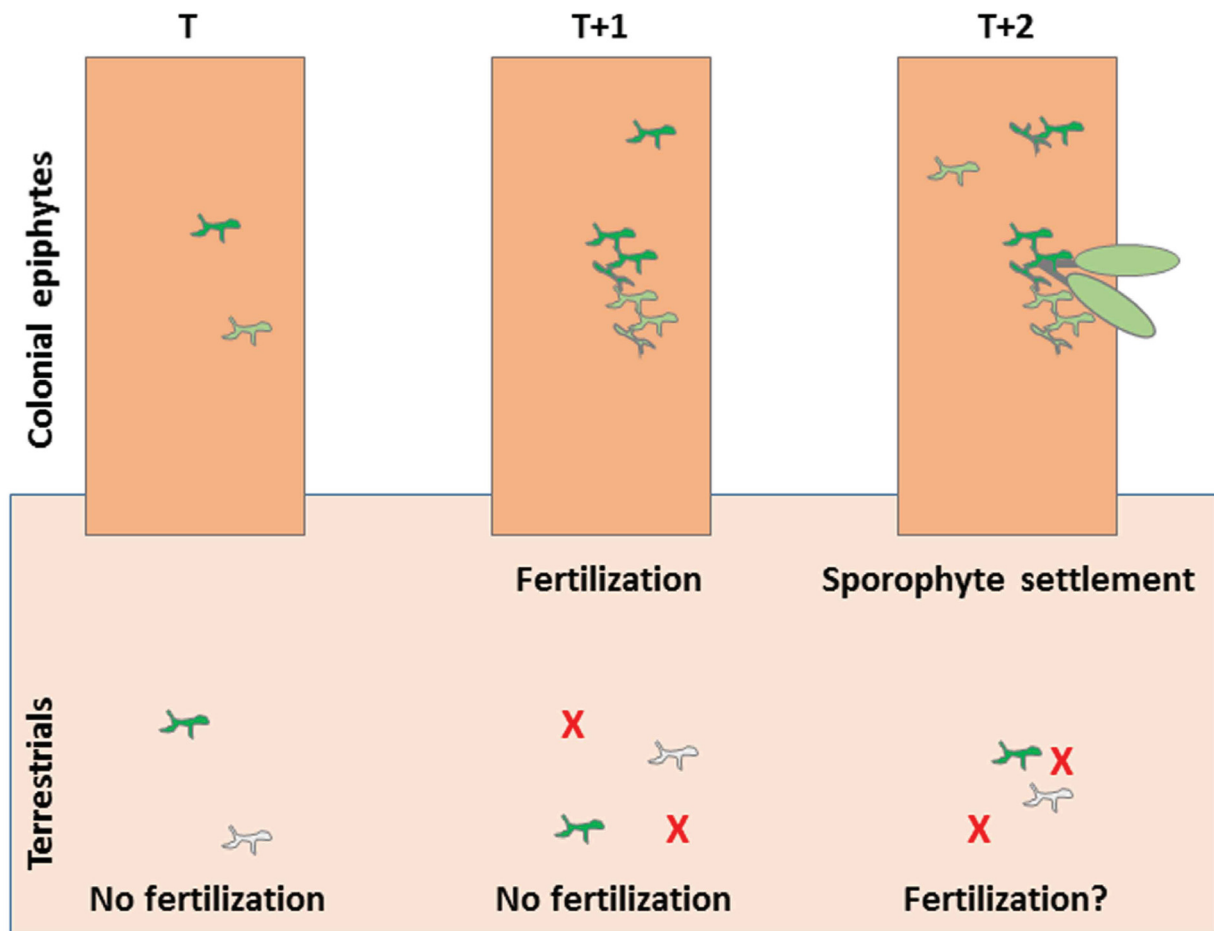
At the specific level, the endemism for Hymenophyllaceae remains low (13%). This contrasts with the endemism of the family in Madagascar, the closest continental island, with at least 16 endemic species out of 43 (37.2%) according to Tardieu-Blot’s data (1951), or with a corrected estimate of 19 out of 48 (39.6%) according to the recent revisions (F.



Rakotondrainibe, pers. comm.; Roux, 2009; Dubuisson *et al.* 2013, 2016, 2017; Bauret *et al.* 2015; Saïd *et al.* 2017). This is not unexpected if we compare the estimated ages of the isolation of Madagascar and of the appearance of the Mascarene Plateau (85 Myrs vs. 35 Myrs) and if we assume that endemism potentially increases with the age of an island.

