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Hidden and neglected taxa inside a collective taxon: taxonomic revision of *Woodsiaceae* in the Southern Cone of South America

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Abstract: *Woodsiaceae* is a monophyletic fern family comprising around 65 taxa that inhabit mainly mountainous areas of the northern hemisphere but also with numerous species in southern America and Africa. Recent molecular studies recognize two genera in the family: *Woodsia*, restricted to the northern hemisphere, and *Physematium*, present in Central and South America, Africa and East Asia. Traditionally, in South America the family has been considered to include a single species, *Woodsia montevidensis*, very variable morphologically, a treatment that underestimates the diversity of South American taxa. Therefore, we carried out a taxonomic review that included comparative analyses of morphological and palynological characters as well as distributional data. In the Southern Cone, *Physematium* is characterized by sori with saucer- or bowl-shaped lower indusia, splitting into 1–3 lobes in the mature sori. The taxa inhabit mountainous regions, between 200 m to more than 4000 m in altitude. Four species are recognized in the genus *Physematium* in the Southern Cone: one new species, *P. hieronymi*, and three that were previously treated as synonyms of *P. montevidense*, publishing here the corresponding new combinations. A key, descriptions, illustrations and distribution maps of the species are provided.

Keywords: cliff ferns, morphology, palynology, *Physematium*, South America, Southern Cone, taxonomy, *Woodsiaceae*

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Introduction

The family *Woodsiaceae* was validly published by Herter (1949) based on *Woodsieae* A. Gray. However, at that time, the system of Alston (1956) was the most used for the classification of ferns in South America, which subordinated the woodsioid group and others, such as the cystopteroids, into the family *Athyriaceae* (de la Sota 1967; 1977). Later, these groups were included in *Dryopteridaceae* by Tryon & Tryon (1982). That treatment divided the family into five tribes, with the tribe *Physematieae* including *Woodsia* R. Br. and the athyrioid genera (e.g. *Athyrium* Roth and *Diplazium* Sw.) as well as *Cystopteris* Bernh. and other small genera. The subsequent classification of ferns by Smith & al. (2006, 2008) resurrected *Woodsiaceae*, according to updated phylogenies based on morphological and molecular data, but with a broad circumscription that included *Athyriaceae* and *Cystopteridaceae*.

Only more recently have the woodsioid ferns been treated as a separate, monophyletic family based on the most recent molecular phylogenies (Rothfels & al. 2012; Shao & al. 2015; PPG I 2016). The species included in *Woodsiaceae* are plants predominantly lithophytic, with lamina 1-pinnate to bipinnatifid, elliptic-lanceolate to narrowly lanceolate, herbaceous or papery, frequently covered with articulate, pauci- to multicellular, glandular and simple trichomes, sometimes with capitate glands, and sori characterized by the unique inferior indusia, saucer-shaped or bowl-shaped or composed of multiple

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scale-like or filamentous segments, occasionally as a single globose or subglobose structure enclosing the sorus.

The generic circumscription within *Woodsiaceae* has been variable as well. *Woodsia* is a very difficult genus with respect to both systematics and understanding its evolutionary history. Before its recognition by Brown (1810), the taxa were included in the nakedly soriate group of ferns called *Acrostichum* by Linnaeus (1753). Swartz (1806) placed the type species in *Polypodium* L. because of its round sori. According to Brown (1964), the first researcher to notice the rather obscure inferior indusium of *Woodsia* was Schkuhr (1809), but he included it in the old "catch all" genus *Aspidium* Sw. It is interesting to note that Brown (1810) characterized *Woodsia* only by "involucrum membranaceum, apertum, lacero-multifidum, … capsulas includit pedicellatas, receptaculo communi elevato nullo" to differentiate it from *Alsophila* R. Br.

Most recent treatments have adopted a single broad genus *Woodsia* (sensu Rothfels & al. 2012; Larsson 2014; Shao & al. 2015; PPG I 2016) even though Shmakov (2003, 2015, 2018) recognized the segregation of seven genera on the basis of morphology (*Cheilanthopsis* Hieron., *Eriosoriopsis* (Kitag.) Ching & S. H. Wu, *Hymenocystis* C. A. Mey., *Physematium* Kaulf., *Protowoodsia* Ching, *Woodsia*, *Woodsiopsis* Shmakov), Most recently, phylogenetic reconstructions have revealed two strongly supported, monophyletic groups within the family *Woodsiaceae*, corresponding to two genera (Lu & al. 2020). These in turn can be subdivided into monophyletic subgenera, many of which predate previously described genera (Lu & al. 2020).

We here follow this classification, recognizing two genera in *Woodsiaceae*: *Physematium* (including *Cheilanthopsis*, *Hymenocystis*, *Protowoodsia* and *Woodsiopsis*) and *Woodsia* (including *Eriosoriopsis*). This treatment is supported by a divergence time of c. 45 Ma, morphology, chromosome numbers and geographical distribution (Lu & al. 2020). Also, it is marked by a remarkably deep split between a clade with about 37 holarctic species distributed in East Asia and circumboreal regions of the Old World (*Woodsia*), and a "Gondwanic" clade with 28–30 species distributed in America (mainly Central and South America), Asia and Africa including Madagascar (*Physematium*). This profound dichotomy is also supported by a groundplan-divergence analysis based on morphological characters (Wagner 1980).

Traditionally, the floristic works in South America, following Brown (1964), de la Sota (1977), Tryon & Tryon (1982) and Tryon & Stolze (1991) treated the genus *Woodsia* as represented by a single, highly morphologically variable species, *Woodsia montevidensis* (Spreng.) Hieron., ranging from Venezuela and Colombia to central and southern Argentina and southern Brazil. This was followed by the treatment of *Woodsiaceae* for countries such as Argentina (Arana & Mynssen 2016), Bolivia (Kessler & Smith 2018), Brazil (Mynssen & Arana 2020+), Chile (Rodriguez & al. 2018) and Peru (Tryon & Stolze 1991).

New morphological studies on herbarium specimens and field work have shown us that treating all South American specimens in a highly morphologically variable species does not reflect the true diversity of the genus in South America, as previously noted by Arana & Mynssen (2016) and Arana & al. (2016). The latter have already lectotypified the names of six species with the intention of providing nomenclatural stability in the genus *Woodsia* (= *Physematium*) in South America (Arana & al. 2016).

In this work we provide a taxonomic revision of the species described for the Southern Cone that have remained cryptic and overlooked under the collective taxon "*Woodsia montevidensis*", verifying diagnostic features and re-evaluating the quality and interpretations of poorly applied morphological characters. In addition, we provide biogeographical extensions from new collections in the region.

Material and methods

For taxonomic treatment and to resolve the delimitation of taxa and their synonyms, as well as for the application of the correct name of each species, we applied the taxonomic species concept combined with the analysis of the overall distribution.

In this work only the names of *Physematium* (= *Woodsia*) species referred to the Southern Cone of South America were analysed. Although *Physematium* is distributed in South America from Venezuela to south-central Argentina, mainly along the Andean mountainous region, we have not been able to analyse with the same detail and number of specimens the taxa from northern South America as those studied for the south of the continent. Therefore, we prefer to be cautious and in this first contribution limit the review to the Southern Cone.

Images of about 55 type specimens available in JSTOR Global Plants (https://plants.jstor.org/) were consulted for all taxon names cited from the study area. Type specimens are cited with their barcodes, if available, unless an accession number is specified. In addition, specimens from the following herbaria were examined and determined: B, BA, BAB, BM, CONC, CORD, CTES, HB, JUA, K, L, LE, LIL, LP, LZ, MA, MERL, MO, MVFA, NY, OXF, P, PR, PRC, QCA, QCNE, R, RB, RCVC, RIOC, S, SGO, SI, US and W (acronyms according to Thiers 2024+). In cases in which the specimens could be reliably identified, we also used the repositories SpeciesLink (http://splink.cria.org.br/), Pteridophyte Collections Consortium (https://www.pteridoportal.org/) and Global Biodiversity Information Facility (https://www.gbif.org/) in order to better document the geographical distribution of species.

The distribution maps of the species of *Physematium* from the Southern Cone were constructed using QGIS v. 2.16.3 (QGIS Development Team 2009), with shape-

Fig. 1. Habit of *Physematium* from the Southern Cone. – A: *P. hieronymi*; B: *P. pallidum*; C: *P. jujuiense*; D: *P. montevidense*. – Photographs by: Marcelo Arana (A, D); Javian Gallardo (B); Alberto Slanis (C).

files provided by Romano (2017), Arana & al. (2021) and Morrone & al. (2022), representing the biogeographic regionalization of the Neotropical and Andean regions and the South American Transition Zone proposed by Morrone (2017, 2018) and Morrone & Ebach (2022). This biogeographic scheme, based on areas of endemism, is very useful for characterizing the typical environments where *Physematium* species live.

Fieldwork and the recent collections were undertaken in the Andean and sub-Andean mountains of central and northern Argentina, covering most of the type localities of previously described species in *Woodsia*. Herbarium

specimens were deposited mainly in LIL and SI. To delimit the taxa and elaborate the key to the species present in the Southern Cone of South America, we carried out a comparative morphological analysis of sporophyte characters with stable and recognized diagnostic value. Some of them had not been used in previous revisions and are reflected in the molecular phylogenetic patterns (Sundue & Rothfels 2013; Shmakov 2015; Lu & al. 2020). The following characters were considered for this study: rhizome habit; type, colour and position of rhizome and stipe scales; colour and indumentum of stipes; lamina division, shape of pinnae and margin of pinnules or last segments; type and position of leaf indumentum; shape of indusium. Species distributions and habitats are based on herbarium label information and data obtained by field observations.

The spores were studied with a light microscope (LM) and a scanning electron microscope (SEM). For the LM analysis, the material was not subjected to any previous treatment. This is because abrasive processes such as acetolysis (Erdtman 1960) can generate distortions, e.g. rupture of the perispore and consequent increase in size, especially in spores with folds (Nayar & Devi 1964; Prada 1990; Gorrer & al. 2022). For the SEM analysis, the spores without treatment were placed on stubs with adhesive double-faced tape and coated with gold. The LM observations were made with a Leica DM500 with an incorporated Leica ICC50 digital camera at Laboratorio de Análisis Palinológicos, Facultad de Ciencias Agrarias, Universidad Nacional de Jujuy. The SEM observations were made with a SUPRA 55VP at Centro Integral de Microscopía Electrónica (CIME-CONICET-UNT). The spore characteristics analysed were: colour, shape, equatorial and polar diameters, laesura length, and ornamentation. Mean measurements were calculated from 20 spores in each sample. We used the terminology proposed by Tryon & Lugardon (1991), Lellinger (2002) and Punt & al. (2007) for the descriptions of the spores. Gametophyte characters and development were taken from Martinenco & al. (2023).

Results

Morphology

The species belonging to *Physematium* from the Southern Cone have monomorphic, polystichous fronds; rhizomes mainly suberect, extended or compact, scaly; stipes non-articulate with scales at base; laminae pinnate-pinnatifid, pinnate-pinnatisect or bipinnate, covered with pilose-glandular indumentum, hairs uniseriate, pauci- or multicellular, articulate, glandular; veins free, visible and widening at end. Sori dorsal along veins, subterminal or terminal, round, indusiate; soral receptacle flat; indusia inferior, subglobose or saucer-shaped to cup-shaped, margin glandular-ciliate, dividing into 1–3 strap-shaped, narrowed lobes as sorus matures.

