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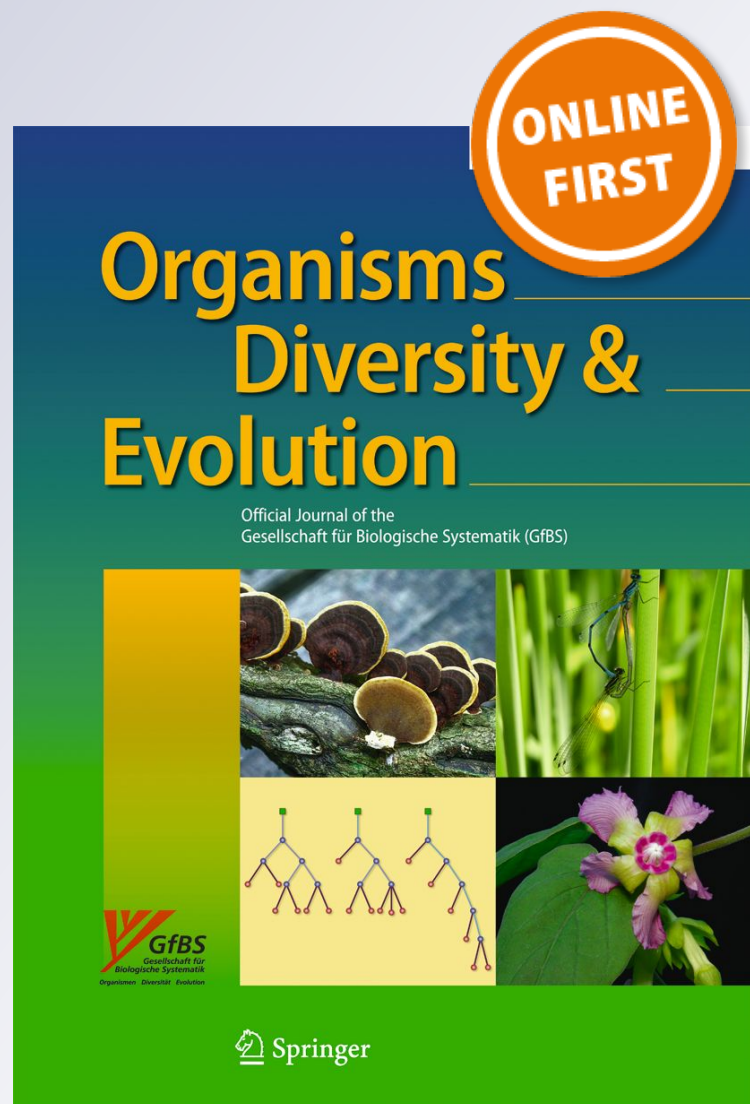
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# Further progress towards the delimitation of *Cheilanthes* (Cheilanthesoideae, Pteridaceae), with emphasis on South American species

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## Abstract

Cheilantheid ferns (Cheilanthesoideae sensu PPG 1 2016) constitute an important group within the Pteridaceae and are cosmopolitan in distribution. In South America, there are 155 species distributed in 13 genera, among which the largest are *Adiantopsis* (35), *Cheilanthes* (27), and *Doryopteris* (22). Most of the cheilantheid species are morphologically adapted to grow in arid to semi-arid conditions and show convergent evolution, which has implied difficulties in defining the genera throughout their taxonomic history (Copeland 1947, Tryon & Tryon 1973, Gastony & Rollo 1995, 1998, Kirkpatrick *Systematic Botany*, 32: 504–518, 2007, Rothfels et al. *Taxon*, 57: 712–724, 2008). Here, we sequenced two plastid markers (*rbcL* + *trnL-F*) of 33 South American cheilantheid species, most of which have not been included in phylogenetic analyses previously. The South American species were analyzed together with South African and Australasian *Cheilanthes* and representatives of related cheilantheid genera. The phylogenetic analysis showed that most *Cheilanthes* species are related to the genus *Hemionitis*, constituting different groups according to their distribution; moreover, three species—*C. hassleri*, *C. pantanalensis*, and *C. obducta*—appear as the sister clade of *Hemionitis*. *Cheilanthes micropteris*, the type species, is strongly supported in a clade with Australasian *Cheilanthes* plus five South American *Cheilanthes* species, all of which show a reduction in the number of spores per sporangium; this feature would be a synapomorphy for core *Cheilanthes* s.s. We found no support uniting other South American *Cheilanthes* to either the group of South African *Cheilanthes* or to core *Cheilanthes* s.s. On the other hand, *C. geraniifolia*, *C. goyazensis*, and *C. bradei* formed a clade related to *Doryopteris* that, with further study, could be considered as a new genus. The phylogenetic hypotheses presented here contribute substantially to the delimitation of *Cheilanthes* s.s. and related groups and provide the basis for re-examining the generic taxonomy.

**Keywords** *Cheilanthes* · *Hemionitis* · Phylogeny · *rbcL* · *trnL-trnF* · South America

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## Introduction

In South America, the cheilantheid ferns (Pteridaceae) are represented by the genera *Adiantopsis* Fée, *Argyrososma* (J. Sm.) Windham, *Astrolepis* D.M. Benham and Windham, *Cheilanthes* Sw., *Doryopteris* J. Sm., *Gaga* Pryer, F. W. Li and Windham, *Hemionitis* L., *Lytoneuron* (Klotzsch) Yesilyurt, *Myriopteris* Fée, *Notholaena* R. Br., *Ormopteris* J.Sm., *Pellaea* Link, and *Trachypteris* André ex Christ (Tryon et al. 1990; Ponce et al. 2008a, 2016). Recent treatments of the subfamily Cheilanthesoideae (sensu PPG 1 2016) transferred several Neotropical species of *Cheilanthes* to the genera *Adiantopsis* (Link-Perez et al. 2011, Ponce and Scataglini

2012), *Gaga* (Li et al. 2012), and *Myriopteris* (Grusz and Windham 2013), and several Paleotropical species to the genera *Allosorus* Bernh. and *Aleuritopteris* Fée (Christenhusz 2012; Zhang et al. 2013). As a result *Cheilanthes* now comprises about 100 species (PPG I 2016), with around 30 species in South America (Ponce et al. 2016), including *C. micropteris*, the type species.