This relatively low endemism is nevertheless more or less equivalent to that found in the archipelago for the fern families Aspleniaceae (13%), Blechnaceae (20%), Polypodiaceae (17.4%), Pteridaceae (10%), and Thelypteridaceae (14.3%), but contrasts to that of Dryopteridaceae (and principally genus *Ctenitis*; 52.2%), Lomariopsidaceae (3 out of 4 species; 75%), and Cyatheaceae (all 4 *Alsophila* species; 100%), according to Hennequin *et al.* (2014). The high diversity (at least 23 species) combined with the low endemism and the fact that all the three endemic species are not phylogenetically closely related (i.e., they do not cluster into a single distinct clade), suggest that the diversity of the Hymenophyllaceae in the archipelago would have originated from multiple colonization events rather than local diversification following few colonization. All non-endemic Hymenophyllaceae are present in Madagascar and the three endemic Mascarenan species also are closely related to species present in the western Indian Ocean (Ebihara *et al.* 2007; Hennequin *et al.* 2003, 2010; Dubuisson *et al.* 2013, 2016, 2017; pers. unpublished molecular data). This strongly suggests a Malagasy origin for the Mascarenan Hymenophyllaceae flora, in addition to a probable local anagenetic origin for each of the three endemic species.

Most Hymenophyllaceae taxa are colonial epiphytes and the gametophytes in the family are usually colonial and perennial. Dassler & Farrar (1997, 2001) proposed that colonial-epiphytic taxa with colonial long-lived gametophytes would have more success in colonizing distant oceanic islands than terrestrial taxa which have less strongly colonial and shorter-lived gametophytes (Fig. 19). The colonial and long-lived status of epiphytic gametophytes would actually increase the probability of fertilization between two distinct gametophytes, allowing relatively fast colonization and installation of epiphytic sporophytes. According to Dassler & Farrar's proposition, we could hypothesize that on distant oceanic islands (1) there are more epiphytic than terrestrial taxa, and (2) under competition, numerous species which would have succeeded in colonizing the same habitat at more or less the same time, would have fewer possibilities to diversify but could coexist if niches are not fully overlapping or if the available area is large enough to host them. On the Mascarenes, the first hypothesis seems probable: of the 23 species currently present on the archipelago, 20 are colonial epiphytes, one is hemi-epiphytic, one is an individual epiphyte, and a single is terrestrial (*A. parviflorum*) (4.3%), whereas Madagascar hosts at least 8 terrestrial species out of 48 species (16.7%) including *A. parviflorum*. The Mascarenan rainforests host many colonial epiphytic Hymenophyllaceae species that would have originated from numerous colonization events, resulting in a maximum of 17 colonial epiphytic taxa in the lowland rainforest and up to 13 taxa in the montane rainforest (see Table 3 and Fig. 20). This does not contradict the second hypothesis. By contrast, the twelve Mascarenan endemic and terrestrial *Ctenitis* species (Dryopteridaceae) have derived from a single common ancestor, hence illustrating a local cladogenetic radiation (Hennequin *et al.* 2017). The single Mascarenan terrestrial Hymenophyllaceae species, *A. parviflorum*, does not show an equivalent local radiation. With its gametophytes that are more long-lived than those of Dryopteridaceae and its ecological opportunism allowing a widespread distribution in all rainforest types on almost the entire elevational gradient in the western Indian Ocean (except the Comores), *A. parviflorum* would have quickly succeeded in colonizing the wet forests of the archipelago. This rapid colonization appears to have prevented a diversification process as well as, perhaps, the colonization by other terrestrial species of Hymenophyllaceae. By comparison, on the Comores archipelago, which is equidistant between Madagascar and southern Africa (see Fig. 1) and has more or less the same age as the current Mascarene islands, *A. parviflorum* is lacking and replaced by the terrestrial and closely related *A. pseudorigidum* Bauret & Dubuisson (Dubuisson *et al.* 2016: 161), also widespread in Madagascar, which occupies the same niches along the entire local elevational gradient (Dubuisson *et al.* 2016, 2017; Saïd *et al.* 2017). The latter species appears to have succeeded in colonizing the Comores archipelago instead of *A. parviflorum*, by competition or stochastically, and reciprocally on the Mascarenes for *A. parviflorum*. Both examples of species of Hymenophyllaceae and genus *Ctenitis* would therefore illustrate the importance of history, ecological preferences, and especially the gametophyte biology, too often neglected in ecological studies on ferns (as reviewed Walker *et al.* 2010), for explaining the local assemblage of the fern flora and contrasted patterns between lineages and localities.



