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Do two South American species of *Cheilanthes* (Pteridaceae) traditionally linked to the *Cheilanthes marginata* group, belong to *Gaga*?

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Abstract

The phylogenetic positions of *Cheilanthes hieronymi* and *C. poeppigiana* are tested using DNA sequences of plastid *matK* and *rbcL* markers. These South American species are historically linked to *Cheilanthes marginata*, now transferred to the new genus *Gaga*. The results showed that *C. hieronymi* and *C. poeppigiana* are located outside *Gaga*. The study corroborated that the morphological similarities between the two species and the genus *Gaga* were resulted from convergences.

Key words: *Cheilanthes hieronymi*, *Cheilanthes poeppigiana*, *Gaga marginata*, homoplasy, Pteridaceae, South America

Introduction

Cheilanthes Swartz (1806: 126), a member of the subfamily Cheilanthoideae of Pteridaceae (Tryon 1990, Christenhusz *et al.* 2011), is a globally distributed genus that comprises around 120 species. At present, numerous *Cheilanthes* species have been transferred to new or formerly described genera that have been segregated based on recent molecular phylogenies. Most cheilanthoids species grow in arid and semiarid mountainous environments leading to a very variable morphology and to adaptive convergence (Tryon & Tryon 1973, Gastony & Rollo 1995, 1998). These phenomena, together with hybridization, polyploidy, and apogamy (Windham & Yatskiewych 2003) have hampered the generic delimitation for decades. Until now, the morphological features that define a natural genus *Cheilanthes* remain elusive.

In the past few years, based on molecular phylogenetic analyses, several monophyletic genera have been circumscribed within the cheilanthoids. These include *Adiantopsis* Fée (1852: 145) (Link-Perez *et al.* 2011), *Argyrochosma* (J. Smith) Windham (1987: 38) (Sigel *et al.* 2011), *Calciphilopteris* Yesilyurt & H.Schneid. (2010: 52–53) (Yesilyurt & Schneider 2010), *Doryopteris* J. Sm. (1841: 404–405) (Yesilyurt *et al.* 2015), *Lytoneuron* (Klotzsch) Yesilyurt (2015: 116) (Yesilyurt *et al.* 2015), *Myriopteris* Fée (1852: 148) (Grusz & Windham 2013), *Notholaena* R. Br. (1810: 145) (Rothfels *et al.* 2008) and *Ormopteris* J. Sm. ex J. Sm. (1875: 281) (Yesilyurt *et al.* 2015). However, *Cheilanthes* and *Pellaea* Link (1841: 59) still remain polyphyletic (Kirkpatrick 2007, Rothfels *et al.* 2008, Bouma *et al.* 2010, Eiserhardt *et al.* 2011, Yesilyurt *et al.* 2015).

Here we focus on a particular case concerning the species related to *Cheilanthes marginata* Kunth (1815[1816]: 22). The *Cheilanthes marginata* group, informally recognized by Tryon & Tryon (1982) was recently transferred to a new genus *Gaga* Pryer, Li & Windham (2012: 855) by Li *et al.* (2012) based on molecular and morphological evidence.

Tryon & Tryon (1982) characterized the species of the *Cheilanthes marginata* group by lamina glabrous or sometimes glandular; continuous, glabrous and membranaceous pseudoindusia with papillae on margin, confined to the segments or extending along the rachis. In addition, traditionally the group includes species that have 2–4-pinnate, pentagonal or deltate-ovate outline lamina, and rachis adaxially sulcate with green wings.

The genus *Gaga* is defined broader than the *Cheilanthes marginata* group by Li *et al.* (2012) by adding the following features: the form of segments ovate, oblong or linear, with rounded to attenuate apices; the margins minutely bullate in mature leaves; the vein endings forming prominent hydathodes; the sporangia clustered at vein tips; the strongly differentiated, inframarginal pseudoindusia with margins entire, papillate, fimbriate, or spiculate; the production of 64 small or 32 large spores per sporangium; and the base number presumably $x = 30$.

Moreover, Li *et al.* (2012) showed that the analyzed species of the *Cheilanthes marginata* group were grouped by a molecular synapomorphy in the *matK* alignment: the nucleotides “GAGA” aligned in position 598–601, a pattern that is not present in species of closely related genera like *Aspidotis* (Nuttall ex Hooker 1867: 131) Copeland (1947: 68) and *Cheilanthes*.

