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Discussion on taxonomy of the fern genera *Crepidomanes* and *Polyphlebium* (Hymenophyllaceae) in Argentina and south-eastern South America, and description of a new local variety for *Crepidomanes pyxidiferum*

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ABSTRACT

The fern genera *Crepidomanes* and *Polyphlebium* are clearly distinct, yet often confused in the wild and in collections. Morphological and molecular investigations were performed to find taxonomic characters for discriminating species occurring in southeastern South America (southern Brazil and northeastern Argentina). Our results show that the genus *Polyphlebium* is represented in the area by two species: *Polyphlebium angustatum* and *Polyphlebium diaphanum*. In addition *P. diaphanum* is a pantropical species that includes as synonyms neotropical *Polyphlebium hymenophylloides* and palaeotropical *Polyphlebium borbonicum*. We also show that southeastern South American *Trichomanes emarginatum* is a local variety of *Crepidomanes pyxidiferum*, here named *C. pyxidiferum* var. *australe*. A key for the species is provided and new taxonomic treatments are discussed.

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Introduction

The fern genera *Polyphlebium* Copel. and *Crepidomanes* (C. Presl) C. Presl (Hymenophyllaceae) are often confused because they share the same ecology and exhibit a similar appearance. Both are epiphytic or lithophytic in the understorey of wet forests, and display long-creeping filiform rhizomes bearing small to large (from few to more than 20 cm), pendent (pinnatifid) bipinnatifid to more-dissected fronds. Molecular phylogenetic studies, however, clearly show that they are distinct (Ebihara et al. 2006). This distinction is expressed morphologically by the root system. *Crepidomanes* is rootless, but produces short rhizome branches that superficially resemble roots. These branches are usually covered by the same dark hairs as on the main rhizome. As such, they correspond to "root-like shoots" as defined by Schneider (2000). In contrast, *Polyphlebium* does not bear root-like shoots, and has true roots. These true (sometimes greatly reduced) roots are not covered by the same hairs as on the rhizomes. Furthermore, many species of *Crepidomanes* exhibit false veins (i.e. rows of non-conducting cells with thickened walls) in the laminae or parallel folds on either side of the segment midribs that mimic false veins. Such false veins or folds are never observed in *Polyphlebium*.

Both genera are primarily pantropical. According to the revision by Ebihara et al. (2006, 2009), *Polyphlebium* includes 13 species, four of which strictly occur in the Neotropics (*Polyphlebium angustatum* (Carmich.) Ebihara & Dubuisson, *Polyphlebium capillaceum* (L.) Ebihara & Dubuisson, *Polyphlebium exsectum* (Kunze) Ebihara & Dubuisson, *Polyphlebium philippianum* (J.W. Sturm) Ebihara & Dubuisson), and one which is restricted to Juan Fernandez Island (*Polyphlebium ingae* (C.Chr.) Ebihara & Dubuisson). In the Old World, one species occurs in New Guinea (*Polyphlebium werneri* (Rosenst.) Ebihara & K. Iwats.), and four in Australia and/or on Pacific islands (*Polyphlebium colensoi* (Hook.f.) Ebihara & K. Iwats., *Polyphlebium endlicherianum* (C. Presl) Ebihara & K. Iwats., *Polyphlebium venosum* (R.Br.) Copel., *Polyphlebium vieillardii* (Bosch) Ebihara & K. Iwats.). Furthermore, a pantropical complex involves the Afro-western Indian Ocean *Polyphlebium borbonicum* (Bosch) Ebihara & Dubuisson, neotropical *Polyphlebium hymenophylloides* (Bosch) Ebihara & Dubuisson and *Polyphlebium diaphanum* (Kunth) Ebihara & Dubuisson, in addition to Pacific populations related to *P. borbonicum* (Ebihara et al. 2009). *Crepidomanes* is mostly palaeotropical, with more than 30 species distributed from tropical Africa to the Pacific islands

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(Ebihara et al. 2006; Dubuisson et al. 2013). Only two of its species are in the New World: *Crepidomanes pyxidiferum* (L.) Dubuisson & Ebihara and *Crepidomanes intricatum* (Farrar) Ebihara & Weakley. The former is widely distributed from Central America and Greater Antilles to southern South America, and the latter is known only as gametophytes in North America and is closely related to the Asiatic *Crepidomanes schmidtianum* (Zenker ex Taschner) K. Iwats. (Farrar 1992; Ebihara, Farrar, and Ito 2008).

Preliminary investigations on neotropical *P. hymenophylloides*, *P. diaphanum* and *C. pyxidiferum* at P (Herbaria acronyms follow Thiers 2016) revealed that these species are often confused in collections. Almost all specimens identified as *C. pyxidiferum* at P were in fact *P. hymenophylloides* or the closely related *P. diaphanum* (Dubuisson et al. 2013; pers. obs.). This explains why *Trichomanes pyxidiferum* was first combined under *Polyphlebium* by Ebihara et al. (2006). In other collections, particularly in South America, the same confusion could occur, and re-examination of herbarium specimens is therefore needed. This confusion in identification was pointed out by Slosson (1915), who clarified that true *T. pyxidiferum sensu* Plumier (1705) (currently combined in *Crepidomanes*) is distinct from many specimens (including the "*T. pyxidiferum*" illustrated by Hooker and Greville 1831) that should be or had finally been attributed to *P. hymenophylloides* or *P. diaphanum*. Besides the presence or absence of roots, both species differ in the length : width ratio of the indusiate sorus (Dubuisson et al. 2013). The sori of *P. hymenophylloides* and *P. diaphanum* are typically twice, or slightly more, as long as wide, whereas those of *C. pyxidiferum* are typically as long as wide.

In conjunction with a global study in progress on the diversity and evolution of Hymenophyllaceae in southeastern South America involving Argentina (Ponce and de la Sota 2008; Arana, Larsen, and Ponce 2016), we assessed the diversity of *Polyphlebium* and *Crepidomanes* in this area by a careful re-examination of local collections. We checked the generic status of previously problematic specimens and populations using morphological and molecular methods. In particular, many specimens from northeastern Argentina (Misiones) and southern Brazil were originally identified as *Trichomanes emarginatum* C. Presl (Capurro 1970; Ponce and de la Sota 2008) and cited as closely related to *C. pyxidiferum* by Presl in 1847. The present study also examines the validity and status of this local taxon.

Material and methods

We first checked the occurrence of *Polyphlebium* and *Crepidomanes* in Argentina and neighbouring areas (southern Brazil, Bolivia, Paraguay, Uruguay, Chile) by using local databases (Flora del Conosur: http://www2.darwin.edu.ar/Proyectos/FloraArgentina/fa.htm; Ponce and de la Sota 2008; Windisch 2016). Morphological investigations on root system, rhizome, fronds and sori were performed on representative herbarium specimens to compare and discriminate between taxa. A list of examined specimens is reported in Appendix 1.

A molecular phylogeny using chloroplast *rbc*L sequences was then constructed, including all *Polyphlebium* (except *P. werneri* and *P. philippianum*, which were lacking) and representative *Crepidomanes* taxa, including an Argentinean specimen first identified as *T. emarginatum* and thought to be closely related to *C. pyxidiferum*. We also extended the sampling of Ebihara et al. (2009) concerning the clade involving *P. hymenophylloides*, *P. diaphanum* and *P. borbonicum*, with three new additional *P. hymenophylloides* specimens, respectively from Brazil, Guadeloupe and Mexico. To root the phylogeny, we selected species representative of the seven other genera of the trichomanoid lineage (Ebihara et al. 2006). All species used in phylogenetic analysis, including distribution and voucher information, are reported in Appendix 2. The *rbc*L gene was amplified and sequenced following the protocol of Ebihara et al. (2007). For phylogenetic analyses we selected the Bayesian metropolis-coupled Markov chain Monte Carlo approach that was used in previous studies on Hymenophyllaceae, especially trichomanoids (Dubuisson et al. 2013; Bauret et al. 2015). The analyses were conducted using MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). The GTR + I + Γ nucleotide substitution model was selected using ModelTest 3.06 (Posada and Crandall 1998). We conducted two runs of 10,000,000 generations using the online CIPRES server (https://www.phylo.org/). We sampled 100,000 trees, and a majority-rule consensus tree was computed based on the last 75,000 trees, excluding the 25,000 trees found in the 'burn-in period'. The support for each node was estimated by the posterior probability (PP) calculated from the 75,000 sampled trees.

Results

Diversity and distribution of Crepidomanes and Polyphlebium in southeastern South America

Literature and databases indicate the occurrence of one species of *Crepidomanes* (*C. pyxidiferum*) and seven species of *Polyphlebium* (*P. angustatum*, *P. capillaceum*, *P. diaphanum*, *P. exsectum*, *P. hymenophylloides*, *P. ingae* and *P. philippianum*) in addition to *T. emarginatum* in Argentina and/or neighbouring areas (southern Brazil, Bolivia, Paraguay, Uruguay and Chile) (Table 1). In contrast, only three species in these genera have been reported from Argentina: *C. pyxidiferum*, *P. angustatum* and *T. emarginatum*. *Polyphlebium hymenophylloides* seems to be absent from Argentina, although it is found nearby in southeastern Brazil. *Polyphlebium diaphanum* is also present in Paraguay. Flora del Cono Sur reports *P. capillaceum*

Table 1. List of *Polyphlebium* and *Crepidomanes* species in addition to *Trichomanes emarginatum* C.Presl and their distribution in southern South America (Argentina and neighbouring areas) according to "*Flora del Conosur (IBODA)*: http://www2.darwin.edu.ar/Proyectos/FloraArgentina/fa.htm" databases and present study.

