DARWINIANA
NUEVA SERIE
www.ojs.darwin.edu.ar
ISSN 0011-6793 impresa - ISSN 1850-1699 en línea

DARWINIANA, nueva serie 13(1): 153-166. 2025
Versión de registro, efectivamente publicada el 26 de junio de 2025
DOI: 10.14522/darwiniana.2025.131.1258

A NEW FERN HYBRID FROM NORTHWESTERN ARGENTINA: *PLEOPELTIS* × *ALBORNOZEANA* (POLYPODIACEAE)

Marcelo D. Arana[1,2,3], M. Gabriela Romagnoli[4], Aldo Rubén Andrada[5], Valeria de los Ángeles Páez[5] & Ana Inés Ruiz[6]

[1]*Instituto Criptogámico, Área Botánica, Fundación Miguel Lillo, Miguel Lillo 251, T4000JFE San Miguel de Tucumán, Argentina;* mdarana@lillo.org.ar (author for correspondence).
[2]*Departamento de Ciencias Naturales, Facultad de Ciencias Exactas, Físico-Químicas y Naturales, Instituto de Ciencias de la Tierra, Biodiversidad y Ambiente (ICBIA, UNRC-CONICET), Universidad Nacional de Río Cuarto, Ruta 36 km 601, X5804ZAB, Río Cuarto, Córdoba, Argentina.*
[3]*IUCN SSC Temperate South American Plants Specialist Group, Species Survival Commission (SSC).*
[4]*Facultad Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán. Miguel Lillo 205, T4000JFE San Miguel de Tucumán, Argentina.*
[5]*Instituto de Genética y Microbiología, Área Biología Integrativa, Fundación Miguel Lillo, Miguel Lillo 251, T4000JFE San Miguel de Tucumán, Argentina.*
[6]*Instituto de Morfología Vegetal, Área Botánica, Fundación Miguel Lillo, Miguel Lillo 251, T4000JFE San Miguel de Tucumán, Argentina.*

Abstract. Arana, M. D.; M. G. Romagnoli, A. R. Andrada, V. de los Á. Paez & A. I. Ruiz. 2025. A new fern hybrid from Northwestern Argentina: *Pleopeltis* × *albornozeana* (Polypodiaceae). *Darwiniana*, nueva serie 13(1): 153-166.

A new hybrid in the genus *Pleopeltis*, distributed in the Yungas of the northwestern, Argentinean Andes is described and illustrated. This is the first *Pleopeltis* hybrid recorded in Argentina and continental Southern Cone and the third of all South America. The hybrid co-occurs with its two putative progenitors, *Pleopeltis macrocarpa* and *Pleopeltis tweediana*, and is readily recognizable by its rhizome scales of different shapes (ovate, ovate-apiculate to lanceolate and long caudate vs. ovate-acuminate to oblong-acuminate in *P. tweediana*, and lanceolate to caudate in *P. macrocarpa*), also the intermediate lamina dissection (pinnate at the base and pinnatifid towards the apex vs. pinnatifid, sometimes with lobed pinnae in *P. tweediana*, and simple in *P. macrocarpa*), irregularly lobed pinnae and also its cryptochlorophyllous spores. Morphological and cytogenetic relationship with the putative parents and with other similar species is discussed. *Pleopeltis* × *albornozeana* is the first taxa of *Pleopeltis* from Argentina in which cryptochlorophyllous spores are reported. It is noteworthy that in the hybrid, the smallest chromosomes have the shortest lengths reported to date.

Keywords. Cryptochlorophyll; Ferns; Polypodiales; South America; Taxonomy.

Resumen. Arana, M. D.; M. G. Romagnoli, A. R. Andrada, V. de los Á. Paez & A. I. Ruiz. 2025. Un nuevo helecho híbrido para el Noroeste de Argentina: *Pleopeltis* × *albornozeana* (Polypodiaceae). *Darwiniana*, nueva serie 13(1): 153-166.

Se describe e ilustra un nuevo híbrido en el género *Pleopeltis*, cuya distribución abarca las Yungas del Noroeste de los Andes argentinos. Este es el primer híbrido de *Pleopeltis* registrado para Argentina y para el Cono Sur continental, y el tercero para Sudamérica. El híbrido coexiste con sus dos progenitores putativos, *Pleopeltis macrocarpa* y *Pleopeltis tweediana*, y es fácilmente reconocible por sus escamas rizomáticas, de diferentes formas (ovadas, ovado-apiculadas a lanceoladas y largamente caudadas vs. ovado-acuminadas a oblongo-acuminadas en *P. tweediana*, y lanceoladas a caudadas en *P. macrocarpa*), además por la disección intermedia de la lámina de las frondes (pinnada en la base y pinnatifida hacia el ápice vs. pinnatifida, a veces con pinnas lobuladas en *P. tweediana*, y simple en *P. macrocarpa*), las pinnas irregularmente lobadas y además por sus esporas criptoclorofílicas.

Original recibido el 25 de abril de 2025, aceptado el 13 de junio de 2025
Editor Asociado: Fernando Biganzoli

Se discuten las relaciones morfológicas y citogenéticas con los parentales putativos y otras especies similares. *Pleopeltis* × *albornozeana* es el primer taxón de *Pleopeltis* de Argentina en el que se reportan esporas criptoclorofílicas. Es de destacar que, en el híbrido, los cromosomas más pequeños tienen las longitudes más cortas reportadas hasta la fecha.

Palabras clave. Criptoclorofila; Helechos; Polypodiales, Sudamérica; Taxonomía.

INTRODUCTION

The importance of hybridization in speciation, especially in disturbed or novel habitats, has long been recognized (Anderson & Stebbins, 1954). Among ferns, over 1200 hybrids have been reported, presumably because ferns have fewer reproductive barriers to hybridization than Angiosperms (Smith, 1972; Barrington et al., 1989; Knobloch, 1996; Ranker & Sundue, 2015). The survival of hybrids is associated with availability of disturbance-created habitat conditions intermediate between those of the progenitors (Folk et al., 2013), and the potential for hybridization between closely related species increases when both taxa have higher similarity in their ecological niches and have sympatric distributions (Andújar et al., 2014; Zhang et al., 2018).