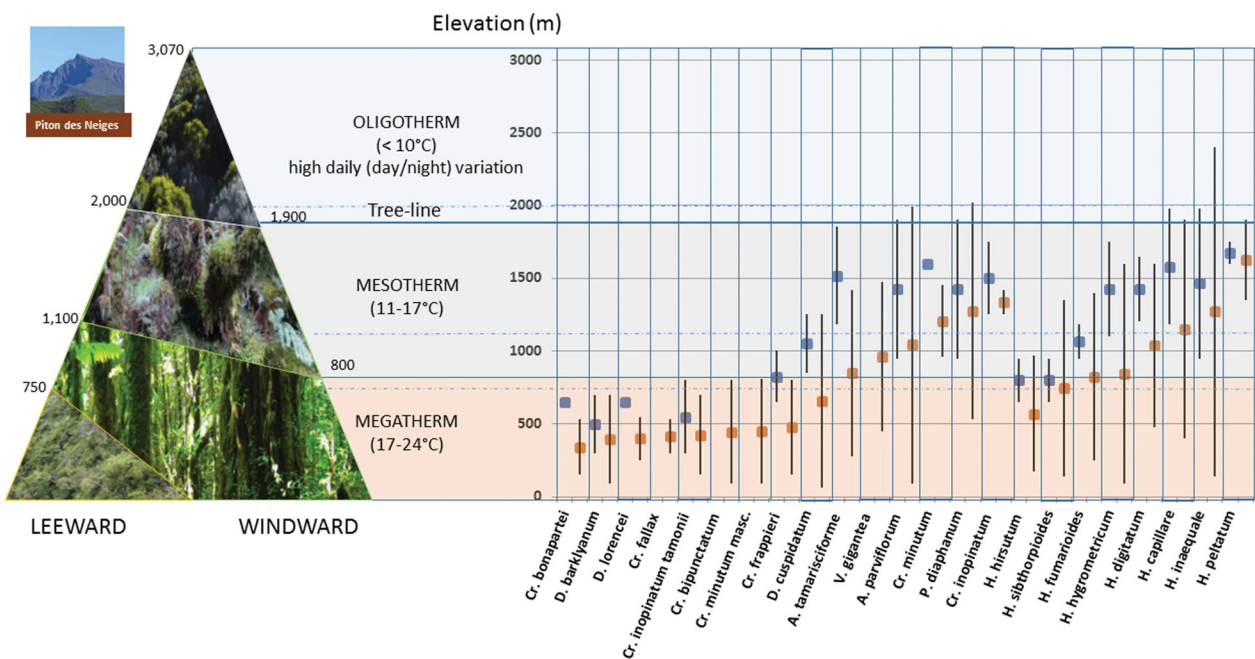
$$P(\text{settlement epiphytes}) > P(\text{settlement terrestrials})$$

**FIGURE 19.** Importance of gametophyte ecology and biology for the sporophyte settlement on distant islands according to Dassler & Farrar's (2001) hypothesis. The long-lived and colonial epiphytic gametophytes (above) would have the possibilities to realize fertilization many seasons/years (T) after the spore germination, whereas short-lived and non-colonial terrestrial gametophytes (below) would fail in realizing the fertilization if they are not close enough, and die at the end of the season (red crosses). Hence, the epiphytic taxa with long-lived and colonial gametophytes would have a higher probability of establishment than terrestrial taxa. Hymenophyllaceae and the genus *Ctenitis* (Dryopteridaceae) illustrate such contrasts in the Mascarene archipelago, explaining the difference in the level of endemism (see text for an in-depth discussion).

#### ***Hymenophyllaceae and elevational distribution***

We discuss here only the La Réunion data for which we have more or less complete transects and because Mauritian data are too fragmented and lack montane ecosystems. For La Réunion, Cadet (1980) linked the different ecosystems and their elevational range to thermal preferences and ranges (as also reviewed by Blanchard 2000). As such, the lowland rainforest, montane rainforest, and ericoid thickets were respectively named megathermous rainforest, mesothermous rainforest, and oligothermous thickets. On the windward side, the megathermous status corresponds to annual temperature averages between 24°C and 17°C, the range for mesotherm is 17–11°C and oligotherm shows temperature averages below 11°C (as reported in Fig. 20). We can thus classify Hymenophyllaceae taxa according to such thermal ranges or preferences. Our data allow defining at least three classes. The megathermous class groups the twelve taxa restricted to lowland forests or mostly present in lowland forests with possible occurrence up to the lowest part of the montane forests (and below 1,500 m): *C. bonapartei*, *C. bipunctatum*, *C. frappieri*, *C. inopinatum* var. *tamonii*, *C. minutum* var. *mascarenense*, *D. barklyanum*, *D. cuspidatum*, *D. lorencei* (thus all the *Didymoglossum* species), *H. fumarioides*, *H. hirsutum*, *H. sibthorpioides*, and *V. gigantea*. The mesothermous class groups the seven taxa restricted to montane forests with possible occurrence in the upper part of the lowland forests (foothills) and on the lower part of the oligotherm close to the tree-line: *A. tamarisciforme*, *C. inopinatum* var. *inopinatum*, *C. minutum* var.