	Argentina	Uruguay	Paraguay	Brazil	Bolivia	Chile
C. pyxidiferum (L.) Dubuisson & Ebihara	X (Yungas *)		X	X		
T. emarginatum C.Presl	X (Misiones)			X		
P. hymenophylloides (Bosch) Ebihara & Dubuisson				X		
P. diaphanum (Kunth) Ebihara & Dubuisson			X	X		
P. capillaceum (L.) Ebihara & Dubuisson				X (Paraná**)	X	
P. angustatum (Carmich.) Ebihara & Dubuisson	X	X	X	X		
P. exsectum (Kunze) Ebihara & Dubuisson						X
P. ingae (C.Chr.) Ebihara & Dubuisson						X ((***))
P. philippianum (Sturm) Ebihara & Dubuisson						X

*Typical populations are observed only in northwestern Argentina close to Bolivia (see text).
**Doubtful (see text).
***Endemic to Juan Fernandez Island.

in Brazilian Paraná state, but the species appears absent in Brazilian databases and collections. Its real presence in southern Brazil therefore remains doubtful.

Phylogeny

The molecular phylogeny shows *T. emarginatum* nested in *Crepidomanes*, closely related to *C. pyxidiferum* and the palaeotropical *Crepidomanes inopinatum* (Pic. Serm.) J.P. Roux (Figure 1). The *rbc*L sequences of *T. emarginatum* and *C. pyxidiferum* are 100% identical. According to our phylogeny, neither *P. hymenophylloides* nor *P. diaphanum* is monophyletic; these species are included in a robust clade that also involves a polyphyletic *P. borbonicum* (here represented by one La Réunion specimen and two specimens from Pacific islands) and *Trichomanes debile* Bosch.

Morphological comparisons

Our morphological investigations of *T. emarginatum* (from Misiones in Argentina and from neighbouring Paraná, Rio Grande do Sul and Santa Catarina states in Brazil) and comparisons of it with *P. hymenophylloides* (and *P. diaphanum*) and typical *C. pyxidiferum* (as illustrated in Figure 2, and reported in Table 2), support the placement of *T. emarginatum* in *Crepidomanes*. All specimens of *T. emarginatum* that we examined are rootless. The sori or indusia are about as wide as long, as is typical of *C. pyxidiferum* (Figures. 2B, and 2C), and never significantly longer than wide, as is typical of *P. hymenophylloides* (Figure 2D). Such similar observations are also confirmed with the *T. emarginatum* type (*Beyrich s.n.*, isosyntype B 20 0103898). This suggests that *T. emarginatum* as well as typical *C. pyxidiferum* can be distinguished morphologically from *P. hymenophylloides* and *P. diaphanum*. Furthermore, as reported in Table 2, our *T. emarginatum* specimens exhibit a few subtle differences from typical *C. pyxidiferum*. First, all the *C. pyxidiferum* specimens, especially the continental ones, have flat fronds with margins (of stipe, rachis and segments) that are sometimes slightly undulating but most often quite flat and not significantly undulate (Figure 2C). In contrast, most *T. emarginatum* exhibit slightly to significantly undulate margins (see Figure 2B), especially on the stipe, rachis and at the base of the pinnae. Second, most typical *C. pyxidiferum* exhibit peculiar longitudinal folds on segments (Figure 2C), whereas most of our *T. emarginatum* do not display such folds (Figure 2B).

Discussion

Diversity and distribution of Crepidomanes and Polyphlebium in southeastern South America

Concerning Argentinean species, *P. angustatum* is a clearly distinct taxon and their occurrence in the area is not questionable (Arana, Larsen, and Ponce 2016); however, there is still discussion concerning *C. pyxidiferum* and our *T. emarginatum* specimens, which will be developed here-after.

The presence of *C. pyxidiferum* in southern Brazil, especially in the Atlantic forest (*Mata Atlantica*) of "Sudeste" states such as Rio de Janeiro, Minas Gerais and São Paulo, deserves discussion because our investigations reveal that most specimens from these states and identified in collections as *C. pyxidiferum* appear actually to be *P. diaphanum* or *P. hymenophylloides* (as discussed below). The same observation was also made for the types of *Trichomanes brasiliense* Desv., *Trichomanes tranninense* Fée, *Trichomanes eximium* Kunze, which are synonyms of *C. pyxidiferum* or *T. emarginatum*, and the types of *T. pyxidiferum* L. var. *organense* Rosenst. and *T. pyxidiferum* L. f. *gracile* Rosenst. (Appendix 1). All these taxa are *P. diaphanum* or *P. hymenophylloides* (as discussed below). Conversely, numerous specimens identified as *P. diaphanum*, especially from Brazilian Santa Catarina state, appear in fact to be similar to *T. emarginatum* (Appendix 1). According to Brazilian databases (Windisch 2016), *C. pyxidiferum* is present in Brazil only in the "Sudeste" (Espírito Santo, Rio de Janeiro, São Paulo and Minas Gerais; especially in the Atlantic forest or *Mata Atlantica*) and "Sul" (Paraná, Rio Grande do Sul, Santa Catarina) states. However, our observations reveal that most populations belonging to *Crepidomanes* including *T. emarginatum* in Brazil

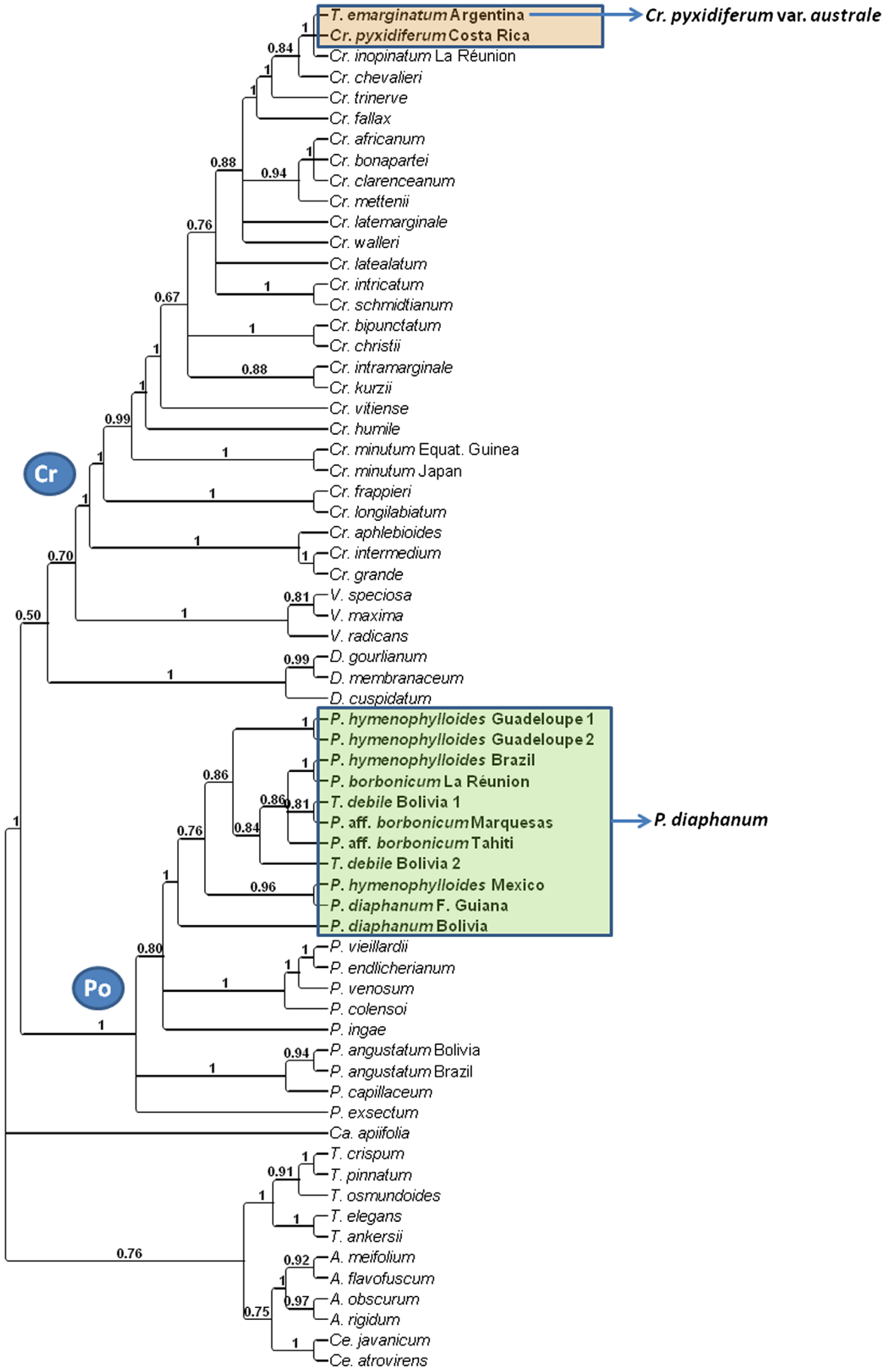

Figure 1. Bayesian phylogeny inferred from *rbc*L sequences showing relationships among Hymenophyllaceae genera *Crepidomanes* (noted as Cr) and *Polyphlebium* (noted as Po). Support values on nodes are posterior probabilities. The species/populations studied and compared here are in boxes. Names on the right correspond to new taxonomic treatment discussed in the text.