The family Polypodiaceae is notable for being one of the richest, most diverse, and abundant groups of ferns in tropical and subtropical forests (Schneider et al., 2004, PPG I, 2016). The diversification of Neotropical Polypodiaceae may have happened in the later Cenozoic as indicated by occurrences in the Californian Miocene (Kvacek et al., 2004) and divergence time estimates indicating the Polypodiaceae are not older than the Eocene (Schneider et al., 2004). The lineage currently comprises 65 genera and approximately 1655 species (PPG I, 2016). One of the genera, *Pleopeltis* Humb. & Bonpl. ex Willd. is monophyletic and comprises more than 90 species, mainly in the New World, but with two species and one hybrid in Africa, India, and Sri Lanka (Smith & Tejero-Díez, 2014). The species of *Pleopeltis* have special ecological preferences for forest canopy in the temperate sub-humid and humid zones of the Neotropics (Wolf & Flamenco-S., 2006), where scaly blades, poikilohydrous character, and bifacial anatomy of laminae in some species are obviously advantageous (Moran, 2004; Sánchez González, 2008; Dubuisson et al., 2009; Smith & Tejero-Díez, 2014). American xeric habitats also harbour several *Pleopeltis* species, as the case of the Prepuna (South America) and southern Mexico (Central America), where there are several species, many of them endemic, adapted to the seasonal dry habitats (Arana et al., 2024), mainly owing to a dense cover of epidermal indument, either hairs or scales, particularly on the abaxial side of the lamina (Hietz, 2010; Sprunt et al., 2011).

In Polypodiaceae, hybridization is dynamic and frequent, and one of the principal process of speciation and adaptation to epiphytism (Wagner & Wagner, 1975; Hooper & Haufler, 1997; Haufler et al., 2000), particularly in *Pleopeltis*, lineage where numerous hybrids have been described, mainly in Central America (Otto et al., 2009; Smith & Tejero-Díez, 2014; Cerón-Carpio et al., 2017; Smith et al., 2018).

In Argentina, with the recent described *P. glandulosa* Arana, Bulacio & Slanis, *Pleopeltis* comprises nine taxa (Arana et al., 2024), distributed mainly in the Neotropical area of the country. Surprisingly, there is no hybrid of *Pleopeltis* registered for the flora of continental Southern Cone. Smith et al. (2018) mentioned *Pleopeltis* × *cuspidata* (Desv.) Boudrie, Cremers & Viane (as *Pleopeltis* × *leucospora* (Klotzsch) T. Moore) for Southern Brazil, but in the taxonomic treatment of *Pleopeltis* for Brazil (De Souza & Salino, 2021) is not mentioned. Accurate taxonomic identification is essential to estimate the biodiversity and constitutes the basis to carry out anatomical and biochemical analysis, as well as ecological, biogeographical and evolutionary studies. Therefore, this work aims to describe the new hybrid *Pleopeltis* × *albornozeana*, including a detailed analysis of the diagnostic morphological, palynological, and cytological traits of this taxon. Additionally, information on distribution and habitat is provided.

MATERIALS AND METHODS

In order to obtain information about the habitat and habit of the putative hybrid and the potential parents, field observations in several localities representing the Yungas biogeographical province in Argentina during 2013-2025 were carried out and at least five plants representing all taxa of *Pleopeltis* were collected and preserved with usual techniques. Photographs of the habitat and the plants were taken "in situ" by the former author. The specimens were deposited in herbarium LIL (Thiers, 2025). Fresh and herbarium samples to compare the characteristics of the new hybrid with the putative parents and related taxa were used. The analysed characteristics were rhizome habit, scales of rhizome (shape, length, margins and apex), lamina division, shape, indument and margin, venation and presence of hydathodes. Also, if the sporangia and spores were well-formed or malformed was studied. Specimens from CORD, CTES, JUA, LIL, LP, RB, RCVC and SI herbaria were consulted. We also examined specimens online, through the websites of IBODA (http://www2.darwin.edu.ar/), SpeciesLink (http://www.splink.org.br/) and Tropicos (http://tropicos.org), including types, mainly from JSTOR (https://www.jstor.org/). Also, specific bibliography was consulted (Cerón-Carpio et al., 2017; Lagoria et al., 2018; Smith et al., 2018).

Descriptions of general morphological characters follow Lellinger (2002). Rhizome and frond scales, and spores were mounted in 20% glycerin without prior treatment. Frond laminae were treated with KOH 10%, stained with astra blue to observe the venation pattern (D'Ambroggio de Argüeso, 1986). The analysed characteristics of spores were colour, shape in polar and equatorial view, laesura type and perispore ornamentation, and compared with the available descriptions (Giudice et al., 2004). Observations were made with a stereoscopic microscope (Olympus SZX7, Olympus Co., Tokyo, Japan), light microscope (Carl Zeiss, Axiostar Plus, Göttingen, Germany), fluorescence microscopes (Optika-02493, Model B-383LD, Ponteranica, Italy, and Olympus BX43, Tokyo, Japan), and photographs were taken with an Olympus Q colour-5 camera (5 mp, Ontario, Canada). The microscopic slides used in this study are stored in the Instituto de Morfología Vegetal, Fundación Miguel Lillo.