*minutum*, *H. capillare*, *H. digitatum*, *H. peltatum* (restricted to the upper part of the mesotherm zone), and *P. diaphanum*. The opportunistic class groups the three taxa more or less present on the whole gradient and up to the oligotherm zone: *A. parviflorum*, *H. hygrometricum*, and *H. inaequale*, the latter species having the widest distribution, from almost the sea-level up to 2,400 m. *Hymenophyllum inaequale* is also the most abundant species on the whole gradient, being observed in 63 of the 107 plots (by excluding the leeward semi-dry forest; 56%). The secondmost abundant species is *H. hygrometricum* observed in 49 plots (45.8%) and the third one is *A. parviflorum* with 42 plots (39.3%). However, the most abundant within their typical elevational ranges are some megathermous species such as *D. cuspidatum* (from sea-level to 1,250 m) with occurrences in 69.4% of plots on the windward side and *C. bipunctatum* in 62% of such plots (here from 85 m to 800 m). In addition, the mesothermous *A. tamarisciforme* is observed in 50% of plots on the windward side (from 270 to 1,520 m). Except for the single *C. trinerve* population, the rarest species appears to be the megathermous *C. bonapartei*, observed in 3 localities only, including one population in a wet ravine on the leeward side. There is no oligotherm class and thus no species restricted to ericoid thickets. Actually, the presence of Hymenophyllaceae in the oligotherm is exceptional and anecdotal. The specimens are found in rare places, often as lithophytic on wet ravines close to streams or as low epiphytes on rare small trees at high elevations in sheltered areas (pers. obs.). We can note that *A. tamarisciforme* is mostly observed as epiphytic on tree-fern trunks (*Alsophila* spp.). Hence, its distribution is likely related to that of such phorophytes. The specific relationship between epiphytes and phorophytes was not been tested here, but should be taken into consideration in further studies, as suggested here for *A. tamarisciforme* and as evidenced by Moran & Russel (2004) on a neotropical species. Lehnert *et al.* (2017) further suggested that the connections of the root mantle of tree ferns to the soil allows the upward growth of mycorrhizal fungi which may also be important in determining the growth of epiphytic Hymenophyllaceae.



**FIGURE 20.** Elevational distribution on each Hymenophyllaceae taxon on the windward (red plots) and leeward (blue plots) sides of La Réunion, and correspondence with thermal zones or ranges according to Cadet (1980) and provided here for the windward side, with ranges of annual average temperatures. The dotted horizontal lines correspond to the limits of leeward ecosystems. The plots indicate the average elevation. *Crepidomanes trinerve* is here lacking because it was only observed at a single locality on the leeward side ('Les Canots' at ~800 m). The range of each taxon, as illustrated by the vertical lines, is assumed to correspond to the range between the minimum and the maximum elevation at which they have been observed, even if the taxon has not been observed in all the intermediate localities between such limits.

On the leeward side, the elevational ranges of wet ecosystems are shift upwards, especially for the megathermous rainforest which is thus restricted to the foothills. One consequence could be that elevational ranges of hygrophilous taxa are also modified. But as shown in Fig. 20, apart from a few examples (*A. tamarisciforme* and the single population of *C. minutum* var. *minutum*), the distribution of each taxon present on the leeward side is more or less embedded into

their distribution on the windward side. This could suggest that the elevational distribution of Hymenophyllaceae species is mainly conditioned by the thermal preferences. The presence of some species in wet ravines within the leeward semi-dry forests more or less at the same elevations as populations in windward lowland rainforests would add support to this hypothesis.

The existence of the three elevational species groups might explain the elevational distribution of species richness (Fig. 5), which displays three modes: the first and highest one in the megatherm zone (~450–600 m), a second one in the mesotherm zone (~1,200–1,500 m) below the ‘Tamarinaie’, and a small third one close to the tree-line (~1,950–2,100 m). The third mode is actually due to three opportunistic species. Similar peaked richness patterns based on the zonation of fern distributions have also been observed in the Andes (Kessler 2000) and Costa Rica (Kluge *et al.* 2008).

We assume here that most Mascarenan Hymenophyllaceae would have a Malagasy origin. We also hypothesize that the ecology and elevational gradient of the Mascarenan taxa would reflect the ecology and elevational distribution of the same taxa in Madagascar. In order to understand the patterns observed on the Mascarenes and the related processes, a comparison with Madagascar and neighboring areas is needed. Further studies and analyses should include Malagasy data and the phylogenetic historical background, including molecular dating, that will allow clarifying the assemblage and distribution of Hymenophyllaceae at the western Indian Ocean level.

