

Research Article

Phylogenetic position of South American *Cheilanthes* (Cheilanthoideae, Pteridaceae): Advances in the generic circumscription and segregation of the new genus *Mineirella*Marta Mónica Ponce[†] and María Amalia Scataglini^{†*}

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Abstract This analysis corroborates and expands our previous results regarding the phylogenetic position of *Cheilanthes* species from South America. We sequenced three plastid genetic regions, one genic (*rbcl*) and two genic plus intergenic spacers (*trnL* + *trnL-F* and *rps4* + *rps4-trnS*) from 25 South American cheilanthoid species. This allowed us to elucidate phylogenetic relationships that have been historically unresolved or were lowly supported. Here, we analyzed 45 *Cheilanthes* species (23 from South America) and circumscribed *Cheilanthes* s.s. in a strongly supported clade that contains three subclades: (i) exclusively from South America, (ii) from Australasia + South America, and (iii) from Africa. The position of three South American species, previously referred to the informal “*Cheilanthes geraniifolia* group”, is confirmed as a highly supported group outside *Cheilanthes* s.s. and within the *Adiantopsis–Doryopteris* clade. This group is described here as the new genus *Mineirella*. The new combinations for the genus and illustrations are included. Additionally, we discuss the morphological innovations that provide evidence to support the different clades.

Key words: *Cheilanthes*, hemionitids, *Mineirella*, phylogeny, South America, taxonomy

1 Introduction

Cheilanthes Sw. (Pteridaceae) is a genus of ferns described more than 200 years ago. The generic limits in *Cheilanthes* have been based on a range of morphological characteristics that allowed the inclusion of extremely variable species under this genus. The first monograph of the genus was performed by Mettenius (1859) and included 84 species, with heterogeneous morphology and ecology, and worldwide distribution. Subsequent treatments were increasing the number of *Cheilanthes* species: more than 180 species according to Copeland (1947) and about 150 species, sensu Mickel (1979). These authors treated *Adiantopsis* Fée (1852), *Myriopteris* Fée (1852), *Notholaena* R. Br. (1810), and other minor genera as synonyms of *Cheilanthes* on the basis of their similar morphology. The classic revision of the neotropical species of *Notholaena* (Tryon, 1956) included dissimilar and contrasting species of *Cheilanthes* within a broad circumscription of *Notholaena*. On the contrary, centered mainly on treatments of the Old World, Pichi-Sermolli (1977) postulated a narrow circumscription of the cheilanthoid genera on the basis of each of the morphological variants, some of which are currently accepted (PPG I, 2016).

Considering the controversial delimitation of genera, major efforts were made to explore further palynological, cytological, reproductive, and geographic evidence to determine natural boundaries between cheilanthoid genera. Accordingly, *Adiantopsis*, *Hemionitis* L. (1753), *Notholaena*, and *Cheilanthes* were recognized on the basis of the spore structure, the types of simple or glandular trichomes, and the presence or absence of farina-producing glands (Tryon & Tryon, 1973, 1982; Tryon et al., 1990). Potentially informative, additional morphoanatomical, cytological, and chemical features were used to segregate genera such as *Argyroschisma* (J. Sm.) Windham, *Astrolepis* D.M. Benham & Windham, and *Bommeria* E. Fourn., among others (Windham, 1987; Ranker, 1990; Benham & Windham, 1992). The monophyly of these genera was corroborated later by molecular phylogenetic analyses (Rothfels et al., 2008; Windham et al., 2009). Despite these achievements, the morphological homoplasy remained widespread across the characters used to determine the generic level. The different states of these characters can be found, alternatively, in *Cheilanthes* s.l. species as well as in those of *Adiantopsis* and *Notholaena*: for example, sporangia at the vein tip or along the veins; sori more or less contiguous or discrete, scarcely

or totally covered by the recurved, continuous, subcontinuous, or lobed foliar margin (pseudoindusia) or without false indusium; indument composed by simple and glandular trichomes, or by trichomes and scales, or only scaly. Thus, the generic relationships remain cryptic, primarily due to the extensive evolutionary convergence resulting from adaptation to arid environments, which potentially masked characters with phylogenetic signals.

In the last 25 years, the use of DNA sequences for phylogenetic analyses has allowed remarkable progress to elucidate the relationships between cheilanthoid ferns (Gastony & Rollo, 1995; Prado et al., 2007; Zhang et al., 2007). The result of these studies has led to the circumscription of numerous, monophyletic cheilanthoid taxa. Currently, the most important results of phylogenetic analyses to resolve the monophyly of American *Cheilanthes* have been the new circumscription and re-arrangement of the related *Adiantopsis* (Link-Pérez et al., 2011) and *Gaga* (Li et al., 2012), and the distantly related *Myriopteris* (Grusz & Windham, 2013) and *Baja* (Windham & George, 2019), with all of them being defined on the basis of morphological and molecular data. Despite these new generic delimitations, *Cheilanthes*, the primordial representative of the subfamily Cheilanthoideae, remained in its polyphyletic condition, mainly due to its large number of species and widespread geographical distribution.

Currently, *Cheilanthes* s.l. includes about 100 species (PPG I, 2016) with 35 of them from South America (Ponce, 2016). Here, the analysis of the South American *Cheilanthes* is frameworked in the called "distant cheilanthoids" clade (Kirkpatrick, 2007) and the hemionitids clade (Windham et al., 2009; Eiserhardt et al., 2011; Ponce & Scataglieni, 2018). The hemionitids clade includes *Adiantopsis* Fée, *Aleuritopteris* Fée; *Aspidotis* (Nut. ex Hook.) Copel.; *Astrolepis* D. M. Benham and Windham, *Cheilanthes* Sw., *Doryopteris* J. Sm., *Gaga* Pryer, F.W. Li and Windham, *Hemionitis* L., *Lytoneuron* (Klotzsch) Yesilyurt, *Oeosporangium* Vis., *Ormopteris* J.Sm., *Trachypteris* André ex Christ., and several unassigned species.

At present, within hemionitids and focusing on *Cheilanthes*, two natural, phylogenetic groups of species have been recognized: South African clade, with about 15 species (Eiserhardt et al., 2011), and the Australasian–South America clade, including 3 Australasian species and the South American type species of the genus, *Cheilanthes micropteris* Sw. (Rothfels et al., 2008; Bouma et al., 2010). This last clade shows particular cytological characters due to the production of 32 spores per sporangium in contrast to the 64 spores per sporangium produced by the majority of the remaining, sexually reproducing *Cheilanthes* species (Grusz & Windham, 2013; Martínez et al., 2017; Ponce & Scataglieni, 2018).

In a previous molecular phylogeny (Ponce & Scataglieni, 2018), we delimited a *Cheilanthes* s.s. clade by adding a large number of South American cheilanthoid species that have not been sampled in the past. The results of that first study, based on *rbcl* and *trnL + trnL-F* sequences, were promising but not conclusive: five species of South American *Cheilanthes* were included in the "core" of *Cheilanthes* s.s. formed by the Australasian species, whereas at least other ten South American *Cheilanthes* species appeared to be

related to this "core" of *Cheilanthes* s.s. and to the South African *Cheilanthes* clade. However, this relation was not well supported.

In the present study, we aimed for an improved phylogeny by including a third marker, the *rps4 + rps4-trnS*, to clarify the unresolved questions of our previous research. In particular, we attempt to determine which taxa of South America are properly included within *Cheilanthes* s.s. Additionally, as a result of the achieved phylogeny, a new genus is recognized and segregated from *Cheilanthes*. We also discuss the potentially informative morphological characters that might support further circumscriptions of cheilanthoid ferns.

2 Material and Methods

2.1 Taxon sampling

Species sampling was aimed to include as many members of *Cheilanthes* as possible: 45 *Cheilanthes* species were analyzed, including the type species *C. micropteris* and 22 South American *Cheilanthes*, with most of them being sampled for the first time in Ponce & Scataglieni (2018). A total of 21 new sequences, mainly corresponding to the *rps4 + rps4-trnS* marker, were obtained from the South American species for the present work. Also, four species that have not been included in Ponce & Scataglieni (2018) were amplified for the *rbcl* and *trnL + trnL-F* markers. The 21 new accession numbers in GenBank are MW245809–MW245829. The details of our South American samples analyzed are listed in Table 1. Representatives of related cheilanthoid genera obtained from GenBank were also included in the analysis: two *Adiantopsis*, three *Aleuritopteris*, six *Doryopteris*, one *Gaga*, two *Hemionitis*, one *Lytoneuron*, four *Myriopteris*, one *Notholaena*, one *Ormopteris*, six *Pellaea*, and *Calciophlopteris ludens* as the root, yielding a total of 73 cheilanthoid taxa. The detail of these 73 species, including the authors of their scientific names and their GenBank accession numbers, is provided in Appendix I.

2.2 DNA sequencing

Total genomic DNA was extracted from silica-dried leaves and from herbarium specimens. DNA from silica samples was extracted with a CTAB protocol (Doyle & Doyle, 1987), whereas DNA from herbarium material was obtained with a DNeasy Plant Mini Kit (Qiagen, Hilden, Germany). The *rps4 + rps4-trnS* marker, including the complete gene of the ribosomal protein small subunit 4 (*rps4*) plus the intergenic spacer *rps4-trnS*, was amplified using the primers specified by Kirkpatrick (2007). The *rbcl* and *trnL + trnL-F* sequences were obtained using primers designed by Gastony & Rollo (1995) and Taberlet et al., (1991), respectively. The polymerase chain reaction (PCR) reactions were performed in 25 μ L of final volume with 50 \pm 100 ng of template DNA, 0.2 μ M of each primer, 25 μ M of dNTP, 5-mM MgCl₂, and 0.3 units of Taq polymerase provided by Invitrogen Life Technologies (Brazil). PCR was carried out using the following parameters: one cycle of 94 °C for 5 min, 35 cycles of 94 °C for 30 s, 48 °C for 1 min, and 72 °C for 1 min 30 s, and a final extension cycle of 72 °C for 10 min. PCR products were run out on a 1% TBE agarose gel stained with SYBR Safe DNA gel stain (Invitrogen) and visualized in a blue-light transilluminator.