Chromosome counting

The rootlets were pre-treated with 8-hydroxyquinoline for a period of six hours at room temperature, then fixed in farmer's solution (ethyl alcohol - acetic acid 3:1) for 24 hours and kept in 70% ethyl alcohol until use (Sharma & Sharma, 1965). To soften the material, it was subjected to acid hydrolysis in 1N HCl for 20 minutes at 60 °C, then rinsed with distilled water, stained with basic fuscin for 20 minutes, and mounted with a drop of 45% acetic acid. Chromosome counts were performed on 10 cells in mitotic metaphase. The preparations were observed under an Olympus BX43F light microscope (Tokyo, Japan) and microphotographs were taken with an Olympus Qcolor5 camera (5 mp, Ontario, Canada). The measurement of total chromosome lengths was conducted utilising the MicroMeasure 3.3 software (Reeves, 2001).

RESULTS

Pleopeltis × albornozeana Arana & Romagnoli, **hybr. nov**. (= *P. tweediana* (Hook.) A. R. Sm. × *P. macrocarpa* (Bory ex Willd.) Kaulf.). TYPE: ARGENTINA. **Tucumán.** Depto. Monteros, Río Los Sosa, 27°02'54.5''S, 65°40'01.6''W, 1065 m a.s.l., 5-XII-2023, *G. Romagnoli, P. Albornoz & M. Arana 29* (Holotype, LIL 618341). Figs. 1-4.

Diagnosis. hybrid between *Pleopeltis tweediana* (Hook.) A.R. Sm. and *P. macrocarpa* (Bory ex Willd.) Kaulf., as proposed putative parentals, with intermediate characters. It is characterized by having rhizomes slender, long creeping, rhizome scales orbiculate, ovate, lanceolate and long caudate, concolorous (orbiculate and ovate scales) and bicolorous (lanceolate to long caudate) intermingled, with glandular papillae at the apex and sometimes on margins; fronds distant, with stipes (and rachis) green, lamina lanceolate to triangular-lanceolate, 1-pinnate at the base, pinnatifid and gradually tapering towards the apex; basal pinnae and medial segments with (1-)2-3 pairs of long lobo-crenate segments; medial and apical segments with lobo-crenate margins; scales scattered on both surfaces, orbicular to ovate-apiculate, centre obscure brown to black, margin pale brown; margins dentate, fimbriate at base; venation free to partially areolate, without include veinlets; sori rounded, naked.

Plants epiphytic (Figs. 1A and 2A); rhizomes slender, long-creeping (Fig. 2B), scaly; scales peltate, concolorous to bicolorous, clathrate or not, comose or glabrous, orbiculate, ovate (Fig. 3A) to lanceolate (Fig. 3B) and long caudate (Fig. 3C); margins entire (Fig. 3A-C), sometimes denticulate or papillose, fimbriate or erose, with glandular apical cell at the apex and sometimes on margins (Fig. 3A-C). Fronds monomorphic, distant; stipes ¼ to ½ the length of the lamina (Fig. 1A, 2A), with or without wings, green, scaly; scales peltate, bicolorous, clathrate, lanceolate, margin erose to dentate, teeth bipapillate, with glandular papillae at the apex and sometimes on margins (Fig. 3D); laminae lanceolate to triangular-lanceolate, 1-pinnate at the base, pinnatifid towards the apex, with last segments lobulate, particularly the basal pinnae and medial segments, basal pinnae and medial segments with (1-)2-3 pairs of long lobo-crenate segments; medial and apical segments linear to oblong, with lobo-crenate margins, irregularly scaly (Fig. 2E), sparsely scaly near midvein (Fig. 2F) to densely scaly on lobes (Fig. 2G); scales peltate, orbiculate to ovate-apiculate, margin erose to dentate, teeth bipapillate, with glandular papillae at the apex and sometimes on margins (Fig. 3E