### ***Hymenophyllaceae and conservation biology in the Mascarenes***

The montane forest (lacking on Mauritius) hosts a high diversity in Hymenophyllaceae with up to 15 taxa in the mesotherm and a maximum of 12 taxa for one locality. The ferns are also abundant in the understory covering most of the tree trunks as shown in ‘Avoune végétation’ and ‘Tamarinaie’ (see Fig. 3A, B). This seems to be in accordance with the global observations of high diversity characterizing mesothermous montane and cloud forests at the pantropical level, especially concerning vascular epiphytes (as reviewed by Krömer *et al.* 2005; Kluge *et al.* 2006; Kluge & Kessler 2011). However, we here show that the maximum diversity for Hymenophyllaceae, at least in Mascarenes, is observed in the megathermous rainforest, as also shown locally for orchids (Jacquemyn *et al.* 2005). This habitat hosts 21 of the 26 total taxa, and a maximum of 16 taxa for one locality, including 2 of the 3 endemic species and the 2 varieties restricted there. Megathermous ecosystems have been mostly replaced on La Réunion and Mauritius by crops and urban zones, and most remnants are invaded by exotic species (Strasberg *et al.* 2005; Virah-Sawmy *et al.* 2009; pers. obs.). By replacing the indigeneous trees, which are potential phorophytes for the numerous epiphytic species, exotic species would likely have a negative impact on the growth of indigeneous epiphytes. Furthermore, by comparison with La Réunion and because the island is older, Mauritius could host at all of the 21 La Réunion taxa present in the megatherm zone. The six lacking taxa (*C. fallax*, *C. frapperi*, *H. sibthorpioides*, *H. capillare* and its dwarf form, *P. diaphanum*, and *V. gigantea*) present at the western Indian Ocean level would likely have been present in the original Mauritian rainforests and would have disappeared since the human colonization in the 17<sup>th</sup> century. As examples, *V. gigantea* and *H. sibthorpioides* are reported in collections but have not been recently observed. Furthermore, many species have been reported recently or in collection from a single or two localities only: *C. bonapartei*, *C. inopinatum* var. *tamonii*, *C. minutum* var. *mascarenense*, *C. trinerve*, *D. barklyanum*, *D. lorencei*, *H. fumarioides*, and *H. hygrometricum*; and this correspond to 53.3% of the current Mauritian species diversity. The Hymenophyllaceae, in addition to orchids, highlight therefore the importance of lowland ecosystems for the preservation of local biodiversity that should benefit from equivalent protections (if possible) as montane ecosystems. Most of the protected areas on La Réunion actually belong to the mesotherm and oligotherm zones within the National Park.

The leeward lowland semi-dry forests have also suffered from human activities and remain at only a few sites (Strasberg *et al.* 2005). We show here that on La Réunion such threatened ecosystems host an unexpected diversity of hygrophilous plants, comprising at least 8 Hymenophyllaceae taxa (38% of the megathermous diversity). Semi-dry forests are crossed by numerous shady ravines with streams that maintain rocks permanently humid, even during the dry winter (see Fig. 4D). Such shaded, wet rocks are suitable to host some Hymenophyllaceae populations that are usually also present in the rainforest at the same elevations. In addition, the present species are all small to dwarf (including the dwarfed *C. inopinatum* var. *tamonii*) and as such appear to have lower hygrophilous requirements than large epiphytic species, growing as dense colonies on vertical or inclined rocks close to streams or waterfalls (see Fig. 9C and Fig. 11A). Some emblematic species such as *C. inopinatum* var. *tamonii* and *C. frapperi* have most, or a significant part, of their populations located in such ravines in semi-dry forests with 68.2% and 38.5% of their populations, respectively. In addition, on the windward side, many megathermous species (*C. fallax*, *C. frapperi*, *C. inopinatum* var. *tamonii*, *D. barklyanum*, *D. cuspidatum*, and *D. lorencei*) are observed below 500 m as lithophytic on rocks in ravines, often in degraded forests close to urban zones and crops (see Appendices 1 & 3). Kluge & Kessler

(2011) have already reported the high fern diversity in ravines compared to adjacent forests. The Hymenophyllaceae are not only emblematic of rainforests, but they also support the importance of the floristic diversity of wet ravines at the lowest elevations, that should mobilize the same conservation attention as other habitats.

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**Appendix 1 (Supplementary material 1).** List of Hymenophyllaceae taxa observed per locality in La Réunion with corresponding elevation.

Locality	Elevation (m)	A. par	A. tam	C. bip	C. bon	C. fal	C. fra	C. ino	C. ino	C. min	C. min	D. bar	D. cus	D. lor	H. cap	H. dig	H. fum	H. hir	H. hyg	H. ina	H. pel	H. sib	P. dia	V. gig	Total species
<b>Windward side</b>																									
Ravine Petit Saint-Pierre	18												X												1
Ravine Cayenne	35												X												1
Ravine –Rivière Ste Anne	50						X																		1
Ravine Bois blanc	60												X												1
Ravine –Rivière Ste Anne	70						X					X													2
Rivière des Roches	85			X			X					X	X												4
Ravine Bois blanc	90	X		X						X		X	X						X						6
Le Tremblet GRR2	140			X									X							X		X			4
Rivière St Denis	150												X												1
Mare Longue Sentier pédagogique de l'Enclos	150			X	X								X										X		4
Rivière du Mât	150			X			X		X			X	X												5
Ravine Bois blanc	170	X		X						X		X	X						X				X		7
Le Tremblet GRR2	180			X														X		X		X			4
Brulé de Takamaka	200			X								X	X					X							4
Ravine Bois blanc	250			X						X		X					X	X	X	X		X			8
Ravine des Orangers	250	X		X			X						X	X											5
Le Tremblet GRR2	250			X									X					X		X		X			5
Mare Longue	250			X									X				X	X		X		X			6
Le Tremblet GRR2	280	X		X						X			X				X	X		X		X			8
Sentier des ravenales	280		X	X								X	X	X											5
Ravine Bois blanc	300	X		X									X				X	X	X	X		X			8
Ravine Tanan	300								X			X													2
Rivière des Marsouins	300					X																			1
Cascade Chaudron	300								X			X													2
Ravine sèche	300					X																			1
Terre Rouge	300					X	X																		2
Ravine Cambourg	300						X					X													2
Rivière des Marsouins	350					X																			1
Mare Longue	350			X								X					X			X		X			5
Le Tremblet GRR2	380			X						X		X						X		X					5
Ravine sèche	400					X																			1
Terre Rouge	400					X	X																		2