Table 1 List and voucher information of our South American species

Species	Location	Herbarium voucher
<i>Adiantopsis dichotoma</i>	Argentina, Misiones, Candelaria, Cerro Santa Ana	M. E. Múlgura 3819 (SI)
<i>Adiantopsis tweediana</i>	Argentina, San Luis, General San Martín, Chacras	F. Biganzoli et al. 2068 (SI)
<i>Cheilanthes arequipensis</i>	Peru, Arequipa, Ojo del Milagro	B. León et al. 5737 (USM)
<i>Cheilanthes buchtienii</i>	Argentina, Tucumán, Tafí del Valle, Ruta Prov. 325, El Rincón	M. M. Ponce 90 (SI)
<i>Cheilanthes fraseri</i>	Peru, 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. Jimenez 1928 (LPB)
<i>Cheilanthes hieronymi</i>	Argentina, Buenos Aires, Tornquist, 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 mollis</i>	Chile, Valparaíso, Petorca, Quebrada Los Durazos	S. Teillier et al. 8274 (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 peruviana</i>	Bolivia, Chuquisaca, Oropeza, Chataquilla	I. Jiménez et al. 6719 (LPB)
<i>Cheilanthes aff. pilosa</i>	Bolivia Potosí, Chayanta, Pocoata, Sarijchi	I. Jiménez et al. 7398 (LPB)
<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, Quillacollo, Incarragay	I. Linneo & D. Enriques 824 (LPB)
<i>Cheilanthes squamosa</i>	Argentina, San Luis, Junín, Merlo a Mirador Los Cóndores	F. 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>Gaga marginata</i>	Argentina, Tucumán, Tafí del Valle, Ruta 307, La Quebradita	M. M. Ponce 95 (SI)
<i>Hemionitis tomentosa</i>	Argentina: Misiones, Cainguaés, Reserva Cuña Pirú	G. J. Márquez 73 (LP)

Herbarium acronyms following Thiers (2020, continuously updated).

Automated sequencing was performed by Macrogen, Inc. (Seoul, Korea). Alignment was manually performed using BioEdit ver. 5.0.9 (Hall, 1999). A region of about 80 base pairs of the *rps4-trnS* marker, at position 3080 of the concatenated alignment, mainly corresponding to an insertion in *Myriopteris* and other cheilanthoid genera, was excluded from the analysis, because it made alignment difficult.

2.3 Phylogenetic analyses

The aligned matrix including the three concatenated plastid regions, *rbcl*, *trnL + trnL-F*, and *rps4 + rps4-trnS*, is available in TreeBase under study number TB2: S25300.

The matrix was analyzed under Bayesian and parsimony approaches.

The Bayesian analysis was conducted with 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). GTR + I + Γ was the model chosen in BEAUti to cover the range of the simpler nested models obtained for the used markers. Also, the choice of the GTR + I + Γ model was in concordance with our

previous phylogeny and previous cheilanthoid studies using the same three markers proposed here (Eiserhardt et al., 2011). Other parameters were set as follows: site rate heterogeneity modeled with four gamma categories, estimated base frequencies, a lognormal uncorrelated relaxed clock, random starting tree, a Yule process as a tree prior, and default values for all other operators. Two independent runs, each using four Markov chains (one cold and three hot) of 10 million generations, were sampled every 1000 generations. 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 et al., 2014). On the basis of this convergence diagnostic, the first 2500 sampled trees were discarded as burn-in from each analysis using TreeAnnotator 1.7.1 (Drummond et al., 2012). Trees of the two runs were combined using LogCombiner 1.8.4 and the maximum credibility tree was displayed in FigTree 1.3.1 (Rambaut, 2009). Statistical support was determined by assessing the Bayesian posterior probabilities. Parsimony analysis was performed using TNT (Goloboff et al., 2008). The search strategy consisted of heuristic searches using 10 000 series of random

addition sequences (ras), followed by TBR branch rearrangements and retaining two trees per series. Retrieved trees were saved in memory and, additionally, TBR swapped retaining a maximum of 20000 trees. Branches with ambiguous lengths of 0 or 1 were collapsed, according to the collapsing rule. A strict consensus tree was generated from the most parsimonious trees. To assess the relative support for clades, bootstrap analyses were performed using 10 000 replicates of the matrix and heuristic searches were executed using 100 ras, holding 5 trees per ras and TBR swapping.

3 Results

The matrix analyzed consisted of 73 taxa \times 3336 positions, including the three plastid markers concatenated (*rbcl*:1-1267, *trnL* + *trnL-F*: 1268-2307, and *rps4* + *rps4-trnS*: 2308-3336). From the 3336 characters, 961 were phylogenetically informative.

The parsimony analysis yielded two most parsimonious trees, 3407 steps long, with $Ci = 0.44$ and $Ri = 0.59$ (data not shown, the analysis and the consensus tree are available in TreeBase TB2: S25300).

The Bayesian analysis of this matrix resulted in a maximum credibility tree (Fig. 1) that was mostly congruent with the parsimony strict consensus tree.

The two major clades proposed in previous studies (Rothfels et al., 2008; Windham et al., 2009; Grusz & Windham, 2013) were recovered by the maximum credibility tree obtained with maximum support: the clade of the myriopterids plus the pellaids and the clade of the hemionitids plus the notholaenids (names *sensu* Windham et al., 2009). Within the hemionitids, three highly supported, major clades were recognized: the *Adiantopsis*–*Doryopteris* clade ($PP = 1$), including its related smaller genera; the *Hemionitis* clade ($PP = 1$) with *Gaga* as its sister genus ($PP = 0.79$); and a large *Cheilanthes* clade including the type species ($PP = 1$), referred here to *Cheilanthes* s.s.

The *Cheilanthes* s.s. clade was formed by three biogeographical groups displaying maximum support ($PP = 1$): (i) 12 African *Cheilanthes*, (ii) 10 exclusive South American *Cheilanthes*, and (iii) four Australasian + nine South American *Cheilanthes*, including the type of the genus *C. micropteris*.

The positions of three South American *Cheilanthes* species: *C. geraniifolia* (sequenced here) together with *C. goyazensis* and *C. bradei* (sequenced by Prado et al., 2007 and Eiserhardt et al., 2011, respectively), form a strongly supported group ($PP = 1$) within the *Doryopteris*–*Adiantopsis* group, but isolated from *Cheilanthes* s.s.

4 Discussion

In the present study, we included 45 *Cheilanthes* species (23 from South America) along with 27 representative taxa of cheilanthoid genera and analyzed them with three plastid DNA markers. The obtained phylogeny agrees with Ponce & Scatagliani (2018), but in contrast to our previous work, the *Cheilanthes* s.s. clade is now defined with maximum support and includes 19 species from South America.

Other studies (Grusz & Windham, 2013; Zhang & Yatskievych, 2013) have recognized the “core” of *Cheilanthes* as a small group of Australasian species and the type of the genus, the South American *C. micropteris*, sharing particular cytological characteristics, for example, the production of 32 spores/sporangium in the sexual condition. In our study, we found that this hypothesis is generally supported, but in addition (i) the Australasian + *C. micropteris* clade includes at least nine other South American species, (ii) this clade is sister to the African *Cheilanthes* clade of Eiserhardt et al., (2011), and (iii) both clades together are the sister group of an exclusive South American *Cheilanthes* clade that includes ten species. According to these results, we propose to recognize *Cheilanthes* s.s. as a genus that includes these three geographical groups: South American–Australasian clade with 32 spores per sporangium, and African and exclusively South American clades, both with 64 spores per sporangium (Fig. 1).

Seven remaining South American *Cheilanthes* species not sampled in this study could be placed in the South American–Australasian clade due to their morphological similarities to species of this clade or their sporangia with 32 spores: *C. andina* Hook. (aff. *C. sarmientoi*); *C. cantangensis* (R. M. Tryon) R. M. Tryon and *C. hassleri* (Weath.) Ponce (both aff. *C. obducta*); *C. incarum* Maxon and *C. lonchophylla* (R. M. Tryon) R. M. Tryon & A. F. Tryon (both aff. *C. squamosa*); *C. juergensii* Rosenst. (aff. *C. micropteris*); and *C. fractifera* R. M. Tryon, displaying 32 spores per sporangium (cfr. George et al., 2019). Thus, the South American–Australasian clade would include 16 South American species. The other 10 sampled South American species are grouped in the exclusively South American clade and contain the typical 64 spores per sporangium: *C. buchtienii*, *C. fraseri*, *C. glauca*, *C. glutinosa*, *C. hypoleuca*, *C. mollis*, *C. pilosa*, *C. poeppigiana*, *C. pruinata*, and *C. rufopunctata*. (see Fig. 1). In total, the number of South American species in the *Cheilanthes* s.s. clade would be 26.