For delimitation of the species inhabiting the Southern Cone, we found variation in the following characters to be informative (Table 1):

Rhizomes — suberect or decumbent, separated or spreading vs erect or suberect aggregated or compacted.

Rhizomatic and stipe scales — concolorous vs bicolorous; wide margin (several rows of cells wide) vs narrow margin (2 or 3 rows of cells wide); entire margin vs sparsely pilose or fimbriate margin.

Stipes — straw-coloured or stramineous vs dark brown or blackish; pilose vs glabrous; smooth vs scabrous; rigid vs brittle.

Lamina division — pinnate-pinnatifid vs pinnate-pinnatisect or bipinnate.

Rachises — pilose-glandular vs pilose-glandular + scattered scales.

Indument — uniseriate hairs, multicellular, jointed, with an acute, hyaline, glandular apical cell vs uniseriate, clavate hairs, paucicellular, with a yellowish, glandular apical cell.

Indusia — symmetric, globose or saucer-shaped, divided into 2 or 3 filamentous lobes vs asymmetric with 1 incised lobe.

Spores — monolete, plane-convex to convex in outline in equatorial view, elliptic to suborbicular in polar view; major equatorial diameter 32–59 μm (Table 2); exospore smooth; perispore folded-reticulate or consisting of reticles of threads; colour yellowish-brown to dark brown. In LM analysis, aborted and collapsed spores and broken perispore were observed in *Physematium hieronymi* (Fig. 4M–O). In SEM analysis, collapsed spores were also seen in *P. pallidum* and *P. hieronymi*, but this may be due to the vacuum applied to the sample, prior to gold plating.

Taxonomic treatment

Physematium Kaulf. in Flora 12: 341. 1829. – Type: *Physematium molle* Kaulf. in Flora 12: 341. 1829.

Morphological description — Plants small to medium-sized (up to 40 cm tall); usually lithophytic. Roots blackish, wiry, inserted radially. Rhizomes usually long-creeping or erect, bearing scales at apex, non-clathrate, brown to blackish-brown, centre usually sclerotic, margin entire to toothed. Fronds clustered, monomorphic, deciduous or sometimes evergreen; stipes stramineous or dark purple throughout, or proximally darkened, usually covered with scales and septate hairs, non-articulate, rigid or brittle. Lamina pinnate-pinnatifid or pinnate-pinnatisect to 2-pinnate-pinnatifid, elliptic-lanceolate to narrowly lanceolate, membranous to subcoriaceous, glabrous or frequently covered with articulate hairs, sometimes with glandular hairs or capitate glands. Veins free, pinnate, usually ending in enlarged hydathodes. Sori dorsal along veins, subterminal or terminal, round, indusiate; soral receptacle flat; indusia inferior, globose, sacciform or

Table 1. Comparison of diagnostic characters of the four species of *Physematium* occurring in the Southern Cone of South America.

		Physematium hieronymi	***P. jujuiense***	***P. montevidense***	***P. pallidum***
Rhizome	type	ascending to decumbent	ascending	ascending to decumbent	ascending
	growing type	paucicipital	multicipital	paucicipital	multicipital
Rhizomatic scales	form	narrowly triangular or triangular	narrowly triangular	ovate-triangular or triangular	linear or narrowly triangular
	colour	bicolorous	bicolorous	bicolorous and concolorous	bicolorous and concolorous
	centre/margin colour	dark brown/reddish or pale	dark brown/pale edge	brown to reddish/pale or hyaline	shiny blackish-brown/pale, very thin or absent
	centre type	sclerotic	sclerotic	partially sclerotic	sclerotic
	margin type	medium wide, entire or with spaced hairs	thin, entire	wide, with spaced fimbriae or hairs	thin, entire
	apex	largely attenuate, sinuate, capillary tip	sharp, attenuate	attenuate, capillary tip	sharp, attenuate
Stipes	phyllotaxis	laxly fasciculate	fasciculate, very approximate	laxly fasciculate	fasciculate, very compact
	colour	brown, base dark brown	brown, base blackish	pale brown	straw-coloured
	basal scales	narrowly triangular, bicolorous or concolorous	linear-lanceolate, bicolorous	ovate-lanceolate, bicolorous or concolorous	linear-ovate or linear-lanceolate, bicolorous
	consistency	firm	somewhat brittle	firm	brittle
Trichomes	types	simple and glandular	simple and glandular	simple and glandular	simple and glandular
		uniseriate, pauci- to multicellular	uniseriate, paucicellular	uniseriate, pauci- to multicellular	uniseriate, paucicellular
	colour	hyaline	hyaline	hyaline and yellowish glandular	hyaline
Laminae	form	linear or elliptic-lanceolate	elliptic-lanceolate	elliptic-lanceolate or ovate-lanceolate	elliptic-lanceolate
	division	pinnate-pinnatifid, pinnate-pinnatisect to bipinnate	pinnate-pinnatifid	pinnate-pinnatifid to bipinnate-pinnatifid	pinnate-pinnatifid
Segments	margin	crenate, dentate or bidentate	entire to crenate	crenate or bicrenate	undulate
	base	decurrent	adnate	adnate	adnate
Indusium	type	inconspicuous, fimbriate, margin glandular-pilose	1- or 2(or 3)-lobed, asymmetric, margin glandular-pilose	saucer split into 2 or 3 lobes, symmetric, margin glandular	saucer 2- or 3-lobed, symmetric, margin glandular

saucer-shaped to cup-shaped, margin ciliate, or indusia developed into strap-shaped or filamentous segments. Spores ellipsoid or somewhat spheric, monolete, non-chlorophyllous, yellowish, tan or brown, perispore folded, cristate or echinate. x = 38.

Distribution — A genus with three subgenera (*Physematium* subg. *Cheilanthopsis* (Hieron.) Li Bing Zhang & al., *P.* subg. *Physematium* and *P.* subg. *Woodsiopsis* (Shmakov) Li Bing Zhang & al.) and c. 30 species distributed in Asia, Africa, Madagascar and America, with at least six species in South America, four in the Southern Cone, with the highest diversity in Andean and Pampean mountainous habitats, reaching its southern distribution limit in the highlands of Río Negro, Argentina. All species inhabiting the Southern Cone belong to *P.* subg. *Physematium*.

Remarks — In *Physematium montevidense*, the germination pattern of the gametophyte corresponds to the *Vittaria*-type and the development is *Aspidium*-type. Gametangia appeared 30–40 days after spore germination. The sporophytes emerged near 3 months after spore sowing (Martinenco & al. 2023).

Key to the species of *Physematium* in the Southern Cone

1. Fronds gracile, pendulous; pinnae subremote to remote; last pinna segments (pinnules) toothed, with rounded to obtuse teeth; pinnule bases broadly decurrent to rachis, rachis becoming winged; spores reticulate, without folds . . . . . **1. *P. hieronymi***
– Fronds erect to patent; pinnae approximate to subremote; last segments (or pinnules) slightly to strongly crenulate or bicrenulate; pinnule bases of last segments or pinnules adnate or slightly decurrent to rachis; spores reticulate-folded, with conspicuous folds **2**
2. Stipes robust, 1.5–2 mm in diam., not brittle; stipe scales dull, concolorous or partly bicolorous, light brown, orange or reddish, triangular, broadly triangular or ovate-triangular, when bicolorous, with sclerotic, dark brown centre sections, and with broad, membranous margin, hyaline to light brown, with distant hairs or fimbriae on margin, apex attenuate with a terminal hair; indusium 3-lobed; spores yellowish, with numerous, small, complete and incomplete reticles . . . . . **3. *P. montevidense***
– Stipes thin, 0.5–1 mm in diam., notably brittle; stipe scales shiny, strongly bicolorous, dark brown to blackish, sclerotic, linear-triangular or subulate, with narrow or wide, membranous, pale brown, entire or sparsely pilose margin; indusium 1–3-lobed; spores brownish or yellowish, if yellowish, never with small reticles **3**
3. Plants more than 20 cm tall; stipes dark brown or dark purple to burgundy proximally, sometimes up to or through rachis; laminae pinnate-pinnatifid to almost bipinnate; pinnae proximate, triangular, acute apex, fertile ones usually with recurved margin; indusia with 1–3 strap-shaped lobes, usually 1 lobe more developed than others; spores yellowish with few and large, complete and incomplete reticles . . . . . **2. *P. jujuiense***
– Plants to 15 cm tall; stipes straw-coloured or straminеous, rarely darkened only very proximally; laminae pinnate; pinnae subremote, oblong or oblong-triangular, apex rounded, fertile ones usually with flat or slightly curved margin; indusia divided into 2 or 3 strap-shaped lobes at maturity; spores brownish with numerous and small, complete and incomplete reticles . . . . . **4. *P. pallidum***

1. *Physematium hieronymi* Ponce & Arana, **sp. nov.**
Holotype: Argentina, Jujuy, Depto. Dr. Manuel Belgrano, 9 km del desvío de la Ruta Nacional 9 camino a Tiraxi, selva con dominancia de *Myrtaceae* y *Junglandaceae*, 1600 m, 10 Dec 1998, *O. Morrone & al. 3208* (SI [accession no. 154134!]).

Diagnosis — *Physematium hieronymi* is similar to *P. montevidense* (Spreng.) Shmakov but differs by several characters: pendulous, gracile fronds (vs erect to patent); rhizomatic scales linear-triangular to narrowly lanceolate, strongly bicolorous, shiny, dark brown, totally sclerotic or with a very thin margin, blackish with castaneous to brown or reddish margin, margin entire, largely attenuate apex (vs ovate-lanceolate or triangular-lanceolate, concolorous, dull, light brown or orange becoming bicolorous, in this case with a central stripe partially to totally sclerotic, brown, margin membranous, broad (twice as wide as central stripe), fimbriate, apex ending with an apical hair); stipe scales narrowly triangular-filiform, shiny, bicolorous, dark brown at centre, sclerotic or light membranous (vs ovate-lanceolate, dull, concolorous, pale brown, orange or reddish, membranous); laminae bipinnate or bipinnate-pinnatisect, pinnules usually sharply toothed, base of pinnules broadly decurrent to rachis, rachis becoming winged (vs pinnate-pinnatifid, rarely bipinnate, pinnules slightly to strongly crenulate or bicrenulate, bases adnate to rachis); spores reticulate, without folds (vs spores reticulate-folded, with conspicuous folds).