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**Appendix 1. (Continued)**

Locality	Elevation (m)	A. par	A. tam	C. bip	C. bon	C. fal	C. fra	C. ino	C. ino tam	C. min	C. min mas	D. bar	D. cus	D. lor	H. cap	H. dig	H. fum	H. hir	H. hyg	H. ina	H. pel	H. sib	P. dia	V. gig	Total species	
Cascade	400								X			X													2	
Chaudron																										
Forêt de Bois blanc	400			X						X		X		X				X	X	X		X			8	
Ravine	400						X					X													2	
Cambourg																										
Bassin Bœuf	400					X																			1	
Mare Longue	450		X	X									X	X			X	X	X	X				X	9	
Le Tremblet GRR2	475	X	X	X						X			X	X	X	X	X	X	X	X		X			13	
Le Tremblet GRR2	480	X	X	X									X				X	X	X	X					8	
Rivière des Marsouins	500					X																			1	
Ravine Tanan	500								X			X													2	
Mare Longue	500	X	X	X									X	X			X	X	X	X		X		X	11	
Forêt Mourou- vin	500	X	X	X									X				X		X	X					7	
Bassin Bœuf	500					X																			1	
Grand Etang	530	X	X	X	X	X				X	X	X	X	X		X	X	X	X	X		X		X	16	
Mare Longue	530	X	X	X									X			X	X	X	X	X		X		X	11	
Mare Longue	550	X	X	X									X	X	X	X	X	X	X	X			X	X	13	
Le Tremblet GRR2	600	X	X							X			X		X	X	X	X	X	X		X	X		12	
Forêt Dioré	600		X	X								X	X			X		X	X						7	
Mare Longue	650	X	X	X									X		X	X	X	X	X	X		X	X		12	
Mare à Poule d'eau	680								X																1	
Ravine	700											X													1	
Chaudron																										
Forêt Dugain	700			X		X		X					X												4	
Vallée Heureuse	800	X	X	X												X			X	X		X			7	
Plaine des palmistes / anthropized ravine	810	X	X							X		X		X	X	X	X	X	X	X		X	X	X	13	
Plaine des Palmistes / Pandanaie	850		X									X						X		X					4	
Sentier de la cascade	950		X										X					X	X						4	
Biberon																										
Vallée Heureuse	950	X	X									X		X					X		X	X	X		7	
Mornes de l'Etang	960	X	X							X				X	X	X	X	X	X	X		X	X		11	
Piton des Songes	970		X											X	X			X	X	X		X	X		8	
Sentier de la Petite Plaine	1,200	X	X											X	X			X	X				X		7	
Ilet Patience	1,250	X	X					X		X			X		X	X		X	X			X	X		12	
Piton de l'eau	1,250	X												X	X			X	X			X			6	
Sentier pédagogique de bras Cabot	1,300	X	X							X				X				X	X						6	
Ravine Petit Bras Piton	1,300	X													X	X		X	X			X			6	
Ravine du grand Bras Piton	1,340		X					X		X				X	X			X	X			X			8	
Forêt de Grand Coude	1,350	X	X					X						X	X			X	X	X	X	X	X	X	11	