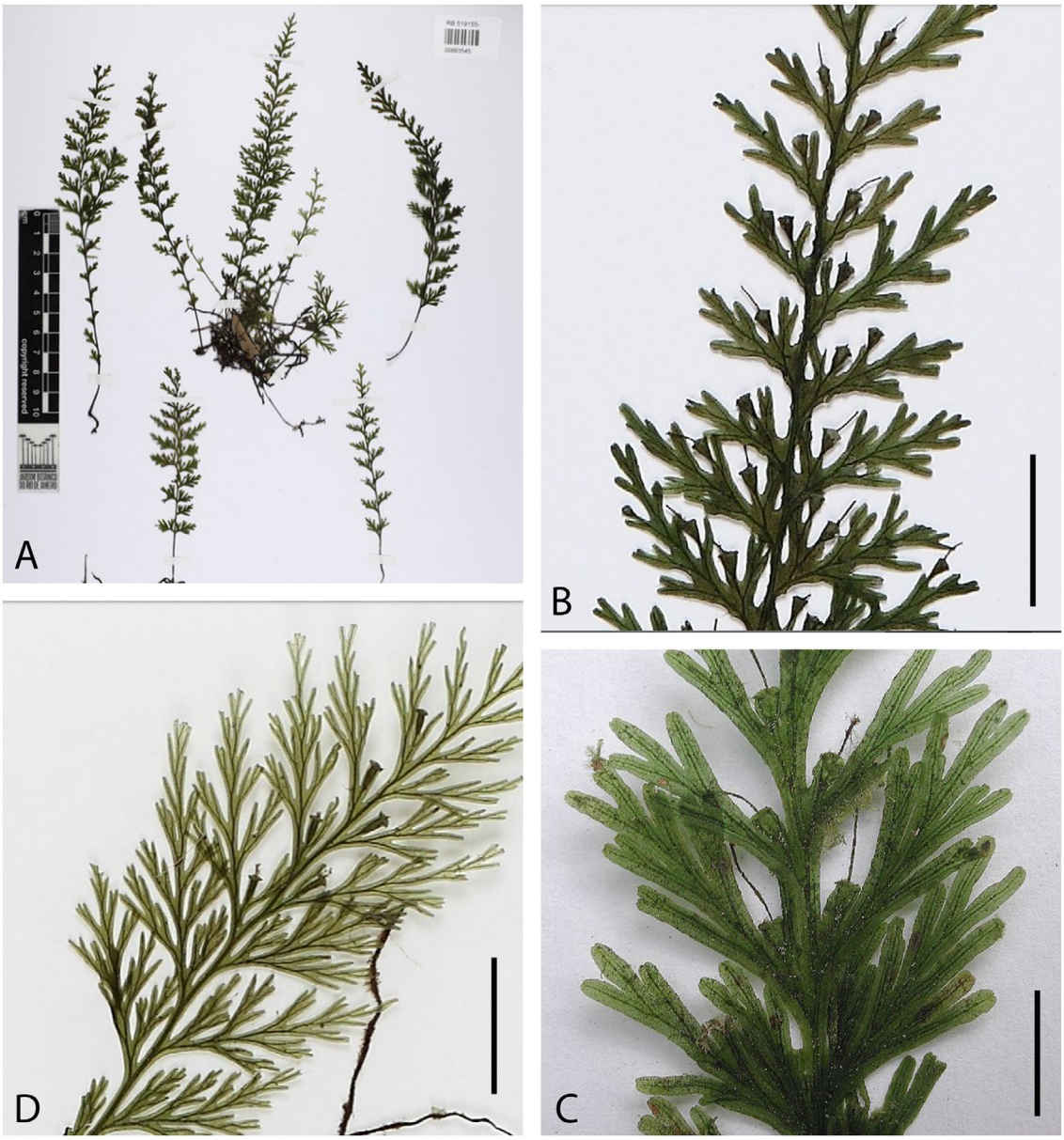

Figure 2. Comparison of three similar neotropical species of Hymenophyllaceae. **(A)** *Trichomanes emarginatum* C. Presl from Brazil (*P.H. Labiak 3900*, RB 00663545 & UPCB 56751) also identified as *Crepidomanes pyxidiferum* (L.) Dubuisson & Ebihara. **(B)** *T. emarginatum*, detail of sori and undulating rachis wing margins, scale = 1 cm. **(C)** Typical *C. pyxidiferum*, here from Costa Rica (photograph by R. Moran, NY) showing plane (not undulate) margins and typical longitudinal folds in the laminae, scale = 5 mm. **(D)** *Polyphlebium* cf. *hymenophylloides* (Bosch) Ebihara & Dubuisson, from Brazilian Rio de Janeiro state (*E.R. Damasceno 307*, RB 00581905), and showing typical sori significantly longer than wide, scale = 1 cm.

Table 2. Morphological comparison of three similar neotropical species of Hymenophyllaceae.

	Crepidomanes pyxidiferum from Central America and northern South America	*Trichomanes emarginatum* and *C.* cf. *pyxidiferum* from southern South America	*Polyphlebium hymenophylloides* or *Polyphlebium diaphanum*
Root system	Rootless	Rootless	Always present even if quite reduced
Root-like shoots *sensu* Schneider (2000)	Present	Present	Absent
Longitudinal laminar folds imitating false veins	Often present	Sometimes present	Absent
Rachis wing and segment margins	Margins usually not undulated or sometimes slightly undulate	Margins often significantly undulate	Margins sometimes undulate, especially rachis wing
Sorus length/width ratio	Sori always significantly less than twice as long as wide, usually as long as wide	Sori always significantly less than twice as long as wide, usually as long as wide	Sori usually at least twice as longer as wide

are mostly in "Sul" states, in addition to some localities in São Paulo, Rio de Janeiro and southern Minas Gerais, whereas they seem mostly replaced in "Sudeste" by *P. diaphanum* or *P. hymenophylloides* (as discussed below). Nevertheless, these last two taxa extend to Paraná and Santa Catarina, but apparently not further south, and are therefore absent in Rio Grande do Sul and neighbouring Argentina.

Genus Polyphlebium

Three species of *Polyphlebium* occur in southeastern South America: *P. angustatum*, *P. hymenophylloides* and *P. diaphanum*. However, the distinction between *P. hymenophylloides* and *P. diaphanum* is not obvious. According to Pacheco (1994) based on Mexican populations, the two are distinguished solely by the development of the stipe wing: stipe fully winged in *P. diaphanum* and stipe wingless or only winged at the upper part in *P. hymenophylloides*. We have studied here a large sampling of specimens belonging to both species, and we actually observe a range of intermediate cases from a wingless stipe to a fully winged stipe. Consequently the distinction between the two species based on this highly variable character is highly questionable and so not supported. Nevertheless both species exhibit a fully winged rachis, which allows them to be distinguished from *P. angustatum*, which displays a rachis that is wingless or winged only on its upper part.

Our phylogeny (see Figure 1) indicates that neither *P. hymenophylloides* nor *P. diaphanum* is monophyletic and both taxa are embedded into a clade with Palaeotropical *P. borbonicum*. In addition, we cannot detect any diagnostic morphological characters for discriminating between these three species. The clustering of these taxa and their strong morphological resemblance suggest that all the specimens belonging to the clade should be considered a single widespread species. By calculating genetic distances (according to JC69's model; Jukes and Cantor 1969) for *rbc*L sequences between clearly distinct species within the *Polyphlebium* genus (and so excluding distances within the clade defined above), we obtain a mean value of 0.034, whereas the mean distance between the species in the *diaphanum*/ *hymenophylloides*/ *borbonicum* clade is 0.014. Such a low value combined with morphological uniformity supports the hypothesis of a single widespread taxon. According to our phylogeny, this single species appears have neotropical origins with secondary independent dispersals respectively to Africa and the Indian Ocean, and to Pacific Islands (see Figure 1). African specimens are lacking in our sampling and would be required in addition to new markers for confirming the here-above biogeographical scenario. Because of the anteriority rule, this single species is *P. diaphanum* (see taxonomic treatment here-after). This new treatment corrects the previous proposition (Ebihara et al. 2009) to name some neotropical populations (especially those first attributed to *T. debile*) *P. borbonicum*.

Genus Crepidomanes *and* T. emarginatum

Our investigations reveal that most *T. emarginatum* specimens exhibit slightly to significantly undulate margins, especially on the stipe, rachis and at the base of pinnae, and only rarely have folds on the laminae, the latter being usually observed in typical *C. pyxidiferum*. Such undulation has already been noted as diagnostic by Presl (1847) in the original description of the species. However, rachis undulation is also observed in some *C. pyxidiferum* specimens from Greater Antilles (especially the Cuban and Jamaican ones), and discrimination based on this feature is therefore not always possible. Furthermore, our *T. emarginatum* specimens occur in a large southeastern area with a mostly wet sub-tropical to warm temperate climate, especially in sub-montane forests of the coastal *Serra do Mar*, whereas typical *C. pyxidiferum* is a tropical element more widespread in montane rainforests of Central America, Greater Antilles and northern South America (Figures 3 and 5). Typical *C. pyxidiferum* is usually observed in sub-montane to montane cloud forests above 1000 m (more

Figure 3. Geographical distribution of typical variety of *Crepidomanes pyxidiferum* (in grey) and *Trichomanes emarginatum* or *C. pyxidiferum* var. *australe* (encircled) in tropical America.