The cheilanthoids live in tropical and temperate regions, in mountainous or rocky locations, from sea level to more than 4000 m elevation. The majority of the species grow in arid to semi-arid environments, and therefore exhibit xeromorphic characteristics as well as apogamy, hybridization, and polyploidy, as these phenomena allow them to perpetuate and reproduce under xeric conditions that are sometimes very extreme. All these features have generated adaptive convergences within the group that have persistently hampered the delimitation of genera and are reflected in the polyphyletic condition of *Cheilanthes* (Gastony and Rollo 1995; Prado et al. 2007; Schuettpelz et al. 2007; Rothfels et al. 2008).

Although *Cheilanthes* s.l. has not been fully monographed, its species have been extensively treated in the floras of North America (Editorial Committee 1993), Mesoamerica (Yatskievych and Moran 1995), Mexico (Mickel and Smith 2004), Peru (Tryon and Stolze 1989), Chile (Rodríguez 1995), Bolivia (Kessler, et al. 2017), Brazil (Prado 1992, 2004), and Argentina (de la Sota 1977, 1998; Ponce et al. 2008a; Ponce, 2016). In the Paleotropics, *Cheilanthes* has been studied taxonomically in South Africa, Australia, New Zealand, and Asia (Anthony 1984, Chamber and Farrant, 1991, Quirk et al. 1983; Zhang and Yatskievych 2013).

The classic works on *Cheilanthes*, from Mettenius (1859), through Christensen (1906) and Copeland (1947) to Tryon et al. (1990), have used the following morphological characters to define the genus: sorus circular in the vein apex, discrete or contiguous to maturity, barely or totally covered by the recurved foliar margin, thin lobed, subcontinuous or continuous. Also, the indument type, shape, and composition, e.g., hairs simple and/or glandular, and presence of hairs and scales or only scales, were used. All these attributes are widely variable and easily encompass all the cheilanthoids; however, they are classically used in taxonomic treatments to separate genera.

Since the 1980s, systematic studies using morpho-anatomical, palynological, chromosomal, and biochemical attributes have segregated a number of genera that present their own combination of characters and appear to be natural, including *Argyrochosma* (Windham 1987), *Bommeria* (Ranker 1990), and *Astrolepis* (Benham and Windham 1992). Later on, with advances in molecular phylogenetic methods, the family Pteridaceae and, in particular the subfamily Cheilanthoideae, were analyzed using the plastid gene *rbcL* by Gastony and Rollo (1995, 1998), Prado et al. (2007), and Bouma et al. (2010), while Zhang et al. (2007) added the *trnL-trnF* region to

analyze the Asian cheilanthoid ferns and Schuettpelz et al. (2007) added the *atpB* and *atpA* markers to analyze the Neo- and Paleotropical species. Additionally, new multigenic analyses of cheilanthoids have revealed that they can be divided into the following groups, sensu Windham et al. (2009): *Calciphilopteris*, bommeriids, skinneri clade, myriopterids, pellaeids, notholaenids, and hemionitids. In the following years, more studies have focused on different genera of the cheilanthoids, circumscribing *Pellaea* (Kirkpatrick 2007), *Notholaena* (Rothfels et al. 2008), *Adiantopsis* (Link-Perez et al. 2011); *Gaga* (Li et al. 2012, Ponce and Scataglini 2016); *Myriopteris* (Grusz and Windham 2013); and *Doryopteris*, *Lytoneuron*, and *Ormopteris* (Yesilyurt et al. 2015). Also, monophyletic groups have been recognized within *Cheilanthes* in South Africa (Eiserhardt et al. 2011) and Australia (Bouma et al. 2010). However, a molecular analysis including a broad sample of South American species is still lacking.

The variable morphology of cheilanthoids makes it difficult to find morphological features that distinguish the genera defined by the molecular analyses mentioned above. Some morpho-anatomical, palynological, and chromosomal synapomorphies have been established for *Argyrochosma* (Windham 1987) and *Astrolepis* (Bentham and Windham 1992), and the presence of waxy glandular hairs in the gametophyte is exclusive for *Notholaena* (Johnson et al. 2012). Glandular hairs were observed in the gametophyte of *Argyrochosma nivea* var. *nivea* by Gabriel y Galán and Prada (2012), but in none varieties of *A. nivea* according to Martínez and Hernández (2017). Furthermore, presence of bicarinate axes and microscopic two-cellular capitate hairs were used to differentiate *Cheilanthes* from *Adiantopsis* (Link Pérez et al. 2011; Ponce and Scataglini 2012). Another two features were proposed as putative characters to distinguish *Myriopteris* from *Cheilanthes*: the shape of the vein ends (Pryer et al. 2010) and the reduction in the number of spores per sporangium (64 to 32 small spores in sexual and 32 to 16 large spores in asexual reproduction) due to “the elimination of a premeiotic mitosis in spore-forming cells” (Grusz and Windham 2013). Nevertheless, few species of *Cheilanthes* from South America were analyzed for these two features and more morphological evidence is still necessary, to clarify the differences between *Cheilanthes* and related groups.

The present study represents a further effort towards the resolution and circumscription of *Cheilanthes* s.s. and closely related groups of cheilanthoid species. We perform a phylogenetic analysis based on two plastid markers including 33 South American cheilanthoids, most of these *Cheilanthes* species not sampled previously, analyzed together with *Cheilanthes* from South Africa, Australia, and Asia and representatives of related cheilanthoid genera; we also score the putative diagnostic characters for *Cheilanthes* in the South American species sampled.

## Material and methods

### Taxon sampling

Species sampling was designed mainly to circumscribe *Cheilanthes* s.s.: we sequenced the *rbcL* and *trnL-F* markers in the type species *C. micropteris*, plus 17 South American *Cheilanthes*; additionally, South American representatives of other cheilanthoid genera were sequenced: four *Adiantopsis*, two *Argyrochosma*, three *Doryopteris*, one *Gaga*, one *Hemionitis*, three *Myriopteris*, and one *Pellaea*, yielding a total of 33 taxa. Most of the South American *Cheilanthes* were sequenced for the first time, except *C. bradei*, *C. goyazensis*, *C. micropteris*, and *C. rufopunctata*. Voucher information for the 33 sampled species is shown in Table 1. For the phylogenetic analysis, we included a broad array of taxa representing the genera listed above, plus representatives of *Aleuritopteris*, *Allosorus*, *Aspidotis*, *Lytoneuron*, *Notholaena*, *Pentagramma*, and *Trachypteris*, yielding a total of 119 taxa analyzed. *Calciophilopteris ludens*, belonging to the “*ludens* clade,” sister, the rest of the cheilanthoid clade (Rothfels and Schuettpelz 2014) was chosen to root the trees. Details of the 119 taxa included in the analysis and their GenBank numbers are listed in Appendix.