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**Appendix 1. (Continued)**

Locality	Elevation (m)	A. par	A. tam	C. bip	C. bon	C. fal	C. fra	C. ino	C. ino	C. min	C. min	D. bar	D. cus	D. lor	H. cap	H. dig	H. fum	H. hir	H. hyg	H. ina	H. pel	H. sib	P. dia	V. gig	Total species	
Bébour	1,400		X												X				X	X	X		X		6	
- Sentier des mares																										
Ravine Petit Bras Piton	1,400	X														X	X		X	X			X		6	
Piton de l'eau	1,450	X								X					X	X			X	X			X		7	
Ravine Petit Bras Piton	1,470	X													X				X	X			X	X	6	
Bélouve - chemin de la Tamarinaie	1,520	X	X					X		X					X	X			X	X			X		9	
Piton de l'eau	1,600	X													X	X			X	X	X		X		7	
Bivouac de la Rivière de l'Est	1,730	X																		X					2	
Fournaise- Sentier Nez de Boeuf-Rivière des Remparts	1,800	X																							1	
Bélouve - str vers Piton des Neiges	1,900													X											1	
Fournaise - sentier du Fond de la Rivière de l'Est	1,900																			X					1	
Plaine des Chicots	1,995	X																			X				2	
Chicots - Bras Détour	2,020																			X			X		2	
- Ravine à Sophora																										
Fournaise - Enclos Fouqué	2,210																			X					1	
Côteau Kervelen - sentier du Piton des Neiges	2,400																			X					1	
<b>Leeward side</b>																										
Grande Chaloupe	300								X			X													2	
Grande Chaloupe	400								X			X													2	
Ravine du Trou	500								X																1	
Ravine du Trou	600								X																1	
Sentier Pièce Jeanne	600								X																1	
Grand Bassin	600								X																1	
Ravine des Cafres	600								X			X													2	
Les Canots	650				X		X		X					X								X			5	
Sentier Pièce Jeanne	700								X																1	
Grand Bassin	700								X																1	
Bois de Nèfles	700								X																1	

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**Appendix 1. (Continued)**

Locality	Elevation (m)	A. par	A. tam	C. bip	C. bon	C. fal	C. fra	C. ino	C. ino tam	C. min	C. min mas	D. bar	D. cus	D. lor	H. cap	H. dig	H. fum	H. hir	H. hyg	H. ina	H. pel	H. sib	P. dia	V. gig	Total species	
Les Canots	700						X	X																	2	
Ravine des Cafres	700							X				X														2
Grand Bassin	750								X																	1
Les Canots	800						X	X																		2
Ravine de la Chaloupe	850												X													1
Grand Bassin	900						X																			1
Forêt de Bon accueil	950	X															X			X		X	X			5
Grand Bassin	1,000						X																			1
Forêt de Bon accueil	1,100											X							X							2
Forêt de Bon accueil	1,180	X	X										X		X	X	X		X	X			X			9
Forêt de Sainte Thérèse	1,200		X									X							X				X			4
Forêt des hauts de Montvert	1,200	X	X																X	X						4
Bois de San Souci	1,250	X	X					X				X		X	X				X	X			X			9
Bois de San Souci	1,400	X	X					X						X	X				X	X			X			8
Forêt des hauts de Montvert	1,500	X	X																X	X						4
Sentier de la Plaine des Cafres	1,550													X	X				X	X			X			5
Pitons Mare à Boue	1,580													X					X	X						3
Ravine Leclerc	1,600	X	X							X				X					X	X	X					7
Sentier du Piton des Neiges (Plaine des Cafres)	1,600													X						X						2
Pitons Mare à Boue	1,650	X												X	X				X	X	X		X			7
Notre Dame de la Paix	1,650	X	X					X						X					X	X						6
Piton bleu	1,690													X					X	X	X		X			5
Piton tortue	1,750							X												X						2
Piton bleu	1,750													X					X	X						3
Piton Lepervenche	1,770													X					X							2
Sentier du Piton des Neiges by la Plaine des Cafres	1,900	X												X					X				X			4
Sentier du Piton des Neiges by la Plaine des Cafres	1,980													X					X							2
Total of localities		42	34	31	3	10	15	8	22	7	10	21	42	8	35	26	22	22	46	63	10	26	30	9		