Most species of *Gaga* grow in North and Central America, only three are distributed in northern South America, *G. angustifolia* (Kunth) Fay-Wei Li & Windham, *G. cuneata* (Link) Fay-Wei Li & Windham, and *G. kaulfussii* (Kunze) Fay-Wei Li & Windham, while the type species, *G. marginata* (Kunth) Fay-Wei Li & Windham, range from Mexico to Argentina.

Among *Cheilanthes* from the Southern Cone (Ponce *et al.* 2008) two species, not included in the analysis of Li *et al.* (2012), are historically associated with the *C. marginata* group: *Cheilanthes poeppigiana* Kuhn, from Ecuador, Peru, Bolivia, and Argentina, placed by Tryon & Tryon (1982) within *C. marginata* group, and *C. hieronymi* Herter, endemic to Argentina, Uruguay, and southern Brazil, linked to *C. marginata* by Capurro (1968) and de la Sota (1969), and originally described as *C. marginata* var. *gracilis* Hieronymus (1897: 388).

Cheilanthes poeppigiana and *C. hieronymi* share morphological characteristics with genus *Gaga*, such as deltate or pentagonal lamina, hairless, ridged rachis with green wings, enlarged veins apex (hydathodes), continuous and membranaceous pseudoindusia that are confined to the segments.

In a global phylogeny of *Cheilanthes* using *rbcL* and *trnL-trnF* (Ponce & Scataglini, unpubl. data.) *C. hieronymi* appears in the clade of *Cheilanthes* s. s. related to *C. micropteris* Swartz (1806: 126), the type species of the genus, while *C. poeppigiana* is included in the clade of Asian *Cheilanthes* (Zhang *et al.* 2007); however the genus *Gaga* was not recovered in our phylogeny probably because *matK* was not used.

Therefore the aim of this study is to test the inclusion of *Cheilanthes poeppigiana* and *C. hieronymi* in the genus *Gaga*, obtaining sequences of *matK* for both species. A morphological study was also carried out to establish similarities and differences of the two analyzed species with those assigned to *Gaga*.

Materials & Methods

Morphological analysis

For the morphological analysis, *Cheilanthes hieronymi* and *C. poeppigiana* plus *C. micropteris* and *Gaga marginata* specimens housed in G, HAS, ICN, K, LP, LPB, MERL, NY, P, PACA, SI, and US (*Index Herbariorum* <http://sweetgum.nybg.org/ih/>) were examined. (Appendix 1).

The following characters considered diagnostic in *Cheilanthes* (Tryon 1990, Ponce 1994, Morbelli & Michelena 1989, Morbelli & Ponce 1997, Li *et al.* 2012) were studied for comparative analysis: petiole length in relation to the total length of the frond, petiole cross section, outline of the lamina, rachis cross section, presence/absence of laminar wings in the rachis, presence/absence of indument, forms the apex of the veins, degree of modification of the margin, pseudoindusia shape, size and number of spores, sculpture and wall structure of the spores.

Molecular phylogeny analysis

Sequences of *matK* and *rbcL* belonging to *Cheilanthes hieronymi* and *C. poeppigiana* were obtained and analyzed along with 15 species included in the phylogeny of *Gaga* proposed by Li *et al.* (2012). Details of taxa analyzed and GenBank accession numbers are available in Appendix 2.

DNA extraction, amplification and sequencing: Total genomic DNA was extracted from the silica dried leaves with cetyl-trimethylammonium bromide protocol (Doyle & Doyle 1990). Amplification of *matK* and *rbcL*, were performed using primers proposed by Kuo *et al.* (2011) and (Gastony & Rollo 1995) respectively. PCR reactions were performed in 25 µL final volumes with 50–100 ng of template DNA, 0.2 µM of each primer, 25 µM dNTP, 5 mM MgCl₂ 1× buffer and 0.3 units of Taq polymerase from Invitrogen Life Technologies (Brazil). PCR was carried out using the following parameters: 1 cycle of 94°C for 5 min, 39 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. Automated sequencing was performed by Macrogen, Inc. (Seoul, Korea). The sequence alignment was performed manually using BioEdit ver. 5.0.9 (Hall 1999).