One of the taxonomic implications of our analysis is the recognition of the strongly supported assemblage of three *Cheilanthes* subclades. We prefer to retain the totality of the subclades under the genus *Cheilanthes* s.s. rather than to recognize three different genera with the necessary nomenclatural changes and the unstable taxonomic definitions that these modifications would imply. The circumscription of *Cheilanthes* proposed here includes species with a circumaustral distribution, distributed across three geographic distinct zones (South America, Africa, and Oceania). These species are morphologically heterogeneous, but mainly present the following diagnostic traits: a small sporophyte of 5–30 cm height, usually with glanduliferous indument on the rhizome scales and fronds; 1-3-pinnate-pinnatifid lamina, and glabrous gametophytes (see description below for more details). This new circumscription of *Cheilanthes*, like those of related genera such as *Adiantopsis*, *Gaga*, and the distant *Myriopteris*, is mainly based on molecular phylogenies, but diagnostic morphoanatomical features reinforce these findings (Link-Pérez et al., 2011; Li et al., 2012; Grusz & Windham, 2013). In search of morphological evolutionary patterns, we found that *Cheilanthes* s.s. differs from the *Adiantopsis*–*Doryopteris* clade (also including *Lytoneuron* and *Ormopteris*) by their root

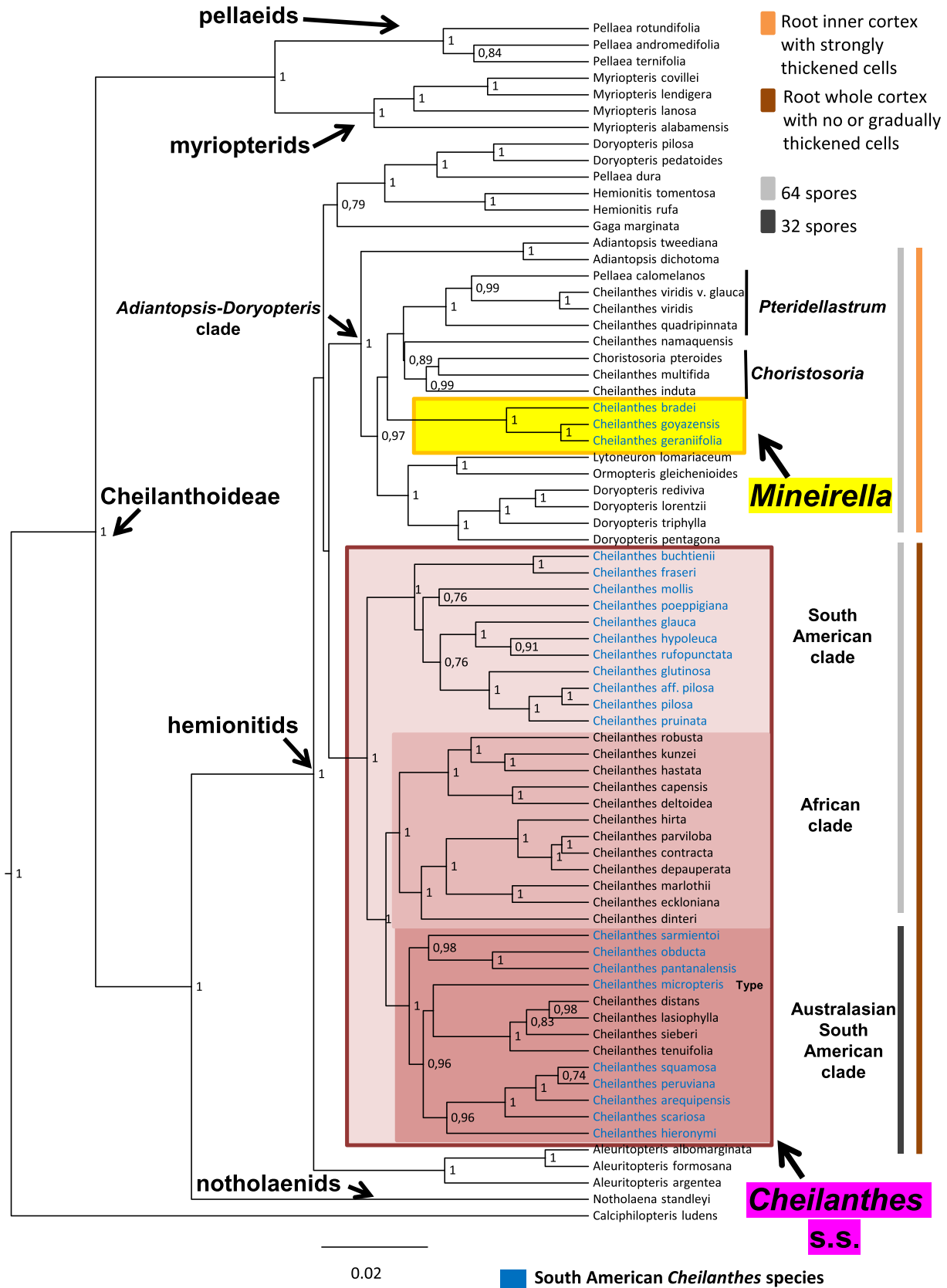


Fig. 1. Continued

anatomy characterized by a whole cortex with thin cell walls or gradually thickened cell walls and wide lumen versus the inner cortex with strongly thickened cell walls and narrow lumen (Hernández, 2019; Hernández et al., 2019). The difference between *Cheilanthes* and *Hemionitis* is illustrated by the very different patterns of the sporangia disposition (at the vein tips versus along the veins) and the glabrous gametophytes of *Cheilanthes* versus pilose gametophytes of *Hemionitis* [*H. tomentosa*] (Hernández, 2019). Finally, *Cheilanthes* and most of the genera included in the hemionitids clade differ from myriopterids and pellaids by possessing widened vein endings (hydathodes) versus not or slightly widened vein tips (Pryer et al., 2010; Hernández 2019; Hernández et al., 2019). These potentially informative synapomorphies require further investigation by analyzing an increasing number of species to test their evolutionary patterns.

4.1 Newly segregated genus

We found that three South American species, *Cheilanthes geraniifolia* (sequenced here), together with *C. goyazensis* and *C. bradei* (sequenced by Prado et al., 2007 and Eiserhardt et al., 2011, respectively), form a strongly supported group within the *Doryopteris*–*Adiantopsis* group, but isolated from *Cheilanthes* s.s.

This association has already been recognized by Ponce & Scataglioni (2018) and informally named as the “*C. geraniifolia* group” (also including *C. eriophora* (Fée) Mett., not sampled until now). These four taxa display a particular distribution in the Brazilian and Guiana Massif, and they have historically been treated as members of *Notholaena* (Weatherby, 1946; Tryon, 1956) and later of *Cheilanthes* (Tryon & Tryon, 1982), and grouped with the pilose species. Some of the diagnostic characters used by Weatherby (1946) for their identification were as follows: the horizontal, creeping rhizomes with bicolored scales, pedate, pentagonal, lobate-pinnatifid, bipinnatifid, or pinnatifid to basally pinnate lamina, usually with simple trichomes, sometimes with a gland at the apex. We corroborated these traits and also added the number of spores (64) per sporangium and rugate spore ornamentation.

This Neotropical “*C. geraniifolia* group” appears related with groups of South African/Madagascan *Cheilanthes* and *Pellaea* species, which had been already obtained in previous works (Kirkpatrick, 2007; Eiserhardt et al., 2011; Yesilyurt et al., 2015), all of them included in the “*Choristosoria* grade”, *sensu* Yesilyurt et al., (2015).

The phylogeny reconstructed by Yesilyurt et al. (2015) included in the “*Choristosoria* grade” three nested groups related to the clade *Doryopteris* + *Lytoneuron* + *Ormopteris*. The first group was formed by *Cheilanthes bradei* + *C. goyazensis*; the second corresponded to *Choristosoria* Mett. ex Kuhn (1879), based on *Choristosoria pteroides* (L.) Mett. &

Kuhn (\equiv *Pellaea pteroides* (L.) Prantl), the type species of the genus, together with *Cheilanthes multifida* (Sw.) Sw. and *C. induta* Kunze; and the third group is consistent with “*Pteridellastrum*” Prantl (1882, infrageneric unranked group), based on *Cheilanthes viridis* (Forssk.) Sw., also containing *C. quadripinnata* (Forssk.) Kuhn and *Pellaea calomelanos* (Sw.) Link. The three groups were well supported, but the relationships among them were uncertain. In our analysis, we recovered the “*Choristosoria* grade”, according to Yesilyurt et al. (2015), with *Cheilanthes geraniifolia* included, with maximum support, in the first clade, together with the other two neotropical species *Cheilanthes goyazensis* and *C. bradei*. We consider segregating this highly supported first clade as the new genus *Mineirella* due to its particular geographical distribution and its morphological differences described above. A review and more extensive sampling are necessary to confirm the definition and range of other groups of the “*Choristosoria* grade”, and the relationships between them and *Mineirella*. At the moment, the new genus would be the sister clade of the remaining groups of the *Choristosoria* grade.

5 Taxonomic Treatment

5.1 *Cheilanthes* s.s

Cheilanthes Sw., Syn. Fil.: 5, 126. 1806, nom. cons. Lectotype species: *Cheilanthes micropteris* Sw. (designated by Maxon, Sci. Surv. Porto Rico and Virgin Islands 6(3): 428. 1926).

Plants terrestrial, saxicolous, 5–30(40) cm tall; rhizomes decumbent or shortly creeping, compact, nodose, sometimes branched, rarely erect, scaly; rhizome scales linear-lanceolate to ovate-lanceolate, colorless, ferruginous or pale to dark castaneous, or less commonly bicolorous, with dark central stripe and hyaline margins; scales with glandular cells usually present at the apex or margins. Fronds monomorphic, fasciculate; petioles terete or semi-terete, sometimes grooved adaxially, light to dark castaneous; laminae linear, elliptic, ovate triangular, narrowly triangular or less commonly pentagonal in outline, 1-3-pinnate-pinnatifid, ultimate segments sessile, adnate or briefly petiolulate, not articulate; rachises terete, rarely grooved adaxially with lateral edges; veins free, 1-4-furcate, widest at the tip (hydathodes); margins slightly to strongly modified, usually recurved, with pale green to hyaline border. Foliar indument with uniseriate, 2-pluricellular, frequently simple, capitate, rarely scamiform or stellate, mostly glandular trichomes; sometimes partially or totally scaly. Sori marginal, sporangia borne on the vein tips, or rarely in a short distal portion of the veins, protected by the recurved foliar margin, continuous or in discrete lobes (false indusia); 32 or 64 spores per sporangium in sexual condition, or 16 or 32 spores per sporangium in asexual condition, globose or globose tetrahedral, of (35-)40-60(-70) μ m of equatorial diameter,

Fig. 1. The maximum credibility tree obtained from the Bayesian analysis of the combined matrix including the three markers concatenated (*rbcl*, *trnL* + *trnL-F*, and *rps4* + *rps4-trnS*). Posterior probabilities up to 0.75 are shown. The major clades of Cheilantheoideae, *sensu* Windham et al. (2009), and the groups of the “*Choristosoria* grade”, *sensu* Yesilyurt et al. (2015), are indicated. The clades proposed here are resalted in colors. Bars indicating the number of spores per sporangium and morpho-anatomical feature is also shown.

with one- to three-layered perispore, compact to reticulate, rugged, granulate, cristate, reticulate-cristate, or rarely verrugate surface. Gametophyte orbicular, cordiform, elongated cordiform, or ribbon-like, glabrous, rarely with glandular (not farinose) trichomes, unisexual, bisexual or vegetative, sometimes with propagules. The base number of chromosomes $x = 30$.