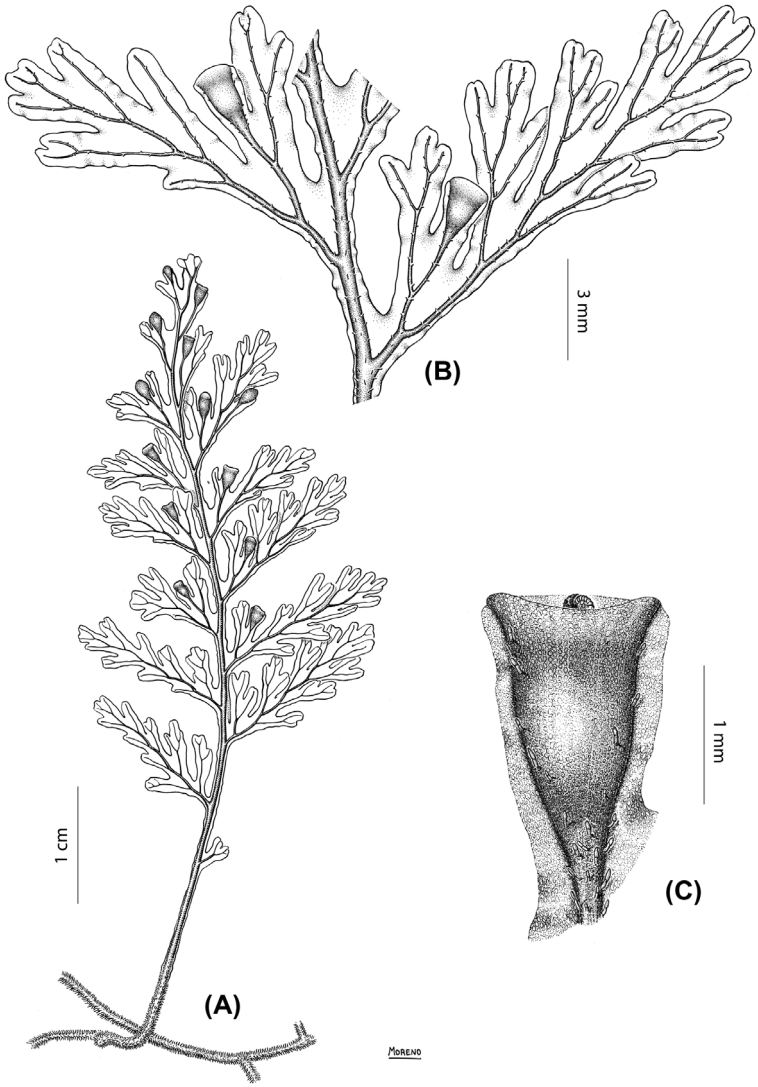

Figure 4. *Crepidomanes pyxidiferum* (L.) Dubuisson & Ebihara var. *australe* Ponce & Dubuisson, var. nov. (*C. Zanotti* et al. *568,* SI). **(A)** Habit. **(B)** Detail of pinnae. **(C)** Detail of sorus (drawing by M. Moreno).

rarely below, and usually at least from 500 to 600 m). The southernmost populations of *T. emarginatum* can occur in wet forests close to sea level, and the taxon reaches 1600 m only in its northernmost tropical localities (in Rio de Janeiro state, especially in *Parque Nacional do Itatiaia*, and southern Minas Gerais). Outside southern Brazil and Argentinian Misiones, the closest typical *C. pyxidiferum* populations are Bolivian and from the neighbouring northwestern Argentina (Southern Yungas; Arana, Larsen, and Ponce 2016), resulting in the geographical isolation and disjoint distribution of southern *C. pyxidiferum* populations occurring in Argentinean Misiones and southeastern Brazil (Figure 3).

Some Brazilian *T. emarginatum* specimens (as *Rosenstock 253*, from Rio Grande do Sul) have also been named *T. brasiliense*. The type of this species (from Rio de Janeiro state) is actually *P. diaphanum* (as already indicated above). Hence, the name does not apply to *T. emarginatum*. The type of *T. emarginatum* (*Beyrich s.n.*) is cited as collected in Rio de Janeiro (in fact *Capitania de Rio de Janeiro*) in the Serra da Estrella. This latter locality does not exist in the current state of Rio de Janeiro. In Brazil Serra da Estrela (with a single "l") is a locality of Rio Grande do Sul where occurrence of *T. emarginatum* is equally probable. In the nineteenth century, most goods from the south (including the scientific collections) in Brazil were sent to Europe by boat from Rio de Janeiro's harbour. This could explain the reference to Rio de Janeiro for a plant that could have been collected in a distinct *Capitania*. Hence, the true locality of the type remains questionable.

The combination of significantly undulating rachis wing, rarity of laminar folds (nevertheless with exceptions) and geographical distribution allowed us to define a distinct morpho-taxon for populations occurring in southern Brazil and northeastern Argentina (Misiones), including the specimens first named *T. emarginatum*. However, based on genetic similarity (at least with *rbc*L sequences) and absence of clear discriminating morphological characters, we do not propose that these southern populations belong to a new distinct species. Rather, we propose here to define a new local variety of *C. pyxidiferum*, including *T. emarginatum*.

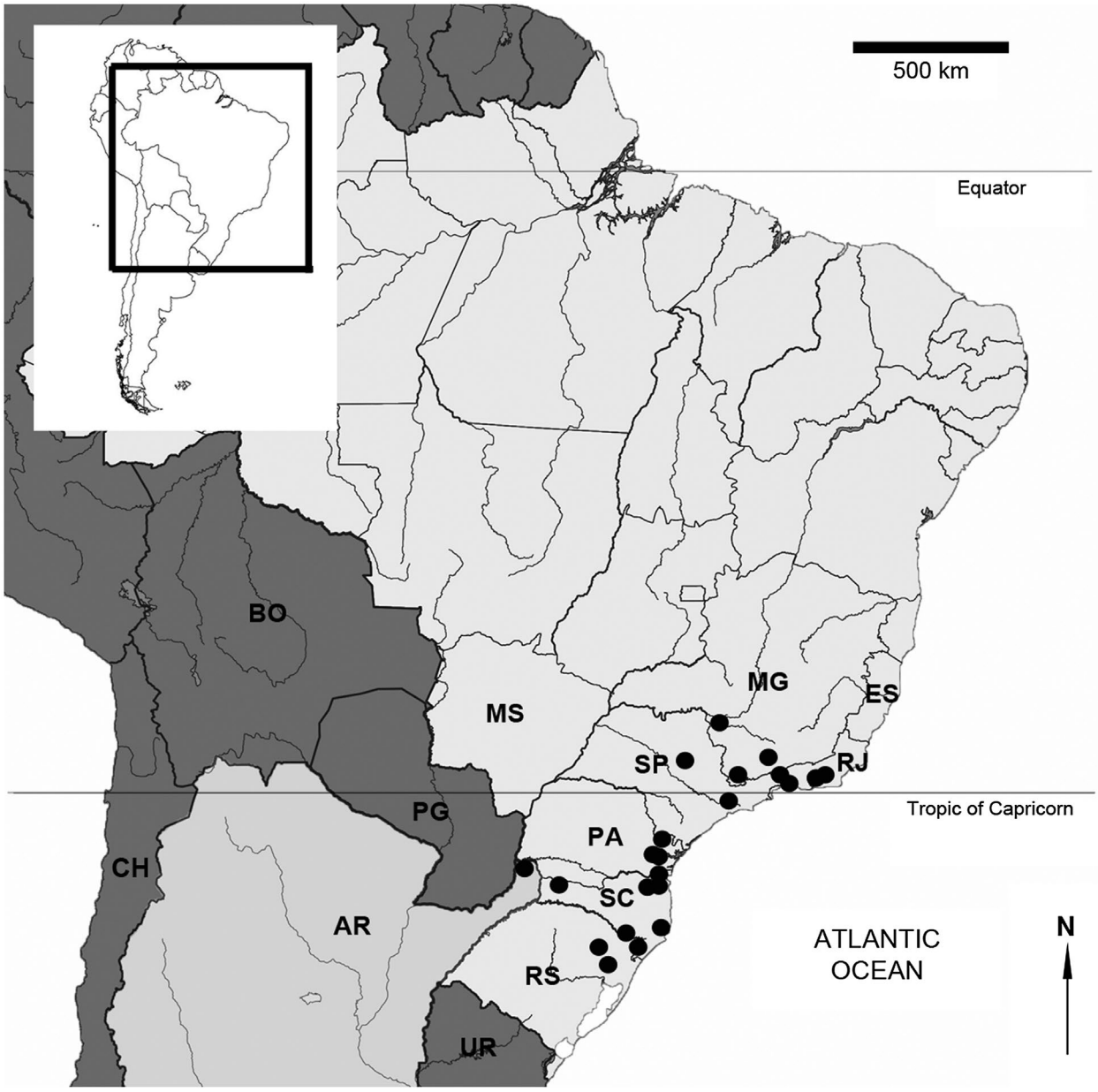

Figure 5. Geographical distribution of *Crepidomanes pyxidiferum* var. *australe* (black circles) in southeastern South America. Argentina and Brazil, where the variety is observed, are in light grey. Abbreviations for countries: AR = Argentina, BO = Bolivia, CH = Chile, PG = Paraguay, UR = Uruguay; Abbreviations for Brazilian states: ES = Espírito Santo, MG = Minas Gerais, MGS = Mato Grosso, PA = Paraná, RJ = Rio de Janeiro, RS = Rio Grande do Sul, SC = Santa Catarina, SP = São Paulo.

