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Original article

The Ferns of the Calilegua National Park: a look through their spores. Part I

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ABSTRACT

Calilegua National Park is located in the Southeast of the province of Jujuy, Argentina. It is comprised of different districts within the Yungas Biogeographic Province, where conditions are optimal for fern development. The palynological studies with light microscopy in this area are very limited. The aim of this work is to present the morphology of spores from 42 taxa belonging to 9 families of isosporate ferns that grow in this protected area. The study was carried out with herbarium material. The families studied are Anemiaceae, Aspleniaceae, Athyriaceae, Blechnaceae, Cyatheaceae, Cystopteridaceae, Dennstaedtiaceae, Dryopteridaceae, and Equisetaceae. According to the spore aperture type, 35 taxa are monolete, five trilete, and two alete. The spores are yellowish, light to dark brown or brown greenish. The largest spores belong to *Anemia australis* and the smallest to *Asplenium argentinum*. Equinate, folded, cristate, alate, reticulate, ridged, psilate, verrucate, and baculate spores were observed. For the first time, the spores of 27 species are illustrated under a light microscope. An identification key of the spores is also provided. The morphological characteristics of the spores allowed for the identification of 23 species, contributing to spore bank analysis, aeropalynological and paleopalynological studies, and taxonomic identifications.

Keywords: Atlas; Calilegua National Park; Isosporate ferns; Palynology; Spores.

Introduction

Calilegua National Park (CNP) is located in the Southeast of the province of Jujuy, Argentina, between 23°27' and 23°56' S latitude and between 64°33' and 65°02' W longitude (Torres *et al.* 2008). It was established in 1979 and has 76306 hectares that comprise different districts of the Yungas Biogeographic Province (Ganem *et al.* 2013a). According to Arana *et al.* (2021), there are 3 districts. The Transition Jungle (elevation: 350-600m) has an annual rainfall record of 700 mm. The Mountain Jungle (elevation: 500-1500m) corresponds to the lower part of the mountain slopes, with rainfall that reaches up to 3000mm per year, an addition to the humidity produced by mists. Lastly, the Montane Forest district (elevation: 1200-2500m) has an annual rainfall of 400mm that is limited to the summer season. The climate

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in CNP is subtropical mountain with a dry winter season. Average temperatures range from 28 °C in summer to 17 °C in winter; absolute maximum records of 40 °C indicate hot summers (National Parks [Parque Nacional Calilegua], s.f.).

These environmental conditions are optimal for the development of ferns and lycophytes (Ponce *et al.* 2002) and given that up to 40-50% of the country's species diversity is confined to less than 2% of the Argentine national territory, these environments are of great importance in terms of biodiversity (Arana *et al.* 2021). Therefore, they have been included by UNESCO within the World Biosphere Reserves (Ganem *et al.* 2013a).

Given the disturbance of practically all known ecosystems, due to physiognomic changes in the landscape from human activity, Torres *et al.* (2008) affirm that it is very important to increase knowledge about biodiversity. As a result, it has become evident in recent years that it is necessary to carry out surveys in order to know what there is, with the purpose of implementing tasks for conservation. In this sense, some taxa that grow in the CNP and are endemic to the Yungas have been classified as threatened by Giudice *et al.* (2011), such as *Alsophila odonelliana* (Cyatheaceae), *Asplenium argentinum* (Aspleniaceae), *Austroblechnum squamipes*, *Lomariocycas moritziana* (=*Lomariocycas yungensis*) (Blechnaceae), *Diplazium lilloi* (Athyriaceae), and *Elaphoglossum crassipes* (Dryopteridaceae).

The following palynological atlases offer a great reference for paleopalynological, aeropalynological, and forensic studies, among others (Farfán-Santillán *et al.* 2016). For the Neotropics, the studies carried out by Heusser (1971) in Chile, Contreras-Duarte *et al.* (2006) in Colombia, Coelho and Esteves (2008) and Lebrão *et al.* (2014) in Brazil, and Gorrer *et al.* (2021) and Di Pasquo *et al.* (2016) for Argentina, are of importance.