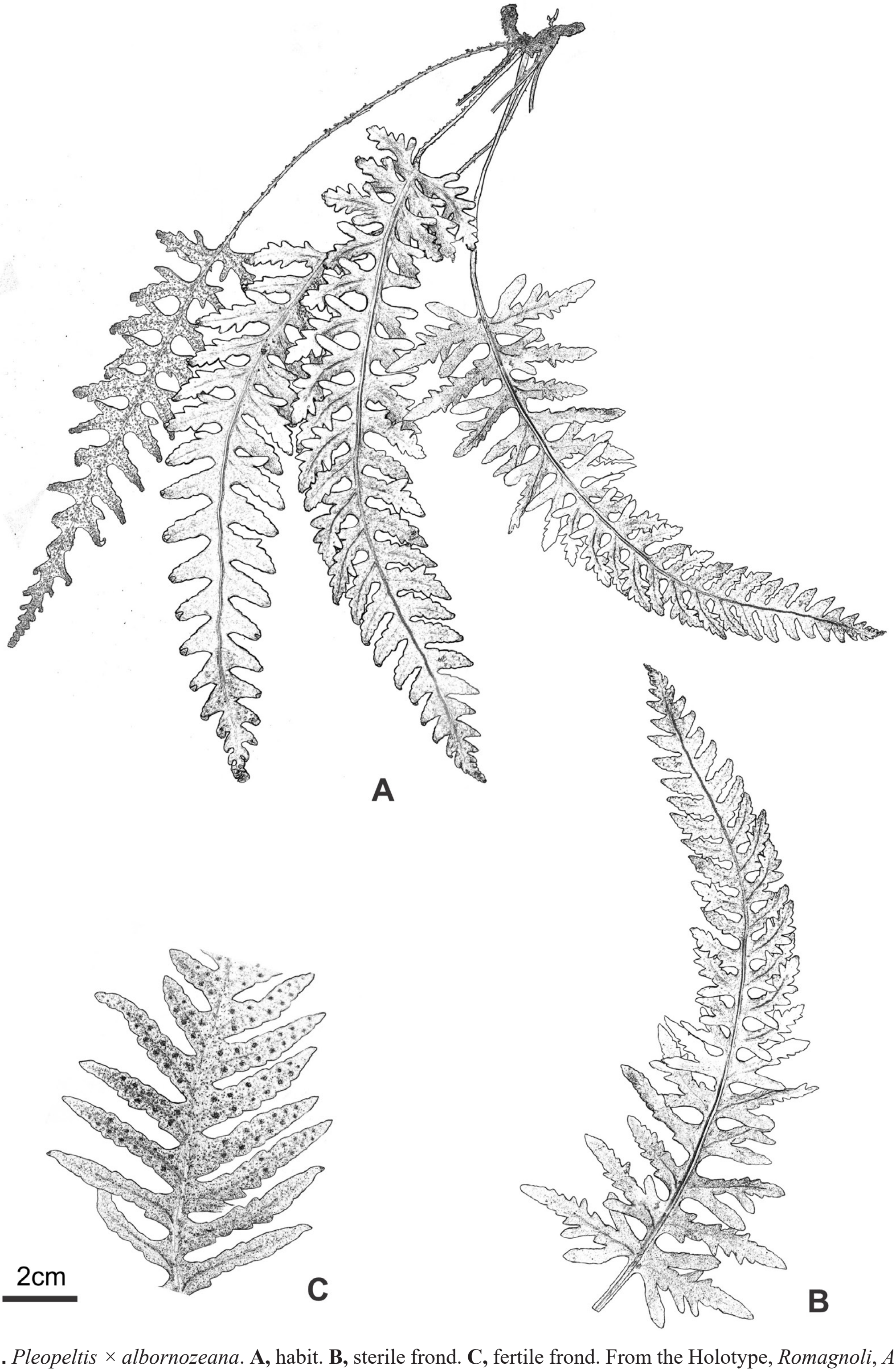

Fig. 1. *Pleopeltis* × *albornozeana*. **A,** habit. **B,** sterile frond. **C,** fertile frond. From the Holotype, *Romagnoli*, *Albornoz* & *Arana* 29 (LIL).

Fig. 2. *Pleopeltis* × *albornozeana*. **A,** habit. **B,** rhizome. **C,** detail of sterile frond. **D,** detail of fertile frond, red arrows indicate sori. **E-G,** distribution of the scales in laminae. **E,** irregularly scaly. **F,** sparsely scaly near midvein. **G,** densely scaly on lobes. From the Holotype, *Romagnoli*, *Albornoz* & *Arana* 29 (LIL).

and inset); segments with or without auricle; margin crenate with some lobes; venation free or partially anastomosing without included veinlets (Fig. 3F, G); hydathodes present (Fig. 3G). Sori rounded, medial, (Figs. 1C and 2D), glabrous or with peltate scales near the margins; sporangia glabrous, sometimes malformed (Fig. 4A-C); spores many irregularly formed, and typically show reduced or entirely absent cytoplasm, causing them to appear collapsed and translucent (Figs. 4E-K), well-formed spores yellow, ellipsoidal, 45-68 µm, monolete, generally verrucose, low to high verrucose (Fig. 4G, K), sometimes papillate, baculate and with sparse to dense globules, cryptochlorophyllous (Figs. 4D, F). The chromosome number of sporophytic metaphase cells is 2n = 70 (Fig. 6A). The length of the chromosomes ranges from 1.05-4.45 µm (Fig. 6B).

Etimology. The hybrid is dedicated in honour to Dr. Patricia Liliana Albornoz (FML-LIL), who made many remarkable generous and disinterested contributions to our knowledge of the morphology, anatomy and mycorrhizal associations of Argentinian ferns and lycophytes.