Morphological description — *Plants* terrestrial, 30–50 cm tall. *Rhizomes* ascending, spreading, scaly, covered by persistent stipe bases; rhizomatic scales 2–3 × 0.2–0.4 mm, linear-triangular to narrowly lanceolate, strongly bicolorous, shiny, dark brown, totally sclerotic or with a very thin margin, blackish with castaneous to brown or reddish margin, margin entire, sometimes with scarce hairs, largely attenuate apex. *Fronds* fasciculate. *Stipes* very short, terete, 1.5–2 mm in diam., dark brown, of-

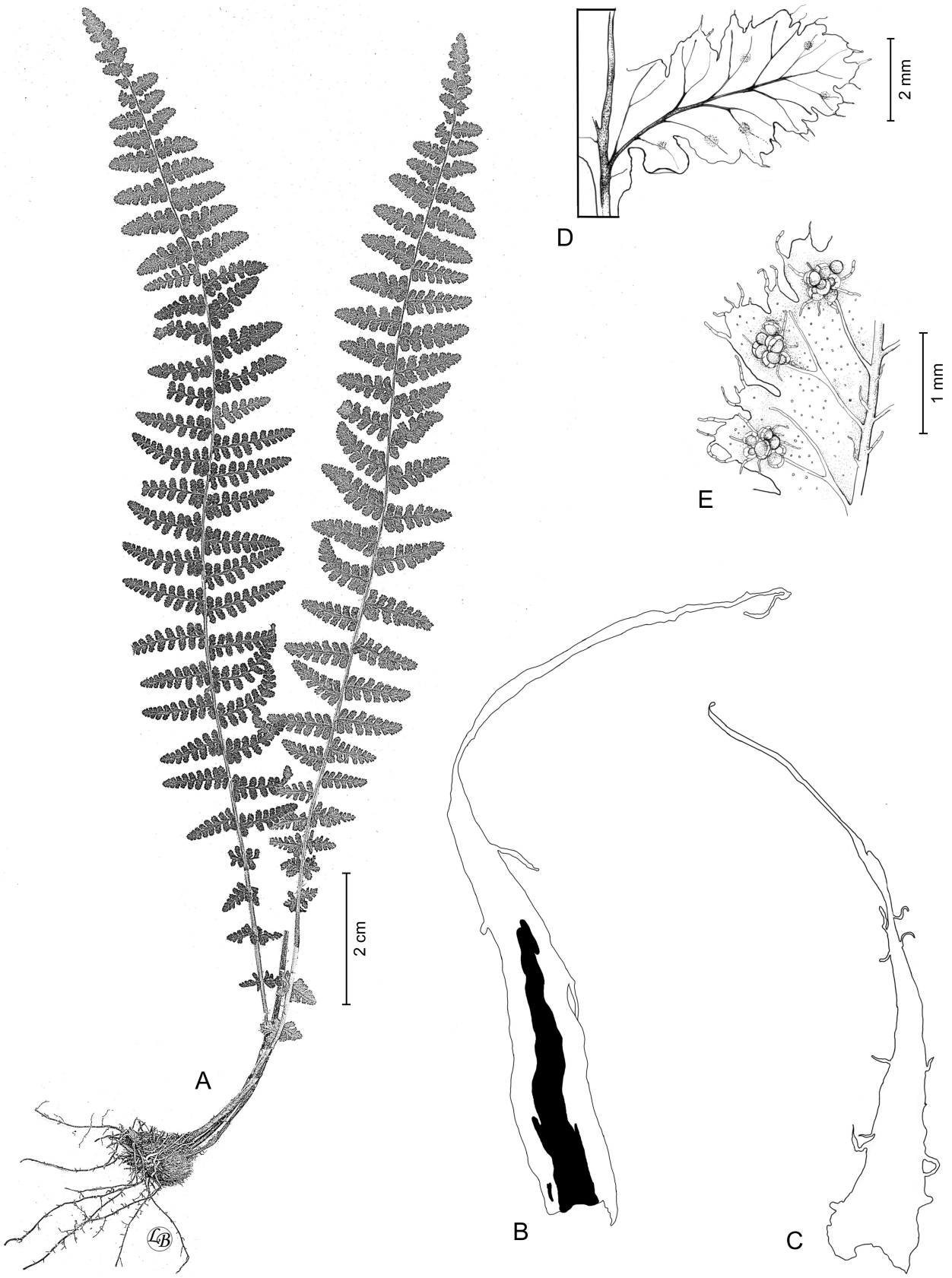


Fig. 2. *Physematium hieronymi* – A: habit; B: rhizomatic scale; C: stipe scale; D: adaxial surface of fertile pinnule; E: detail of abaxial surface of fertile pinnule showing indument and sori position. – Drawn by Leila Bordón from *R. Delgado 415* (LIL).

ten blackish proximally, scabrous, glabrescent, sometimes with paucicellular, uniseriate, glandular hairs and scaly proximally, scales narrowly triangular to filiform at apex, shiny, bicolorous, dark brown, sclerotic at centre, or sometimes light membranous. *Blades* linear-lanceolate to elliptic-lanceolate, bright green or light green, bipinnate or bipinnate-pinnatisect. *Rachises* sulcate, stramineous to pale brown, scabrous or covered by scattered, multicellular, uniseriate, glandular hairs. *Pinnae* numerous, remote or subremote, ascendant, nearly opposite, triangular-lanceolate to long triangular, narrow, almost 1 cm wide at base, basal pinnae reduced gradually to become auriculiform. *Pinnules* opposite to subopposite, obtuse to rounded at apex, basally decurrent, margin sharply toothed, teeth at bases of segments rounded to subacute, apical ones acute, margin hairy, veins visible, furcate, tips enlarged to form whitish hydathodes visible adaxially; adaxial and abaxial lamina surfaces densely covered with two types of glandular trichomes, first type tortuous, uniseriate, articulate, multicellular with acute apical cell, second type erect, capitate, apparently composed of 2 or 3 cells, uni- or bicellular stalk and an apical cell globose, pale yellow, without any apparent exudate. *Sori* circular, with inferior indusium, membranous, inconspicuous at maturity, divided into small lobes with glandular hairs. *Spores* with perispore reticulate, apparently without folds, large reticles formed by thick cords or many stacked, thin cords, also micro-reticulate surface pattern formed by smaller cords. – Fig. 1A, 2, 3S–W, 4J–O, 5M–P.

Distribution — Northwestern Argentina (Catamarca, Jujuy, Salta and Tucumán), also probably in Bolivia. This rare species occurs mainly in the Yungas (Montane Forest district) and Monte biogeographic provinces. – Fig. 6.

Habitat — *Physematium hieronymi* inhabits sunny or shady, humid rock crevices close to meadows in open habitats of the Yunguean montane forest, which develops on the upper slopes of the mountains at 1500–3500 m. These forests constitute an area of endemism dominated by *Podocarpus parlatorei* Pilg. (*Podocarpaceae*), *Alnus acuminata* Kunth (*Betulaceae*), *Cedrela angustifolia* DC. (*Meliaceae*) and several species of *Polylepis* Ruiz & Pav. (*Rosaceae*) (Arana & al. 2021). In the Monte biogeographic province, *P. hieronymi* is found in shady places close to meadows in canyons and valleys, mainly in the undergrowth of woodland formations at median altitudes, intermingled with several species of *Poaceae*.

Etymology — The species is named in honour of the German botanist Georg Hans Hieronymus (1845–1921). Hieronymus was born in Silesia. In September 1872 he travelled to Argentina. Living in Córdoba, he dedicated himself intensely to the study of the flora, describing new species in various taxonomic groups of angiosperms and ferns. In 1883 he returned to Germany and in 1892 became a curator at the Botanic Garden and Botanical Museum Berlin-Dahlem. Hieronymus advanced the taxonomy of ferns in South America, with the description of several new taxa, especially on the genus *Woodsia* (= *Physematium*).

Remarks — *Physematium hieronymi* is similar to ***Physematium peruvianum*** (Hook.) Ponce & Arana, **comb. nov.** ≡ *Woodsia peruviana* Hook., Sp. Fil. 1: 61. 1844. – Lectotype (designated by Arana & al. 2016: 16): Peru, "Shady places, Huamantanga", 1834–1835, *A. Mathews 602* (K [K000632731!]; isolectotypes: B [B 20 0094655!, B 20 0171563!], BM [BM000937848 digital image!], GH [00022287 digital image!], K [K000632730 digital image!]). However, the two species differ in several characters. In addition to the very different geographical distribution and habitats, the rhizomatic scales of *P. peruvianum* are lanceolate with an acute apex, castaneous, flaccid, with micro-dentate margins (vs rhizomatic scales linear-triangular, bicolorous, dark brown, with pale brown or reddish margin, entire border, sometimes with scarce hairs, and largely attenuate apex in *P. hieronymi*). Also, the last segments of the fronds are fully dentate, with acute teeth with a hyaline apex, sometimes with bicuspidate teeth in *P. peruvianum* (vs last segments not completely toothed at bases, with obtuse to subacute teeth in *P. hieronymi*). Although the type material of *P. peruvianum* lacks a rhizome, we were able to analyse specimens from Peru (and also high-quality digital images of specimens from Ecuador) collected in the same area from which the type material comes.

In the Southern Cone, *Physematium hieronymi*, owing to its habit and overall appearance, can be confused with *P. jujuiense*, but *P. hieronymi* has fronds gracile, fragile and pendulous, with laminae pinnate-pinnatifid or pinnate-pinnatisect or usually bipinnate, and pinnae more or less remote (vs fronds erect, firm and rather rigid, with laminae pinnate-pinnatisect to rarely pinnate, and pinnae more approximate in *P. jujuiense*). Also, *P. hieronymi* grows at intermediate elevations, whereas *P. jujuiense* grows at higher elevations.

Additional specimens examined — **Argentina:** Catamarca: Belén, Quebrada de los Potrerillos, 2700 m, 28

Fig. 3 (page 37). A–E: *Physematium jujuiense*; A: base of stipes and rhizomes; B: rhizomatic scales; C, D: stipe scales; E: fertile pinna. – F–L: *P. montevidense*, F, G: base of stipes and rhizomes; H, I: stipe scales; J, K: rhizomatic scales; L: fertile pinnae. – M–R: *P. pallidum*; M: base of stipes and rhizome; N, O: base of stipes with scales; P: rhizomatic scale; Q: basal stipe scale; R: fertile pinna. – S–W: *P. hieronymi*; S: rhizome apex and base of stipes; T, U: stipe scales; V: rhizomatic scale; W: fertile pinnae. – Photographs by: Marcelo Arana (A, F, G, M, S, W); Rita Morero (L); Juca San Martín (B–D, H–K, N–Q, T–V); Christian Zanotti (E, R). – Scale bars: W = 5 cm; L = 1.5 cm; A, E, F, G, M, S = 1 cm; O = 5 mm; N = 2.5 mm; R = 1 mm; C, H–K, T–V = 0.5 mm; B, D = 0.25 mm; P, Q = 0.1 mm.

Jan 1952, *H. Sleumer & F. Vervoorst 2460* (LIL); Pomán, Saujil, quebrada del Poca Agua, camino a la Casa de Piedra, 2000 m, 22 Feb 1952, *F. Vervoorst 3550* (LIL); Rodeo, Quebrada de las Peñas, 27 May 1910, *L. Castillón 11592* (LIL). — Jujuy: Dr. Manuel Belgrano, Quebrada de Lozano, Río Lozano camino a Cerro Azul, 1950 m, *O. Morrone & al. 3282* (SI); Tumbaya, Volcán, cantera al SE del pueblo, 2200 m, 13 Feb 1985, *Kiesling & al. 5178* (SI). — Tucumán: Anfama, 1800 m, 8 Jun 1906, *L. Monetti s.n.* (LIL 40876); Tafí, San José, 2100 m, 17 Feb 1949, *R. Sparre 5836* (LIL); Tafí del Valle, La Ciénaga, 2567 m, 20 Apr 2013, *R. Delgado 415* (LIL); La Ciénaga, entre rocas, 17 Apr 1904, *M. Lillo 3714* (LIL). Tafí, La Hoyada, 1200 m, 3 May 1922, *S. Venturi 1825* (LIL, SI); Cumbre del Taficillo, 1800 m, 4 Mar 1928, *S. Venturi 6013* (SI); Abra del Infiernillo, c. puesto vialidad, 3000 m, *E. Gomez-Sosa & M. E. Múlgura 144, 146* (SI). — Salta: Quebrada del Río Toro y Río Blanco, *I. Vattuone 4* (SI).