According to Ganem *et al.* (2013a), there have been numerous floristic and survey studies carried out in CNP, although palynological studies are relatively limited. The studies that focus on the palynology of ferns from Northwest Argentina (NWA) focus on genera or families and were mostly performed using scanning electron microscopy (SEM) (Morbelli & Giudice 2005; Marquez *et al.* 2009; Ramos Giacosa *et al.* 2009; 2012; Ganem *et al.* 2013b). However, in these studies, the spores were not described nor illustrated using a light microscope (LM).

For Argentina, Zuloaga *et al.* (2019) cite 397 fern taxa, while for CNP, 100 taxa are cited (Ganem *et al.* 2013a; 2014; 2016; Arana *et al.* 2016; 2017; Jaimez & Martínez 2016). The spores of about 40 of these taxa have been illustrated using SEM in the previously mentioned works and only about 25 with LM (Contreras-Duarte *et al.* 2006; Coelho & Esteves 2008; Gómez-Noguez *et al.* 2013; Gorrer *et al.* 2021). Therefore, of the fern spores that inhabit CNP, approximately 60% and 75% have not yet been illustrated using SEM and LM, respectively.

The aim of this work is to provide the spore morphology of 42 taxa belonging to nine isosporate ferns families that grow in the CNP, mainly through LM analysis, as a contribution to aeropalynological, paleopalynological, and systematic studies of Neotropical ferns.

Materials and methods

The families studied are Anemiaceae, Aspleniaceae, Athyriaceae, Blechnaceae, Cyatheaceae, Cystopteridaceae, Dennstaedtiaceae, Dryopteridaceae and Equisetaceae.

The study was carried out with herbarium material from the following Argentine institutions: LP, JUA, LIL, MCNS, RCV and SI (Thiers 2022) (Table 1). When specimens from the CNP area were found to be infertile or with insufficient numbers of spores, herbarium specimens from other locations were selected. Material of only three species could not be obtained: *Megalastrum ciliatum* M. Kessler & A.R. Sm., *Elaphoglossum lorentzii* (Hieron.) H. Christ (Dryopteridaceae) and *Diplazium divergens* Rosenst. (Athyriaceae).

The spores were studied with LM and after the analysis with LM five species were selected as representative for the study with SEM.

For the analysis with LM, the material was acetolized according to the method of Erdtman (1960). For the study with SEM, the spores without treatment were placed into stubs with adhesive double-faced tape and coated with gold.

The observations were made with a Leica DM500 with Leica ICC50 digital camera incorporated from Laboratorio de Palinología, Facultad de Ciencias Agrarias, Universidad Nacional de Jujuy and with SUPRA 55VP SEM from Centro Integral de Microscopía Electrónica (CONICET- UNT).

The characteristics analyzed were: color, shape, equatorial and polar diameters, laesura length and ornamentation. The measurements of the spores were estimated on 20 spores in each sample.

The terminology proposed by Punt *et al.* (2007) and Tryon and Lugardon (1991) was used for the descriptions of the spores.

Results

Measurements of the spores are given in Table 2.

Descriptions of the spores

ANEMIACEAE

Anemia australis: Fig. 1A-C

Aperture: trilete; Color: brown; Shape in equatorial view: Convex/hemisferic; Amb: Triangular, convex sides and prominent angles; Ornamentation: Parallel ridges separated by narrow grooves, echinulate surface.

Anemia herzogii: Fig. 1D-F

Aperture: trilete; Color: Light brown; Shape in equatorial view: Plane-convex/convex; Amb: Subglobose to triangular,

Table 1. Material studied. COL AND N. C.: collector and number collection; HERB.: herbaria.