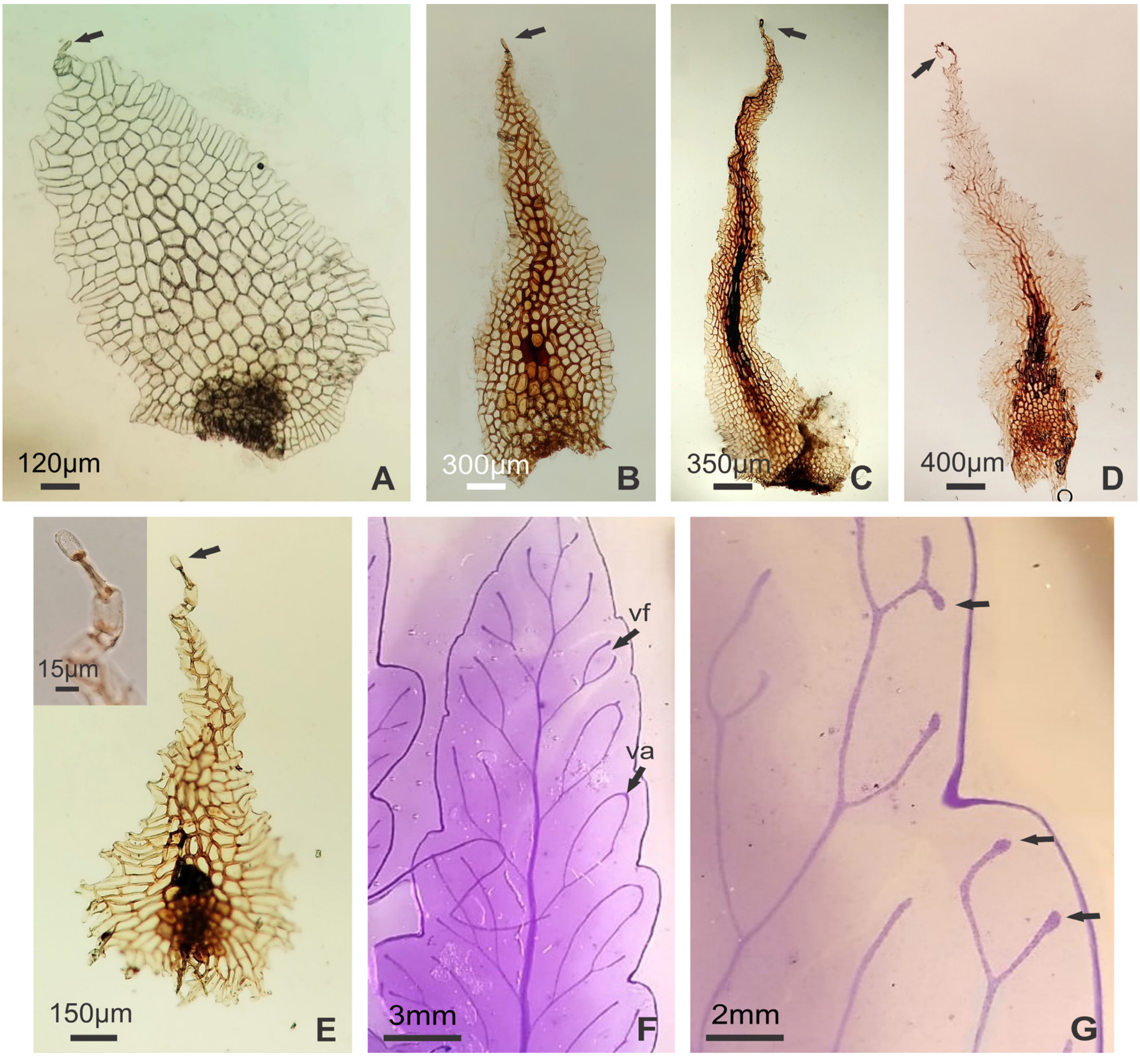

Fig. 3. *Pleopeltis* × *albornozeana*. **A-C,** rhizome scales with glandular apical cell. **A,** ovate scale. **B,** lanceolate scale. **C,** long caudate scale. **D,** petiole scale with glandular apical cell. **E,** laminae scale with glandular apical cell. **F,** venation. **G,** venation and hydathodes. Abbreviations: **va,** venation anastomosing; **vf,** venation free. **A-E,** arrows indicate apical gland. In **G** arrows indicate hydathodes. From the Holotype, *Romagnoli*, *Albornoz* & *Arana* 29 (LIL).

Distribution and habitat. This hybrid is known only from two localities of North-western Argentina. *P.* × *albornozeana* is growing in humid montane forests of Tucumán province, in habitats of the Yungas biogeographic province, growing epiphytically on *Blepharocalyx salicifolius* (Kunth) O. Berg ("horco molle"), Myrtaceae, *Tipuana tipu* (Benth.) Kuntze, Fabaceae, two typical tree species from Yungas (Arana et al., 2021), and also on *Salix humboldtiana* Willd. ("sauce criollo"), Salicaceae, near yunguean watercourses. Despite numerous field trips and the study of hundreds of herbarium specimens in Argentina we have been unable to find additional records of this hybrid, but it likely occurs elsewhere, as both putative progenitors grow together throughout Yungas.

Additional specimen examined (Paratypes): ARGENTINA. **Tucumán.** Depto. Capital: Parque 9 de julio, epífito sobre tipa, 9-IV-2024, *M. Arana & M. Catania 7381* (LIL 618342). Depto. Lules, Quebrada de Lules, 26°54'06.8"S 65°22'14.5"W, epífito sobre sauce criollo, 15-IV-2025, *M. Arana, G. Romagnoli & V. Paez 7405* (LIL).