2. *Physematium jujuiense* (Copel.) Ponce & Arana, **comb. nov.** ≡ *Woodsia jujuiensis* Copel. in Univ. Calif. Publ. Bot. 19: 297. 1941. – Holotype: Argentina, Jujuy, Rio Yala, 15 km west of Yala, on half-shady banks, alt. 1900 m, 8 Mar 1936, *J. West 6235* (UC [UC 561572!]).

= *Woodsia montevidensis* var. *fuscipes* Hieron. in Hedwigia 46: 322. 1907. – Lectotype (designated by Arana & al. 2016: 16): Argentina, Salta, "Prov. de Salta, Los Potreros al pie del Nevado del Castillo, 24.03.1827", *P. G. Lorentz & G. H. E. W. Hieronymus 138* (B [B 20 0171577!]; isolectotypes: B [B 20 0171580!, B 20 0171581!], CORD!).

Morphological description — Plants saxicolous, 10–40 cm tall. *Rhizomes* suberect, ascending, nodose, compact, scaly, covered by many persistent stipe bases; rhizomatic scales 2–2.8 × 0.4–0.7 mm, triangular-lanceolate, strongly bicolorous, shiny, castaneous to dark brown, with dark brown to blackish central stripe completely sclerotic, margin pale brown, entire or scarcely hairy, apex acute, short or elongate. *Fronds* fasciculate or approximate. *Stipes* terete or subterete, brittle, 1/5–1/3 of length of frond, 0.5–1 mm in diam., brown, dark brown to burgundy, blackish at base, basal part with linear-triangular, sclerotic scales, glabrescent, smooth. *Blades* linear-lanceolate to elliptic-lanceolate, bright green or light green, pinnate-pinnatifid. *Rachises* subterete to sulcate, stramineous to pale brown, with dense, glandular, uniseriate, pauci-multicellular, articulate hairs. *Pinnae* numerous, 20–30 pairs, approximate, ascending, triangular, almost 1 cm wide at base, basal pinnae sometimes strongly reduced. *Last segments* triangular, with margin sparsely incised-crenate, margin hairy, lateral veins visible, free, furcate, tips enlarged to form hydathodes visible adaxially; adaxial and abaxial lamina surfaces with multicellular, uniseriate, articulate hairs, dense on both surfaces, antrorse on adaxial surface. *Sori* circular, indusium inferior, membranous, with 1–3 striped lobes, usually one of them larger, with marginal, glandular hairs. *Spores* with folded-reticulate perispore, with complete and incomplete reticules, with some perforations, significant number of spheroids on surface, crest of folds microbaculate. – Fig. 1C, 3A–E, 4A–C, 5A–D.

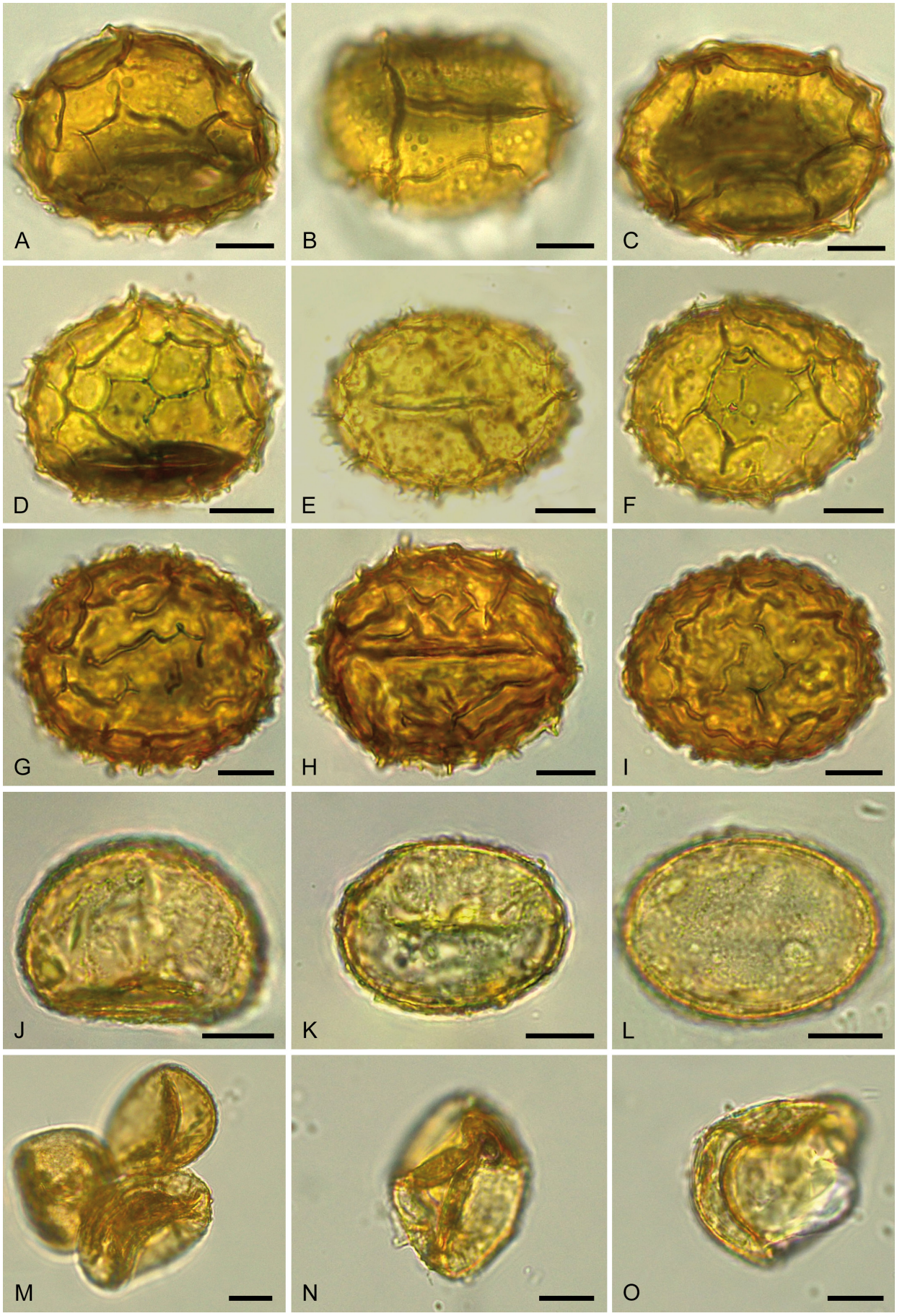
Distribution — Northwestern Argentina (Catamarca, Jujuy, La Rioja, San Juan, Salta and Tucumán), in Bolivia (Cochabamba) and Peru (Cuzco). This species occurs mainly from the Monte (only in Prepuna district) to Puna biogeographic provinces. – Fig. 7.

Habitat — Physematium jujuiense grows in the high Andean environments, above 2000 m in elevation, on outcrops in rock crevices.

Remarks — This species is very well characterized by its narrowly elliptic blades; stipes thin and brittle, dark brown to almost burgundy, blackish at the bases; and by the rhizomatic and stipe scales linear-lanceolate, shiny and sclerotic.

Additional specimens examined — **Argentina:** Catamarca: Ambato, El Potrero, 15 Mar 1904, *Castillón 713* (LIL); Ambato, Rodeo, cerro Lamedero, 1600 m, 12 Feb 1959, *V. Carenzo 941* (LIL); Andalgalá, Capillitas, 3000 m, Apr 1944, *A. O'Donell 1365* (LIL); Capillitas, Refugio Minero, cerca de arroyo, 3046 m, 13 Jan 2017, *J. M. Acosta & S. von Mering 613* (SI); Andalgalá, Río Potrero, 2700 m, *H. Sleumer 1845* (LIL); Andalgalá, Rio Pisavil, cerce de El Suncho, 2000 m, 21 Feb 1951, *H. Sleumer 1621* (LIL). — Jujuy: Sierra de Zanta, 3500 m, Mar 1931, *E. Martin 7513* (LIL); Humahuaca, Ruta Provincial 13, cerca del límite con la provincia de Salta hacia Iruya, 3800 m, 15 Mar 2018, *F. O. Zuloaga & al. 16337* (SI); Tumbaya, Volcán, Chilcayo camino a Abra Morada, 2550 m, 26 Feb 1985, *R. Kiesling & al. 5708* (SI). — La Rioja: Famatina, Sierra de Famatina, camino a la mina La Mexicana, Cuevas de Noroña, 2850 m, 20 Feb 1986, *R. Kiesling & al. 6348* (SI); Pelagio Luna, Sierra de Velazco, rancho la Esperanza, 2100 m, *Sparre 8650* (LIL); Malanzán, Quebrada de los Nogués, Apr 1940, *A. Agüero Vera de Gaudio s.n.* (LIL 232851). — San Juan: Angaco, Sierra de Pie de Palo, camino a Mogote de los Corralitos, Aguada del Caño, 2500 m, 15 Feb 1984, *R.*

Fig. 4 (page 39). Spores of *Physematium* with LM. – A–C: *P. jujuiense*; A: spore in equatorial view; B: spore in proximal view; C: spore in distal view. – D–F: *P. montevidense*; D: spore in equatorial view; E: spore in proximal view; F: spore in distal view. – G–I: *P. pallidum*; G: spore in equatorial view; H: spore in proximal view; I: spore in distal view. – J–O: *P. hieronymi*; J: spore in equatorial view; K: spore in proximal view; L: spore in distal view; M: aborted spore cluster; N: collapsed and twisted spore; O: aborted spore with broken perispore. – A–C from *Zuloaga & al. 16337* (SI); D–F from *Acosta 590* (SI); G–I from *Acosta & al. 1171* (SI); J–O from *Morrone & al. 3208* (SI). – Scale bars: A–O = 10 µm.