Data analysis: We analyzed both the combined matrix and the *matK* and *rbcL* matrixes separately. Maximum parsimony analyses were performed using TNT ver. 1.1 (Goloboff *et al.* 2008). All characters were equally weighted,

treated as unordered, and gaps were scored as missing data. The searches involved 1,000 replicates, each of which generated a Wagner tree using a random addition sequence of taxa from the data matrix, swapping the initial tree with TBR (tree bisection and reconnection) and retaining a maximum of 10 trees in each replicate. Subsequently, all optimal trees were swapped using TBR, holding a maximum of 20,000 trees. A strict consensus tree was generated from the most parsimonious trees. Branch supports were estimated using bootstrap (Felsenstein 1985) with a total of 10,000 replicates. Each replicate was analyzed using 10 Wagner trees as starting point followed by TBR branchswapping, saving only one tree per replicate. The combined data matrix and the analysis performed can be found in TreeBase (Study Accession URL <http://purl.org/phylo/treebase/phylows/study/TB2:S18355>).

Results

Morphological analysis

The states of morphological characters with taxonomic value are summarized in Table 1.

TABLE 1. Morphological structures potentially informative in the analyzed cheilanthsoids.

	<i>Cheilanthes microptera</i>	<i>Cheilanthes hieronymi</i>	<i>Cheilanthes poeppigiana</i>	<i>Gaga marginata</i>
Petiole length / frond length	-1/4	2/3	1/2	+2/3
Petiole section	terete	terete	semiterete-sulcate	semiterete-sulcate
Petiole fragility (fresh)	firm	brittle	firm	firm
Petiole color	brown	blackish brown	reddish brown	reddish-brown to blackish brown
Lamina outline	linear	deltate to pentagonal	deltate	pentagonal
Rachis section	terete	sulcate-alate	sulcate-alate	sulcate-alate
Segments outline	ovate	ovate, elliptic	triangular	linear, elliptic
Petiolule	free short axis	laminar short axis	adnate	laminar short axis
Indument	glandular trichomes	glabrous	glabrous	glabrous
Vein apices	slightly enlarged	enlarged	enlarged	enlarged
Pseudoindusium	subcontinue-lobate	continue	continue	continue-decurrent
Spore numbers	32	32	64	32
Spore sizes (μm)	52–70; 66–80	41–52	50–60; 55–70	64–87
Spore sculptures	reticulate-cristate	reticulate-cristate	rugate	anastomosing ridged
Perispore structure	3 layered	3 layered	3 layered	3 layered
Perispore outer layer	closed	closed	closed	closed

Cheilanthes hieronymi and *C. poeppigiana* have no clear synapomorphies to separate them from *Gaga*. Both species and *G. marginata* are similar in forms of lamina, rachis, and segments, and the absence of indument (Table 1, Fig. 1). Also, the three species bear enlarged vein endings forming hydathodes (Fig. 1), a feature that is absent in other cheilanthsoids genera such as *Argyrochosma*, *Myriopteris*, and *Notholaena*. The differences noted in the shape and tissues of the petiole (Hernández 1992; Hernández & Albornoz 2001) and the characteristics, size and numbers of the spores (Fig. 2) (Morbelli & Michelena 1989, Michelena, 1989; Morbelli & Ponce 1997) would indicate the need to further investigate these attributes, which may separate *Cheilanthes* s. s. from the remaining genera.