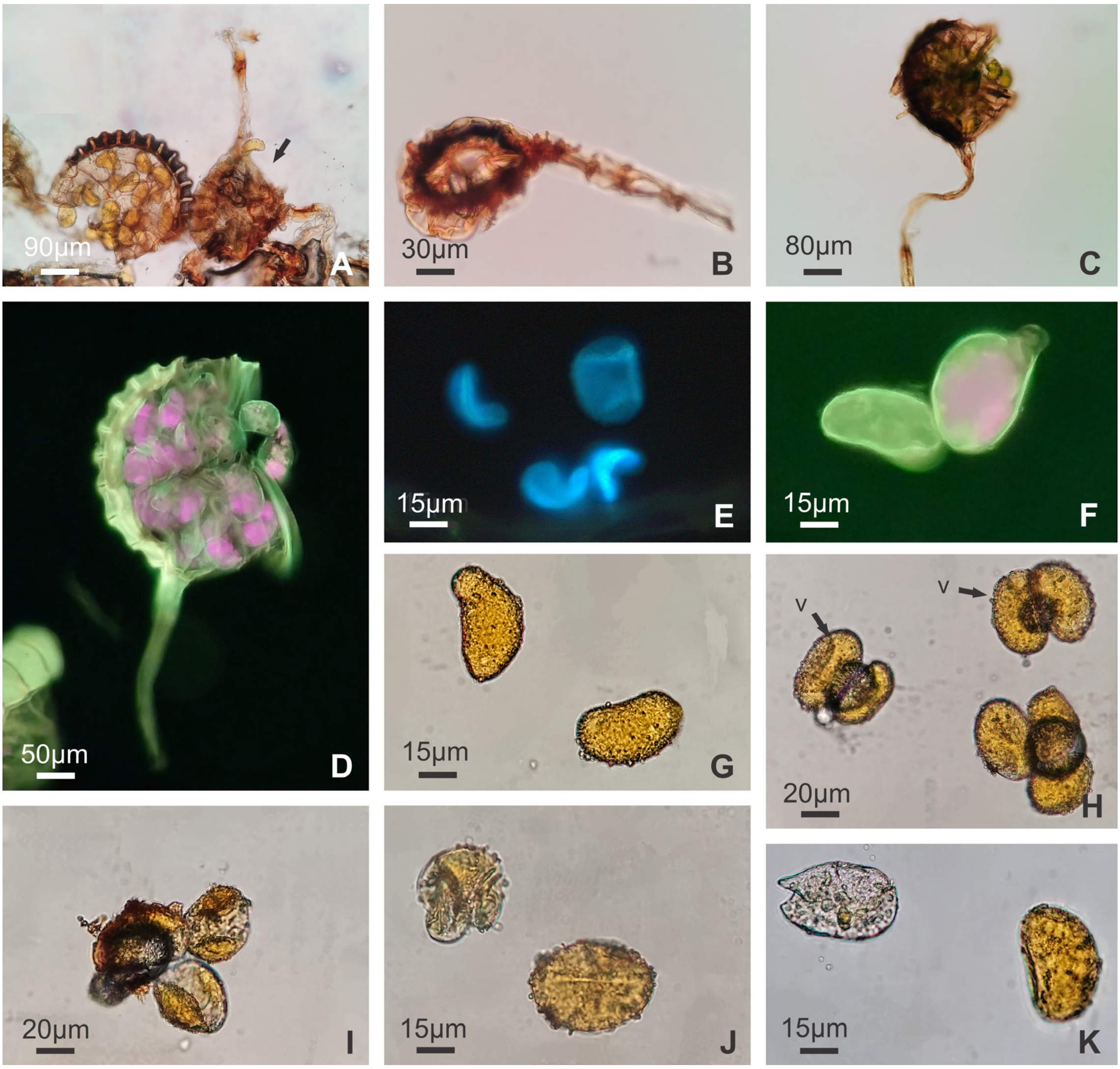

Fig. 4. *Pleopeltis* × *albornozeana*. **A-C,** malformed sporangia. **D,** sporangia with cryptochlorophyllous spores (fluorescence light microscopy). **E,** spores without cellular content (epifluorescence microscopy). **F,** cryptochlorophyllous spores (fluorescence microscopy). **G-K,** verrucose spores, many irregularly formed. Abbreviations: v, verrucae. From the Holotype, *Romagnoli*, *Albornoz* & *Arana* 29 (LIL).

DISCUSSIONS AND CONCLUSIONS

The existence of hybrids in nature is of considerable floristic, ecological and evolutionary importance (Tseng et al., 2024). About 10-30% of multicellular animal and plant species hybridize regularly in sympatry (Mallet, 2005), which might contribute to adaptive divergence between populations, and it also result in the generation of new populations of mixed ancestry that remain distinct from both parental taxa (Mallet, 2007; Abbott et al., 2010). Several studies have shown that potential for hybridization between closely related taxa increases when both taxa have higher similarity in their ecological niches (Andújar et al., 2014; Rueda et al., 2021), similar habitats and they have sympatric distributions (Liao et al., 2015; Zhang et al., 2018). Hybridization is common in ferns (Barrington et al., 1989), thought to have fewer reproductive barriers to hybridization than angiosperms (Smith, 1972; Ranker & Sundue, 2015), over 1200 instances of inter- and intrageneric hybrids have been reported, and is thought to be one of the major processes in their evolution (Knobloch, 1996; Sigel, 2016). Closely related species tend to hybridize more often, in particular, species in rapidly diversifying adaptive radiations may be particularly prone to hybridization (Price & Bouvier, 2002; Seehausen, 2004; Gourbiere & Mallet, 2010). One example is the very modern (not older than the Eocene) and highly diverse fern family Polypodiaceae (Kvacek et al., 2004; Schneider et al., 2004).

By combining field observations, studies of meiotic chromosome behaviour, as well as surveys of macro- and micro-morphological features using living and preserved specimens, new species have been discovered and the reticulate patterns of hybridization and polyploidy have been elucidated (Haufler & Windham, 1991). The discovery of a hybrid in *Pleopeltis* is usually based at first sight on the presence of