### DNA extraction and sequencing

Plants were field collected, dried in silica gel, and total DNA was extracted using the modified CTAB (cetyltrimethylammonium bromide) protocol from Doyle and Doyle (1987). The DNeasy plant mini kit (Qiagen, Hilden, Germany) was used for material from herbarium specimens. The plastid markers *rbcL* and *trnL-F* were amplified. For the *rbcL* gene, the pairs of primers 1F-675R and 660F-1351R designed by Gastony and Rollo (1995) were used. The *trnL-F* region was amplified using the primer pair denoted c-d and e-f as described by Taberlet et al. (1991). The PCR reactions were performed in 25  $\mu$ l final volume of 50–100 ng of template DNA, 0.2  $\mu$ M of each primer, 25  $\mu$ M of dNTPs, 5  $\mu$ M MgCl<sub>2</sub>, buffer 10 $\times$ , and 1.5 units of Taq polymerase provided by Invitrogen (Brazil). The reaction conditions were an initial period of denaturation at 94 °C for 5 min, followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at 48 °C for 1 min, extension at 72 °C for 1 min and 30 s, and a final extension at 72 °C for 6 min terminated the reactions. PCR products were run out on a 1% TBE agarose gel and stained with SybrSafe (Invitrogen). Sequencing reactions were performed by Macrogen, Inc. (Seoul, Korea). Sequences obtained were edited and manually aligned using the program BioEdit version 5.0.9 (Hall 1999). The sequences obtained were analyzed along with a selection of cheilanthoid sequences available in GenBank yielding a

total 119 for *rbcL* and 50 for *trnL-F*. The two plastid matrices were combined; the combined matrix can be found in S1 and in TreeBase: <http://purl.org/phylo/treebase/phyloids/study/TB2:S22441>

### Scoring of putative diagnostic morphological characters

Two morphological characters, the number of spores per sporangium and the shape of the vein endings, were scored for the 33 South American species analyzed. The data for the remaining species were obtained from the published literature (Knobloch 1966, 1969; Anthony 1984; Morbelli and Michelena 1989; Morbelli and Ponce 1997; Yesilyurt 2004; Martínez et al. 2017; Hernández in prep.). Dry and/or fresh specimens were examined using a Wild M5 binocular and Wild M20 microscope to observe the vein endings and the spores. To count the spores, a single mature, unopened, sporangium was placed in a drop of glycerol on a glass slide and covered with a coverslip; each sporangium was forced open by pressing carefully the coverslip and its spores were released into the glycerol. The results of these observations are summarized in Table 2. The number of spores per sporangium was also mapped onto the phylogenetic tree obtained.

### Phylogenetic analysis

Data were analyzed under Bayesian inference using BEAST 1.8.1 (Drummond et al. 2012). The appropriate model of nucleotide substitution for each marker was selected by the Akaike information criterion (AIC) implemented in jModelTest 2.1.4 (Darriba et al. 2012). In the case of *trnL-F*, the best-fitting model identified by jModeltest could not be implemented in BEAUti, so the next more complex model was used, which was coincident with the GTR + I + G selected as the best-fitting model for *rbcL*. So, the Bayesian analysis was conducted on the combined matrix with settings as follows: GTR + I + G substitution model, site-rate heterogeneity modeled with four gamma categories, estimated base frequencies, a lognormal uncorrelated relaxed clock, random starting tree, a Yule process as tree prior, auto-optimization option for all operators, and default values for all other settings. Two independent runs of 10 million generations were sampled every 1000 generation. To identify when the analyses had reached stationarity, we checked the output files for convergence and effective sample size (ESS) > 200 with Tracer v1.6 (Rambaut and Drummond, 2013). Based on this convergence diagnostic, the first 2500 sampled trees were discarded as burn-in from each analysis. Trees of the two runs were then combined using LogCombiner 1.8.4. The maximum clade-

**Table 1** List of the 33 species sampled and sequenced for this study. The collection localities and herbarium voucher information are indicated