FAMILY	TAXA	COL. AND N.C.	HERB.	ORIGIN
Anemiaceae	*Anemia australis* (Mickel) M. Kessler & A.R. Sm.	Larsen & Arana 134	SI	Jujuy, PN Calilegua, Descendiendo desde el Monolito hacia Mesada de las Colmenas, 23°40'58''S-64°54'04''W, 1720 snmn
Anemiaceae	*Anemia herzogii* Rosenst.	Ramos Giacosa et al. 36	LP	Jujuy, PN Calilegua, Sendero Tataupá
Anemiaceae	*Anemia phyllitidis* var. *phyllitidis* (L.) Sw.	Ramos Giacosa 117	LP	Jujuy, PN Calilegua, Mesada de las Colmenas, Sendero de la Cascada, 1100 msnm
Aspleniaceae	*Asplenium argentinum* Hieron.	Ramos Giacosa et al. 49	LP	Jujuy, PN Calilegua, Sendero Tataupá
Aspleniaceae	*Asplenium auritum* Sw.	Larsen & Arana 130	RCV	Jujuy, PN Calilegua, Sendero que une el camino principal con Arroyo El Negrito (Sendero 4), 23°44'20''S-64°51'14''W, 758 msnm
Aspleniaceae	*Asplenium claussenii* Hieron.	Ganem et al. 17	LP	Jujuy, PN Calilegua, Zona pozos de petróleo, yacimiento El Caimancito
Aspleniaceae	*Asplenium cuspidatum* Lam.	Ganem et al. 29	LP	Jujuy, PN Calilegua, Camino a Mesada de las Colmenas
Aspleniaceae	*Asplenium gilliesii* Hook.	Fabris 6968	LP	Jujuy, Valle Grande, Finca Pozuelos, a 6 km de Caspalá
Aspleniaceae	*Asplenium harpeodes* Kunze	Ganem 223	JUA	Jujuy, PN calilegua, Ledesma
Aspleniaceae	*Asplenium inaequilaterale* Willd.	Ramos Giacosa et al. 125	LP	Jujuy, PN Calilegua, Camino de Abra de las Cañas a Mesada de las Colmenas, 23°41'S-64°54'W, 1650 msnm
Aspleniaceae	*Asplenium lorentzii* Hieron.	Ganem et al. 32	LP	Jujuy, PN Calilegua, Camino a Mesada de las Colmenas
Aspleniaceae	*Asplenium monanthes* L.	Fabris, Crisci & Petriella 5933	LP	Jujuy, PN Calilegua, Serranía de Calilegua, Tolditos
Aspleniaceae	*Asplenium serra* Langsd. & Fisch.	Larsen & Arana 155	SI	Jujuy, PN Calilegua, Aguada de Tigre, 23°41'03''S-64°53'40''W, 1630 msnm
Aspleniaceae	*Asplenium squamosum* L.	Ganem et al. 31	LP	Jujuy, PN Calilegua, Camino a Mesada de las Colmenas
Athyriaceae	*Diplazium cristatum* (Desr.) Alston	Ahumada 7158 b	JUA	Jujuy, PN calilegua, Ledesma
Athyriaceae	*Diplazium lilloi* (Hicken) R.M. Tryon & A.F. Tryon	Ganem et al. 38	LP	Jujuy, PN Calilegua, Camino a Mesada de las Colmenas
Blechnaceae	*Austroblechnum squamipes* (Hieron.) Gasper & V.A.O. Dittrich	Ramos Giacosa et al. 37	LP	Jujuy, PN Calilegua, Aguada de Tigre
Blechnaceae	*Blecnhum laevigatum* Cav.	Zuloaga et al. 7548	LP	Jujuy, PN Calilegua, 1100 msnm
Blechnaceae	*Blechnum occidentale* L.	Ramos Giacosa 104	LP	Jujuy, PN Calilegua, Camino de Aguas Negras a Mesada de las Colmenas, 23°41'S-64°52'W, 1100 msnm
Blechnaceae	*Cranfilia caudata* (Baker) V.A.O. Dittrich & Gasper	Meyer 14034	LIL	Tucumán, Chicligasta, entre Puesto Las Pavas y Saladillo, 1000 m
Blechnaceae	*Lomariocycas moritziana* (Klotzsch) Gabriel y Galán & Vicent	Ramos Giacosa et al. 60	LP	Jujuy, PN Calilegua, Camino hacia Abra de las Cañas
Blechnaceae	*Parablechnum cordatum* (Desv.) Gasper & Salino	Ramos Giacosa et al. 45	LP	Jujuy, PN Calilegua, Camino hacia Abra de las Cañas
Cyatheaceae	*Alsophila odonelliana* (Alston) Lehnert	Vervoorst 440	LIL	Salta, Orán, A° El Negrito, afluente de Río Santa María, 846 msnm
Cystopteridaceae	*Cystopteris diaphana* (Bory) Blasdell	Larsen & Arana 142	RCV	Jujuy, PN Calilegua, Camino desde Monolito hacia Mesada de las Colmenas, 23°40'58''S-64°54'04''W, 1720 msnm
Dennstaedtiaceae	*Mucura globulifera* (Poir.) L.A. Triana & Sundue	Ganem et al. 14	LP	Jujuy, PN Calilegua, Zona pozos de petróleo, yacimiento El Caimancito
Dennstaedtiaceae	*Hypolepis poeppigii* (Kunze) R. Rodr.	Larsen & Arana 147	SI	Jujuy, PN Calilegua, Camino desde Monolito hacia Mesada de las Colmenas, 23°41'08''S-64°53'47''W, 1616 msnm
Dryopteridaceae	*Bolbitis serratifolia* (Mert. ex Kaulf.) Schott	Ramos Giacosa et al. 18	LP	Jujuy, PN Calilegua, Sendero Guaraní