Key for *Crepidomanes* and *Polyphlebium* species in southeastern South America

Polyphlebium capillaceum is noted as present in southern Brazil by Flora del Conosur, but as already noted above this presence is doubtful according to Brazilian databases. The species nevertheless occurs in neighbouring Bolivia. Because we cannot exclude the possibility of finding it in the wild in the area, the species is included in the following key.

(1) Indusia usually twice, or more, as long as wide 3
(2) Indusia mostly as long as wide, never twice as long as wide *C. pyxidiferum*.
(3) Ultimate segments not capillaceous, with lamina more than three cells wide along the veins 5.
(4) Ultimate segments capillaceous, with lamina not exceeding two to three cells wide along the veins *P. capillaceum*.
(5) Rachis always fully winged *P. diaphanum*
(6) Rachis wingless or winged only on its upper part *P. angustatum*

Taxonomic treatment for *Crepidomanes* and *Polyphlebium* in southern Brazil and northwestern Argentina

***Crepidomanes pyxidiferum* (L.) Dubuisson & Ebihara var. *australe* Ponce & Dubuisson, var. nov.** (Figure 4)

Resembles *C. pyxidiferum* but differs by geography (southeastern Brazil and Argentinean Misiones),

conspicuously undulate rachis margins, and longitudinal folds of the segment laminae rarely present.

Type. Argentina, Misiones: Departamento San Pedro, Puente López, sobre el Arroyo Yabotí Guazú, 27°04'10" S, 53°53'38" W, 410 m, 27 November 2013, *C. Zanotti* et al. *568* (holotype, SI; isotype, P).

= *Trichomanes emarginatum* C. Presl, Abhandlungen der Königlichen Böhmischen Gesellschaft der Wissenschaften, ser. 5(5): 332. 1847[1848], nom. illeg. hom., non Poir., 1808. Type: Brazil. Rio de Janeiro. Serra da Estrella, H. K. Beyrich s.n. (PRC; isotype: B 20 0103898!).

Epiphytic or lithophytic ferns. Rhizomes long-creeping, filiform, branched, c. 0.3 mm in diameter, densely covered with long, slender, simple, dull brown hairs, rootless or with root-like shoots covered by the same hairs as on rhizomes. Fronds up to 2–4 cm apart. Stipes 0.5–3.0 cm long, fully winged or winged at the upper part, with base thickened, blackish, bearing hairs similar to those on the rhizomes, other parts flattened or shallowly grooved ventrally, with short, pale brown clavate hairs on entire surface. *Laminae* 3.0–10.0(–15.0) × 1.0–4.0 cm, green or olive-green, diaphanous, glabrous, narrowly oblong-elliptic to narrowly ovate-elliptic, or ovate, or slightly lanceolate with well attenuated to sharp apex, bipinnatifid to tripinnatifid, and with anadromous venation. Rachis widely winged with mostly significantly undulate margins. Pinnae alternate, pinnatifid to bipinnatifid, ovate or lanceolate to oblong, with margin base mostly undulate. Segments entire, linear, apically emarginate, often with undulating margins, and sometimes but not always with longitudinal folds parallel to true veins (especially when dry), false veins absent. Costae and veins prominent on both sides, with clavate hairs similar to those on the stipe. Lamina cells thin-walled, slightly elongate, mostly hexagonal. Sori paratactic, adaxially borne on the proximal pinnae and/or pinnules, (4–)6 to more than 15 (in largest specimens) per fertile frond; indusia obconical to campanulate, 1.0–1.5 × 0.8–1.2 mm, slightly bordered on both sides by laminar cells, forming a wing, and with few clavate hairs; mouth of indusia slightly dilated; receptacles cylindrical and filiform, short to long-exerted up to twice or more the sorus length.

Distribution and habitat. Restricted to southeastern South America, Argentina (Misiones) and Brazil (Rio Grande do Sul, Santa Catarina, Paraná, Rio de Janeiro, São Paulo, southern Minas Gerais), especially in *Serra do Mar* of southeastern Brazil (Figure 5). Epiphytic, sometimes epipetric on shady rocks, in wet forests in lowland to middle-elevations (sea level for the Brazilian southernmost populations up to 1600 m in Rio de Janeiro state).

The type variety is widely distributed in the Neotropics, occurring from the Greater Antilles, Central America to northern South America and western South America by following the Andes to Amazonian Bolivia and neighbouring northwestern Argentina (Yungas) (Figure 3), in sub-montane to montane cloud forests, usually above 1000 m. It seems to be absent in Amazonian lowlands, Guianas and Lesser Antilles (Proctor 1977; Lellinger 1994; Windisch 2016). In the Lesser Antilles, as in Guadeloupe, the species seems to be replaced by *P. hymenophylloides* (pers. obs.; Proctor 1977) or *P. diaphanum* according to the taxonomic treatment hereafter.

Etymology. The varietal name refers to the southern distribution of the new variety compared with the typical variety, which occurs further north.

Specimens examined: – See Appendix 1.

***Polyphlebium angustatum* (Carmich) Ebihara & Dubuisson**, *Blumea* 2006;51(2):240

Basionym. *Trichomanes angustatum* Carmich, *Transactions of the Linnean Society of London* 1819;12:513.

Type. Tristan da Cunha, *D. Carmichael s.n.* (holo?: BM 001,044,269!)

≡ *Vandenboschia angustata* (Carmich.) Copel., *Philippine Journal of Science* 1941;73:466.

= *Trichomanes tenerum* Spreng., *Systema Vegetabilium, editio decima sexta* 1827;4(1):129.

Type. Brazil, *Anon s.n.* (holotype: LZ) ≡ *Vandenboschia tenera* (Spreng.) Copel., *Philippine Journal of Science* 1938;67(1):53.

= *Trichomanes fulvum* Klotzsch ex Sturm, *Flora Brasiliensis* 1859;1(2):272, pl. 18, f. 6.

Type. Brazil, *F. Sellow 3878* (holotype: B 20 0106 887!).

***Polyphlebium diaphanum* (Kunth) Ebihara & Dubuisson**, *Blumea* 2006;51(2): 240

Basionym. *Trichomanes diaphanum* Kunth, in Humb., Bonpl. & Kunth, *Nova Genera et Species Plantarum* (*quarto ed.*) 1: 25, 1815[1816].

Type. Venezuela, *Humboldt & Bonpland s.n.* (isotype: B 20 0086870!) ≡ *Vandenboschia diaphana* (Kunth) Copel., *Philippine Journal of Science* 1938;67(1):53.

= *Trichomanes borbonicum* Bosch, *Nederlandsch Kruidkundig Archief* 1861;5(2):158, 159.

Type. 'Hab. Ins. Borboniae', *L.H. Boivin 908* (lectotype: B20 0103881, isolectotype: P00065006!), designated by Schelpe & Anthony (1986: 76).

≡ *Vandenboschia borbonica* (Bosch) G. Kunkel; *Nova Hedwigia* 1963;6(1/2):213.

≡ *Crepidomanes borbonicum* (Bosch) J.P. Roux, *Conspectus of southern African Pteridophyta*: 45, 2001.

≡ *Polyphlebium borbonicum* (Bosch) Ebihara & Dubuisson, *Blumea* 2006;51(2):240.

= *Trichomanes brasiliense* Desv. *Mémoires de la Société Linnéenne de Paris* 1827;6:328, t. 7, f. 4.

Type. Brazil, *s.d., s.c.* (holotype: P 00,624,517!).

= *Trichomanes eximium* Kunze, *Flora Brasiliensis* 1(2): 271, 1859.

Type. Brazil, Rio de Janeiro, Serra dos Orgaos, *P. von Luetzelburg 6095* (holotype: W 19,270,020,949!).

= *Trichomanes debile* Bosch, *Nederlandsch Kruidkundig Archief* 1861;5(2):154.

Type. Venezuela, Carabobo, *Funck & Schlim 596* (isotypes: BR0000006988135!, BR0000006987466!, BR0000006988128!, BR0000006987794!).

≡ *Trichomanes pyxidiferum* var. *debile* (Bosch) Sodiro, *Anales de la Universidad Central del Ecuador* 1890;4:290.

= *Trichomanes hymenophylloides* Bosch, *Nederlandsch Kruidkundig Archief* 1863;5(3):209.

Type. St Vincent, *Guilding s.n.* (isotype?: GH 00022242!).

≡ *Vandenboschia hymenophylloides* (Bosch) Copel., *Philippine Journal of Science* 1938;67(1):53.

≡ *Polyphlebium hymenophylloides* (Bosch) Ebihara & Dubuisson, *Blumea* 2006;51(2):240.

= *Trichomanes tranninense* Fée, *Cryptogames Vasculaires du Brésil* 1869;1:187, t. 69, f. 1.