Species	Location	Herbarium voucher
<i>Adiantopsis radiata</i>	Argentina, Misiones, Cainguás, Reserva Cuña Pirú	G. J. Márquez 19 (LP)
<i>Adiantopsis dichotoma</i> ,	Argentina, Misiones, Candelaria, Cerro Santa Ana	M. E. Múlgura 3819 (SI)
<i>Adiantopsis orbignyana</i>	Perú, Cajamarca, Guzmango	A. Sagástegui 11235 (F)
<i>Adiantopsis tweediana</i>	Argentina, San Luis, General San Martín, Chacras	F. Biganzoli et al. 2068 (SI)
<i>Argyrosma nivea</i> var. <i>flava</i>	Argentina, Córdoba, Calamuchita, Santa Rosa, Calmayo	L. Zavala-Gallo 1 (SI)
<i>Argyrosma nivea</i> var. <i>tenera</i>	Argentina, La Rioja, Chilecito	S. Donadio et al. 94 (SI)
<i>Cheilanthes buchtienii</i>	Argentina, Tucumán, Tafí del Valle, La Quebradita	M. M. Ponce 95 (SI)
<i>Cheilanthes fraseri</i>	Perú, Cusco, Machu Pichu, Ruinas Ollantaitambo	F. Biganzoli 2195 (SI)
<i>Cheilanthes geraniifolia</i>	Brazil, Minas Gerais, Itinga	T. E. Almeida 1340 (BHCB)
<i>Cheilanthes glauca</i>	Argentina, Rio Negro, P.N. Nahuel Huapi, Cerro Cresta de Gallo	PN-DTP, G.F. 77 (BCRU)
<i>Cheilanthes glutinosa</i>	Bolivia, La Paz, Parque Nacional Madidi, arriba Tambo Quemado	I. Jiménez 1928 (LPB)
<i>Cheilanthes hassleri</i>	Brazil, MS, Bonito, Faz. Remanso	Damasceno Jr. et al. 4196 (SI)
<i>Cheilanthes hieronymi</i>	Argentina, Buenos Aires, Tomquist, Sierra de la Ventana	M. D. Arana s.n. (SI)
<i>Cheilanthes hypoleuca</i>	Chile, Coquimbo, La Higuera, Caleta Los Hornos	M. M. Ponce 116 (SI)
<i>Cheilanthes micropteris</i>	Argentina, Córdoba, Calamuchita, Río Santa Rosa	L. Zavala-Gallo 7 (SI)
<i>Cheilanthes obducta</i>	Brazil, MS, Corumbá, Estrada Parque	E. Assis & G. Damasceno Jr. 280 (SI)
<i>Cheilanthes pantanalensis</i>	Brazil, MS, Corumbá, Serra de Amolar	E. Assis 1002 (SI)
<i>Cheilanthes pilosa</i>	Argentina, Salta, Cachi, Brealito	F. O. Zuloaga et al. 9453 (SI)
<i>Cheilanthes poeppigiana</i>	Argentina, Tucumán, Tafí del Valle, El Rincón	M. M. Ponce 88 (SI)
<i>Cheilanthes pruinata</i>	Argentina, Jujuy, de Tilcara a Alfarcito	F. O. Zuloaga et al. 9234 (SI)
<i>Cheilanthes rufopunctata</i>	Bolivia, Chuquisaca, Oropezca, Loma Guerrero a Punilla	J. R. L. Wood 14579 (LPB)
<i>Cheilanthes sarmientoi</i>	Argentina, San Juan, Jáchal, El Salto del Divisadero	M. M. Ponce 112 (SI)
<i>Cheilanthes scariosa</i>	Bolivia, Cochabamba, Quillaocollo, Incarragay	I. Linneo & D. Enriques 824 (LPB)
<i>Cheilanthes squamosa</i>	Argentina, San Luis, Junín, Merlo a Mirador Los Cóndores	Biganzoli et al. 2102 (SI)
<i>Doryopteris lorentzii</i>	Argentina, Tucumán, Burruyacu, Sierra del Campo, Arroyo Cajón	Hernández & Varela 757 (LIL)
<i>Doryopteris pentagona</i>	Argentina, Misiones, Gral. Belgrano, Res. Vida Silvestre Uruguái	M. E. Múlgura 3906 (SI)
<i>Doryopteris triphylla</i>	Argentina, Entre Ríos, Colón, P.N. El Palmar, La Glorieta	O. Morrone et al. 5881 (SI)
<i>Gaga marginata</i>	Argentina, Tucumán, Tafí del Valle, Ruta 307, La Quebradita	M. M. Ponce 95 (SI)
<i>Hemionitis tomentosa</i>	Argentina, Misiones, Cainguás, Reserva Cuña Pirú	G. J. Márquez 73 (LP)
<i>Myriopteris aurea</i>	Argentina, Jujuy, Humahuaca, Ruta 9, Arroyo Yallagua	M. E. Múlgura et al. 4227 (SI)
<i>Myriopteris microphylla</i>	Bolivia, Sud Yungas, de La Plazuela a La Paz	M. Kessler et al. 5688 (LPB)
<i>Myriopteris myriophylla</i>	Argentina, Jujuy, de Tilcara a Alfarcito, Garganta del Diablo	F. O. Zuloaga et al. 9232 (SI)
<i>Pellaea ternifolia</i>	Argentina, Córdoba, Río Cuarto, de Punilla a Achiras	Biganzoli et al. 2115 (SI)

credibility tree (MCC) showing posterior probabilities (PP) was displayed with FigTree.

## Results

A total of 33 *rbcL* and 23 *trnL-F* sequences were obtained for the South American cheilanthoid species. The combined matrix consisted of 119 taxa and 2261 bp (1266 bp *rbcL* + 995 bp *trnL-F*) of which 632 were parsimony-informative.

Consistent with previous results (Rothfels et al. 2008; Windham et al. 2009), the topology was resolved in two major

clades: one including the myriopterids (PP = 1) and pelleaids (*Pellaea* s.s., PP = 1 and *Argyrosma*, PP = 0.99) and the other formed by the notholaenids (*Notholaena*, PP = 1) and the hemionitids (PP = 0.99; names follow Windham et al. 2009; Fig. 1).

The hemionitids included many genera and different groups of *Cheilanthes* species: a clade with PP = 1 groups *Adiantopsis* (PP = 1), *Doryopteris* (PP = 0.97) plus the smaller genera *Lytoneuron* (PP = 1) and *Ormopteris* (PP = 1), and two groups of *Cheilanthes* species: the “*Cheilanthes geraniifolia* group” joining *C. geraniifolia*, *C. goyazensis*, and *C. bradei* with PP = 1 and the “*Choristosoria* group” (Yesilyurt et al. 2015) including *C. multifida*, *C. induta*, and *P. pteroides* (PP = 0.97).