Table 1. Cont.

FAMILY	TAXA	COL. AND N.C.	HERB.	ORIGIN
Dryopteridaceae	*Ctenitis submarginalis* (Langsd. & Fisch.) Ching	Capurro 229	LIL	Jujuy, PN Calilegua
Dryopteridaceae	*Dryopteris patula* (Sw.) Underw.	Larsen & Arana 146	RCV	Jujuy, PN Calilegua,Camino desde Monolito hacia Mesada de las Colmenas, 23°41'08''S-64°53'47''W, 1616 msnm
Dryopteridaceae	*Dryopteris wallichiana* (Spreng.) Hyl.	Ganem et al. 36	LP	Jujuy, PN Calilegua, Camino desde Monolito hacia Mesada de las Colmenas
Dryopteridaceae	*Elaphoglossum crassipes* (Hieron.) Diels	Ramos Giacosa et al. 67	LP	Jujuy, PN Calilegua,Aguada de Tigre
Dryopteridaceae	*Elaphoglossum gayanum* (Fée) T. Moore	Legname y Cuezzo 5932 c	LIL	Jujuy, Ledesma, RP n°3 camino a Valle Grande (10 km antes del Río Jordán)
Dryopteridaceae	*Elaphoglossum hybridum* (Bory) Brack.	Larsen & Arana 149	SI	Jujuy, PN Calilegua, Camino desde Monolito hacia Mesada de las Colmenas, 23°41'08''S-64°53'47''W, 1616 msnm
Dryopteridaceae	*Elaphoglossum sellowianum* (Klotzsch ex Kuhn) T. Moore	Ganem et al. 43	LP	Jujuy, PN Calilegua, Aguada de Tigre
Dryopteridaceae	*Elaphoglossum spathulatum* (Bory) T. Moore	Ganem et al. 38	LP	Jujuy, PN Calilegua, Camino a Mesada de las Colmenas
Dryopteridaceae	*Elaphoglossum yungense* de la Sota	Guantay 8	LIL	Tucumán, Chicligasta, La Banderita
Dryopteridaceae	*Megalastrum adenopteris* (C. Chr.) A.R. Sm. & R.C. Moran	Tolaba, Arentsen, Juárez & Acuña 5005	JUA	Jujuy, PN Calilegua, Área afectada a Yacimiento petrolífero Caimancito, próximo a Serranías de Socabón, 15-20 km NW Caimancito, 589 m, 23°38'28,3'' S 64°36'48,9'' W
Dryopteridaceae	*Megalastrum fugaceum* R.C. Moran, J. Prado & Sundue	Sleumer 2097	MCNS	Jujuy, PN Calilegua, Aguada de Tigre, RP83, 1600 msnm
Dryopteridaceae	*Polystichum montevidense* (Spreng.) Rosenst.	Ganem et al. 37	LP	Jujuy, PN Calilegua, Camino a Mesada de las Colmenas
Dryopteridaceae	*Polystichum platyphyllum* var. *platyphyllum* (Willd.) C. Presl	Ramos Giacosa et al. 43	LP	Jujuy, PN Calilegua, Sendero El Negrito
Equisetaceae	*Equisetum bogotense* Kunth	Rotman 727	JUA	Jujuy, PN calilegua, Ledesma
Equisetaceae	*Equisetum giganteum* L.	Filipovich 340	LIL	Salta, Rosario de Lerma, Campo Quijano, 1588 msnm