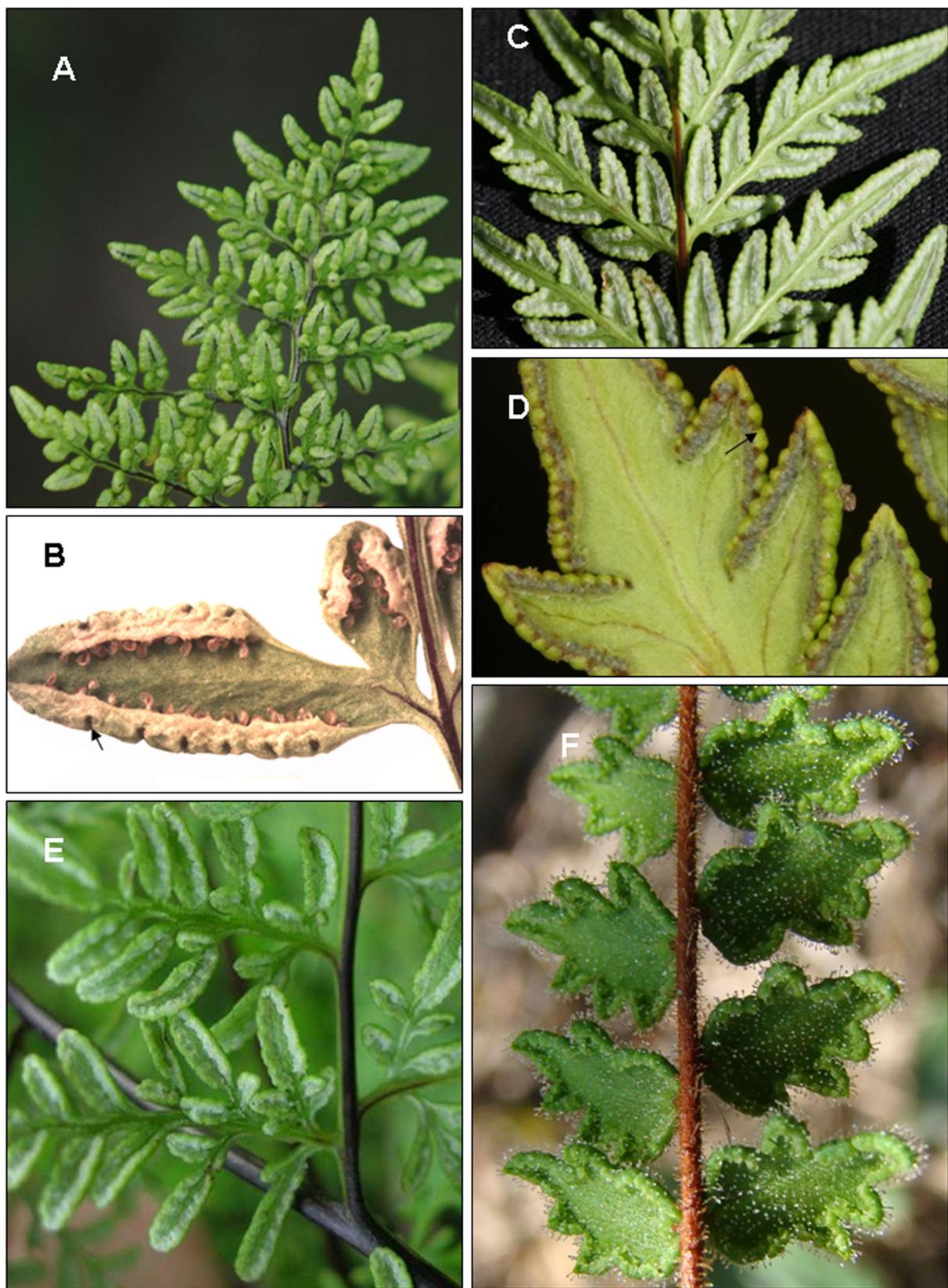


FIGURE 1. Morphology of *Cheilanthes* and *Gaga*. A–B: *Cheilanthes hieronymi*, A: lamina; B: ultimate segment, showing hydathode; C–D: *Cheilanthes poeppigiana* C: lamina; D: ultimate segment, showing hydathode; E: *Gaga marginata* lamina; F *Cheilanthes micropteris*, lamina.

Molecular phylogeny analysis

A total of 17 taxa were analyzed. The *matK* matrix has 1303 characters, 125 of which are informative; the analysis

of the matrix yielded two most parsimonious trees, 240 step-long ($C_i = 0.63$; $R_i = 0.75$). The *rbcL* matrix has 1267 characters, 51 of which are informative; the parsimony analysis resulted in three trees of 94 steps ($C_i = 0.58$; $R_i = 0.65$). Combined matrix showed a total of 176 informative characters and resulted in two trees of 691 step-long with $C_i = 0.75$ and $R_i = 0.64$. The strict consensus trees of the combined analysis (Fig. 3) and the *matK* consensus, were congruent, while in the *rbcL* consensus a basal polytomy was obtained and the genus *Gaga* could not be recovered as monophyletic.