Type. Brazil, *Glaziou 2251* (holotype: P 00624521!).

= *Trichomanes pyxidiferum* L. f. *gracile* Rosenstock, *Repertorium specierum novarum regni vegetabilis* 1924;20:90.

Type. Brazil, Rio de Janeiro, Coreorado, 1910, *P. von Luetzelburg 262* (isotype: NY 00144726!).

= *Trichomanes pyxidiferum* L. var. *organense* Rosenstock, *Repertorium specierum novarum regni vegetabilis* 1924;20:89.

Type. Brazil, Rio de Janeiro, Serra dos Orgaos, *P. von Luetzelburg 92* (isotype: NY 00144725!).

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Disclosure statement

No potential conflict of interest was reported by the authors.

Notes on contributors

M. M. Ponce is a researcher at the National Council of Scientific and Technical Research (Argentina) working on systematics, diversity and biogeography of ferns of the Southern Cone of America. *Contribution:* initiated the study and wrote the manuscript.

C. del Rio (MNHN, Paris) defended his Master thesis in 2015 at the MNHN on the systematics of *Hymenophyllum* in New Caledonia. He is currently a PhD student also at the MNHN. *Contribution:* provided molecular data during his Master's, especially from the Argentinean material.

A. Ebihara (NMNS, Tsukuba) has worked on the systematics of filmy ferns in collaboration with J.-Y. Dubuisson. He is also interested in complex speciation in ferns and is also conducting studies on gametophytes in the wild using DNA barcoding. *Contribution:* has provided most of the molecular data and contributed to the taxonomic discussion.

J.-Y. Dubuisson (UPMC, Paris) has worked on the systematics and evolution of filmy ferns (Hymenophyllaceae), with a special interest on *Trichomanes s.l.*, for more than 23 years. He has conducted many field studies in the Mascarenes and one in Brazilian Mata Atlantica, focusing on the diversity and ecology of ferns. *Contribution:* performed the final analyses and co-wrote the manuscript.

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APPENDIX 1.List of specimens examined.

Crepidomanes pyxidiferum var. *australe* Ponce & Dubuisson (Paratypes)
First identified as *Trichomanes emarginatum* C. Presl.
ARGENTINA–**Misiones**: Parque Nacional Iguazú, 19 Dec. 1991, *Vanni 3006* (ASU 0006825); Dep. San Pedro, Parque Provincial Moconá, Sendero La Gruta, 27 Nov. 2013, *C. Zanotti 561* (SI); Dep. General Manuel Belgrano, Refugio Uruguaí de la Fundación Vida Silvestre Argentina, 25°58' S, 54°07' W, 400 m, 15 Nov. 2000, *M.E. Múlgura 2685* (SI).

BRAZIL–**Rio Grande do Sul**: 1905, *Rosenstock 254* (W 18,860, 002,860); São Leopoldo, Aug. 1940, *A. Rohr 3* (RB 00649 468); São Leopoldo, 1941, *R. Reitz 257* (RB 00649465), *R. Reitz H211* (RB 00649473); Municipio de Santa Tereza, Reserva, Linha Pederneira, Reserva Brum, 1 May 2012, *F. Gonzatti 488* (RON 00007283, FURB 09396); **Santa Catarina**: Rio dos Cedros, Rio Esperança, 8 Dec. 2010, *M. Verdi 5838* (FURB 00,127); Itajaí, 14 Jan. 1941, *R. Reitz c656* (RB 00649472); Serra da Pedra, Araranguá, 7 Dec. 1943, *R. Reitz c426* (RB 00649470); **Paraná**: S. do Mar- Est Eng Lange até Prainhas, 13 Feb. 1951, *G. Tessmann 459* (RB 00649480); **São Paulo**: Serra da Cantareira, Jun. 1913, *L. Toledo 842* (RB 00649506); **Rio de Janeiro**: Serra d'Estrella, *s.d.*, *D. Pohl? 4481* (W 0056060); Duque de Caxias, Rio Pedra Branca, 1 Sep. 1999, *J.M.A. Braga 5443* (RB 00778086); Duque de Caxias, Trilha ao redor do lago da Barragem, Duque de Caxias, 6 May 1997, *S. J. Silva Neto 3998* (RB 00778085 Parque Nacional do Itatiaia. Rio Campo Belo, Lote 37, 27 March 1942, *A.C. Brade 17293* (RB 00649453).

First identified as *Trichomanes brasiliense* Desv.
BRAZIL–**Rio Grande do Sul**: Boa Vista, 1906, *Rosenstock 253* (W 19070016260).

First identified as *C. pyxidiferum* (list not exhaustive, only representative specimens)
BRAZIL–**Santa Catarina**: Blumenau, Parque Nacional da Serra do Itajaí – Spitzkopf, 14 Sep. 2009, *T.J. Cadorin 62* (FURB 00138); Parque Natural Municipal São Francisco de Assis, 20 Jan. 1999, *R. Hiendlmayer s.n.* (FURB 09541); Jaraguá do Sul, 30 Apr. 2011, *T.J. Cadorin 3160* (FURB 09537); **Paraná**: Curitiba, Bosque Municipal Reinhard Maack, 6 Mar. 2001, *Borgo 1146* (UPCB 45104); Tunas do Paraná, Estrada de Tunas do Paraná para a Fazenda Berneck, 21 Apr.

2007, *P.H. Labiak 3900* (RB 00663545); **São Paulo**: Matão, Fragmento G-09, 12 Dec. 2007, *J. Prado 1765* (RB 00836814); **Rio de Janeiro**: Parque Nacional do Itatiaia, Cachoeira do Poranga, próximo a antiga entrada do Hotel Simon, 15 Dec. 2008, *E.R. Damasceno 196* (RB 00581792); Parque Nacional do Itatiaia. Rio Campo Belo, próximo as parcelas do PMA, 30 May 2009, *E.R. Damasceno 272* (RB 00581791); Parque Nacional do Itatiaia, Trilha para os Três Picos, 31 May 2009, *E.R. Damasceno 292* (RB 00581795); Guapimirim, Estação Ecológica Estadual do Paraíso, rio Paraíso, margem esquerda na direção da subida da trilha, Parcela 5, 1 Dec. 2008, *C.E.S. Jascone 1146* (RB 00655244); Mangaratiba, Reserva Ecológica Rio das Pedras, trilha para a Toca da Aranha, 11 Jan. 1999, *C. Mynssen 245* (RB 00649906).

First identified as *Polyphlebium diaphanum* (Kunth) Ebihara & Dubuisson
BRAZIL–**Santa Catarina**: Forcação, 26 Jan. 2010, *T.J. Cadorin1016* (FURB 09531); Braço esquerdo, 10 May 2010, *T.J. Cadorin 2109* (FURB 09,527); Pinhalzinho, 27 Jan. 2010, *A. Korte 3127* (FURB 09529); Braço do Salão – Fazenda Sabiá, 27 Oct. 2009, *J.L. Schmitt 410* (FURB09536); Chicão – Vargem do Cedro/Parque Estadual da Serra do Tabuleiro, 1 Jun. 2010, *J.L. Schmitt 2582* (FURB 09526); **Minas Gerais:** Camanducaia, Mata do Trevo de acesso a Camanducaia, 01 Jun. 2001, *A. Salino 6914* (BHCB 60224);
First identified as *Polyphlebium hymenophylloides* (Bosch) Ebihara & Dubuisson

BRAZIL– **São Paulo:** Juquiá, Reserva Votorantim, 28 Mar 2013, *T.E. Almeida,* (BHCB 163019); **Minas Gerais:** Lambari, Parque Estadual de Nova Baden, 13 Jul. 2007, *A. Salino 12536* (BHCB 111,414); São Roque de Minas, Parque Nacional da Serra da Canastra, 31 Jan. 2007, *A. Salino 11588* (BHCB 104457).

Representative specimens of typical ***Crepidomanes pyxidiferum*** (L.) Dubuisson & Ebihara.

COSTA RICA – Puntarenas, Cantón de Coto Brus, Las Cruces Biological Station, sendero Rio Jaba, 15 Jun. 2004, *R.C. Moran 7021* (ASU 0006814).
CUBA – Southern Oriente and Pico Turquino, Arroyao Bayajá, 8 Aug. 1922, *E.L. Ekman 14760* (NY 01840964); Southern Oriente and Pico Turquino, Serra Maestra, 15 Aug. 1922, *E.L. Ekman 14852a* (NY 01840965).
DOMINIC REPUBLIC – Prov. Elias Piña, Cordillera Central, 4 Mar. 1982, *J.T. Mickel 8681* (NY 01840959); Prov. La Vega, Cordillera Central, 12 May 1982, *T. Zanoni s.n.* (NY 01840979).
JAMAICA – "Old England", below Cinchona, 18 Feb. 1903, *L.M. Underwood 1666* (NY 01840962).
PERU – Tarapoto, 1855, *Spruce 4761* (K 000201009).

First identified as *Trichomanes cavifolium* C. Müller
MEXICO – Cuesta grande de Chiconquiaco, *s.d., Schiede s.n.* (Holotype – B 20 0106081); *s.loc., s.d., Schaffner s.n.* (K 000589424).

First identified as *Trichomanes olivaceum* Kunze ex Klotzsch
VENEZUELA – Merida, *s.d., Moritz 341* (Type – B 20 0103901, B 20 106093).