5.1.1 Observations

Despite the stricter generic description given here, *Cheilanthes* species continue exhibiting a heterogeneous gross morphology, particularly in those characters that have been used traditionally to delimit the cheilanthoid genera (e.g., shape and division of the lamina, indument types, and pseudoindusia forms) (Fig. 2). Differences in the anatomical

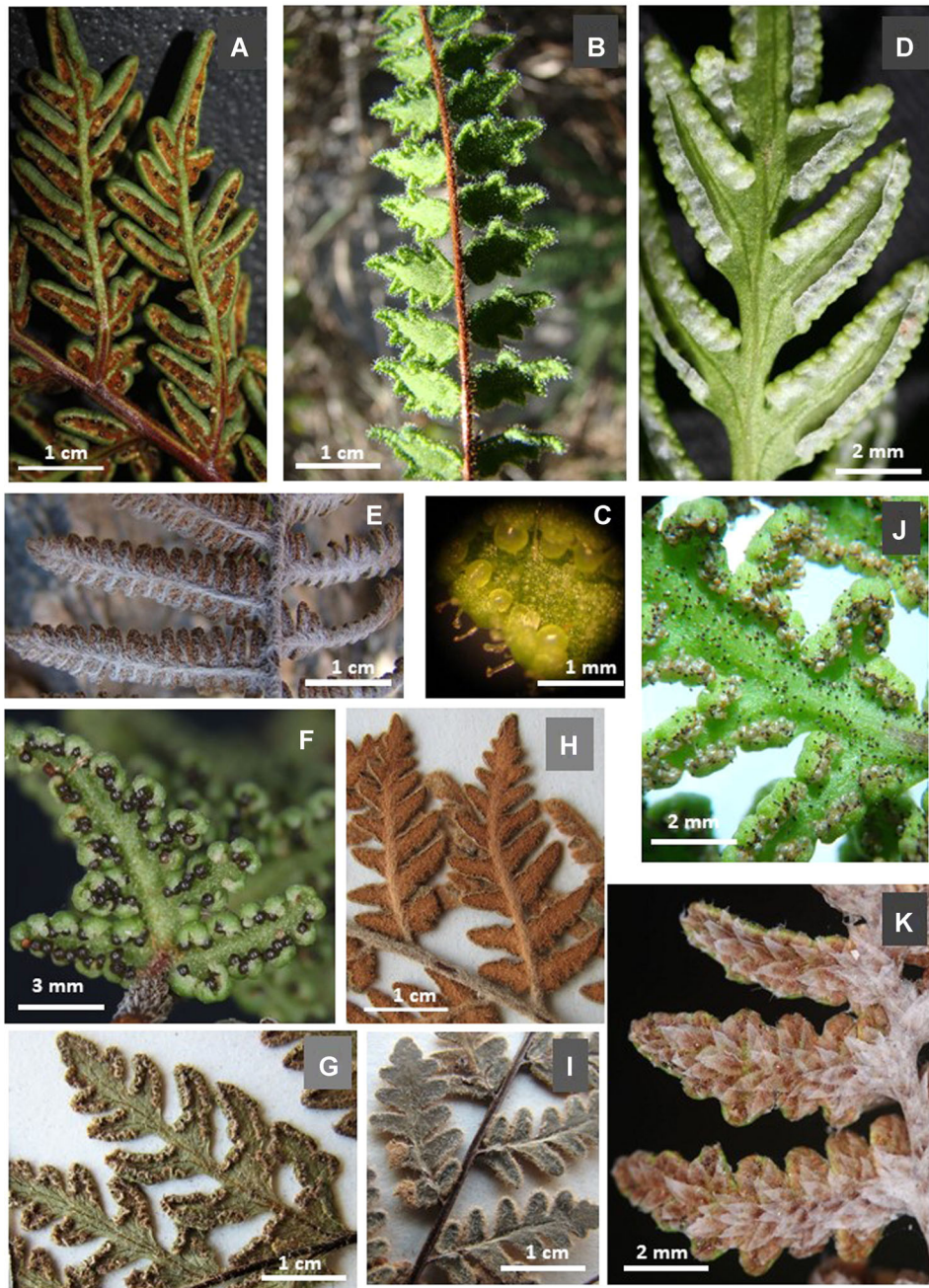


Fig. 2. *Cheilanthes* species from South America. **A**, *Cheilanthes glauca* abaxial pinnae side (Zuloaga 12639, SI). **B**, *C. micropteris* middle portion of the frond. **C**, *C. micropteris* abaxial segment (Arana s.n., RCVC). **D**, *C. poeppigiana* abaxial pinnae side (Zuloaga 10726, SI). **E**, *C. obducta* middle portion of the frond (Arana s.n., RCVC). **F**, *C. pruinata*, abaxial pinnae side (Zuloaga 16323, SI). **G**, *C. fractifera* abaxial pinnae side (Saunders 353, US). **H**, *C. buchtienii* abaxial pinnae side (Buchtien 4225, US). **I**, *C. hypoleuca* adaxial pinnae side (Hasting 100, US). **J**, *C. sarmientoii* abaxial pinnae surface (Martínez s.n., MCNS). **K**, *C. squamosa* abaxial pinnae surface (Zuloaga 16241, SI). Photo authors: A, D, F, G, K: Documenta Florae Australis, IBODA; B, C, E: M.D. Arana; G, H, I: M.M. Ponce; J: O.G. Martínez.

characteristics of roots and axes (Hernández 2019) in gametophytes and in the number and size of spores (Sigel et al., 2011; Grusz & Windham, 2013; Martínez et al., 2017; George et al., 2019) were recently found among *Cheilanthes* s.s. and the genera excluded from it. These findings appear to be significant in elucidating the relationships between cheilanthoid ferns.

5.1.2 Distribution

Cheilanthes is a circumastral genus that comprises about 66 species, based on their phylogenetic and/or morphological similarities: ca. 26 in South America (the present treatment), 25 species in Africa (Anthony, 1984; Eiserhardt et al., 2011), and 15 in Australasia (Quirk et al., 1983). The species of Eurasia, treated under *Cheilanthes* s.l., were not considered here, but their majority was described in the Flora of China (Zhang & Yatskievych, 2013); their phylogenetic position must be corroborated, especially to genera *Aleuritopteris* (Zhang et al., 2013) and *Oeosporangium* (Fraser-Jenkins, 2016; Fraser-Jenkins et al., 2017).

5.1.3 Species List

The following list displays the 26 South American *Cheilanthes* s.s. species:

1. ***Cheilanthes andina*** Hook., *Sp. Fil.* 2: 115. 1852. —Type: Peru. “Lofty Andes of Peru”, *J. McLeans* n. (holotype: K!, photograph US!). ≡ *Cheilanthes valdiviana* Phil., *Linnaea* 29: 106. 1858. —Type: Chile. Valdivia, Huanehue, 1835, C. Gay 2450 (holotype: SGO-82317!, photographs BM!, SI!) **syn. nov.**
2. ***Cheilanthes arequipensis*** (Maxon) R. M. Tryon and A. F. Tryon, *Rhodora* 83: 133. 1981. *Notholaena arequipensis* Maxon, *Smithsonian Misc. Coll.* 65(8): 9. 1915. —Type: Peru, Arequipa, near Tingo, Ms. Rose and J. N. Rose 18797 (holotype: US! US-00142012!; isotype: NY! NY-00144380!).
3. ***Cheilanthes buchtienii*** (Rosenst.) R. M. Tryon, *Fieldiana Bot. N.S.* 29: 34. 1989. *Notholaena buchtienii* Rosenst., *Repert. Spec. Nov. Regni Veg.* 5: 238. 1908. —Type: Bolivia, Suryungas, Sirupaya, 13-XI-1906, O. Buchtien 472 (lectotype, designated by Ponce 290. 2016: S-R-3761!; isolectotypes: B-20-0143765!, GH-00021672!, NY! NY-00144384!, UC-477583!, US! US-00142015!).
4. ***Cheilanthes cantangensis*** (R. M. Tryon) R. M. Tryon, *Fieldiana Bot.* 29: 32. 1989. *Notholaena cantangensis* R. M. Tryon, *Rhodora* 63: 81. 1961. —Type: Peru, Dep. Cajamarca, Prov. Celendín, ruta Celendín-Río Marañón, Cantange, 1450 m, 4-VI-1960, A. López and A. Sagástegui 3366 (holotype: GH-00021675!).
5. ***Cheilanthes fractifera*** R. M. Tryon, *Rhodora* 62: 7. Jan. 1960. —Type: Peru, Ayacucho, D. S. Correll and E. E. Smith P-169 (holotype: GH!, isotype: LL-0037001!). ≡ *Cheilanthes saundersii* Alston, *Lilloa* 30: 110, t. 6. Aug. 1960. —Type: Peru, Dpto. Lima, Huarochiri, S. G. E. Saunders 353 (holotype: BM! BM-000936608!; isotype: US! US-00141682!).
6. ***Cheilanthes fraseri*** Mett. ex Kuhn, *Linnaea* 36: 83. 1869. *Notholaena fraseri* (Mett. ex Kuhn) Baker, *Syn. Fil.* (Hooker & Baker) ed. 2, 514. 1874. —Syntype: Peru, H. Ruiz and J. A. Pavón s.n. (B-20-0101079!); Ecuador, J. Fraser s.n. (B 20 0101078 a!); Ecuador, M. Wagner s.n. (B-20-0101079 b!).
7. ***Cheilanthes glauca*** (Cav.) Mett., *Abh. Senckenberg. Naturf. Ges.* (Cheilanthes) 3: 75, n. 32, t. 3, f. 18-19. 1859. *Acrostichum glaucum* Cav. *Anales Hist. Nat.* 1: 107. 1799. *Pteris glauca* (Cav.) Cav., *Descr. Pl.* 269. 1802. *Pellaea glauca* (Cav.) J. Sm., *Ferns Brit. and For.* 180. 1866. —Type: Chile, V Región, “Cordillera del Portillo en los Andes” L. Née s.n.” (lectotype, designated by Ponce 291. 2016: MA476156!; isolectotype, MA-476155!).
8. ***Cheilanthes glutinosa*** M. Kessler and A. R. Sm., *Brittonia* 59: 188. 2007. —Type: Bolivia, Dpto. Cochabamba, Prov. Carrasco, Km 98 antigua carretera Cochabamba-Villa Tunari, 17° 12' S, 65° 42' W, 3400 m, 27/VI/1996, M. Kessler et al. 6750 (holotype: UC-1615419!; isotypes: GOET-007170!, LPB! LPB-0000036!).
9. ***Cheilanthes hassleri*** (Weath.) Ponce, *Darwiniana* 45: 240. 2007. *Notholaena hassleri* Weath., *Lilloa* 6: 274, t. 4. 1941. —Type: Paraguay. “In regione calcarea cursus superioris fluminis Apa”, 11/1913, E. Hassler 10996 (holotype: K! K-000633271!; isotypes: G-00401740, MO-255612!, NY! NY-00888320!, S05-9887!, UC-950037!, fragment US-00142019!).
10. ***Cheilanthes hieronymi*** Herter, in Osten and Herter (ed.) *Anales Mus. Nac. Montevideo Ser. 2*, t. 1: 361, t. 27. 1925. —Type: Brazil, Rio Grande do Sul, frontier with Uruguay, Sierra de Santana do Livramento, 26-28-V-1907, W. Herter 3153 (lectotype, designated by Ponce 292. 2016: US! US-00141835!; isolectotypes: B-20-0036945!, B-20-0036948!, NY-00144364!, P-00584332!, P-00584333!, P-00584334!; S-R-1061!).
11. ***Cheilanthes hypoleuca*** (Kunze) Mett., *Abh. Senckenberg. Naturf. Ges.* (Cheilanthes) 3: 66, n.11. 1859. *Notholaena hypoleuca* Kunze, *Linnaea* 9: 54. 1834. —Type: Chile, pr. Valparaíso, IV-1827, E. F. Poeppig 262 (lectotype, designated by Ponce. 293. 2016: B-200143796!; isolectotypes: B-20-0143795! (the plant at right on the sheet), HAL-0137747!, MO-255918!, P-00584336!).
12. ***Cheilanthes incarum*** Maxon, *Smithsonian Misc. Coll.* 65(8): 5. 1915. —Type: Peru, near Cuzco, 3300 m, 1/IX/1914, J. N. Rose 19061 (holotype: US! US-00141836!; isotypes: NY! NY-00144365! fragment; P! P-00584337!).
13. ***Cheilanthes juergensii*** Rosenst., *Hedwigia* 46: 84. 1906. —Type: Brazil, Rio Grande do Sul, Mun. Cachoeira, Col. St. Angelo, Arroio Bohemia, 12-5-1905, C. Jürgens 269 (holotype: S05-9870!, verified by Rosenstock; isotypes: NY! NY-00144366!, P-00584340!, UC-442052!).
14. ***Cheilanthes lonchophylla*** (Weath. ex R. M. Tryon) R. M. Tryon and A. F. Tryon, *Rhodora* 83: 133. 1981. *Notholaena lonchophylla* Weath. ex R. M. Tryon, *Contrib. Gray Herb.* 179: 19. 1956. —Type: Peru, Chachapoyas, B. F. Mathews 610 (holotype: K! K-000633281!; isotype: P! P-00586992!).
15. ***Cheilanthes micropteris*** Sw., *Syn. Fil.* (Swartz) 126, 324, t. 3, f. 5. 1836. —Type: Ecuador, “Regni Quitensis, Pelileo” L. Née s. n. (holotype: S!, S-R-1065!; isotype: MA-208972!).
16. ***Cheilanthes mollis*** (Kunze) C. Presl, *Tent. Pterid.* 160. 1836. *Notholaena mollis* Kunze, *Linnaea* 9: 54. 1834. —Type: Chile, ca. Valparaíso, Playa Ancha, VI-1827, E. F.

- Poeppig s. n. (lectotype, designated here: LE-00008529; isolectotype: BM-001067980!).
17. *Cheilanthes obducta* Mett. ex Kuhn, *Linnaea* 36: 83. 1869. —Type: Bolivia, La Laguna (now Padilla), D'Orbigny 386 (holotype: B-20-0102214; isotypes: P! P-00586581!, P-00586582!).
 18. *Cheilanthes pantanalensis* E. L. M. Assis, Ponce and Labiak, *Amer. Fern J.* 98(4): 203, Figs. 1, 2. 2009. —Type: Brazil. Mato Grosso do Sul, Corumbá, Serra do Amolar, Morro do Sucuri, 700 m, 18-X-2002, E. L. M. Assis 364 (holotype: UPCB!; isotypes: MBM!, SI!, SP!).
 19. *Cheilanthes peruviana* (Desv.) T. Moore, *Index Fil.* 250. 1861. *Notholaena peruviana* Desv., *Mém. Soc. Linn. Paris* 6: 220. 1827. —Type: Peru, non-designated locality, *J. Dombey s. n.* (holotype: P-00586588; isotypes: B-200127985, fragment, P-00586540!).
 20. *Cheilanthes pilosa* Goldm., *Nov. Act. Caes. Leopold. Carol. Nat. Cur.* 19 (Suppl. 1): 455. 1843. —Type: Peru, non-designated locality, *F. J. F. Meyen s. n.* (lectotype, designated by Ponce 295. 2016: B-20-0038096; isolectotypes: B-20-0038097!, S-R-1066!).
 21. *Cheilanthes poeppigiana* Mett. ex Kuhn, *Linnaea* 36: 84. 1869. —Syntype: Peru, *E. F. Poeppig s.n.* (not located); Bolivia, *H. Cumming s.n.* (B-20-0038108 a!).
 22. *Cheilanthes pruinata* Kaulf., *Enum. Filic.* 210. 1824. —Type: Peru, non-designated locality, *A. d. Chamisso s. n.* (not located). Note: Until now we have not been successful in the search of the specimen *A. d. Chamisso s. n.* cited by Kaulfuss in the original description, in the oldest herbaria of Europe, such as B, BM, BR, C, HAL, HBG, K, KIEL, L, LE (main collection), LZ (destroyed), M, P, S, W.
 23. *Cheilanthes rufopunctata* Rosenst., *Meded. Rijks-Herb. Leiden* 19: 9. 1913. —Type: Bolivia, La Paz, “in valle Araca, in lapidosis, 3400 m, X-1911”, *T. Herzog* 2366 (holotype: L-0063079; isotypes: UC-478369!, US-00141681!).
 24. *Cheilanthes sarmientoi* Ponce, *Amer. Fern J.* 79: 131, Figs. 4A–E. 1989. —Type: Argentina, San Juan, Dpto. Sarmiento, río de Los Sombreros, NW río Los Leones, 21-I-1986, *R. Guaglianone* 1528 (holotype: SI! SI-000014; isotype: SI SI-000015!).
 25. *Cheilanthes scariosa* (Sw.) C. Presl, *Reliq. Haenk.* 1(1): 65. 1825. *Acrostichum scariosum* Sw., *Syn. Fil.* (Swartz) 16. 1806; nom. nov. for *Acrostichum lanuginosum* Willd., *Schr. Akad. Erf.*: 31, t.3, f4, 1802, non Desf. 1800. —Type: Peru, Exped. Malaspina (holotype: B-W 19554-01 0!). Note: Erroneously labeled as from Nueva España (Mexico).
 26. *Cheilanthes squamosa* Gillies ex Hook. and Grev., *Icon. Filic.* t. 151. 1829. *Notholaena squamosa* (Gillies ex Hook. and Grev.) Lowe, *Ferns Brit. and Exot.* 1: 49, t. 17 B. 1856. —Type: Argentina, San Luis, Cerro del Morro, 1-VII-1828, *J. Gillies s. n.* (holotype: E-00182897; isotype: K!).

5.2 New genus

Mineirella Ponce and Scataglini, **gen. nov.**

Type: *Mineirella geraniifolia* (Weath.) Ponce and Scataglini. Basionym: *Notholaena geraniifolia* Weath.

Etymology: *Mineira*, Portuguese, refers to the distribution range of the genus that includes the State of Minas Gerais (Brazil) and all near mountain and mining regions where the

species grow, and the latin suffix *ella*, alludes to its little size.

Diagnosis: Differs from *Cheilanthes* s.s. in rhizomes creeping, horizontal, elongate; laminae pentagonal, pedate, lobate-pinnatifid, bipinnatifid or basally pinnate (vs. rhizomes rarely erect, mostly decumbent, or short creeping, compact, nodose; laminae linear, elliptic, ovate triangular, 1-2-pinnate-pinnatifid, or rarely pentagonal, 3-pinnate-pinnatifid).