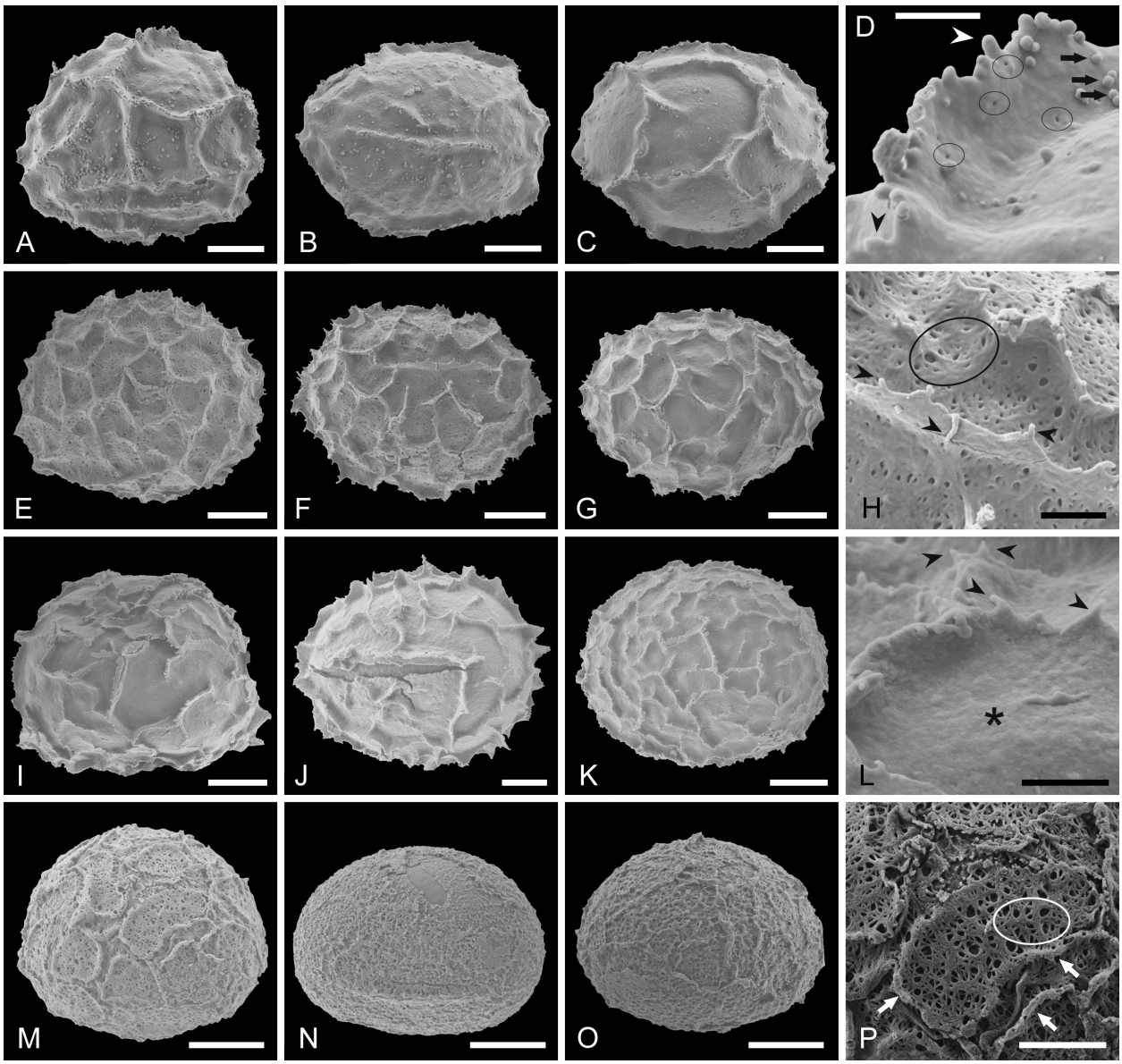


Fig. 5. Spores of *Physematium* with SEM. – A–D: *P. jujuiense*; A: spore in equatorial view; B: spore in proximal view; C: spore in distal view; D: spore detail, small perforations (black circles) and some spheroids (black arrows) are observed on surface, while microbacules (black and white arrowheads) are observed on margin of folds. – E–H: *P. montevidense*; E: spore in equatorial view; F: spore in proximal view; G: spore in distal view; H: spore detail, surface is densely perforated (black circle) forming a microreticle, margins of folds are echinulate (arrowhead). – I–L: *P. pallidum*; I: spore in equatorial view; J: spore in proximal view; K: spore in distal view; L: spore detail, surface is rugulate-scabrate (black asterisk), margins of folds are echinulate (black arrowheads). – M–P: *P. hieronymi*; M: spore in equatorial view; N: spore in proximal view; O: spore in distal view; P: spore detail, large reticles are made up of thick threads (white arrows), while background has microreticles made up of individual units of small threads (white circle). – Scale bars: A–C, E–G, I–K, M–O = 10 µm; D, H, L, P = 3 µm.

Kiesling 4406 (SI). San Luis, Pringles, Ruta Provincial 9 entre los Tapiales y La Arenilla, 1600 m, 20 Nov 1984, *R. Kiesling & al. 4729* (SI). — Salta: Orán, Santa Cruz, 3000 m, 20 May 1945, *S. Pierotti 1264* (LIL). — Tucumán: Rio Chico, Escaba, cumbre del Marbay, pajonal, 2400 m, *L. Monetti 1816* (LIL); Tafí del Valle, La Quebradita, 2200 m, 7 Feb 1959, *de la Sota 2076* (LIL); Sierras Calchaquíes, Peñas Azules, 29 Jan 1933, 3400 m, *A. Burkart 5536* (SI); Calchaquíes, Quebrada honda, 3500 m, 26 Jan 1952, *Sparre 9353* (LIL); Chicligasta, Estancia Las Pavas, Puesto La Cascada, 11 Mar 1924, 2700 m, *S. Venturi 3039* (LIL, SI); Trancas, San Pedro de Colalao, 1700 m, 14 Apr 1955, *de la Sota 274* (LIL). — **Bolivia:** Cochabamba: barrancas del arroyo de Caluya, 3500 m, 20 May 1920, *J. Steinbach 4033, 4034* (LIL); Sacaba, Incachaca, sobre rocas húmedas, 2500 m, 14 Oct 1921, *J. Steinbach 5862* (LIL). — **Peru:** Cuzco: Sicuani, Feb 1903, *C M. Hicken 3* (SI); Cuzco, 3500 m, Mar 1922, *F. Herrera 5* (SI).

3. *Physematium montevidense* (Spreng.) Shmakov in Turczaninowia 18(2): 12. 2015 [“*montividensis*”] ≡ *Dick-*

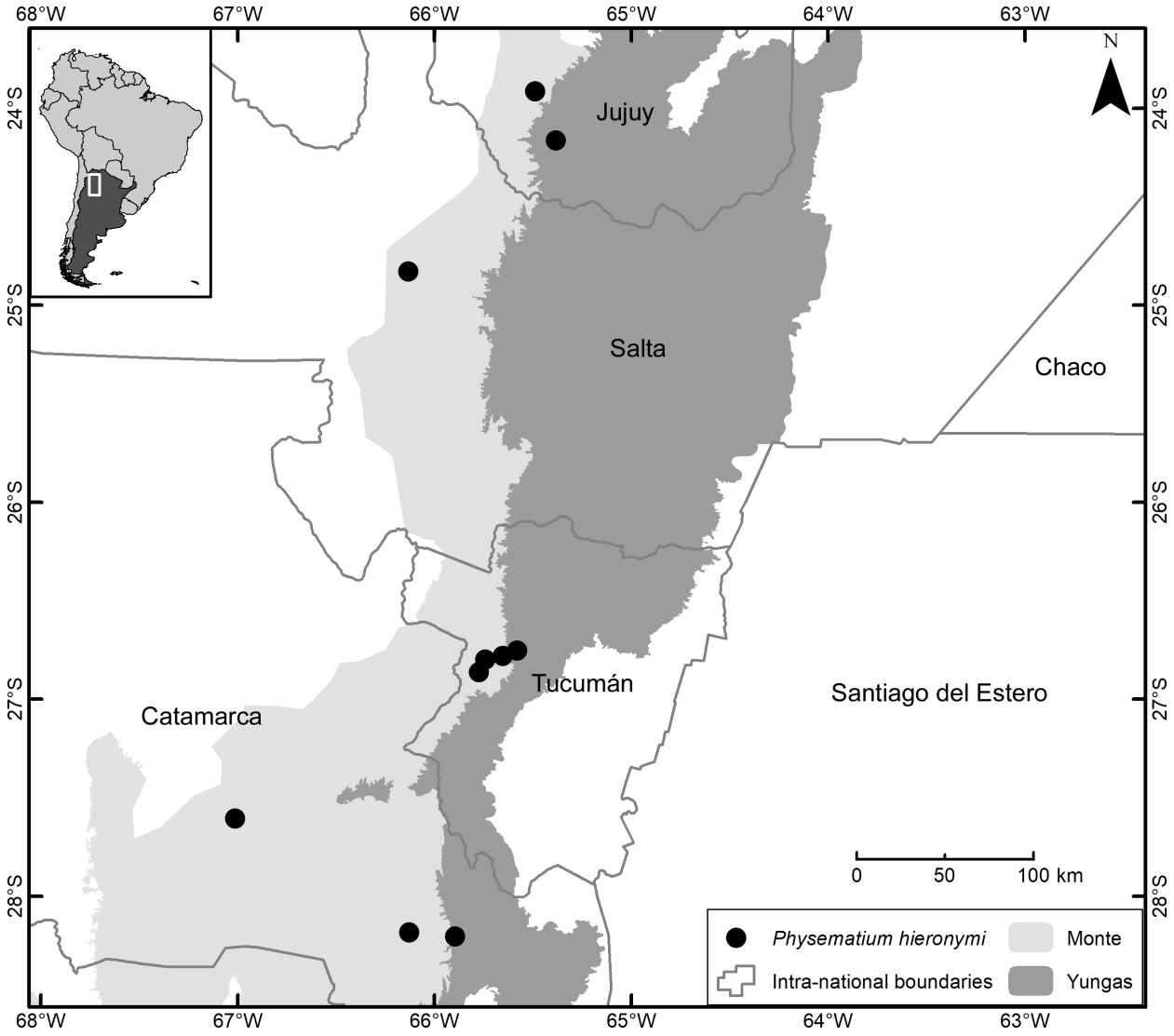


Fig. 6. Geographic distribution of *Physematium hieronymi* throughout Monte and Yungas biogeographic provinces, Argentina.

sonia montevidensis Spreng., Syst. Veg. 4: 122. 1827 ≡ *Woodsia montevidensis* (Spreng.) Hieron. in Bot. Jahrb. Syst. 22: 363. 1896. – Lectotype (designated by Arana & al. 2016: 15): Uruguay, ("Brasilia") [Montevideo], Pan d'Açucar, *F. Sellow d 517* (B [B 20 0094654!]; isolectotype: B [B 20 0120343!]).

= *Woodsia incisa* Gillies ex Hook. & Grev., Icon. Filic. 2: t. 191. 1830 ≡ *Physematium incisum* (Gillies ex Hook. & Grev.) C. Presl, Tent. Pterid.: 66. 1836. – Lectotype (designated by Arana & al. 2016: 15): Argentina, Mendoza, near San Luis, *J. Gillies s.n.* (BM [BM000937851!]; isolectotypes: BM [BM000937850!], K [K000229420!]).