**Table 2** Two morphological features scored for the 33 analyzed species

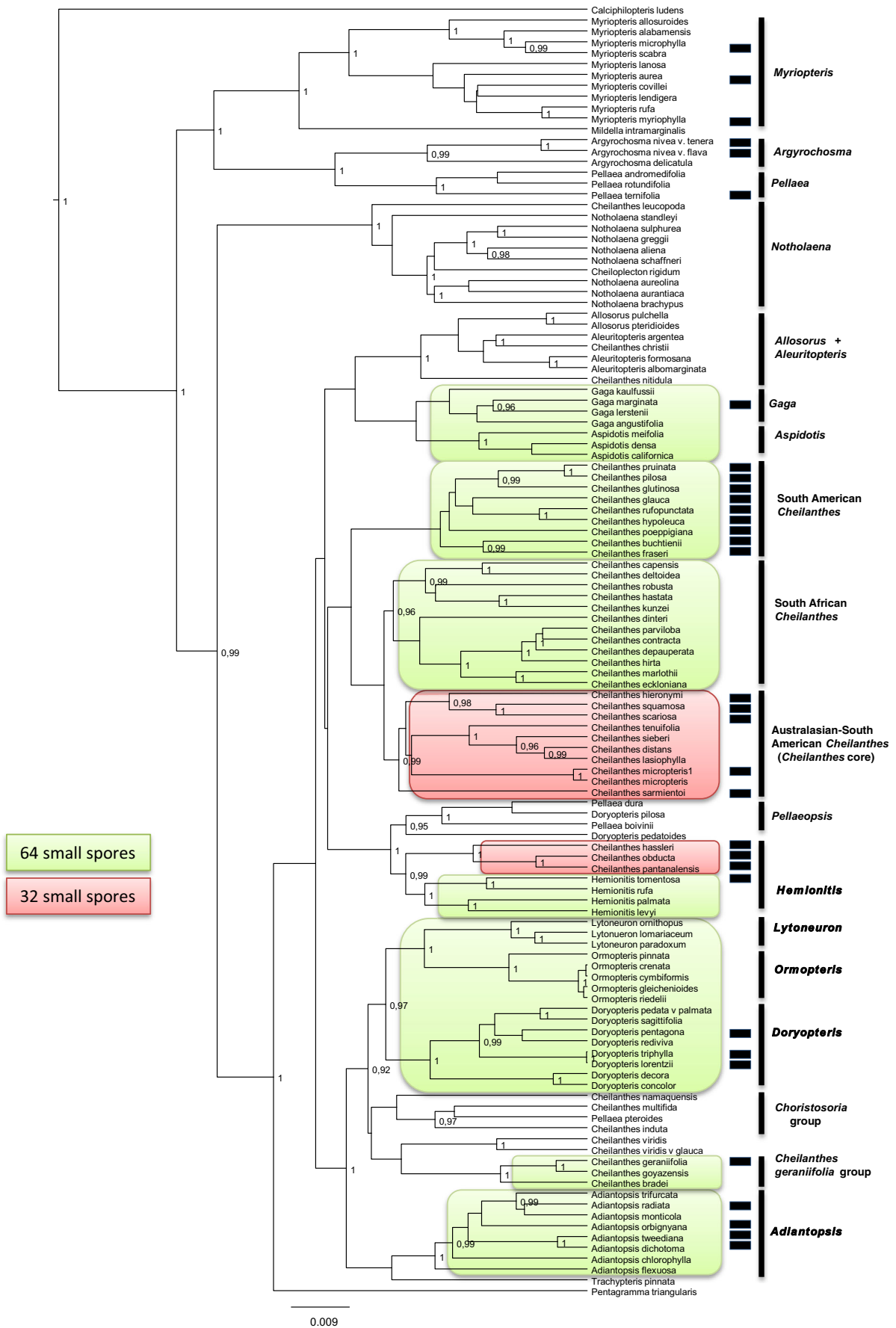
Species	Number of spores per sporangium		Shape of the vein end
	Asexual reproduction Large spores (55–88 µm)	Sexual reproduction Small spores (30–54 µm)	
<i>Adiantopsis radiata</i>		–	Widened
<i>Adiantopsis dichotoma</i>		–	Widened
<i>Adiantopsis orbignyana</i>		64	Widened
<i>Adiantopsis tweediana</i>		64	Widened
<i>Argyroschisma nivea</i> var. <i>flava</i>	32	64	Unwidened
<i>Argyroschisma nivea</i> var. <i>tenera</i>	32	64	Unwidened
<i>Cheilanthes buchtienii</i>	32	64	Widened
<i>Cheilanthes fraseri</i>		–	Widened
<i>Cheilanthes geraniifolia</i>		64	Widened
<i>Cheilanthes glauca</i>		64	Widened
<i>Cheilanthes glutinosa</i>	–	–	Widened
<i>Cheilanthes hassleri</i>		32	–
<i>Cheilanthes hieronymi</i>		32	Widened
<i>Cheilanthes hypoleuca</i>		64	Widened
<i>Cheilanthes micropteris</i>		32	Widened
<i>Cheilanthes obducta</i>		32	Unwidened
<i>Cheilanthes pantanalensis</i>		32	Unwidened
<i>Cheilanthes pilosa</i>		64	Widened
<i>Cheilanthes poeppigiana</i>		64	Widened
<i>Cheilanthes pruinata</i>	32		Widened
<i>Cheilanthes rufopunctata</i>		64	Widened
<i>Cheilanthes sarmientoi</i>	16	32	Widened
<i>Cheilanthes scariosa</i>		32	–
<i>Cheilanthes squamosa</i>		32	Widened
<i>Doryopteris lorentzii</i>		64	Widened
<i>Doryopteris pentagona</i>		64	–
<i>Doryopteris triphylla</i>		64	Widened
<i>Gaga marginata</i>	32		Widened
<i>Hemionitis tomentosa</i>		64	Unwidened
<i>Myriopteris aurea</i>	32	64	Unwidened
<i>Myriopteris microphylla</i>		64	Unwidened
<i>Myriopteris myriophylla</i>	32		Unwidened
<i>Pellaea ternifolia</i>		64	Unwidened

The remaining species of *Cheilanthes* appear in three groups distributed in the hemionitid clade according to their distribution; two of these groups display good support: South African *Cheilanthes* (PP = 0.98) and Australasian-South American *Cheilanthes* (PP = 0.99), the latter including the type species *C. micropteris*. The third group includes exclusively *Cheilanthes* from South American but is weakly supported. The *Hemionitis*—“*Pellaeopsis*” clade (PP = 1) also includes a group (PP = 1) of three *Cheilanthes*: *C. hassleri*, *C. obducta*, and *C. pantanalensis*, constituting with PP = 0.99 the sister clade of *Hemionitis*.

## Discussion

### Phylogenetic analysis

The results presented here recover with good support the clades within the subfamily Cheilantheoideae (PPG I, 2016) proposed in earlier molecular phylogenies: myriopterids, pellaids, notholaenids, and hemionitids (Kirkpatrick 2007; Rothfels et al. 2008, Windham et al. 2009, Eiserhardt et al. 2011, Grusz and Windham 2013). The analysis shows the myriopterids + pellaids as the sister group to notholaenids





◀ **Fig. 1** Maximum credibility tree obtained from the Bayesian analysis of the combined matrix (*rbcL* + *trnL-F*). Numbers at nodes indicate Bayesian posterior probabilities. The scale bar represents divergence times. Species sequenced for this study are denoted with a black rectangle. Major clades are indicated and discussed in the text. The mapping of the number of spores per sporangium in sexual reproduction is shown for the hemionitid clade

+ hemionitids, in agreement with the scheme proposed by Grusz and Windham (2013) for the subfamily.

The cheilanthoid species of *Argyrochosma*, *Myriopteris*, and *Pellaea* sequenced for this study fall in their corresponding genera, as expected; the same occurs with the sequenced species of *Adiantopsis* and *Doryopteris*. These two genera form a strongly supported clade in the hemionitids in agreement with Link-Perez et al. (2011) and Yesilyurt et al. (2015).