Table 2. Spore measurements. Dimensions in µm. MAED: Major Equatorial Diameter; MIED: Minor Equatorial Diameter; PD: Polar Diameter; LL: Laesura Length.

TAXA	MAED	MIED	PD	LL
Alsophila odonelliana	38 - 48	40 - 47	30 - 36	16 - 25
Anemia australis	76 - 91	70 - 91	65 - 77	28 - 42
Anemia herzogii	53 - 67	53 - 70	49 - 57	14 - 26
Anemia phyllitidis var. *phyllitidis*	54 - 74	56 - 70	49 - 65	17 - 28
Asplenium argentinum	28 - 35	21 - 29	23 - 33	11 - 21
Asplenium auritum	39 - 56	26 - 35	26 - 35	14 - 33
Asplenium claussenii	35 - 46	21 - 35	25 - 35	14 - 35
Asplenium cuspidatum	37 - 53	25 - 39	28 - 35	25 - 28
Asplenium gilliesii	31 - 42	25 - 33	25 - 32	17 - 34
Asplenium harpeodes	29 - 41	25 - 32	22 - 32	15 - 24
Asplenium inaequilaterale	32 - 46	23 - 35	23 - 35	18 - 35
Asplenium lorentzii	28 - 35	25 - 32	23 - 32	11- 25
Asplenium monanthes	37 - 53	33 - 42	28 - 42	21 - 32

Table 2. Cont.

TAXA	MAED	MIED	PD	LL
Asplenium serra	28 - 49	28 - 35	28 - 42	12 - 18
Asplenium squamosum	39 - 53	32 - 48	26 - 46	21 - 35
Austroblechnum squamipes	35 - 42	28 - 35	30 - 36	21 - 35
Blechnum laevigatum	35 - 42	23 - 30	25 - 31	21 - 32
Blechnum occidentale	35 - 49	25 - 32	25 - 33	18 - 32
Bolbitis serratifolia	30 - 46	25 - 39	22 - 35	23 - 28
Cranfilia caudata	33 - 42	24 - 32	24 - 31	25 - 34
Ctenitis submarginalis	28 - 49	24 - 43	21 - 44	11 - 43
Cystopteris diaphana	39 - 49	25 - 35	28 - 35	14 - 25
Diplazium cristatum	43 - 54	33 - 47	27 - 43	20 - 35
Diplazium lilloi	49 - 74	39 - 61	40 - 53	23 - 42
Dryopteris patula	40 - 54	28 - 40	30 - 40	18 - 32
Dryopteris wallichiana	39 - 57	27 - 37	29 - 39	22 - 36
Elaphoglossum crassipes	35 - 47	35 - 39	30 - 39	18 - 35
Elaphoglossum gayanum	43 - 58	33 - 44	32 - 43	24 - 34
Elaphoglossum hybridum	35 - 40	27 - 35	23 - 32	18 - 26
Elaphoglossum sellowianum	35 - 46	30 - 39	27 - 34	25 - 34
Elaphoglossum spathulatum	42 - 63	35 - 49	35 - 49	21 - 35
Elaphoglossum yungense	37 - 52	32 - 42	24 - 41	25 - 35
Equisetum bogotense	26 - 38			
Equisetum giganteum	45 - 53			
Hypolepis poeppigii	44 - 52	26 - 33	28 - 35	14 - 28
Lomariocycas moritziana	49 - 70	35 - 49	37 - 56	32 - 46
Megalastrum adenopteris	45 - 64	26 - 43	29 - 40	25 - 45
Megalastrum fugaceum	27 - 34	20 - 25	22 - 27	12 - 20
Mucura globulifera	32 - 40	32 - 42	21 - 28	11 - 14
Parablechnum cordatum	30 - 41	21 - 36	21 - 30	21 - 33
Polystichum montevidense	34 - 48	25 - 38	26 - 38	14 - 30
Polystichum platyphyllum var. *platyphyllum*	28 - 46	26 - 35	27 - 38	16 - 24