Morphological description — Plants saxicolous, 15–40 cm tall. *Rhizomes* suberect to decumbent or suberect, separate or spreading, scaly, covered by persistent stipe bases; rhizomatic scales 2–2.8 × 0.4–0.7 mm, ovate-lanceolate or triangular-lanceolate, concolorous, dull, light brown or orange becoming bicolorous, in this case with a central stripe partial to totally sclerotic, brown, margin membranous, broad (twice as wide as central stripe), fimbriate, with spaced hairs, apex ending with an apical hair. *Fronds* fasciculate. *Stipes* short to very short, terete or semiterete, 1.5–2 mm long, stramineous, often dark brown proximally, scabrous, with paucicellular, uniseriate, glandular hairs and scaly, scales ovate-lanceolate, dull, concolorous, pale brown, orange or reddish, membranous. *Blades* triangular, ovate-lanceolate to elliptic-lanceolate, bright green or light green, pinnate-pinnatifid, rarely almost bipinnate. *Rachises* sulcate, stramineous to pale brown, scabrous or covered by scattered, multicellular, uniseriate, glandular hairs. *Pinnae* numerous, approximate, triangular, patent to ascending, opposite to alternate, 1–1.5 cm wide at base, basal pinnae gradual to strongly reduced to auriculiform. *Last segments* subopposite, with acute apex, base adnate, lobes with slightly to strongly crenate margin, sometimes bicrenate, margin hairy, lateral veins visible, free, furcate, tips enlarged to form whitish hydathodes visible adaxially; adaxial

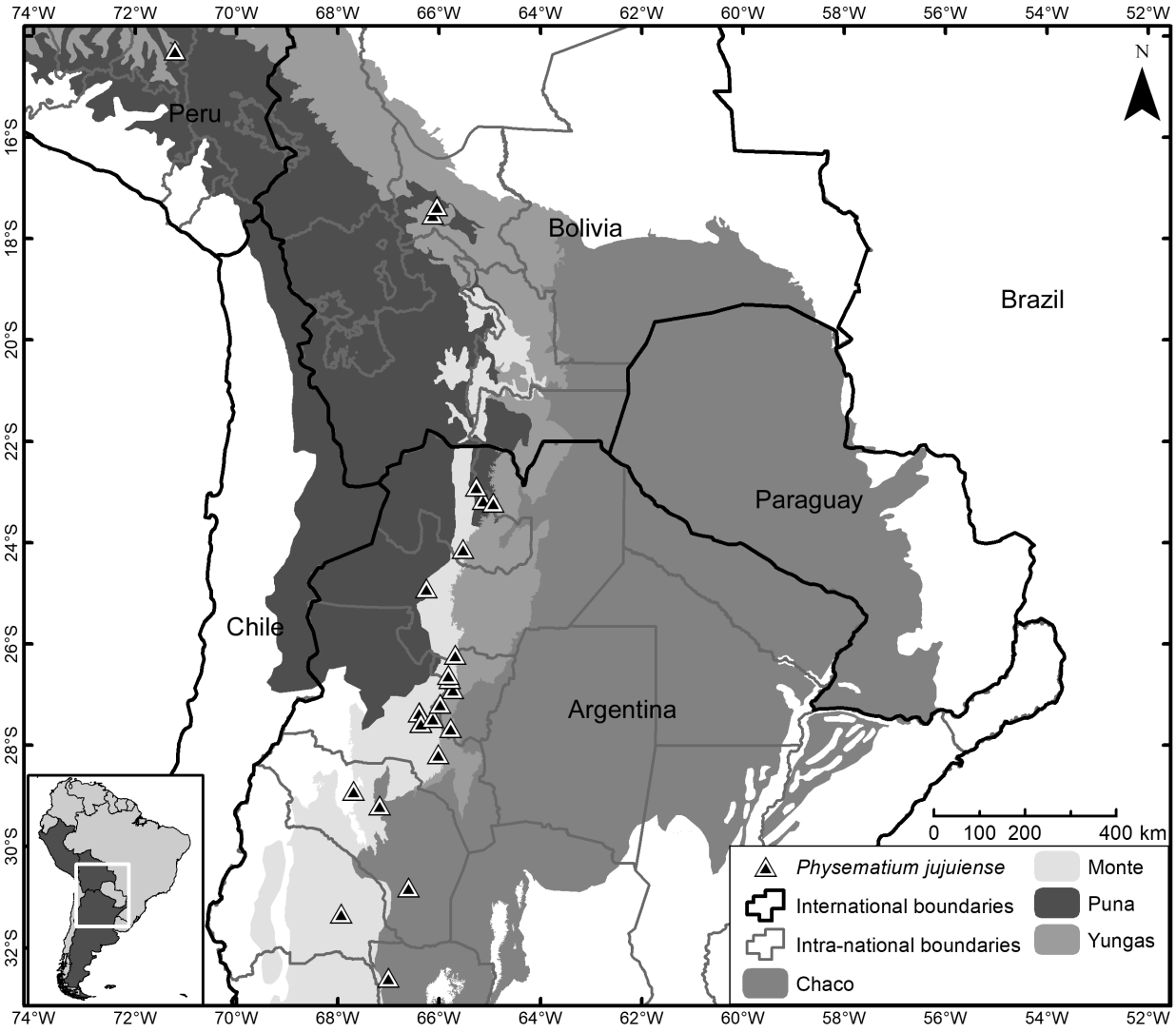


Fig. 7. Geographic distribution of *Physematium jujuiense* throughout Monte and Puna biogeographic provinces, Argentina.

and abaxial lamina surfaces with hyaline, multicellular, articulate, glandular, hairs, dense on both surfaces, antrorse on adaxial surface, frequently with yellowish, paucicellular, glandular hairs on abaxial surface. *Sori* circular, indusium inferior, membranous, saucer-shaped, symmetric, composed of 2 or 3 conspicuous lobes, with glandular hairs on margins. *Spores* folded-reticulate, with complete and incomplete reticles and perforated surface, also with spinules on crests of folds. – Fig. 1D, 3F–L, 4D–F, 5E–H.

Distribution — Central and northwestern Argentina (Buenos Aires, Córdoba, La Rioja, Mendoza, Río Negro, San Juan, San Luis and Tucumán), southeastern Brazil (Rio de Janeiro, Rio Grande do Sul, Santa Catarina and São Paulo) and Uruguay (Lavalleja, Maldonado, Minas, Rocha and Treinta Tres). This species occurs from the Atlantic biogeographic province, through the *Araucaria* Forests, Pampean (in isolated mountain systems) to Chaco (only Montane Chacoan district) and Monte biogeographic provinces. – Fig. 8.

Habitat — The species is common in mountainous forests and grasslands, and is found sunny areas, between rocks or in rock crevices, as well as in humid ravines near rivers.

Remarks — *Physematium montevidense* is distinguished by having rhizomatic and stipe base scales ovate-lanceolate or triangular-lanceolate, concolorous, light brown to orange becoming bicolorous, with centre partially to totally sclerotic, margin broad, with spaced hairs or fimbriate, and apical hair. The stipes are rather robust, especially at the bases, and the laminae are very variable in division, shape and size, depending on the habitats where the plants grow, usually ovate-lanceolate to elliptic-lanceolate, pinnate-pinnatifid to bipinnatifid.

The spore size difference observed in *P. montevidense* is striking, where our specimens were 26 µm smaller than those analysed by Castro (2004), perhaps because she applied a very broad concept of *Woodsia montevidensis*. We were able to revise the specimens analysed by her

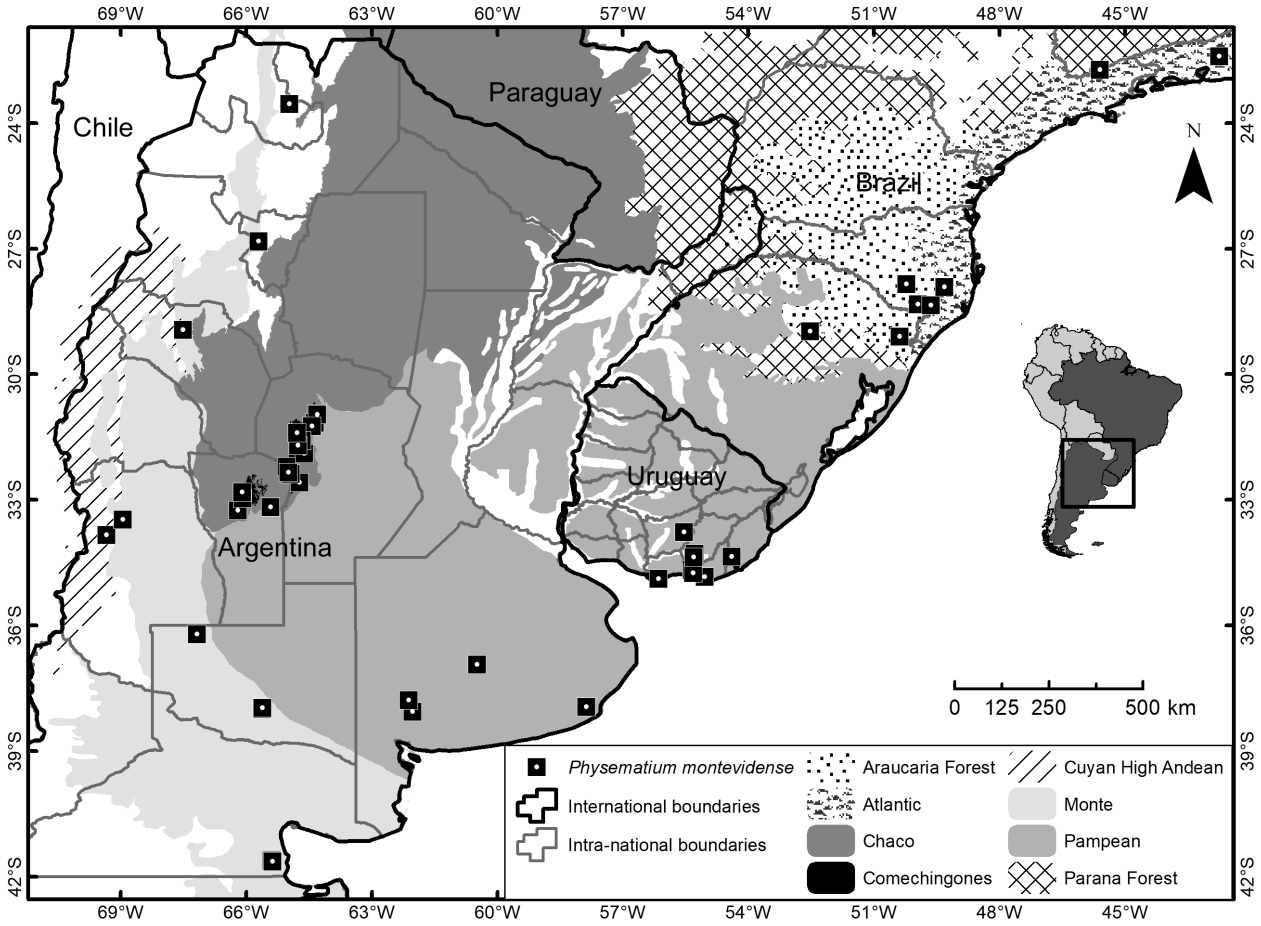


Fig. 8. Geographic distribution of *Physematium montevidense* throughout its distributional range, from Brazil to northwestern Argentina.

and many of them, identified as "*W. montevidensis*" belong to *P. pallidum* (large spores) and *P. hieronymi* (small spores). According to Tryon & Lugardon (1991) *Woodsia* (= *Physematium*) spores with large sizes are related to high ploidy levels. This would indicate that speciation in the genus apparently involves polyploidization.