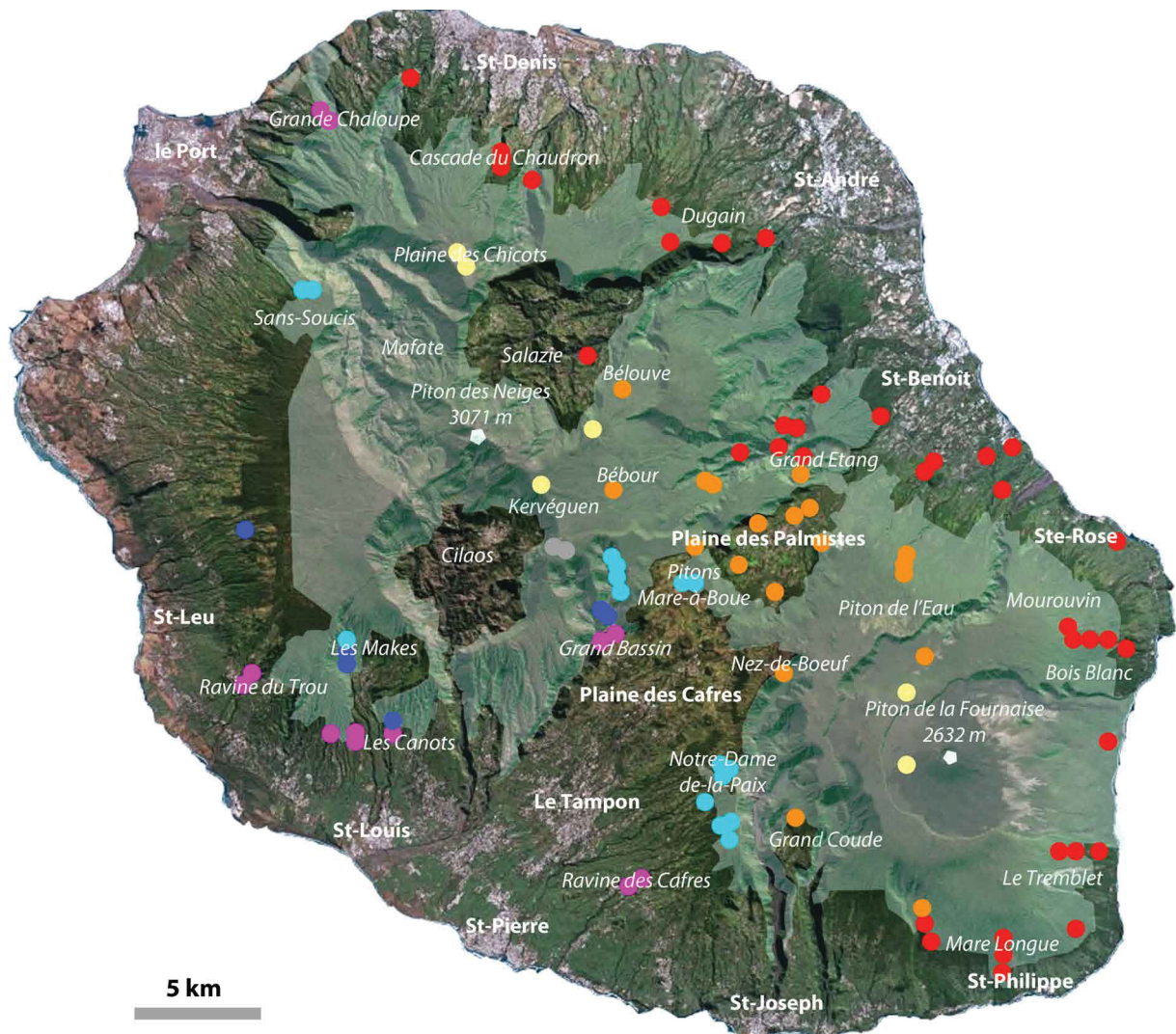
**Appendix 2 (Supplementary material 2).** List of Hymenophyllaceae taxa observed per locality in Mauritius with corresponding elevation.

Locality	Elevation (m)	<i>A. par</i>	<i>A. tam</i>	<i>C. bip</i>	<i>C. bon</i>	<i>C. ino tam</i>	<i>C. min mas</i>	<i>C. trin</i>	<i>D. bar</i>	<i>D. cus</i>	<i>D. lor</i>	<i>H. dig</i>	<i>H. fum</i>	<i>H. hir</i>	<i>H. hyg</i>	<i>H. ina</i>	Total species
Vallée de Ferney	86	X									X						2
Mare D'Australia	174			X													1
Vallée d'Osterlog	260						X	X									2
Bel Ombre	280								X								1
Fayence Mt.	300								X								1
Rambouillet	330			X					X							X	3
Gaulettes Serrées	332															X	1
Alma Hill	470								X							X	2
Calebasses Mt.	514															X	1
Tamarind Falls	520			X	X (*)			X (*)								X	2
Trou aux Cerfs	558			X													1
Bar Le Duc	590		X	X					X							X	4
Brise Fer	597		X								X				X		3
Brise Fer CMA	600			X													1
Grand Bassin	609		X														1
Trou aux Cerfs	611					X			X								2
Rivière du Poste	615										X						1
Mare Longue	627											X					1
Deux Mamelles	630							X (*)									
Pigeon Wood	646													X			1
Mt Cocotte	654	X										X					2
Curepipe Point	655															X	1
Plaine Paul	660													X			1
Macabé	670			X												X	2
Pétrin	670	X	X				X				X		X				5
Mt Cocotte	672														X		1
Corps de Garde	680							X (*)									
Mt Cocotte	704	X															1
Mt Cocotte	735													X			1
Total of localities		4	4	7	1	1	2	2	1	6	1	3	2	4	2	8	

(\*) herbarium data



**Appendix 3 (Supplementary material 3).** Localization of the studied plots on La Réunion. Red plots: windward megathermous lowland rainforest; orange: windward mesothermous montane rainforest; yellow: windward oligothermous ericoid thickets; purple: leeward megathermous semi-dry forest; dark blue: leeward megathermous rainforest (restricted to foothills); light blue: leeward mesothermous montane rainforest; grey: leeward oligothermous ericoid thickets. The area in light green corresponds to the National Park.



Appendix 4 (Supplementary material 4). Localization of the studied plots on Mauritius.