convex sides and and rounded angles; Ornamentation: Parallel and narrow ridges with high bacula, separated by wide grooves.

Anemia phyllitidis var. *phyllitidis*: Fig. 1G-I

Aperture: trilete; Color: Light brown; Shape in equatorial view: Plane-convex/convex; Amb: Subglobose to triangular, convex sides and and rounded angles; Ornamentation: Parallel and narrow ridges with high bacula, separated by wide grooves.

ASPLENIACEAE

Asplenium argentinum: Fig. 1J-L

Aperture: monolete; Color: brown; Shape in equatorial view: Plane/convex; Amb: Ellipsoidal/subcircular; Ornamentation: Alate-folded, short folds, echinulate margin, surface perforated between and on folds.

Asplenium auritum: Fig. 1M-O

Aperture: monolete; Color: dark brown; Shape in equatorial view: Plane/convex; Amb: ellipsoidal; Ornamentation: Alate-folded, long folds, smooth margin, surface perforated between folds.

Asplenium claussenii: Fig. 1P-R

Aperture: monolete; Color: light brown; Shape in equatorial view: Plane/convex; Amb: ellipsoidal; Ornamentation: Alate-folded, long folds, echinulate margin, surface perforated between folds.

Asplenium cuspidatum: Fig. 1S-U

Aperture: monolete; Color: dark brown; Shape in equatorial view: Plane/convex; Amb: ellipsoidal; Ornamentation: Alate-folded, long folds, smooth margin, surface perforated between folds.