Additional specimens examined — **Argentina:** Buenos Aires: General Pueyrredón, Estancia La Brava, Sierra Valdez, ladera oeste, 18 Nov 1977, *O. Boelcke & al. 806* (SI); Olavarría, Cerro Dos Hermanas, 250 m, 21 Apr 1947, *A. Krapovickas 3407* (LIL). Tornquist, Cerro Ventana, 7 Dec 1970, *A. Burkart & M. E. Múlgura s.n.* (SI 28122); Coronel Suárez, Camino de Piscultura, 8 Dec 1970, *A. Burkart & M. E. Múlgura s.n.* (SI 28123); Sierra de La Ventana, 23 May 1938, *A. L. Cabrera 4470* (SI). Saavedra, Pigüé, Cerro Cura Malal, grietas húmedas, 10 Nov 1932, *A. Burkart 4667* (SI); Sierra de Curu Malal, abra de la Comenas, 13 Oct 1979, *O. Boelcke & al. 91198* (SI); Tandil, Sierras de Tandil, Cerro Leones, 2 Nov 1951, *D. Abbiatti 4270* (SI). — Córdoba: Calamuchita, Valle de los Reartes, *A. Castellanos 197* (SI); Las Guindas, pastizal, 30 Mar 2000, *M. Ceballos s.n.* (RCVC 3647). Colón, Ascochinga, Tres cascadas, 900 m, 17 Jan 1932, *B. Veronesi s.n.* (LIL 436491); Río Ceballos, Reserva Hídrica La Quebrada, Colanchanga, margen del sendero que une Los Guindos con el río Los Hornillos, 29 Mar 2015, *R. E. Morero 414, 415* (CORD); Ascochinga, 28 Nov 1936, *E. Nicora 1159* (SI); 28 Nov 1936, *M. L. Giardelli 669* (SI); Punilla, Sierra Chica, Cerro Pan de Azúcar, 16 Dec 1886, *F. Kurtz 4445* (CORD, SI); Copina, 1400 m, 12 Feb 1947, *D. Grassi 2245* (LIL); Los Cocos, 1200, 15 Apr 1962, *J. S. Lichtenstein s.n.* (SI 22855), Capilla del Monte, Feb 1933, *E. Nicora 150* (SI). San Alberto, Pampa de Achala, pastizal, 9 Nov 2000, *M. Arana s.n.* (RCVC 3727); Pampa de Achala, Ruta provincial 14, proximo al cruce Ruta nacional 20, 1800 km, 9 Jan 2017, *J. M. Acosta 590* (SI); San Alberto, Los Gigantes, a 3 km de La Rotonda subiendo por el sendero, 9 Jan 2017, *J. M. Acosta 588* (SI). San Javier, La Paz – Loma Bola, 21 Apr 1952, *J. S. de Lichtenstein s.n.* (SI 18126). Ischilín, Copacabana, 2 Jan 1941, *E. Nicora s.n.* (SI 17677). — Jujuy: Valle Grande, entre Tres Morros y Cerro Hermoso, 2940 m, 16 Apr 2016, *CMM 792* (SI); Alto Calilegua, 2540 m, 19 Jan 1987, *Iudica 387* (SI). — La Pampa: Depto. Chical Co, 20 Dec 1989, *H. O. Troiani 10029* (SRFA). Depto. Lihuel Calel, Sierra de Lihuel Calel, 30 Nov 1959, *A. Burkart s.n.* (SI 20553); Lihuel Calel, poco abundante entre grietas a la sombra, 25 Oct 1978, *Steibel 5942* (SRFA). — La

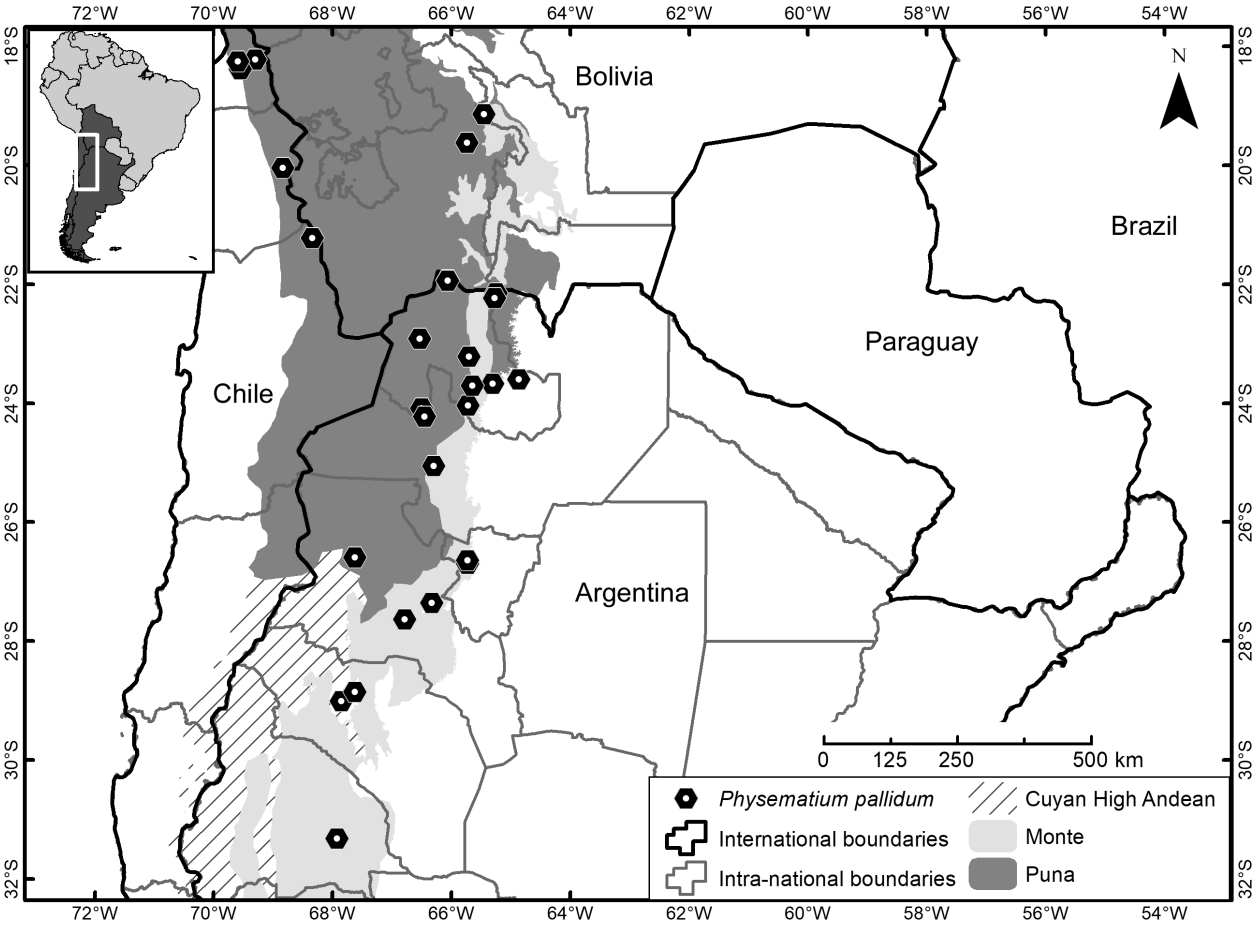


Fig. 9. Geographic distribution of *Physematium pallidum* throughout Monte (Prepuna district), Puna and Cuyan high Andean biogeographic provinces in Argentina, Bolivia and Chile.

Rioja: Cerro Famatina, Guanchin viejo, 25 Jan 1928, *Castellanos 28/20* (LIL 18362); Velasco, 6 Mar 1944, *A. Soriano 981* (SI); cerca de Mina San Juan, 3100 m, Mar 1906, *F. Kurtz s.n.* (SI24713). — Mendoza: San Carlos, Quebrada de Alvarado, 1800–2000 m, 10 Feb 1919, *R. Sanzin 3278* (SI); Tunuyán, 25 km al suroeste de Campo de los Andes, 1800 m, *J. Araque 1146* (LIL); íbid., *M. Cáceres 86* (LIL). — Río Negro: Dpto. San Antonio, Sierra Grande, ladera SE, aprox. 400 m, 8 Feb 1979, *S. Crespo & al. 2231* (BAB); ídem, 4 km al sur de Sierra Grande, entre piedras, en Quebrada, 10 Nov 1988, *M. Correa & al. 9616* (BAB). — Salta: Ruta provincial 33, Cuesta del Obispo, Paraje La Herradura, 3100 m, 12 Jan 2017, *J. M. Acosta 606* (SI). — San Juan: Valle Fértil, Sierra de Elizondo, 1200 m, 16 Nov 1987, *M. E. Múlgura & al. 804* (SI). — San Luis: Cerro el Morro, 14 Oct 1949, *Castellanos s.n.* (LIL 380139); Merlo, Peñón Colorado, 19 Feb 1936, *M. A. Vignati 37* (SI); Juan Martín de Pueyrredón, El Volcán, 25 Jan 1908, *F. Pastore 13* (SI); Coronel Pringles, Ruta Provincial 9, Junin, Piedra Blanca, ladera occidental de Comechingones, 2000 m, *D. Grassi 2166, 2171* (LIL); La Carolina, Monumento – Museo Lafinur, 1680 m, 28 Nov 2008, *F. Biganzoli, R. León & C. Larsen 2037* (SI); Dique La Florida, cerca del vertedero, 15 Dec 1991, *M. E. Múlgura 1173* (SI); Estancia Grande, 28 Feb 1939; *M. A. Vignati 7063* (SI). — Tucumán: Tafí, Valle de Tafí, Mar 1908, *C. Bruch s.n.* (SI 24691); Tafí, San José, 2100 m, 17 Feb 1949, *R. Sparre 5873* (LIL), Los Chamicos, 900 m, 30 Jan 1924, *S. Venturi 2778* (SI). — **Brazil:** Rio de Janeiro: Nova Friburgo, Parque Estadual dos Três Picos, na subida para caixa de Fósforo, 22°24'00"S, 42°44'00"W, 1550 m, Jun 2006, *J. Condack 442* (RB). — Rio Grande do Sul: Soledade, Sep 1913, *C. Jürgens 355* (NY 678816); Santa Anna, 26 May 1907, *W. G. F. Herter 3097* (NY 678817); Jaquirana, Parque Estadual do Tainhas. Estrada para o passo do S, 18 Dec 2021, *F. Gonzatti & al. 6219* (HUCS). — Santa Catarina: São Joaquim, ad saxa aprica juxta flum. S. Matheus, 1907, *L. Spannagel s.n.* (Herb. Rosenstock 381) (P01402552, SI); idem, Bom Jardim da Serra, entre pedras no campo, 1300 m, 15 Dec 1958, *R. Reitz & R. M. Klein 7902* (PACA); Lages, Campo Bello, 27°48'58"S, 50°19'33"W, *sine col.* (NY01016492); Campos dos Padres, em barrancos, 1800 m, 19 Dec 1948, *R. Reitz 2622* (RB). — São Paulo: Campos do Jordão, 20 Feb 1937, *P. Campos Porto 3111* (RB). — **Uruguay:** Uruguai, Banda Oriental Del Uruguay, 1 Jan 1816, *A. Saint-Hilaire C2/2148* (P). — Florida: Cerro Colorado, estancia San Pedro, 2 Oct 1942, *Gallinal, Aragone, Bergalli, Campal & Rosen-*

Table 2. Spore measurements of the four species of *Physematium* occurring in the Southern Cone of South America. – MaED = major equatorial diameter; MiED = minor equatorial diameter; PD = polar diameter; LL = length of laesura; measurements are minimum (mean) maximum in µm.