Description: Plants saxicolous, 3–25(30) cm. Rhizomes creeping, horizontal, sometimes branched; scales linear to ovate-lanceolate, bicolorous, with brown blackish, sclerotic center, and hyaline, narrow to broad border, margin entire to broadly dentate toward the capillar apex. Fronds monomorphic, fasciculate or approximate along the rhizomes. Petiole terete to slightly sulcate distally, 2–5 times longer than the lamina, one vascular bundle, dark brown, base with scales as those of the rhizome, throughout the petiole, with villous or lanate trichomes, generally dense, glabrescent to maturity. Laminae pentagonal in outline, entire, lobate-pinnatifid, bipinnatifid or basally 1-2-pinnate; basal pinnae lobed or pinnatifid basicopically, with basicopic segments elongate, herbaceous to chartaceous, laminar indument villous to lanate (matted), trichomes simple or capitate, multicellular, uniseriate; veins free, 2-4-furcate, with widened tips (hydathodes), laminar margins usually with a membranaceous border, crenate or lobate. Sori marginal, sporangia on the vein tips, covered by crenate or lobed margin (false indusium). Sporangia with 32 spores when apomictic or 64 spores when sexual; spores trilete, tetrahedral to globose, surface rugate, sometimes shortly cristate, inner reticulate. The chromosome number is not counted.

5.2.1 Distribution

This genus is found from the massifs of Brazil and the Guianas to the Amazonian border in Bolivia and Paraguay. Its presence is restricted to xeric habitats with basaltic rocks and sandstone substrates.

5.2.2 Observations

Within the *Adiantopsis–Doryopteris* clade, the genus *Mineirella* appears to be related to South African and Malagasy species groups: *C. quadripinnata* and *C. viridis* (“*Pteridellastrum*”), *Pellaea calomelanos* (*P. sect. Holcochlaena* Baker, see Kirkpatrick, 2007) and *Choristosoria pteroides*, *Cheilanthes induta* and *C. multifida* that had been tentatively included into *Choristosoria* by Yesilyurt et al., (2015). These paleotropical species differ from *Mineirella* and also from *Cheilanthes* s.s. by having large fronds with 2-3-pinnate-pinnatifid lamina and deeply sulcate rachis. A revision of these paleotropical taxa is still required to explore their taxonomic circumscription and relationships. Although these African and Malagasy species are reliably excluded from *Cheilanthes* s.s. and *Pellaea* s.s., further sampling is required to corroborate well-supported monophyletic groups and to establish the relationships among them.

5.2.3 New combinations in *Mineirella*

Mineirella eriophora (Fée) Ponce and Scataglini, **comb. nov.** Figs. 3A, 3B.

Notholaena eriophora Fée, *Mem. Foug.* 5 (Gen. Filic.): 159, t. 13, f.3. 1852. *Polypodium eriophorum* (Fée) Hook., *Icon. Pl.* 6: t.

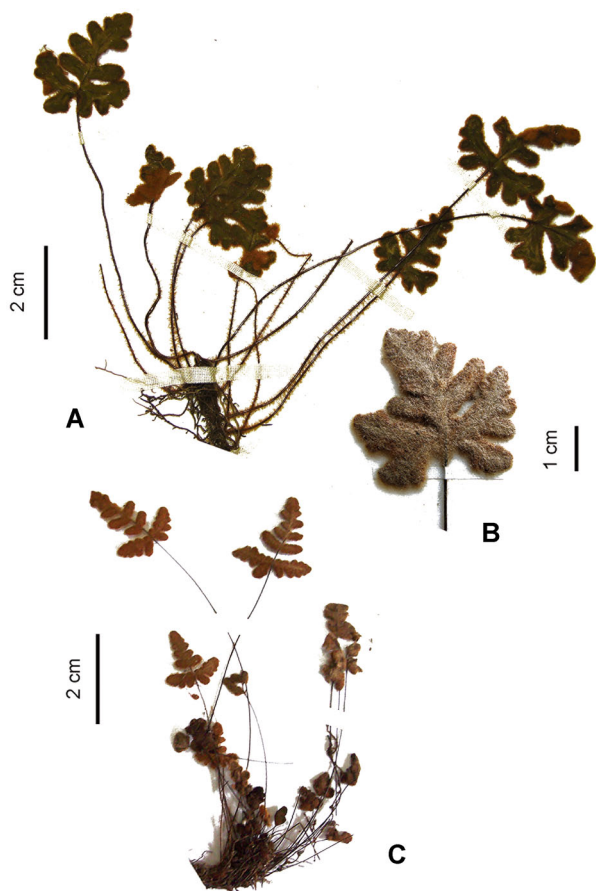


Fig. 3. A, B, *Mineirella eriophora*. A, plant habit. B, lamina abaxial (Gardner 2390). C, *Mineirella venusta*, plant habit (Sehnem 12933). Photo author: M.M. Ponce.

991. 1854. *Cheilanthes eriophora* (Fée) Mett., *Abh. Senckenberg. Naturf. Ges.* (Cheilanthes) 3: 67, n. 14. 1859. —Type: Brazil, Piauí, “Peauhy near Oeiras, shady cliffs on the hills, III-1839”, G. Gardner 2390 (lectotype, designated here: K-000633268!; isolectotypes, fragment “1” B-20-0128131!, BM!, K-000633267!, K-000633269!, NY-00144390!, P-00274406, P-00274407!, US-00142017!).

Notholaena palmatifida Kunze, *Farnkräuter* 1: 148. 1844, nom. nud.

Mineirella geraniifolia (Weath.) Ponce and Scataglini, **comb. nov.** Fig. 4

Notholaena geraniifolia Weath., *J. Arnold Arbor.* 27: 367. 1946. *Cheilanthes geraniifolia* (Weath.) R. M. Tryon and A. F. Tryon, *Rhodora* 83: 133. 1981. —Type: Brazil, Minas Gerais, “prope São Miguel de Jequitinhonha”, A. St. Hilaire 1489 (holotype: P-00274392!, isotypes: fragment “3” B-20-0128131!; P-00274394!).

Mineirella goyazensis (Taub.) Ponce and Scataglini, **comb. nov.** Fig. 5

Notholaena goyazensis Taub., *Bot. Jahrb. Syst.* 21(4): 421. 1895. *Cheilanthes goyazensis* (Taub.) Domin, *Biblioth. Bot.* 20 [Heft 85(1)]: 133. 1915. —Type: Brazil, Goiás, Serra Dourada, I-1893, E. Ule 531/3222 part. A (lectotype, designated here: P-00274399!). Epitype: Brazil, Minas Gerais, São João d'El Rei

(Serra do Lenheiro), 13-X-1886, A. F. M. Glaziou 16643 (designated here: P-00274397!; epitype duplicates B-20-0128137!, K-000633270!, P-00274398!).

Notholaena glaziovii Weath., in herbaria, nom. nud.

Note: The original material deposited in P, labeled “*Notholaena goyazensis* Taubert, nov. sp. ms. in herb. Ulei”, legit Ule 531/3222 (P-00274399!), consists of a few tiny fronds. This specimen was described by Christ (1902) as a small form of *Notholaena goyazensis*, and this criterion was also accepted by Weatherby (1946) and Tryon (1956) who studied the material. Here, we have analyzed this material and duplicates, concluding that P-00274399 and also P-00274409! correspond exactly to small plants of *N. goyazensis*, but other duplicates of Ule 531 (P-004408!) and Ule 531/3222 (CORD-00001413!) agree with *N. eriophora*, which can be easily confused with small specimens of *M. goyazensis*. Therefore, to clarify the current concept of *Mineirella goyazensis*, we designate as lectotype the material with the original label Ule 531/3222 (P-00274399!), because it must be explicitly cited (Art. 9.9 of the CNB); besides, given that this material corresponds to a poor and unrepresentative specimen of *N. goyazensis*, we also designate an epitype to preserve the undoubted identity of the basionym.

Mineirella venusta (Brade) Ponce and Scataglini, **comb. nov.** Fig. 3C

Notholaena venusta Brade, *Anais Prim. Reun. Sul-Amer. Bot.* 2: 7, t.4 f. 1-2. 1940. *Cheilanthes venusta* (Brade) R. M. Tryon and A. F. Tryon, *Rhodora* 83: 133. 1981, hom. illeg., non *Cheilanthes venusta* Fée, *Mem. Foug.* 10: 20. 1865. *Cheilanthes bradei* J. Prado and A. R. Sm., *Amer. Fern J.* 92(2): 110. 2002. —Type: Brasil, Minas Gerais, Diamantina, nos rochedos, 1400 m, A. C. Brade 13949 (holotype: RB-00543350!; isotype: HB!).

Notholaena capillus St. Hil. ex Christ, *Bull. Herb. Boissier ser.* 2, 2: 381. 1902. nom. nud. prosyn.

5.2.4 Putative hybrid

Mineirella steyermarkii (Vareschi) Ponce and Scataglini, **comb. nov.** *Notholaena steyermarkii* Vareschi, *Acta Bot. Venez.* 1(2): 100. 1966. —Type: Venezuela, Bolívar, Chimantá Massif, Torono-tepuí, along the base of SE-facing sandstone bluffs of Torono-tepuí, 1700 m, 21/V/1953, J. A. Steyermark 75534 (lectotype designated here: US!; isolectotypes, GH!, NY!).