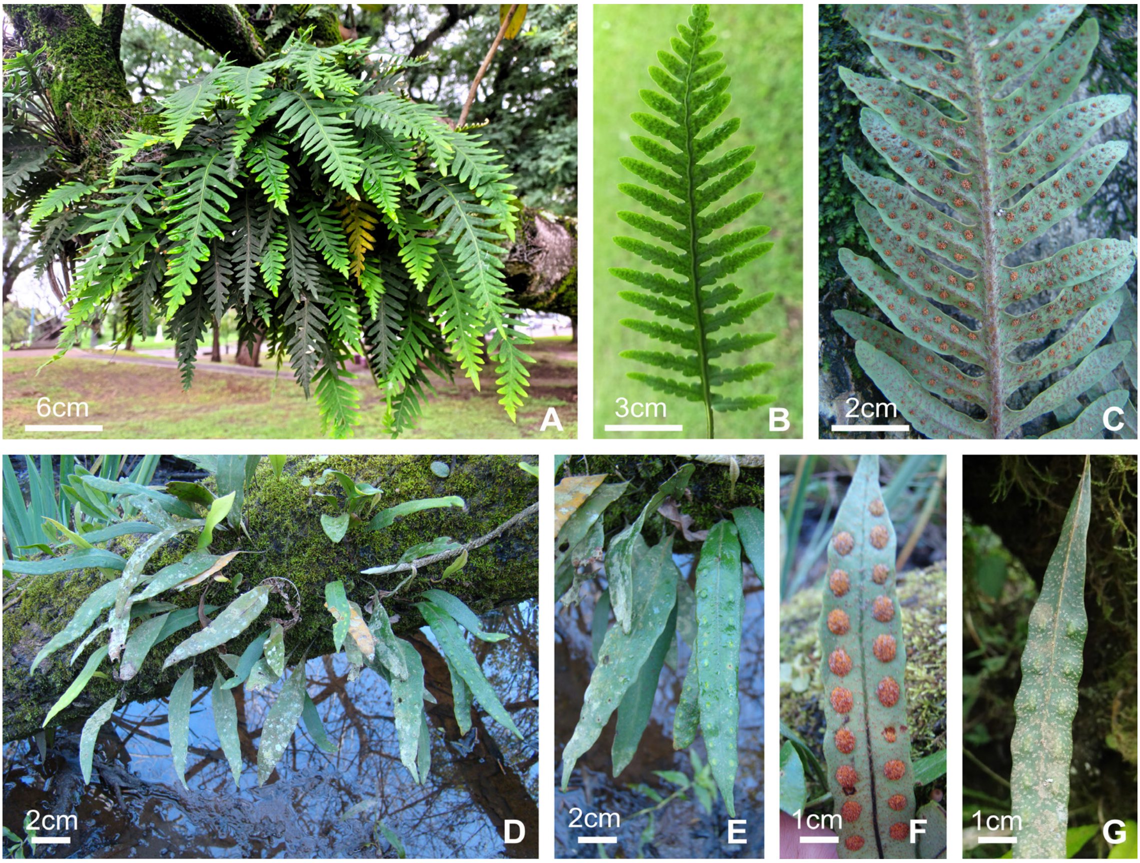

Fig. 5. *Pleopeltis tweediana*. **A,** habit and habitat. **B,** lamina showing division and crenate margins. **C,** detail of fertile frond in abaxial view showing sori position and indument. *Pleopeltis macrocarpa***. D,** habit and habitat. **E-G,** details of fertile fronds. **E,** adaxial side. **F,** abaxial side. **G,** detail of adaxial side showing margins and indument. Photos **A-F**, M Arana, **G**, D. Gorrer.

anomalous fronds (irregular growth or lobing). According to Cerón Carpio et al. (2017) and Sorojsrisom et al. (2023), in several cases, these hybrids are known from one or a few collections (as the case of *P.* × *albornozeana*), but they are so distinct morphologically that their hybrid origins are readily evident, even at first glance. Spores from specimens of hybrid origin tend to display high variability in size and shapes (Taylor et al., 1985; Wagner et al., 1986), and the presence of at least 75% spores exhibiting reduced, absent, or collapsed cytoplasm have been documented in fern hybrids (Wagner et al., 1986; Quintanilla & Escudero, 2006; Ekrt & Koutecky, 2016), as observed in *P.* × *albornozeana* (Fig. 4E), even at the tetrad level (Fig. 3J, K), this also could support the conclusion that *P.* × *albornozeana* is infertile, occasional hybrid and probably incapable of reproducing sexually itself (Wagner & Chen, 1965; Wagner et al., 1986). The apparently normal spores of *P.* × *albornozeana* have similar shape, colour and ornamentation (Table 1) compared to *P. tweediana* and *P. macrocarpa* (described in Giudice et al., 2004).

In Yungas, *P. macrocarpa* and *P. tweediana* share very similar habit (Fig 5A, D), habitats, and have sympatric distribution, so hybridization is possible. Hybrids appear to be relatively common in *Pleopeltis*, sometimes between intrageneric groups exhibiting extreme morphological, disparate characters, such as those observed in the simple-lamina "Pleopeltis macrocarpa group" and any group with pinnatifid or pinnate fronds (Smith & Tejero-Díez, 2014; Cerón Carpio et al., 2017; Smith et al., 2018). The hybrid *Pleopeltis* × *cuspidata* (Desv.) Boudrie, Cremers & Viane (Cremers et al., 2022) is widespread in the Neotropics (Hispaniola; Costa Rica; Colombia to Peru), and Wagner & Wagner (1975) presented evidence that this is a hybrid between *Pleopeltis macrocarpa*, a simple-bladed species (Fig. 5D-G), and *Pleopeltis thyssanolepis* A. Braun ex Klotzsch, a pinnatifid species (Smith et al., 2018).

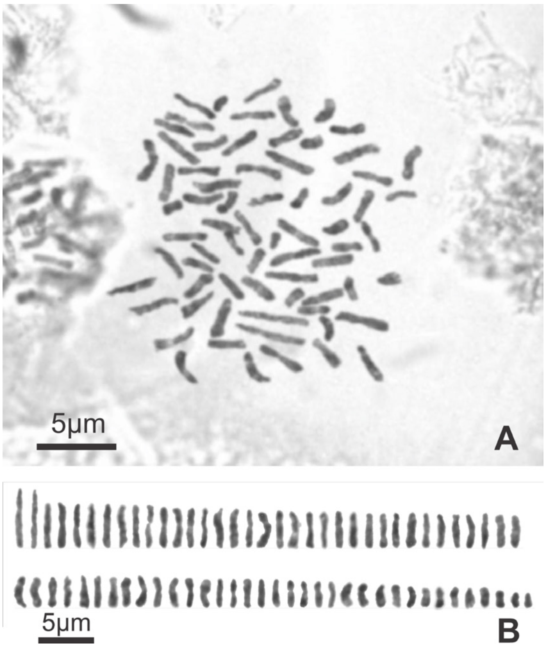

Fig. 6. *Pleopeltis* × *albornozeana*. **A,** mitotic metaphase. **B,** metaphase karyogram shown in A. **A,** From the Holotype, *Romagnoli*, *Albornoz* & *Arana* 29 (LIL). **B,** From the Paratype *Arana & Catania 7381* (LIL).

In light of the aforementioned evidence, it is hypothesised that the probable parents of the hybrid are *P. tweediana* and *P. macrocarpa*. *Pleopeltis tweediana* is a very common species, widespread in Northwest Argentina and shares the pinnatifid, scaly lamina with evident crenate margins (Fig. 5B, C) with *P.* × *albornozeana*. Furthermore, the presence of glandular papillae on the scales of *P.* × *albornozeana* is a character shared with the sympatric *P. macrocarpa* (Lagoria et al., 2018). The only other registered species in which glands are present on scales, at least in Argentine flora, is *P. glandulosa* Arana, Bulacio & Slanis, but the latter inhabits the Prepuna, a completely different biogeographical environment (Arana et al., 2024).