	MaED	MiED	PD	LL
Physematium hieronymi	32 (36) 41	24 (28) 31	22 (27.4) 30	12 (18.3) 21
P. jujuiense	41 (47.5) 55	34 (37.7) 42	29 (36.5) 40	25 (29.5) 43
P. montevidense	41 (45.6) 50	33 (37.8) 42	30 (35.7) 40	22 (26.6) 33
P. pallidum	42 (47.6) 59	32 (39.6) 47	33 (37.8) 45	22 (26.5) 32

gurtt 5030 (LIL). — Lavalleja: en intersticio rocoso, 14 Dec 1948, *Rosengurtt 5318* (LIL); cerro de Arequipa, Apr 1907, *A. Lombardo s.n.* (LIL 225539); Sierra de la Ballena, 4 Aug 1940, *Legrand 2229* (LIL); 12 Jun 1985, Del Puerto, *Davies & Berrutti 17847* (MVFA). — Maldonado: Sierra de las Ánimas, 500 m, 3 May 1931, *W. Herter 885a* (LIL); Sierra de las Ánimas, 6 Mar 1915, *M. B. Berro s.n.* (MFVA); en lugar húmedo y soleado, *E. Marchesi 1359* (MFVA); Sierra de las Ánimas, Cerro Betete, entre piedras, a la sombra, 27 Oct 1996, *M. Bonifacino & E. Mendez s.n.* (MFVA 25864); Cerro Lagunitas entre piedras, 1 Apr 1999, *M. Bonifacino s.n.* (MFVA 28870). — Minas: cerro Verdún, 4 Dec 1900, *M. B. Berro 1420* (MFVA); — Rocha: Cerro de San Miguel, *A. Castellanos 17451* (LIL). — Treinta y Tres: Yerbal, 200 m, Apr 1928, *G. Herter 885* (SI).

4. *Physematium pallidum* (Copel.) Ponce & Arana, **comb. nov.** ≡ *Woodsia pallida* Copel. in Univ. Calif. Publ. Bot. 19: 297. 1941. – Holotype: Argentina, Jujuy, 20 km west of Humahuaca, rock crevices in half-shade, alt. 3600 m, fern 10–30 cm high, 13 Mar 1936, *J. West 6339* (UC [UC 600270!]; isotype: MICH [1191108!]).

Morphological description — Plants saxicolous, 5–15 (–20) cm tall, caespitose. *Rhizomes* suberect, compact, scaly, covered by persistent stipe bases; rhizomatic scales 0.5–1 mm long, strongly bicolorous, linear-lanceolate, dark brown to shiny black, sclerotic, with a thin, pale margin, entire, papillose or hairy, apex hairy. *Fronds* compactly fasciculate. *Stipes* 1/4–1/3 of length of frond, less than 1 mm in diam., brittle, light straw-coloured to stramineous, with paucicellular, uniseriate, glandular hairs, somewhat scabrous, base and along stipe with tiny, linear-lanceolate, black, membranous scales. *Blades* elliptic or subelliptic, 2–3(–4) cm wide, light-green or yellowish, pinnate to pinnate-pinnatifid. *Rachises* light straw-coloured, hairy-glandular, with abundant, uniseriate, glandular hairs, 2-pluricellular, articulate. *Pinnae* subremote, triangular, patent, opposite, basal pinnae strongly reduced. *Last segments* opposite to subopposite, oblong, rounded, with an undulate, sometimes recurved margin, glandular, lateral veins visible, furcate, tips enlarged to form hydathodes; adaxial and abaxial lamina surfaces with abundant, hyaline, uniseriate, glandular hairs, 2-multicellular, articulate. *Sori* circular, few per segment, indusium inferior, membranous, central, bowl-shaped, somewhat globose, divided into 2 or 3 lobes, with glandular hairs on margin. *Spores* with folded-reticulate perispore, with complete and incomplete reticules, with rugulate-scabrate surface; margin of folds echinulate. – Fig. 1B, 3M–R, 4G–I, 5I–L.

Distribution — Northwestern Argentina (Catamarca, Jujuy, La Rioja, San Juan, Salta and Tucumán), Bolivia (Chuquisaca and Potosí), and recorded here for the first time in Chile (Antofagasta, Arica y Parinacota and Tarapacá). This species is endemic to the South American Transition Zone, in the biogeographic provinces of Monte (Prepuna district), Puna and the Cuyan High Andean. – Fig. 9.

Habitat — Physematium pallidum is a xerophytic species that grows in crevices of cliffs or between rocks, close to meadows above 3600 m.

Additional specimens examined — **Argentina:** Catamarca: La Tranca, 4 Feb 1930, *Castellanos 30/316* (LIL); Andalgalá, El Globo, 4015 m, 17 Feb 2010, *F. Zuloaga & al.* 11950 (SI); Belén, Laguna Blanca, 4200 m, 16 Mar 1989, *A. Reca & D. E. Ramadori 139* (SI). — Jujuy: Maimará, Laguna Colorada, 4000 m, 20 Jan 1906, *Budin 18* (LIL); ídem, *M. Lillo 4946* (SI); Rinconada, Reserva Provincial Altoandina La Chinchilla, Pie del Cerro Negro, frente laguna Villamas. 24 Feb 2022, *J. M. Acosta, P. Moroni & C. Zanotti 1171* (SI); Santa Catalina, Río Santa Catalina, 3780 m, 16 Feb 1998, *O. Morrone & al. 2692* (SI); Humahuaca, Mina Aguilares, cerca del molino, 4100 m, 28 Mar 1952, *E. Petersen & P. Hyinting 105, 133* (LIL); Valle Grande, Faldeo oeste Cerro Hermoso, 3380 m, 21 Jan 1995, *H. Ayarde 480* (LIL); Yavi, Cerro Negro, 4000 m, 27 Feb 1940, *T. Meyer s.n.* (LIL 96216); Yavi, Ruta Provincial 5, de La Quiaca a Santa Victoria, 4020 m, 20 Feb 1997, *F. O. Zuloaga & al. 6097* (SI); Dr. Manuel Belgrano, Cerro Chañi, Refugio Militar, 4610 m, 27 Jan 2012, *C. Zanotti & M. Suescún 277* (SI); Susques, Coranzulí, 4703 m, 31 Mar 2019, *V. L. López & al. 176* (SI); idem, Ruta Nacional 40, base del Cerro Tuzgle, 4500 m, 8 Feb 2016, *Zanotti & al. 710* (SI). Santa Catalina, 3650 m, 9 Jan 1901, *F. Claren (Herb. Kurtz) 11402* (SI); Tumbaya, Abra de Lipán, 4000 m, 24 Mar 1979, *A. L. Cabrera & al. 30570* (SI). — La Rioja: Sierra de Famatina, Cerro Nevado, Vega del Real Viejo, 4200 m, 5/6 Mar 1907, *Herb. F. Kurtz 14774* (SI); La Mesada, 3500 m, 29 Apr 1951, *Sparre 8886* (LIL). — Salta: Alrededores del Nevado del Castillo, 23 Mar 1873, *P. Lorentz & G. Hieronymus 52-54* (CORD); Los Andes, Chorrillos, Mar 1930, *Budín 20* (LIL). — San

Juan: Angaco, Sierra de Pie de Palo, Mogote de los Corralitos, 3100 m, 18 Feb 1986, *R. Kiesling & al. 6301* (SI). — Tucumán: Tafí, cumbres Calchaquíes, entre rocas, 4200 m, 30 Jan 1907, *M. Lillo 55426* (LIL); Calchaquíes, Cerro Negrito, 4300 m, 7 Mar 1952, *R. Sparre 9658* (LIL), idem, 4000 m, 25 Feb 1949, *R. Sparre 6042* (LIL). — **Bolivia:** Chuquisaca: Oropeza, camino de Herradura prehispánico que va a Chaunaco y a pinturas rupestres, 3600 m, 9 Dec 2006, *N. Muruaga & H Huaylla s.n.* (LIL 608391). — Potosí: entre rocas, en el borde de la Laguna San Sebastián, 4000 m, May 1932, *M. Cárdenas 159* (LIL); 4000 m, ídem, Apr 1933, *M. Cárdenas 487* (LIL). — **Chile:** antofagasta: El Loa, Queb. Amincha, 1 Jan 2010, *Pfanzelt & Garcia 445* (CONC). —Arica y parinacota: camino Zapahuira a Putre, km 25, en quebrada a orilla de riachuelo, 3450 m, 1 May 1972, *Ricardi, Weldt & Quezada 195* (CONC); Murmuntani, 1 May 1989, *Hoffman 8948* (CONC); Putre, 4800 m, Feb 1952, *U. Levi 44880* (CONC). —Tarapacá: Parinacota, Laguna de Parinacota, 4300 m, 1 Jan 1970, *O. Zöllner 3882* (CONC); Parinacota, wuchs an der Südseite unter grossen Felsblöcken, 30 Jan 1970, *O. Zöllner 3901* (L).

Dubious species

Physematium cumingianum Kunze, Analecta Pteridogr.: 43. 1837 ≡ *Woodsia cumingiana* (Kunze) Hook., Sp. Fil. 1: 61. 1844. – Holotype: "Habitat probabiliter in Chile, misit H. Cuming" (LZ [herb. Kunze, destroyed]).

Kunze (1837) mentioned in the protologue: "Unicum vidi specimen filicis" and "Herb. prop." This is a rare case of evidence that an author used only a single specimen, so it was the holotype (Turland & al. 2018: Art. 9.1). As Arana & al. (2016) stated, there is no isotype or even an illustration of the species. According to Hooker (1844), who had the opportunity to revise the collections immediately after Cuming returned to Europe from Chile or Peru, most probably the type locality was mistaken and was in Peru instead of Chile.

Conclusions

In the Southern Cone of South America, there are four species of *Physematium* that have well-defined morphological and biogeographical limits. They have historically been included in the collective concept of *W. montevidensis*, following Brown (1964), even though this author recognized that he had not seen the type specimen and his treatment for South American taxa was based on quite scarce material. The delimitation of species used here follows the morphological cluster species concept (Mallet 1995) in combination with the distinctive geographical range of distribution. Such combinations of properties are useful lines of evidence for assessing the divergence and delimitation of lineages (de Queiroz 2007).

The factors that contributed to optimizing the taxonomy of *Physematium* from the Southern Cone were: (1) increased sampling in areas that are difficult to access; (2) evaluation of a greater number of characters with taxonomic value, previously tested in phylogenetic studies (Lu & al. 2020); (3) spores of *P. jujuiense*, *P. montevidense* and *P. pallidum* could be easily discerned among the three species, due to the size of the reticule and the coloration of the perispore, and *P. hieronymi* is distinguished by the absence of folds.

Castro (2004) analysed with LM and SEM the spores of three species of *Woodsia* (= *Physematium*) from the Southern Cone. She emphasized that two palynological groups can be distinguished, represented by *W. jujuiensis* (= *P. jujuiense*) on the one hand and *W. montevidensis* (= *P. montevidense*) and *W. pallida* (= *P. pallidum*) on the other. Although all three species analysed by Castro have a folded-reticulate perispore, *P. jujuiense* differs from the others by having a surface with perforations. However, we observed that *P. jujuiense* has small perforations and *P. montevidense* has a microreticle with a densely perforated structure. Likewise, *P. pallidum* has no perforations.

Furthermore, the observed differences in spore size of *Physematium* species would likely be strongly related to different ploidy levels. Since polyploidization can increase both genome size and chromosome number, it has been hypothesized that repetitive polyploidization events, together with possible changes in chromosome composition, explain the evolution of chromosomes and genomes (Wang & al. 2022) and advantage species diversity in ferns (Fujiwara & al. 2021). Because spore size varies significantly between closely related species of different ploidy levels (Barrington & al. 2020), the observed spore size differences among *Physematium* species suggested that their diversification, particularly in the arid environments of the South American Transition Zone, apparently involves polyploidization.

Author contributions

M. M. Ponce performed the taxonomic reviews and the morphological analyses. D. A. Gorrer provided the palynological images and descriptions. M. D. Arana performed fieldwork, taxonomic reviews and morphological and biogeographical analyses. All authors participated in the interpretation of the data and in the preparation and writing of the final version of the manuscript.

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