Asplenium gilliesii: Fig. 1V-X

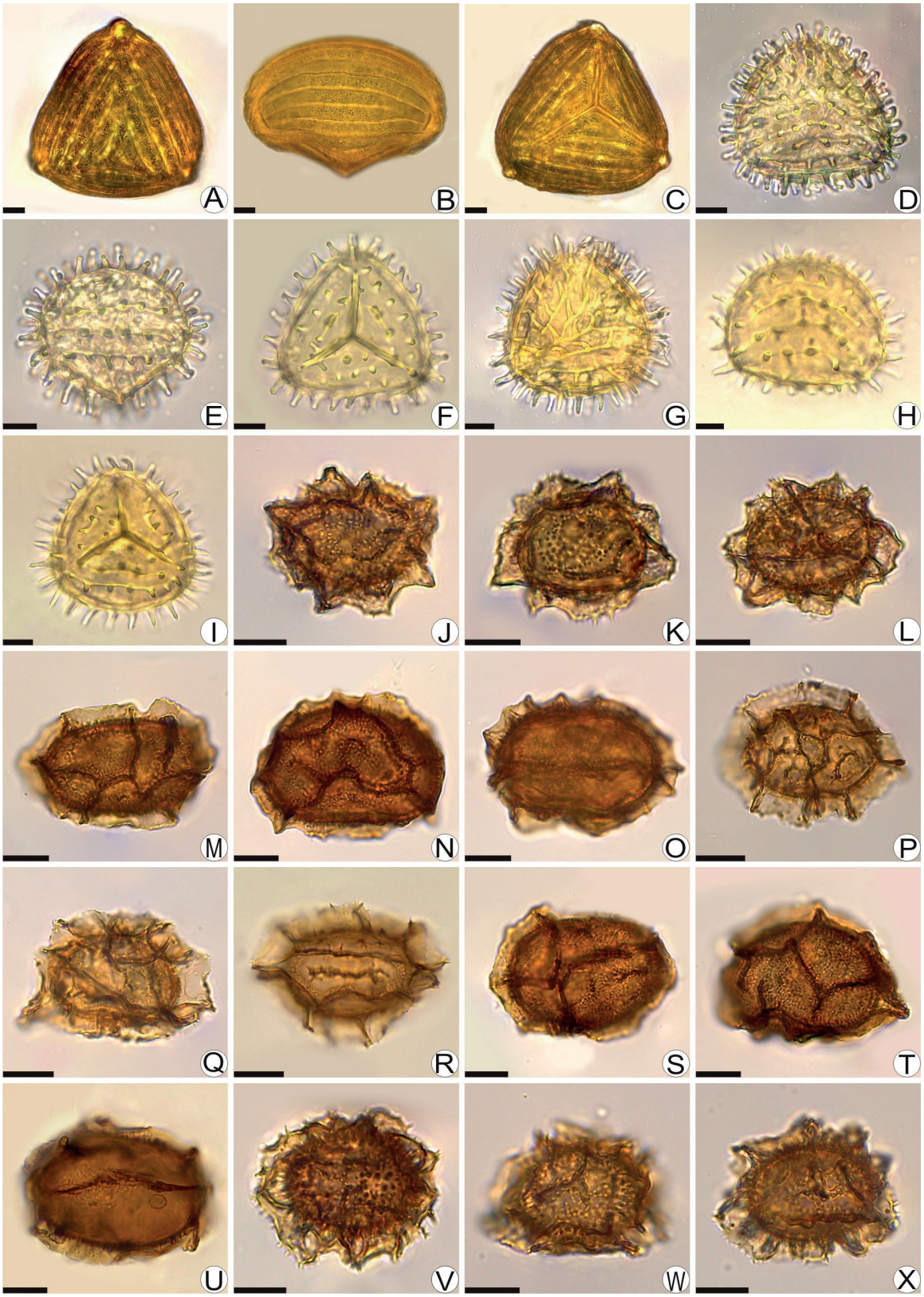

Figure 1. A-C: *Anemia australis*. Ridged with echinulate surface. **D-F**: *Anemia herzogii*. Ridged with baculae. **G-I**: *Anemia phyllitidis* var. *phyllitidis*. Ridged with baculae. **J-L**: *Asplenium argentinum*. Alate-folded with short folds and echinulate margin. **M-O**: *Asplenium auritum*. Alate-folded with long folds and smooth margin. **P-R**: *Asplenium claussenii*. Alate-folded with long folds and echinulate margin. **S-U**: *Asplenium cuspidatum*. Alate-folded with long folds and smooth margin. **V-X**: *Asplenium gilliesii*. Alate-folded with short folds and echinulate margin. Scale bar: 10 μm.