On the other hand, the species traditionally considered within *Cheilanthes* appear in different groups of the hemionitids clade, discussed below.

*Cheilanthes bradei*, *C. geraniifolia*, and *C. goyazensis* compose a strongly supported group, here named “*Cheilanthes geraniifolia* group,” resembling the one described by Weatherby (1946), including these three species plus *C. eriophora* (Fée) Mett., the latter with no sequences available. The species are distributed in central-eastern Brazil, the Guyana massif of Colombia and Venezuela, eastern Bolivia, and Paraguay. The group is characterized by bicolored rhizome scales with sclerotic centers and filiform apices; petioles and rachis terete, blackish; pedate, pentagonal lamina; single and/or capitate, multicellular, long, matted hairs; veins free and widened at the apex; and 64 spores per sporangium (sexual reproduction) and 32 spores per sporangium (asexual reproduction). In the present study, the “*C. geraniifolia* group” appears more closely related to *Doryopteris* than to other groups of *Cheilanthes*. The peculiar morphology, distribution, and habitat of the *C. geraniifolia* group were already pointed out by Weatherby (1946) and Tryon & Tryon (1973) in his work on *Notholaena* of Brazil. Based on the molecular results presented here and the morphological evidence, it is possible that this group could be segregated as a genus (Ponce and Scataglini unpublished).

The remainder of the sampled South American *Cheilanthes* form different groups related to *Hemionitis*, a neotropical genus that includes five species (Mickel 1974, PPG I 2016). Three Andean-Amazonian species included for the first time in a phylogenetic analysis—*C. hassleri*, *C. obducta*, and *C. pantanalensis*—form a strongly supported clade sister to *Hemionitis*. This clade, here named the “*C. obducta* group” shares with *Hemionitis* the combination of terete petioles, sclerotic cortex, bixylic stele, simple and capitate (2–3-cellular) hairs (Hernández and Albornoz, 2001; Graçano et al. 2001), and spores crested to crested-reticulated (Mickel

1974; Ponce et al. 2008b). The species of the *C. obducta* group differ from *Hemionitis* mainly in sori arrangement and in the number of spores per sporangium in sexual reproduction (32 in the *C. obducta* group vs. 64 in *Hemionitis*; Table 2 and Fig. 1).

Other South American species not sampled previously—*C. hieronymi*, *C. sarmientoi*, *C. scariosa*, and *C. squamosa*—are placed in a strongly supported clade that includes the type species *C. micropteris* + the Australasian *Cheilanthes* group obtained by Bouma et al. (2010). These five South American species and the Australasian *Cheilanthes* clade share a combination of soft or sclerotic concolorous rhizome scales, vein apices widened (hydatodes), and 32 small spores per sporangium in sexual species and 16 large spores per sporangium in asexual species (Grusz and Windham 2013, Table 2, Martínez et al. 2017). Due to the inclusion of the type species *C. micropteris*, this clade should be considered the core of *Cheilanthes* s.s. (Fig. 1).

The other well supported group of *Cheilanthes* species is formed by South African species and was obtained by Eiserhardt et al. 2011. The South African species present 64 small spores per sporangium in sexual species (Anthony 1984), differing from the 32 small spores per sporangium of the Australasian-South American clade (Table 2 and Fig. 1).

Most of the South American *Cheilanthes* species sequenced for this study appear grouped in a single unsupported clade. Within this group, there are some morphologically cohesive subclades, such as *Cheilanthes glutinosa*-*C. pilosa*-*C. pruinata*, which are characterized by concolorous, sclerotic rhizome scales, and lamina with glandular-pruinose hairs, and *C. buchtienii*-*C. fraseri*, which have bicolorous rhizome scales and lamina with simple hairs and a not reduced number of spores per sporangium.

Two alternative treatments are possible for the exclusively South American *Cheilanthes* group and the South African clade mentioned above: they may form part of *Cheilanthes* s.s., if further studies provide higher support for this relationship, or alternatively, these two groups may warrant segregation as new genera. New evidence and a more extensive sampling are necessary to elucidate this point.

### Putative diagnostic morphological characters

We corroborated that the vein ends are widened in South American species of *Cheilanthes* as well as in the analyzed species of *Adiantopsis*, *Doryopteris*, and *Gaga*, and unwidened in analyzed species of *Argyrochosma*, *Myriopteris*, and *Pellaea*, confirming that this feature is a putative character to distinguish hemionitids from the rest of the cheilanthoids. However, in *Hemionitis* and in species of the “*Cheilanthes obducta* group,” this feature seems to revert, so more data for these two groups are needed.

With respect of the number of spores per sporangium, Grusz and Windham (2013) pointed out that *Cheilanthes micropteris*, the Australian, and other South American species (*C. obducta* and *C. scariosa* and *C. fractifera* R.M. Tryon) all present 32 small spores in sexual species and 16 large spores in the apomictic mode (vs. 64 small and 32 large spores respectively in the other genera like *Myriopteris* and *Gaga*). In our work, this reduction in the number of spores was verified for the South American species placed in the Australasian + South American clade (*C. hieronymi*, *C. micropteris*, *C. sarmientoi*, *C. scariosa*, and *C. squamosa*) and also for the species of the “*C. obducta* group” (Table 2). Furthermore, we verified 64 small and/or 32 large spores per sporangium in the remaining South American *Cheilanthes* (*C. buchtienii*, *C. glauca*, *C. hypoleuca*, *C. poeppigiana*, *C. pilosa*, *C. pruinata*, and *C. rufopunctata*) and in the analyzed species of *Adiantopsis*, *Gaga*, and *Hemionitis* (Table 2); this not-reduced number of spores was seen also in the South African *Cheilanthes* clade by Anthony (1984) and in *Doryopteris* by Yesilyurt (2004). By mapping this feature on the obtained hemionitid phylogeny, we corroborated that the reduced number of spores constitutes a synapomorphy for the core of *Cheilanthes* s.s. (Fig. 1).

## Concluding remarks

The results presented here contribute substantially to the delimitation of *Cheilanthes* s.s. and provide novelties that add to a better understanding of the genus classification. The group composed of Australasian and five South American *Cheilanthes* species should be considered the core of *Cheilanthes* s.s. since *C. micropteris* is included in it. We believe that generic treatments of the related groups of *Cheilanthes*, such as the exclusive South American group, the South African group, and the *C. obducta* group, require the incorporation of additional molecular markers as well as anatomical, cytological, and gametophyte characters, in order to obtain a definitive classification and circumscription of *Cheilanthes* s.s. and its closely related species groups.