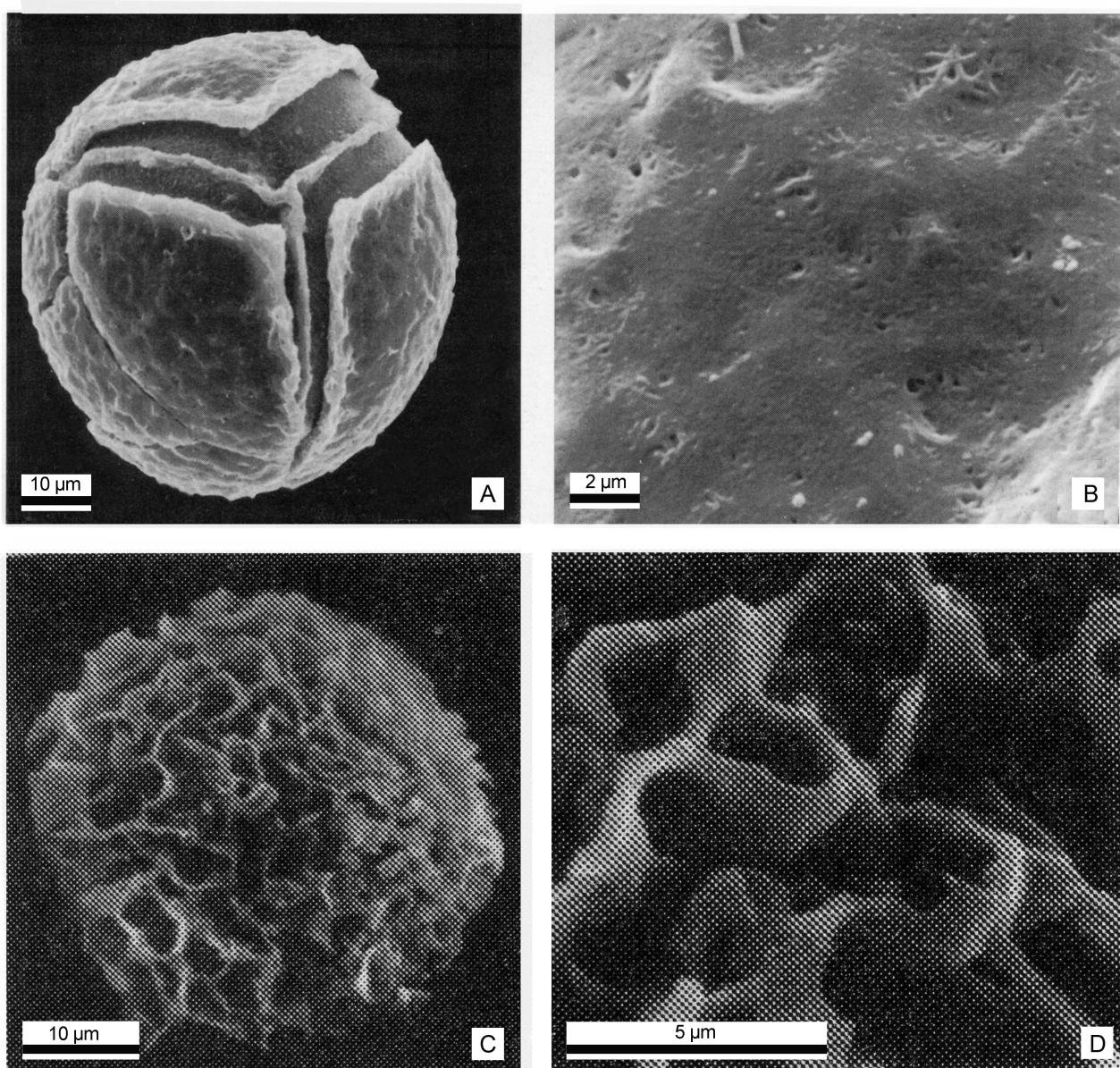


FIGURE 2. Spores sculpture. A–B: *Cheilanthes poeppigiana*, A: Spore in proximal view with partially detached perispore, B: detail of regulate perispore, finely reticulate and perforate; C–D: *Cheilanthes hieronymi*, C: Spore in distal view with cristate perispore, D: detail partly anastomosing ridges. (A–B, from Morbelli & Michelena, 1989; C–D, from Michelena, 1989).

Fig. 3 shows species assigned to *Gaga* grouped in a 100% supported clade, with *Aspidotis* as the sister genus; in concordance with Li *et al.* (2012). The two species tested in this study, *Cheilanthes hieronymi* and *C. poeppigiana*, appeared outside of the *Gaga* clade. *Cheilanthes poeppigiana* is shown in an unresolved position along with the remaining analyzed species, while *C. hieronymi* appears related to *C. micropteris*. The molecular synapomorphy of “GAGA” in positions 598–601 of *matK*, is not present in the two species analyzed: *Cheilanthes hieronymi* and *C. micropteris* showed “GCAG”, and *C. poeppigiana* “GAGG”.