5.3 Incertae sedis

According to the present phylogeny, five South American species assigned to *Cheilanthes* should be placed as *incertae sedis* until further DNA sequence data can be analyzed or their diagnostic morphological characters are compared with other cheilanthoid genera to try to identify their affinities:

1. ***Cheilanthes incisa*** Kunze ex Mett., *Abh. Senckenberg. Naturf. Ges.* (Cheilanthes): n. 65, tab. 3, fig. 28-31. 1859. —Type: Brazil, Rio de Janeiro, Serra d'Estrella, 1822-1823, H. K. Beyrich s.n. (lectotype, designated by Schwartzburd and Prado, 2015. PRC-455086!; isolectotype, LE). Note: Due to its poorly known diagnostic characteristics, the assignment to *Cheilanthes* must be confirmed using molecular data.
2. ***Cheilanthes pohliana*** Kunze ex Mett., *Abh. Senckenberg. Naturf. Ges.* (Cheilanthes): n. 13. 1859. *Notholaena pohliana* Kunze, *Farnkräuter* 1: 45. 1840, nom. nud. —Type: Brasil,

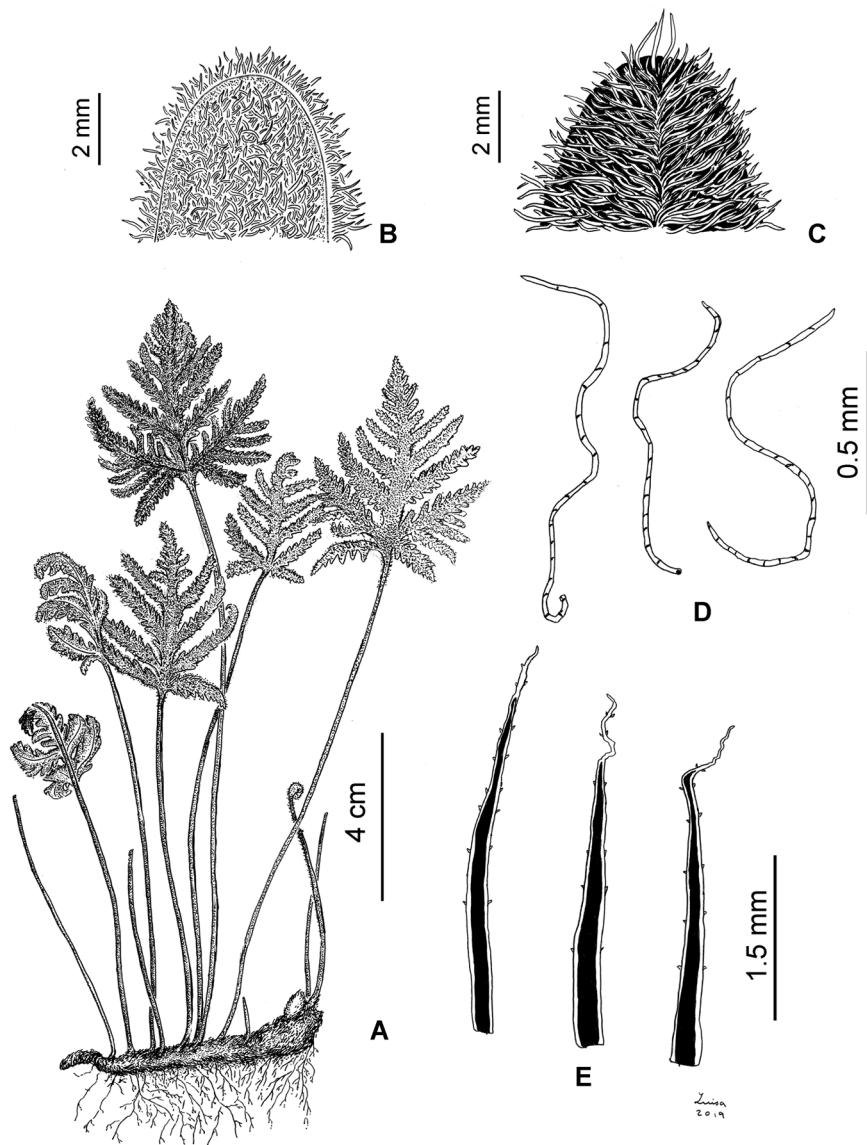


Fig. 4. *Mineirella geraniifolia*. **A**, plant habit. **B**, portion of abaxial segment. **C**, portion of adaxial segment. **D**, petiole trichomes. **E**, rhizome scales. (Mori & dos Santos 11792, NY). Illustration by Luisa Lerman (2019).

Goiás, Serra da Natividade, M. 1839, G. Gardner 3554 (lectotype, designated here: B-20-0128129!; isolectotypes: BM!, K!, F!, G!, P!, US!). Syntype: Brasil, Goiás, “Ad Meia Ponte, Capit. Goyaz”, J. B. E. Pohl 3869 (W!). Note: The generic assignment of this species is in revision, based on its morphology and molecular data.

3. *Cheilanthes regnelliana* Mett. ex Baker, *Fl. Bras.* 1 (2): 391, T. 43, f. 1. 1870. —Type: Brazil, Minas Gerais, “Serra de Caldas”, in fissuris rupis, Pedra Branca, 30-VIII-1875, *Herb. Regnell*: G. Mosén 2071 (lectotype; S! S-R-1067!; isolectotypes; K! K-000633273!, So5-9871! P!, photograph BM!). ≡ *Cheilanthes flexuosa* Kunze var. *minor* Kunze, *Linnaea* 22: 578. 1849. —Type: Brazil, Minas Gerais, Caldas, Serra das Gineta, 12-II-1850, A. F. Regnell II. 320 (holotype: S!, isotypes: B-20-0038455!, K!, US!). ≡ *Cheilanthes flexuosa* Baker, *Syn. Fil. (Hooker & Baker)* 138. 1867. hom. illeg. Non Kunze 1849. —Type: Brazil, Minas Gerais, Rio Capivary, XI-1854, S. O. Lindberg 586 (holotype:

K-000633275!). ≡ *Cheilanthes globuligera* Christ, *Ann. Cons. Jard. Bot. Genève* 3: 40. 1899. —Type: Brazil, Rio de Janeiro, Serra dos Ilheos, près de S. João d’El Rei, 21-II-1889, A. F. M. Glaziou 17958 (holotype: G-00348309!; isotypes: B-200038456!, NY, P, US). Note: On the basis of its morphology, this species probably belongs to *Adiantopsis*.

4. *Cheilanthes volcanensis* de la Sota, *Darwiniana* 17: 78, f. 5 G-H, t. 1, 1. 1972. —Type: Argentina, Jujuy, Estación Volcán, I-1920, L. Castellón 20 (holotype: LIL-17156!; isotype: US!). Note: On the basis of Hernández (2019), this species probably belongs to *Gaga*.
5. *Notholaena solitaria* R. M. Tryon, *Rhodora* 63: 82, tab. 1257, fig. 7. 1961. —Type: Suriname, without locality, F. W. Hostmann 199 (holotype: K-000484092!, photograph S!, US!). Note: Only the type collection from Suriname (North of South America) is known. The specimen consists of two fronds without rhizomes that resemble *C. hassleri*.

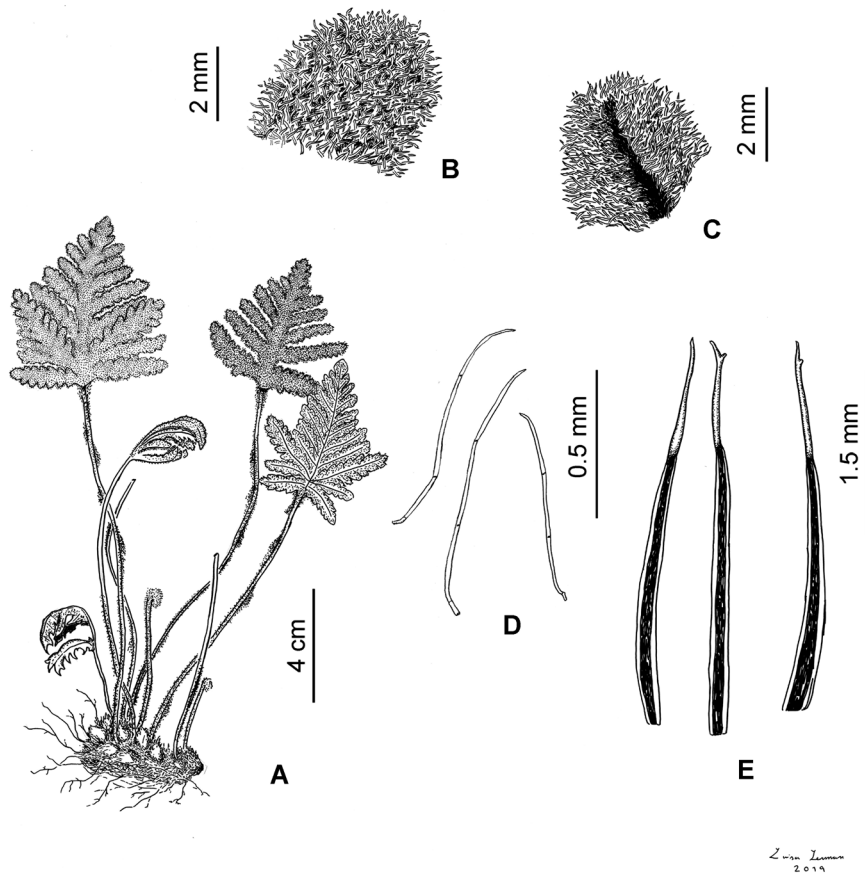


Fig. 5. *Mineirella goyazensis*. **A**, plant habit. **B**, portion of abaxial segment. **C**, portion of adaxial segment. **D**, petiole trichomes. **E**, rhizome scales. (Irwin et al. 13740, NY). Illustration by Luisa Lerman (2019).

6 Concluding Summary

This is the first phylogenetic approach covering almost the entire range of the South American *Cheilanthes*. From a total of ca. 35 South American *Cheilanthes* species (Ponce, 2016), we propose that 26 of them belong to the *Cheilanthes* s.s. (ten to the South American clade and 16 to the South American + Australasian clade). Other four *Cheilanthes* species were transferred to the new genus *Mineirella*, and five species remain as *incertae sedis* until new studies confirm their transfer to other genera.