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## Appendix

Detail of the 119 taxa included in the analysis and their corresponding GenBank numbers (*rbcL*, *trnL-F*). The studies of all previously published sequences are cited. Sequences obtained for this study are in bold and denoted by “\*.” Unavailable sequences are indicated with “–”.

- Adiantopsis chlorophylla* (Sm.) Fée, EF473684 (Prado et al. 2007), –  
*A. dichotoma* (Sw.) T. Moore, \***MG593078**, –  
*A. flexuosa* Kunze, EF473686 (Prado et al. 2007), –  
*A. monticola* (Gardner) T. Moore, JN709729 (Link-Perez et al. 2011), –  
*A. orbignyana* (Kuhn) Ponce & Scataglini, \***MG593080**, –  
*A. radiata* (L.) Fée, \***MG593079**, –  
*A. trifurcata* (Baker) Link-Pérez & Hickey, JN709767 (Link-Perez et al. 20117), –  
*A. tweediana* Hook., \***MG593081**, –  
*Allosorus pulchellus* (Bory ex Willd.) Presl, GU935503 (Eiserhardt et al. 2011), –  
*Allosorus pteridioides* (Reichard) Christenh. GU935505 (Eiserhardt et al. 2011), –  
*Aleuritopteris argentea* (S.G. Gmel.) Fée, AY266410 (Zhang et al. 2005), DQ432667 (Zhang et al. 2007)  
*A. albomarginata* (C.B. Clarke) Ching, AY266411 (Zhang et al. 2005), DQ432665 (Zhang et al. 2007).  
*A. formosana* (Hayata) Tagawa, DQ432643, DQ432671 (Zhang et al. 2007)  
*Argyrososma delicatula* (Maxon & Weath.) Windham, U19500 (Gastony & Rollo 1995), –  
*A. nivea* var. *flava* (Gillies ex Hook.), Ponce, \***MG593082**, –  
*A. nivea* var. *tenera* (Gillies ex Hook.) Ponce, \***MG593083**, \***MG593110**  
*Aspidotis densa* (Brack.) Lellinger, Rothfels et al. 2008, EU268773 (Rothfels et al. 2008), –  
*A. californica* (Hook.) Nett. ex Copel., Gastony & Johnson 2001, AF336101 (Gastony & Johnson 2001), –  
*A. meifolia* (D.C. Eaton) Pic. Serm., JX313527 (Li et al. 2012), –  
*Calciphlopteris ludens* (Wall. ex Hook.) Yesilyurt & H. Schneid. DQ432657 (Zhang et al. 2007), DQ432686  
*Cheilanthes bradei* J. Prado & A.R. Sm., JN122014 (Eiserhardt et al. 2011), –  
*C. buchtienii* (Rosenst.) R. M. Tryon, \***MG593084**, \***MG593111**  
*C. contracta* (Kunze) Mett. ex Kuhn, GU935519, GU935593 (Eiserhardt et al. 2011)  
*C. capensis* (Thunb.) Sw., GU935511 (Eiserhardt et al. 2011), –  
*C. christii* Fraser-Jenk. & Yatsk., DQ432640, DQ432664 (Zhang et al. 2007)  
*C. deltoidea* Kunze, GU935512, GU935605 (Eiserhardt et al. 2011)