Polyphlebium diaphanum (Kunth) Ebihara & Dubuisson
VENEZUELA – *s.d., Humboldt & Bonpland s.n.* (Holotype – P 00669210).
FRENCH GUIANA – Petite Montagne Tortue, Bassin de l'Approuague, 4 Jun. 2005, *M. Boudrie 4087* (P 01419713).
BRAZIL– **Espírito Santo**: Castelo, Trilha para o Forninho, Floresta Ombrófila Densa Altomontana com inselbergues, 17 Jul 2008, *P.H. Labiak 4812* (RB 00532185); Domingos Martins, São Paulo do Aracê, 6 Dec. 2008, *A. Salino 14140* (BHCB) **Rio de Janeiro**: Nova Friburgo, Caminho para o córrego São Thiago, Entrada no Km 13 da Estrada Nova Friburgo – Lumiar, 30 Mar. 1989, *L.S. Sylvestre 206* (RB 00650005); Itatiaia - Lote XVII, Sep. 1934, *Brade 14081* (RB 00650010); **Minas Gerais:** Conceição do Mato Dentro, Parque Natural Municipal do Ribeirão do Campo, 6 Oct. 2003, *A. Salino 8858* (BHCB); Simonésia, RPPN Mata do Sossego, 23 May 2006, *A. Salino 11177* (BHCB); **São Paulo:** Ubatuba, Parque Estadual da Serra do Mar, 5 May 2001, *A. Salino 6752* (BHCB); Eldorado, Parque Estadual do Jacupiranga, 23 Mar. 2005, *A. Salino 10173* (BHCB); **Paraná**: Ponta Grossa, Parque Estadual de Vila Velha, capão da piscina, 7 Jan. 2004, *P. H. Labiak 3084* (RB 00649299);); Morretes, Serra da Graciosa, 9 Apr. 1998, *V.A.O. Dittrich 345* (BHCB); **Santa Catarina**: Braço esquerdo, 10 May 2010, *T.J. Cadorin 2209* (FURB 09523); Rio Manso, 2 Feb. 2010, *T.J. Cadorin 1128* (FURB 09533).

First identified as *P. hymenophylloides*
St VINCENT – *s.d., Guilding s.n.* (Type? - HUH 00022242); Upper valley of Richmond River, 26–27 May 1947, *C.V. Morton 6189* (P 01304661).
TRINIDAD – 1861, Bosch's collection, *Cruger s.n.* (K 000589444).
GUADELOUPE – Matouba, 29 Sep. 1938, *Questel 1822* (P 01304656).
HAITI – Massif des Cahos, 16 Feb. 1926, *E.L. Ekman 5555* (P01304657)
BRAZIL–**Paraná**: Reserva Natural Rio Cachoeira, Trilha do Zé Carlos, 30 Apr. 2006, *Weiss 1134* (UPC B0057092).

First identified as *Crepidomanes pyxidiferum* (L.) Dubuisson & Ebihara
BRAZIL–**Rio de Janeiro**: Entrada Redentor, Serra da Carioca, 6 Jan. 1948, *A.C. Brade 18780* (RB 00649916); Parque Nacional do Itatiaia, Trilha Rui Braga – Rebouças/Sede, 25 Nov. 2009, *E.R. Damasceno 389* (RB 00581796); Parque Nacional do Itatiaia, Trilha Rui Braga – Rebouças/Sede. Próximo ao Abrigo Lamego, 11 Jun. 2009, *E.R. Damasceno 307* (RB 00581905); Chácara do Fonseca, Corcovado (próximo do aqueduto), 17 Mar. 1925, *M.C. Vaughau Bandeira s.n.* (RB 00649492); Guapimirim, Trilha entre o Paraíso e o Jacarandá (Teresópolis), 8 Apr. 2011, *R. A. Engelmann RE1673* (RB 00698457); **São Paulo**: Apiahy, *s.d.*, Ex Herb. Schwacke, *Puiggari 2365* (RB 00651477); Itapecirica, Jun. 1901, *Wettstein s.n.* (W 19,050,001,083); **Minas Gerais**: Córrego da Lapa in Serra da Tiririca, 20 Sep. 1902, *Schwacke 14930* (RB 00652018); **Santa Catarina**: Área Virgem do Parque Nacional da Serra do Itajaí, 23 Nov. 2009, *T.J. Cadorin 757* (FURB 09540); Cubatão, 6 Jul. 2010, *T.J. Cadorin 2918* (FURB 09538).

First identified as *Trichomanes pyxidiferum* L. f. *gracile* Rosenstock
BRAZIL–**Rio de Janeiro**: Coreorado, 1910, *P. von Luetzelburg 262* (Isotype – NY 00144726).

First identified as *Trichomanes pyxidiferum* L. var. *organense* Rosenstock
BRAZIL–**Rio de Janeiro**: Serra dos Orgaos, 1910, *P. von Luetzelburg 92* (Isosyntype – NY 00144725).

First identified as *Trichomanes brasiliense* Desv.
BRAZIL– *s.d., s.c.* (Holotype – P 00624517).

First identified as *Trichomanes eximium* Kunze
BRAZIL–**Rio de Janeiro**: Serra dos Orgaos, Aug. 1915, *P. von Luetzelburg 6095* (W 19270020949).

First identified as *Trichomanes tranninense* Fée
BRAZIL– *s.d.*, *Glaziou 2251* (Holotype – P 00624521).

Appendix 2. Selected taxa with preliminary taxonomic treatment, global geographical distribution of the species, voucher and origin for selected specimens, and GenBank Accession number for *rbcL* sequences (or references). Distribution: WIO = Western Indian Ocean.