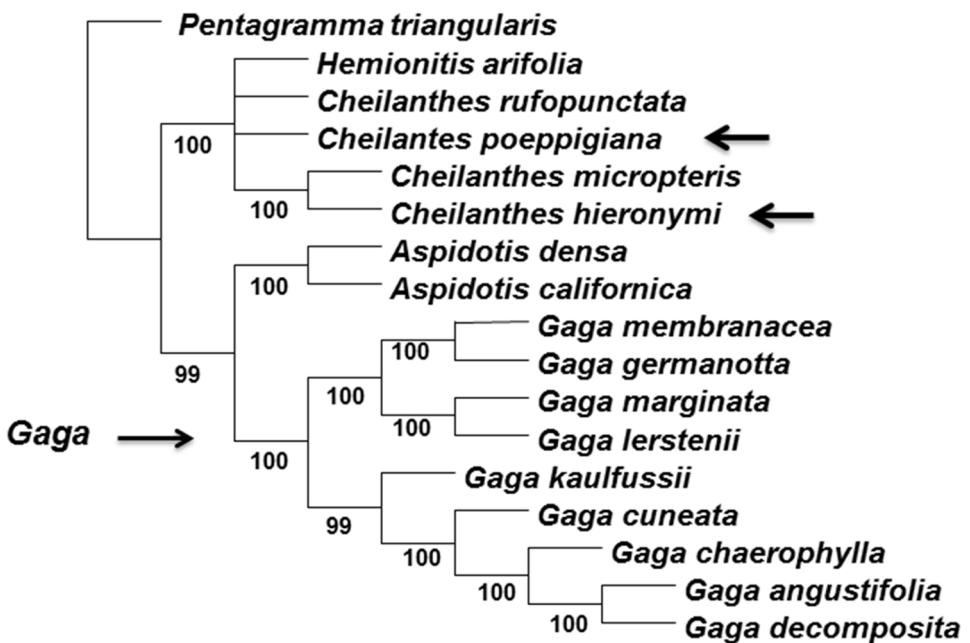


FIGURE 3. Strict consensus of the two most parsimonious trees obtained from the combined dataset (*matK + rbcL*). Bootstrap values are shown below branches.

Discussion

The taxa studied in this work, *Cheilanthes hieronymi* and *C. poeppigiana* are endemic to South America and historically presumed belonging to the group *C. marginata*, although they were not included in the analysis of Li *et al.* (2012). *Cheilanthes poeppigiana*, grows widely through the Central and Southern Andes, while *Cheilanthes hieronymi* lives in a few sites of the Southeastern Mountain Ranges in Southern Brazil and Uruguay, and in Tandilia, Ventania, La Pampa and Cuyo Isolated Massifs in Argentina.

Here we show that the morphological similarities among *C. hieronymi*, *C. poeppigiana*, and *C. marginata* are due to homoplasy. *Cheilanthes hieronymi* is closely related to the type of the genus, *C. micropteris*. Although the two species have a common geographical distribution, they are morphologically very distinct (Table 1, Fig. 1). According to our results, *C. hieronymi* may remain in *Cheilanthes* s. s.

Regarding to *Cheilanthes poeppigiana*, this species is located outside the *Gaga* and *Cheilanthes* s. s. clades (Fig. 3). These results are consistent with the topology of the phylogeny obtained using *rbcL* and *trnL-trnF* genes (Ponce & Scataglini in prep.) in which *C. poeppigiana* is included in the clade of Asian *Cheilanthes* (Zhang *et al.* 2007), called *Aleuritopteris* in Eiserhardt *et al.* (2011), sister of the *Aspidotis* and *Gaga* clades (data not shown).

Finally, we consider that the petiole morpho-anatomy and perispore features should be further investigate as diagnostic characters, since they may separate *Cheilanthes* s. s. from *Gaga* which are currently only separated by molecular differences.

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APPENDIX 1. Specimens examined: Species, locality, voucher number (herbarium)

Cheilanthes hieronymi—ARGENTINA. **Buenos Aires:** Tornquist, Sierra de La Ventana, *H. H. Bartlett* 20046 (US); Sierra de La Ventana, *J.H. Hunziker* 593 (G), Abra de la Ventana, *Pichi Sermolli & Bizzarri* 7321 (K); Sierra de la Ventana, *H. A. Fabris* 3701 (LP). **Mendoza:** San Carlos, Quebrada de Alvarado, *G. Covas* 10595 (MERL). URUGUAY. **Tacuarembó:** Valle Edén, *W. Herter* 1228 (G, NY, P, US); Rivera, frontera del Brasil, Sierra de Santana del Livramento, 250 m, 20-23/IX/1937, *W. Herter* 1228b (G, NY). BRAZIL. **Rio Grande do Sul,** Guaritas, *C. Steffens* 195 (PACA).