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Appendix I. 7 List of the 73 species (including the authors of the scientific names) analyzed in the phylogenetic analysis. Genbank accession numbers (*rbcl*, *trnL* + *trnL-F*, and *rps4* + *rps4-trnS*) and their corresponding sites are indicated. Sequences obtained for this work are bold and marked with *. Not available sequences are indicated as --.

Adiantopsis dichotoma (Sw.) T. Moore, MG593078 (Ponce & Scatagliani 2018), --, --. **A. tweediana** Hook., MG593081, -- (Ponce & Scatagliani 2018), **MW245820***. **Aleuritopteris albomarginata** (C.B. Clarke) Ching, AY266411 (Zhang et al., 2005), DQ432665 (Zhang et al., 2007), --. **A. argentea** (S.G. Gmel.) Fée, AY266410 (Zhang et al., 2005), DQ432667 (Zhang et al., 2007), --. **A. formosana** (Hayata) Tagawa, DQ432643, DQ432671 (Zhang et al., 2007), --. **Calciophilopteris ludens** (Wall. ex Hook.) Yesilyurt & H. Schneid. DQ432657, DQ432686 (Zhang et al., 2007), KU147318 (Pryer et al., 2016). **Cheilanthes arequipensis** (Maxon) R. M. Tryon & A. F. Tryon, **MW245815***, **MW245809***, --. **C. bradei** J. Prado & A.R. Sm., JN122014, JN122019 (Eiserhardt et al., 2011), --. **C. buchtienii** (Rosenst.) R. M. Tryon, MG593084, MG593111 (Ponce & Scatagliani 2018), DQ914145 (Kirkpatrick 2007). **C. contracta** (Kunze) Mett. ex Kuhn, GU935519, GU935593, GU935533 (Eiserhardt et al., 2011). **C. capensis** (Thunb.) Sw., GU935511, --, GU935536 (Eiserhardt et al., 2011). **C. deltoidea** Kunze, GU935512, GU935605, GU935537 (Eiserhardt et al., 2011). **C. depauperata** Baker, GU935516, GU935590, GU935532 (Eiserhardt et al., 2011). **C. dinteri** Brause, GU935506, GU935582, GU935527 (Eiserhardt et al., 2011). **C. distans** (R. Br.) Mett., EU268783 (Rothfels et al., 2008), --, DQ914147 (Kirkpatrick 2007). **C. eckloniana** Mett., GU935513, GU935585, GU935540 (Eiserhardt et al., 2011). **C. fraseri** Mett. ex Kuhn, MG593085, --, -- (Ponce & Scatagliani 2018). **C. geraniifolia** (Weath.) R. M. Tryon & A. F. Tryon, MG593086, MG593112, -- (Ponce & Scatagliani 2018). **C. glauca** (Cav.) Mett. MG593087, MG593113, -- (Ponce & Scatagliani 2018). **C. glutinosa** M. Kessler & A.R. Smith, MG593088, MG593114, -- (Ponce & Scatagliani 2018). **C. goyazensis** (Taub.) Domin, EF473687 (Prado et al., 2007), JN122018, -- (Eiserhardt et al., 2011). **C. hastata** Kunze, GU935510, GU935612, GU935538 (Eiserhardt et al., 2011). **C. hieronymi** Herter, MG593090, MG593116, (Ponce & Scatagliani 2018), **MW245821***. **C. hirta** Sw., GU935515, GU935589, GU935531 (Eiserhardt et al., 2011). **C. hypoleuca** (Kunze) Mett., MG593091, MG593117, -- (Ponce & Scatagliani 2018). **C. induta** Kunze, GU935501, GU935597, GU935542 (Eiserhardt et al., 2011). **C. kunzei** Mett., GU935508, GU935614, GU935539 (Eiserhardt et al., 2011). **C. lasiophylla** Pic. Serm., HM003032, --, -- (Pryer et al., 2010). **C. marlothii** (Hieron.) Domin, GU935514, GU935586, GU935541 (Eiserhardt et al., 2011). **C. micropteris** Sw., MG593092, MG593118, -- (Ponce & Scatagliani 2018). **C. mollis** (Kunze) C. Presl, **MW245817***, **MW245811***, **MW245822***. **C. multifida** (Sw.) Sw., GU935500, GU935596, GU935544 (Eiserhardt

et al., 2011). **C. namaquensis** (Baker) Schelpe & N.C. Anthony, GU935492, GU935583, GU935529 (Eiserhardt et al., 2011). **C. obducta** Mett. ex Kuhn, MG593093, MG593119, -- (Ponce & Scatagliani 2018). **C. pantanalensis** E.L.M. Assis, Ponce & Labiak, **MW245818 *** (Ponce & Scatagliani 2020), MG593120 (Ponce & Scatagliani 2018), **MW245824***. **C. parviloba** Sw., GU935517, GU935591, GU935534 (Eiserhardt et al., 2011). **C. peruviana** (Desv.) T. Moore, **MW245819***, **MW245812***, --. **C. pilosa** Goldm., MG593094, MG593121 (Ponce & Scatagliani 2018), **MW245823***. **C. aff. pilosa** **MW245816***, **MW245810***, --. **C. poeppigiana** Mett. ex Kuhn, MG593095, MG593122, -- (Ponce & Scatagliani 2018). **C. pruinata** Kaulf., MG593096, MG593123, -- (Ponce & Scatagliani 2018). **C. quadripinnata** (Forssk.) Kuhn, GU935496, --, GU935550 (Eiserhardt et al., 2011). **C. robusta** (Kuntze) R. M. Tryon, GU935507, GU935609, GU935535 (Eiserhardt et al., 2011). **C. rufopunctata** Rosenst., MG593097, MG593124, -- (Ponce & Scatagliani 2018). **C. sarmientoi** Ponce, MG593098, MG593125 (Ponce & Scatagliani 2018), **MW245825***. **C. scariosa** (Sw.) C. Presl, MG593099, MG593126, -- (Ponce & Scatagliani 2018). **C. sieberi** Kunze, GU136792 (Bouma et al., 2010), EU831190, EU831154 (Kirkpatrick 2008). **C. squamosa** Gillies ex Hook. & Grev., MG593100, MG593127 (Ponce & Scatagliani 2018), **MW245826***. **C. tenuifolia** (Burm. f.) Sw., KP126965, --, KP126988 (Wang & Zhang, 2015). **C. viridis** Sw., GU935494, GU935603, GU935547 (Eiserhardt et al., 2011). **C. viridis** var. **glauca** Schelpe & N.C. Anthony, GU935495, GU935602, GU935548 (Eiserhardt et al., 2011). **Doryopteris lorentzii** (Hieron.) Diels, MG593101 (Ponce & Scatagliani 2018), **MW245813***, **MW245827***. **D. pedatoides** (Desv.) Kuhn, JN122016, JN122022 (Eiserhardt et al., 2011), --. **D. pentagona** Pichi Serm., MG593102, MG593128 (Ponce & Scatagliani 2018), **MW245828***. **D. pilosa** (Poir.) Kuhn, JN122017, JN122023 (Eiserhardt et al., 2011), --. **D. rediviva** Fée, KP407200, KP407220 (Yesilyurt et al., 2015), DQ914141 (Kirkpatrick 2007). **D. triphylla** (Lam.) Christ, MG593103, MG593129 (Ponce & Scatagliani 2018), DQ914139 (Kirkpatrick 2007). **Gaga marginata** (Kunth) Fay W. Li & Windham, MG593104, MG593130 (Ponce & Scatagliani 2018), **MW245829***. **Hemionitis rufa** (L.) Sw., AY357707 (Geiger & Ranker unpubl.), --, --. **H. tomentosa** (Lam.) Raddi, MG593105 (Ponce & Scatagliani 2018), **MW245814***, --. **Lytoneuron lomariaceum** (Klotzsch) Yesilyurt, KP407209 (Yesilyurt et al., 2015), JN122020, -- (Eiserhardt et al., 2011). **Myriopteris alabamensis** (Buckley) Grusz & Windham, EF452143 (Schuettpeitz et al., 2007), DQ914220, DQ914144 (Kirkpatrick 2007). **M. covillei** (Maxon) Á. Löve & D. Löve, EU268782 (Rothfels et al., 2008), DQ914221, DQ914146 (Kirkpatrick 2007). **M. lanosa** (Michx.) Grusz & Windham, U27205 (Gastony & Rollo 1995), DQ914227, DQ914153 (Kirkpatrick 2007). **M. lendigera** (Cav.) J. Sm., EU268784 (Rothfels et al., 2008), DQ914228, DQ914154 (Kirkpatrick 2007). **Notholaena standleyi** Maxon, EU268804 (Rothfels et al., 2008), --, DQ914169 (Kirkpatrick 2007). **Ormopteris gleichenioides** (Gardner) J. Sm., EF473698 (Prado et al. 2007), KM435287 (Yesilyurt et al., 2015), DQ914138 (Kirkpatrick 2007). **Pellaea andromedifolia** (Kaulf.) Fée, U19501 (Gastony & Rollo 1995), DQ914174,

DQ914072 (Kirkpatrick 2007). *P. calomelanos* (Sw.) Link (G. Forst.) Hook., U28788 (Gastony & Rollo 1995), DQ914181, GU935497, GU935600, GU935549 (Eiserhardt et al., 2011). *P. DQ914084* (Kirkpatrick 2007). *P. ternifolia* (Cav.) Link, *dura* (Willd.) Baker, GU935490, GU935579, GU935523 MG593109, MG593132 (Ponce & Scatagliani 2018), DQ914106 (Eiserhardt et al., 2011). *P. pteroides* (L.) Mett., GU935502, (Kirkpatrick 2007). GU935599, GU935545 (Eiserhardt et al., 2011). *P. rotundifolia*