Genus and species	Subgenus/Section	Geographical distribution	Selected specimens and vouchers (and herbaria)	Origin of the sequenced specimens	GenBank Accession Number or references
Trichomanes emarginatum C.Presl		Southern South America	*C. Zanotti* et al. *568* (SI)	Argentina	This study, KX894450
Crepidomanes (C.Presl) C.Presl					
Cr. africanum (Christ) Ebihara & Dubuisson	*Crepidomanes/Crepidomanes*	Africa	*R. Mauri 14-15* (MPU)	Congo	Dubuisson et al. (2013)
Cr. aphlebioides (Christ) I.M.Turner	*Nesopteris*	Asia	*Matsumoto 01-955* (TNS)	Vanuatu	Ebihara et al. (2007)
Cr. bonapartei (C.Chr.) J.P.Roux	*Crepidomanes/Crepidomanes*	WIO	*F. Rakotondrainibe 6255* (P)	Madagascar	Dubuisson et al. (2013)
Cr. bipunctatum (Poir.) Copel.	*Crepidomanes/Crepidomanes*	Palaeotropics, except Africa	*JY Dubuisson H1601* (MPU)	La Réunion	Dubuisson (1997)
Cr. chevalieri (Christ) Ebihara & Dubuisson	*Crepidomanes/Crepidomanes*	Africa	*C.A.Thorold CP2* (BM)	Cameroon	Dubuisson et al. (2013)
Cr. christii (Copel.) Copel.	*Crepidomanes/Crepidomanes*	Asia	*A. Ebihara 000,226-038* (TI)	Malaysia	Ebihara et al. (2007)
Cr. clarenceanum (F.Ballard) Pic.Serm.	*Crepidomanes/Crepidomanes*	Africa	*A. Mercier s.n.* (P)	Gabon	Dubuisson et al. (2013)
Cr. fallax (Christ) Ebihara & Dubuisson	*Crepidomanes/Crepidomanes*	Africa-WIO	*F. Rakotondrainibe 6467* (P)	Madagascar	Dubuisson et al. (2013)
Cr. frappieri (Cordem.) J.P.Roux	*Crepidomanes/Cladotrichoma*	Africa-WIO	*Y. Robert 1290*	La Réunion	Dubuisson et al. (2013)
C. grande (Copel.) Ebihara & K.Iwats.	*Nesopteris*	Asia	*Kokubo Ponape-8* (TI)	Micronesia	Ebihara et al. 2007)
Cr. humile (G.Forst.) Bosch	*Crepidomanes/Crepidium*	Asia	*A. Ebihara 001,121-04* (TI)	Japan	Ebihara et al. (2007)
Cr. inopinatum (Pic.Serm.) J.P.Roux	*Crepidomanes/Crepidomanes*	Africa-WIO	*E. Grangaud s.n.*	La Réunion	Dubuisson et al. (2013)
Cr. intermedium (Bosch) Ebihara & K.Iwats.	*Nesopteris*	Asia-Pacific Isl.	*Game 83/095* (UC)	Fiji	Dubuisson et al. (2003)
Cr. intramarginale (Hook. & Grev.) C.Presl	*Crepidomanes/Crepidomanes*	Asia	*C. Tsutsumi & M. Kato s.n.* (TNS)	India	Dubuisson et al. (2013)
Cr. intricatum (Farrar) Ebihara & Weakley	*Crepidomanes/Crepidomanes*	North America	*Farrar 06-01-06-02 & 06-01-06-04* (TNS)	Illinois, USA	Ebihara, Farrar, and Ito (2008)
Cr. kurzii (Bedd.) Tagawa& K.Iwats.	*Crepidomanes/Crepidomanes*	Asia	*A. Ebihara 001,121-05* (TI)	Japan	Ebihara et al. (2007)
Cr. latealatum (Bosch) Copel.	*Crepidomanes/Crepidomanes*	Asia	*A. Ebihara 991,205-02* (TI)	Japan	Ebihara et al. (2003)
Cr. latemarginale (D.C.Eaton) Copel.	*Crepidomanes/Crepidomanes*	Asia	*A. Ebihara 031,116-08* (TI)	Taiwan	Ebihara et al. (2007)
Cr. longilabiatum (Bonap) J.P.Roux	*Crepidomanes/Cladotrichoma*	Madagascar	*F. Rakotondrainibe 1860* (P)	Madagascar	Dubuisson et al. (2013)
Cr. mettenii (C.Chr.) Ebihara & Dubuisson	*Crepidomanes/Crepidomanes*	Africa	*R. Mauri s.n.* (MPU)	Congo	Dubuisson et al. (2013)
Cr. minutum (Blume) K.Iwats.	*Crepidomanes/Gonocormus*	Africa-Asia	*Norris 106,043* (UC)	Equatorial Guinea	Ebihara et al. (2007)
Cr. minutum	/	/	*A. Ebihara 001,121-05* (TI)	Japan	Ebihara et al. (2007)
Cr. pyxidiferum (L.) Ebihara & Dubuisson	*Crepidomanes/Crepidomanes*	Neotropics	*Rojas 4360*	Costa Rica	Dubuisson et al. (2013)
Cr. schmidtianum (Zenker ex Taschner) K.Iwats var. *schmidtianum*	*Crepidomanes/Crepidomanes*	Asia	*A. Ebihara 010,509-01* (TI)	Japan	Ebihara, Farrar, and Ito (2008);
Cr. trinerve (Baker)	*Crepidomanes/Crepidomanes*	Mauritius	*M.J. Coode 4103* (MAU, P)	Mauritius	Dubuisson et al. (2013);
Cr. vitiense (Baker) Bostock.	*Crepidomanes/Crepidomanes*	Asia	*Bostock s.n.* (TI)	Australia	Ebihara et al. (2004);
Cr. walleri (Watts) Tindale	*Crepidomanes/Crepidomanes*	Asia	*Ohsawa 001,202-03* (TI)	Australia	Ebihara et al. (2007);
Polyphlebium Copel.					
P. angustatum (Carmich.) Ebihara & Dubuisson		Neotropics	*M. Kessler 10,957* (UC)	Bolivia	Dubuisson et al. (2003);
P. angustatum		/	*A. Salino 13,279* (BHCB)	Brazil	This study, KX913311
P. borbonicum (Bosch) Ebihara & Dubuisson		Palaeotropics	*JY Dubuisson HR1999-2* (P)	La Réunion	Dubuisson et al. (2003);
P. aff. *borbonicum*		/	*Wood 10,501* (PTBG)	Marquesas Isl.	Ebihara et al. (2009);
P. aff. *borbonicum*		/	*J. Nitta 073* (UC)	Tahiti (Moorea)	Ebihara et al. (2009);
P. capillaceum (L.) Ebihara & Dubuisson		Neotropics	*M. Kessler 7316* (GOET, LPB)	Bolivia	Dubuisson et al. (2003);
P. colensoi (Hook.f.) Ebihara & K.Iwats.		New Zealand	*Ebihara 011,216-07* (TI)	New Zealand	Ebihara et al. (2007);
T. debile Bosch (*)		Neotropics	*Jimenez 1568* (UC)	Bolivia (1)	Ebihara et al. (2009);
T. debile		/	*Kromer 1743* (UC)	Bolivia (2)	Ebihara et al. (2009);
P. diaphanum (Kunth) Ebihara & Dubuisson		Neotropics	*JY Dubuisson s.n.* (MPU)	French Guiana	Dubuisson (1997);
P. diaphanum		/	*T. Ohsawa 178-12* (KANA, TI, LPB)	Bolivia	Ebihara et al. (2003);
P. endlicherianum (C.Presl) Ebihara & K.Iwats.		Pacific Isl.-NZ	*A.R. Smith 2600* (UC)	New Zealand	Dubuisson et al. (2003);
P. exsectum (Kunze) Ebihara & Dubuisson		Chile	*A. Ebihara 021,229-01* (TI)	Chile	Ebihara et al. (2007);
P. hymenophylloides (Bosch) Ebihara & Dubuisson		Neotropics	*JY Dubuisson HG-2004-10* (P)	Guadeloupe (1)	Ebihara et al. (2007);
P. hymenophylloides		/	*C. Chaussidon 4-2007* (P)	Guadeloupe (2)	This study, KX913313
P. hymenophylloides		/	*A. Salino 13,269* (BHCB)	Brazil	This study, KX913314

(Continued)

Appendix 2. *(Continued)*

P. hymenophylloides		/	*n.c.*	Mexico	This study, KX913312
P. ingae (C.Chr.) Ebihara & Dubuisson		Juan Fernandez	*Danton s.n.* (P)	Juan Fernandez	Ebihara et al. (2007);
P. venosum (R.Br.) Copel.		Australia-NZ	*A.R. Smith 2598* (UC)	New Zealand	Ebihara et al. (2007);
P. vieillardii (Bosch) Ebihara & K.Iwats.		New Caledonia	*Ebihara 001,220-02* (TI)	New Caledonia	Ebihara et al. (2007);
Didymoglossum Desv.					
D. cuspidatum (Willd.) Ebihara & Dubuisson	*Microgonium*	WIO	*JY Dubuisson HR-1999-5* (P)	La Réunion	Hennequin et al. (2003);
D. gourlianum (Grev. ex J. Sm.) Pic.Serm.	*Didymoglossum*	Neotropics	*JY Dubuisson H701* (MPU)	Colombia	Dubuisson (1997);
D. membranaceum (L.) Vareschi	*Didymoglossum*	Neotropics	*JY Dubuisson H801* (MPU)	Colombia	Dubuisson (1997);
Vandenboschia Copel.					
V. maxima (Blume)Copel.	*Vandenboschia*	Asia-Pacific Isl.	*A. Ebihara 000,225-026* (TI)	Malaysia	Dubuisson et al. (2003);
V. radicans (Sw.) Copel.	*Vandenboschia*	Neotropics	*M. Kessler 11,447* (UC, LPB)	Bolivia	Pryer et al. (2001);
V. speciosa (Willd.) G. Kunkel	*Vandenboschia*	Western Europe	*JY Dubuisson H401-410* (MPU)	France	Dubuisson (1997);
Trichomanes L.					
T. ankersii C. Parker ex Hook. & Grev.	*Lacostea*	Neotropics	*JY Dubuisson H1201* (MPU)	Colombia	Dubuisson et al. (2003);
T. crispum L.	*Trichomanes*	Neotropics	*JY Dubuisson HV-1997-22* (DUKE)	Venezuela	Dubuisson et al. (2003);
T. elegans Rich.	*Davalliopsis*	Neotropics	*JY Dubuisson H901* (MPU)	Colombia	Dubuisson (1997);
T. osmundoides Poir.	*Feea*	Neotropics	*JY Dubuisson H1102* (MPU)	French Guiana	Dubuisson (1997);
T. pinnatum Hedw.	*Trichomanes*	Neotropics	*JY Dubuisson H2601* (MPU)	French Guiana	Dubuisson (1997);
Abrodictyum C.Presl					
A. flavofuscum (Bosch) Ebihara& K.Iwats.	*Abrodictyum*	Asia	*J. Munzinger 316* (P)	New Caledonia	Dubuisson et al. (2003);
A. meifolium (Bory ex Willd.) Ebihara & K.Iwats.	*Pachychaetum*	WIO	*JY Dubuisson HR-1999-21* (P)	La Réunion	Dubuisson et al. (2003);
A. obscurum (Blume) Ebihara & K.Iwats.	*Pachychaetum*	Asia	*A. Ebihara 001,118-06* (TNS)	Japan	Ebihara et al. (2007);
A. rigidum (Sw.) Ebihara & Dubuisson	*Pachychaetum*	Neotropics	*M. Kessler 11,360* (UC)	Bolivia	Hennequin et al. (2003);
Cephalomanes C.Presl					
Ce. atrovirens C.Presl		Asia	*Kokubo Ponape-12* (TI)	Micronesia	Ebihara et al. (2007);
Ce. javanicum (Blume) C.Presl.		Asia	*JY Dubuisson H3001* (MPU)	Brunei	Dubuisson (1997);
Callistopteris Copel.					
Ca. apiifolia (C.Presl) Copel.		Asia-Pacific Isl.	*Matsumoto 0003-054* (TNS)	Taiwan	Ebihara et al. (2007);
Hymenophyllum Sm.					
H. hirsutum (L.) Sw.	*Sphaerocionium*	Pantropics	*M. Kessler et al. 9756* (UC, LPB)	Bolivia	Pryer et al. (2001);
H. polyanthos (Sw.) Sw.	*Mecodium*	Neotropics	*M. Kessler et al. 9866* (UC, LPB)	Bolivia	Pryer et al. (2001);
H. tunbrigense (L.) Sm.	*Hymenophyllum*	Western Europe	*JY Dubuisson H301* (MPU)	France	Dubuisson (1997);
H. nephrophyllum Ebihara & K.Iwats.	*Cardiomanes*	Australia-New Zealand	*A. Ebihara 011,222-07* (TI, CHR)	New Zealand	Ebihara et al. (2003)

(*) Considered as synonym of *P. borbonicum* by Ebihara et al. (2009).