Cheilanthes micropteris—ARGENTINA. **Buenos Aires:** Sierra de la venta, *Ponce* 3 (LP). **Catamarca:** Capital, Río del Valle, *Castillón* 719 (US). **Córdoba:** Calamuchita, Río Santa Rosa, *L. Zavala* 7 (SI); **Corrientes:** Santo Tomé, Estancia Garruchos, *M. Pedersen* 990 (US). **Entre Ríos:** Colón, Humaitá, *R. Guaglianone et al.* 513 (SI); **San Luis:** El Volcán, *R. Kiesling et al.* 4717 (SI). **La Pampa:** Lihuel Calel, II-1975, *R. Fidler s.n.* (SI). **Mendoza:** San Rafael, Los Coroneles y Sierra La Chilena, *Roig* 9573 (MERL). **Misiones:** Candelaria, a Cerro Corá, *Morrone et al.* 1766 (SI); **San Juan:** Sierra de Valle Fértil, Los Bretes, *R. Kiesling et al.* 4964 (SI). **Santiago del Estero:** Choya, Sierra de

Guasayán, E. A. *Ulibarri* 1679 (SI). **Tucumán:** Tafí, Los Chuscos, S. *Venturi* 6454 (US). **Salta:** Cafayate, E. I. Meza Torres *et al.* 412 (SI). BOLIVIA. **Cochabamba:** Mizque, Julpe 20 km S de Totora, P. Labiak *et al.* 2878 (LPB, SI). BRAZIL. **Mato Grosso do Sul:** Borda da Serra de Amambaí, *Hatschbach et al.* 58787 (K, MBM). **Santa Catarina:** Bom Jardim da Serra, *Hatschbach et al.* 78157 (MBM); **Rio Grande do Sul:** Rosario do Sul, Cerro do Caverá, 3/V/1986, R. *Wasum* 1523 (US). PARAGUAY. **Cordillera de Altos,** K. *Fiebrig* 199 (US). URUGUAY. **Tacuarembó,** *Gibert* 1345 (K); **Treinta y Tres:** Arroyo, Carajá del Olimar, *Rosengurt* 4837 (US). **Rivera:** Libramento, G. *Herter* 882 a (US). **Paysandú:** Río Uruguay y arroyo Chapicuy, *Rosengurt B* 3272 (US). **Minas:** Cerro Arequita, *Rosengurt B* 2160 (US).

Cheilanthes poeppigiana—ARGENTINA. **Catamarca:** Andalgalá, *Joergensen* 1491 (SI). **Jujuy:** Lagunas de Yala a Termas de Reyes, F.O. Zuloaga & N. B. Deginani 3430 (SI); **Salta:** Quebrada del Río Toro y del Río Blanco, I-1923, J. C. Vattuone 3 (SI); Santa Victoria a Yaví, F. O. Zuloaga *et al.* 10726 (SI); **Tucumán:** Tafí del Valle, La Ventanita, *Castillón* 43 (K, P, SI); Chilicasta, Las Pavas, Cerro Bayo, S. *Venturi* 3040 (SI), La Ciénaga, 2500 m, 14-IV-1904, M. Lillo 2940 (SI), Trancas, Segunda Cuesta, S. *Venturi* 4191 (SI); BOLIVIA. **Cochabamba:** Mizque, NW of Mizque on road to Arani, J. *Wood* 17145 (LPB); road Quillacollo to Morochata, N. *Ritter & J. Wood* 2814 (LPB); **Chuquisaca:** Tarabuco, ca. 30 km hacia Zudañez, S. *Beck* 6242 (LPB). **Tarija:** Arce, al W de Abra Blanca, cerca de Rejará, 2940 m, 17-XII-1987, S. *Beck & M. Liberman* 16016 (SI). ECUADOR. **Cotopaxi:** Quevedo-Latacunga, *Holm-Nielsen* 3096 (K); **Loja:** Sacapalca-Pampa Bonita, G.P. *Lewis et al.* 3282 (K). PERÚ. **Cuzco:** Urubamba, Machu Pichu, D. *Stafford* 1055 (K); **Tumbes:** Zarumilla, El Cauchó, Matapalo, J. *Schunke* 3031 (US).