- C. depauperata* Baker, GU935516, GU935590 (Eiserhardt et al. 2011)
- C. dinteri* Brause, GU935506 (Eiserhardt et al. 2011), –
- C. distans* (R. Br.) Mett., GU136791 (Eiserhardt et al. 2011), –
- C. eckloniana* Mett., GU935513, GU935585 (Eiserhardt et al. 2011)
- C. fraseri* Mett. ex Kuhn, \*MG593085, –
- C. geraniiifolia* (Weath.) R.M. Tryon & A.F. Tryon, \*MG593086, \*MG593112
- C. glauca* (Cav.) Mett. \*MG593087, \*MG593113
- C. glutinosa* M. Kessler & A.R. Smith, \*MG593088, \*MG593114
- C. goyazensis* (Taub.) Domin, EF473687 (Prado et al. 2007), JN122018 (Eiserhardt et al. 2011)
- C. hassleri* (Weath.) Ponce, \*MG593089, \*MG593115
- C. hastata* Kunze, GU935510 (Eiserhardt et al. 2011), –
- C. hieronymi* Herter, \*MG593090, \*MG593116
- C. hirta* Sw., GU935515, GU935589 (Eiserhardt et al. 2011)
- C. hypoleuca* (Kunze) Mett., \*MG593091, \*MG593117
- C. induta* Kunze, GU935501, GU935597 (Eiserhardt et al. 2011)
- C. kunzei* Mett., GU935508 (Eiserhardt et al. 2011), –
- C. lasiophylla* Pic. Serm., HM003032 (Pryer et al. 2010), –
- C. leucopoda* Link, EU268785 (Rothfels et al. 2008), –
- C. maderensis* Lowe, GU935505 (Eiserhardt et al. 2011), –
- C. marlothii* (Hieron.) Domin, GU935514, GU935586 (Eiserhardt et al. 2011)
- C. micropteris* 1 Sw., EF452145 (Schuettpelz et al. 2007), –
- C. micropteris* Sw., \*MG593092, \*MG593118
- C. multifida* (Sw.) Sw., GU935500, GU935596 (Eiserhardt et al. 2011)
- C. namaquensis*, (Baker) Schelpe & N.C. Anthony, GU935492, GU935583 (Eiserhardt et al. 2011)
- C. nitidula* Wall. ex Hook., DQ432638, DQ432662 (Zhang et al. 2007)
- C. obducta* Mett. ex Kuhn, \*MG593093, \*MG593119
- C. pantanalensis* E.L.M. Assis, Ponce & Labiak, –, \*MG593120
- C. parviloba* Sw., GU935517, GU935591 (Eiserhardt et al. 2011)
- C. pilosa* Goldm., \*MG593094, \*MG593121
- C. poeppigiana* Mett. ex Kuhn, \*MG593095, \*MG593122
- C. pruinata* Kaulf., \*MG593096, \*MG593123
- C. robusta* (Kuntze) R.M. Tryon, GU935507, GU935609 (Eiserhardt et al. 2011)
- C. rufopunctata* Rosenst., \*MG593097, \*MG593124
- C. sarmientoi* Ponce, \*MG593098, \*MG593125
- C. scariosa* (Sw.) C. Presl, \*MG593099, \*MG593126
- C. sieberi* Kunze, GU136792 (Bouma et al. 2010), –
- C. squamosa* Gillies ex Hook. & Grev., \*MG593100, \*MG593127
- C. tenuifolia* (Burm. f.) Sw., KP126965 (Wang & Zhang, 2015), –
- C. viridis* Sw., GU935494, GU935603 (Eiserhardt et al. 2011)
- C. viridis* var. *glauca* Schelpe & N.C. Anthony, GU935495 (Eiserhardt et al. 2011), –
- Cheiloptecton rigidum* (Sw.) Fée, EU268789 (Rothfels et al. 2008), –
- Choristosoria pteroides* (L.) Mett., GU935502 (Eiserhardt et al. 2011), –
- Doryopteris decora* Brack., U27446 (Gastony & Rollo 1995), –.
- D. concolor* (Langsd. & Fisch.) Kuhn, AY266414 (Zhang et al. 2005), DQ432685 (Zhang et al. 2007)
- D. lorentzii* (Hieron.) Diels, \*MG593101, –
- D. pedata* (L.) Fée, U27206 (Gastony & Rollo 1995), JN122021 (Eiserhardt et al. 2011)
- D. pedatoides* (Desv.) Kuhn, JN122016 (Eiserhardt et al. 2011), –
- \**D. pentagona* Pichi Serm., \*MG593102, \*MG593128
- D. pilosa* (Poir.) Kuhn, JN122017 (Eiserhardt et al. 2011), –
- D. rediviva* Fée, EF473694 (Prado et al. 2007), –.
- D. sagittifolia* (Raddi) J. Sm., EF473695 (Prado et al. 2007), –.
- D. triphylla* (Lam.) Christ, \*MG593103, \*MG593129
- Gaga angustifolia* (Kunth) F.W. Li & Windham, JN647782 (Li et al. 2012), –
- G. kaulfussii* F.W. Li & Windham, JQ855930 (Johnson et al. 2012), –
- G. lerstenii* (Mickel & Beitel) F.W. Li & Windham, JX313536 (Li et al. 2012), –
- G. marginata* Humb. & Bonpl. ex Kunth, \*MG593104, \*MG593130
- Hemionitis levyi* E. Fourn., U27725 (Gastony & Rollo 1995), –
- H. palmata* L., AY357708 (Geiger & Ranker unpubl.), –
- H. rufa* (L.) Sw., AY357707 (Geiger & Ranker unpubl.), –
- H. tomentosa* (Lam.) Raddi, \*MG593105, –
- Lytoneuron lomariaceum* (Klotzsch) Yesilyurt, KP407209 (Yesilyurt et al. 2015), JN122020 (Eiserhardt et al. 2011)
- L. ornithopus* (Hook. & Baker) Yesilyurt, EF473691 (Prado et al. 2007), –
- L. paradoxum* (Fée) Yesilyurt, EF473692 (Prado et al. 2007), –
- Mildella intramarginalis* (Kaulf. ex Link) Trevis., U27449 (Mexico, Gastony & Rollo 1995)
- Myriopteris alabamensis* (Buckley) Grusz & Windham, EF452143 (Schuettpelz et al. 2007), *M. allosuroides* (Mett.) Grusz & Windham, U27239 (Gastony & Rollo 1995), –
- M. aurea* (Poir.) Grusz & Windham, \*MG593106, –
- M. covillei* (Maxon) Á. Löve & D. Löve, EU268782 (Rothfels et al. 2008), –
- M. rufa* Fée, EF452144 (Schuettpelz et al. 2007), –

- M. scabra* (C. Chr.) Grusz & Windham, U27448 (Gastony & Rollo 1995), –
- M. lanosa* (Michx.) Grusz & Windham, U27205 (Gastony & Rollo 1995), –
- M. lendigera* (Cav.) J. Sm., EU268784 (Rothfels et al. 2008), DQ914228
- M. microphylla* (Sw.) Grusz & Windham, \*MG593107, –
- M. myriophylla* (Desv.) Sm., \*MG593108, \*MG593131
- Notholaena aliena* Maxon, EU268790 (Rothfels et al. 2008), –
- N. aureolina* Yatsk. & Arbeláez, EU268778 (Rothfels et al. 2008), –
- N. aurantiaca* D.C. Eaton, EU268777 (Rothfels et al. 2008), –
- N. brachypus* (Kunze) J. Sm., EU268781 (Rothfels et al. 2008), –
- N. greggii* (Mett. ex Kuhn) Maxon, EU268796 (Rothfels et al. 2008), –7
- N. schaffneri* (E. Fourn.) Underw. ex Davenp., EU268801 (Rothfels et al. 2008), –
- N. standleyi* Maxon, EU268804 (Rothfels et al. 2008), –
- N. sulphurea* (Cav.) J. Sm., U28254 (Gastony & Rollo 1995), –
- Ormopteris crenata* (R.M. Tryon) T. Barbará, KM081636, KM435285 (Yesilyurt et al. 2015)
- O. cymbiformis* (J. Prado) T. Barbará, KM081637, KM435286 (Yesilyurt et al. 2015)
- O. gleichenioides* (Gardner) J. Sm., EF473698 (Prado et al. 2007), KM435287 (Yesilyurt et al. 2015)
- O. pinnata* (Kaulf.) Lellinger, EF473699 (Prado et al. 2007), KM435288 (Yesilyurt et al. 2015)
- O. riedelii* (Baker) T. Barbará, KM081640, KM435289 (Yesilyurt et al. 2015)
- Pellaea andromedifolia* (Kaulf.) Fée, U19501 (Gastony & Rollo 1995), –
- P. boivinii* Hook., U29132 (Gastony & Rollo 1995), –
- P. dura* (Willd.) Hook., GU935490 (Eiserhardt et al. 2011), –
- P. rotundifolia* (G. Forst.) Hook., U28788 (Gastony & Rollo 1995), –
- P. ternifolia* Link, \*MG593109, \*MG593132
- Pentagramma triangularis* (Kaulf.) Yatsk., Windham & E. Wollenw., EF452165 (Schuettpelez et al. 2007), –
- Trachypteris pinnata* (Hook. f.) C. Chr., U27450 (Gastony & Rollo 1995), –
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