The importance of hybridization in speciation in novel lineages, especially in disturbed or novel habitats, has long been recognized (Stebbins, 1940, 1950; Anderson & Stebbins, 1954; Price & Bouvier, 2002; Seehausen, 2004; Gourbiere & Mallet, 2010; Sorojsrisom et al., 2023). This could be related to the environments in which *P.* × *albornozeana* was found, where the natural landscape has been transformed by urban development, but some native tree species are represented among the park trees. It is precisely in these native species trees that the hybrid was found growing epiphytically. The type localities of *P.* × *albornozeana* highlight the importance of close observation of ferns from both, transformed landscapes, where the natural vegetation has been almost completely replaced by human-made urban environments, or allegedly well-collected areas. The same situation as occurred with other fern hybrids (Sorojsrisom et al., 2023).

Hybridization might result in the generation of new populations of mixed ancestry (Mallet, 2007; Abbott et al., 2010). These new populations may be sexual or asexual, homoploid or polyploid. Hybridization leading to a new taxon, distinct from both parent species (but with no increase in ploidy), is called homoploid hybrid speciation (Mallet, 2007; Mavarez & Linarez, 2008; Abbott et al., 2010), as the case of the diploid

Table 1. Comparative table of morphological and palynological characters between the hybrid *Pleopeltis* x *albornozeana* and the potential parental species.

	P. tweediana	*P. x albornozeana*	*P. macrocarpa*
Rhizome	long-creeping	short-creeping	long-creeping
Scales of rhizome	ovate-acuminate to oblong-acuminate	ovate, ovate-apiculate to lanceolate and long caudate	lanceolate to caudate
Length of rhizome scales (mm)	1.5-2.5	1.3-3.8	1.5-3.5
Margin of rhizome scales	without glandular papillae	with glandular papillae	with glandular papillae
Apex of rhizome scales	without apical glandular papillae	with apical glandular papillae	with apical glandular papillae
Lamina	herbaceous	herbaceous	coriaceous
Division of the lamina	pinnatifid	pinnate at the base and pinnatifid towards the apex, with last segments lobulate	simple
Lobes of lamina	simple	pinnatifid	absent
Lamina margin	crenate	crenate, repand to almost sinuate	entire to repand
Venation	free to partially areolate and evident	partially areolate, without include veinlets and partially evident	areolate and not evident
Hidatodes	absent	present	present
Distribution of lamina scales	homogeneous	heterogeneous	homogeneous
Sporangia	normal	mainly malformed	normal
Spores	normal	mainly malformed	normal
Spores ornamentations	verrucate, with low verrucae, and globules	verrucose to papillate, baculate with sparse to dense globules	verrucate, with few globules
Average equatorial spore size (µm)	69.6	well formed: 56.5 malformed: 36.4	81.6

P. × *albornozeana* (Fig. 4). Schwartsburd et al. (2020) suggested that combinations of sporophyte morphology, palynology, chromosome counts and chloroplast DNA sequences, have the potential to unambiguously reveal diploid hybrids. The homoploid hybrids are derived from hybridization between normal, reduced gametes and have ploidy levels identical to their progenitors (Sigel, 2016). The *P.* × *albornozeana* sporophyte chromosome number 2n = 70 demonstrates its diploid nature, as evidenced by the fundamental chromosome number x = 35 (Hopper, 1995). Previous studies have documented divergent basic numbers for *Pleopeltis*, including x = 34, 35, 36 and 37. Nevertheless, the majority of chromosome counts conducted on *Pleopeltis* species align with the number n = 35 bivalent and 2n = 70 chromosomes (Hopper, 1995; Evans, 1963; Smith & Mickel, 1977; Srivastava, 1985; Winkler et al., 2011). The chromosome numbers of the genus are indicative of the crucial role played by aneuploidy in the process of its evolution (Lewis, 1980). Although the chromosome lengths observed in this putative hybrid (1.05 µm to 4.45 µm) are consistent with the lengths observed in other ferns as the Pteridaceae *Argyrochosma flava* (Hook.) M.

Kessler & A. R. Sm. (2.4 µm to 5.02 µm, Windham & Yatskievych, 2003), and *Doryopteris triphylla* (Lam.) Christ (1.59 µm to 4.38 µm, Neira et al., 2017) and other Polypodiaceae (*Polypodium* ssp., 2.2 µm to 4.5 µm, Rodriguez et al., 2024). It is noteworthy that in the taxon analysed here, the smallest chromosomes have the shortest lengths reported to date.

Pleopeltis × *albornozeana* is the first taxa of *Pleopeltis* from Argentina in which cryptochlorophyllous spores are reported (Fig. 4D, F). These kinds of spores contain chlorophyll but appear nongreen to the naked eye or under a light microscope because chlorophyll is being covered by the perispore pigments (Sundue et al., 2011). Both putative parents were analysed and have not such type of spores (Table 1), which could indicate that aberrant status of the hybrid spores. Compared with species with nongreen spores, species with spores with chlorophyll have greater success in colonizing new habitats (Dassler & Farrar, 2001). That could be the case of *P.* × *albornozeana*, found in novel, anthropic habitats.

The discovery of *Pleopeltis* × *albornozeana* constitutes the first register of an Argentinian and also continental South American Cone hybrid within the genus. Another hybrid described for such area is *Pleopeltis* × *cerro-altoensis* Danton & Boudrie, a hybrid between *P. macrocarpa* and *Pleopeltis masafuerae* (Phil.) de la Sota, but endemic to Robinson Crusoe Island (Masatierra) in Juan Fernández Archipelago in Chile (Danton et al., 2015). In continental South America, *Pleopeltis* × *cuspidata* (Desv.) Boudrie, Cremers & Viane (Cremers et al., 2022) is also found, widespread in the Neotropical region, but mainly in Andean tropical biomes from Venezuela to Peru.

ACKNOWLEDGEMENTS

We are grateful to R. Delgado (Fundación Miguel Lillo, FML) for his technical assistance during field trips in Tucumán, to the scientific illustrator L. Bordón (Iconography section, FML) for her meticulous work, and Daniel Gorrer for facilitating photographs.

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