Gaga marginata—ARGENTINA. **Jujuy:** Yala, Cerros, *Burkart et al.* 11363 (K); **Salta:** Santa Victoria, E.R. *de la Sota* 4117 (US); **Catamarca:** Andalgalá, 27/XI/1946, B. *Sparre* 940 (K); **Tucumán:** Tafí del Valle, A. *Burkart* 5543 (SI). BOLIVIA. **La Paz:** Larecaja, Sorata, G. *Mandon* 1571 (G, K, P); **Cochabamba:** Ayopaya, J.R.I *Wood et al.* 18439 (LPB); **Tarija:** Carichi Mayu – León Cancha, *Gerold* 107 (LPB). COLOMBIA. **Cauca:** Timbío, C. E. *Acosta-Arteaga* 933 (MBM); **Bogotá:** Tunja, C. E. *Acosta-Arteaga* 815 (G, MBM); **Cundinamarca:** Cordillera Oriental, Muchindote Valley, M. L. *Grant* 9572 (US); **Magdalena:** Páramos of the Sierra Nevada de Santa Marta, W. *Seifriz* 424 (US). ECUADOR. **Azuay:** Nudo de Portete, W.H. *Camp E2145* (K, US). **Cañar:** north Rio de Cañar, W.H. *Camp E-2888* (US); **Chimborazo:** Puela, *Sodiro s. n.* (P); **Loja:** southwest of Gonzanama, D. S. *Correll E395* (US); **Pichincha:** Cordillera Occidental, Quito, Quinta Miraflores, J. A. *Ewan* 16474 (US); Km 10 Nono – Tandayapa, 2320 m, 14-V-1981, C&P *Dodson & W&P Clendenin* 10750 (US). PERÚ. **Lima:** Mahuacana a Tambo, A. *Weberbauer* 108 (G); **Cuzco:** Machu-Pichu, R. M. & A. F. *Tryon* 5401 (US); **La Libertad:** Huamachuco, D. S. *Correll & E. E. Smith P935* (US); **Ayacucho:** between Huanta and Río Apurimac, E.P. *Killip & A. C. Smith* 22234 (US); **Cajamarca:** Contumazá, A. *Sagástegui et al.* 14946 (US); **Pasco:** Valle del Paucartambo, F. L. *Herrera* 1601 (US). VENEZUELA. **Trujillo:** Boconó, Páramo de Guirigay, L. *Ruiz-Terán & M. López-Figueiras* 13110 (US); **Mérida:** Sierra del Norte, H. *Humbert* 26718 (P).

APPENDIX 2.

List of taxa used in the molecular analysis and GenBank accession numbers (*matK*, *rbcL*). The taxa listed were used previously in the analysis of Li *et al.* (2012). The voucher information and collection sites of sequences newly generated in this study are also provided.

Aspidotis densa (Brack.) Lellinger JX313625, JX313526; *A. californica* (Hook.) Nutt. ex Copel. JX313624, JX313525; **C. hieronymi** Herter KT932744, KT932742, *Arana s.n.* (SI), **Sierra de La Ventana, Buenos Aires, Argentina;** *Cheilanthes micropteris* Sw. JX313627, EF452145; **C. poeppigiana** Kuhn KT932743, KT932741, *Ponce 88* (SI) **Tafí del Valle, Tucumán, Argentina;** *C. rufopunctata* Rosenst. JX313628, JX313528; *Gaga angustifolia* (Kunth) F.W. Li & Windham JN647724, JN647782; *G. chaerophylla* (M. Martens & Galeotti) F.W. Li & Windham JN647733, JN647791; *Gaga cuneata* (Kaulf. ex Link) F.W. Li & Windham JX313632, JX313532; *G. decomposita* (M. Martens & Galeotti) F.W. Li & Windham JN647741, JN647798; *G. germanotta* JX313646, JX313546; *G. kaulfussii* (Kunze) F.W. Li & Windham JN647753, JQ855930; *G. lerstenii* (Mickel & Beitel) F.W. Li & Windham JX313636, JX313536; *G. marginata* (Kunth) F.W. Li & Windham JX313637, JN647812; *G. membranacea* (Davenp.) F.W. Li & Windham JN647764, JX313538; *Hemionitis arifolia* (Burm. f.) T. Moore JX313629, JX313529; *Pentagramma triangularis* (Kaulf.) Yatsk., Windham & E. Wollenw. JX313631, JX313531.