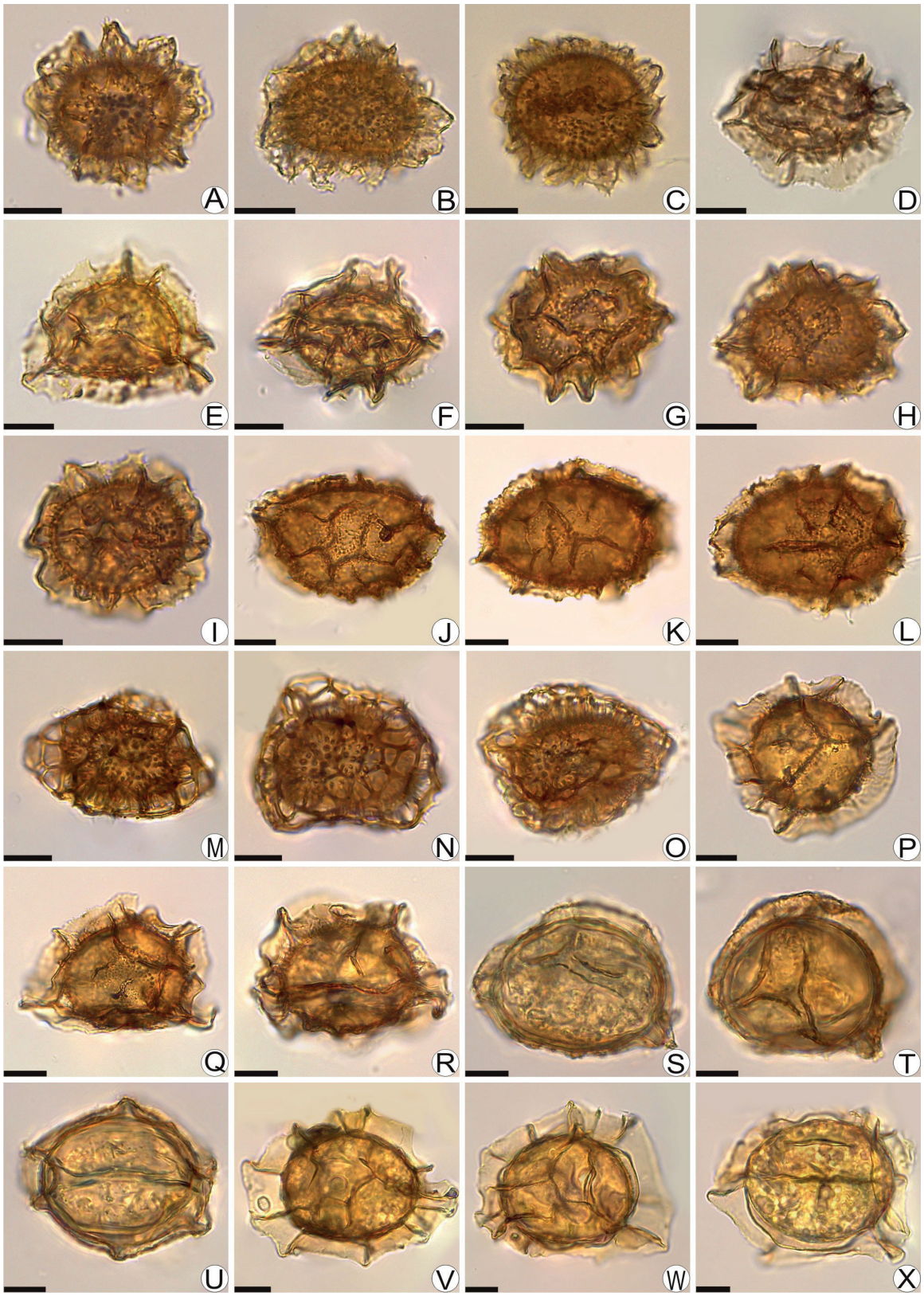

Figure 2. A-C: *Asplenium harpeodes*. Alate-folded with short folds and echinulate margin. **D-F**: *Asplenium inaequilaterale*. Alate-folded with long folds and echinulate margin. **G-I**: *Asplenium lorentzii*. Alate-folded with short folds and echinulate margin. **J-L**: *Asplenium monanthes*. Alate-folded with long folds and echinulate margin. **M-O**: *Asplenium serra*. Reticulate mesh supported by spines or baculae. **P-R**: *Asplenium squamosum*. Alate-folded with long folds and echinulate margin. **S-U**: *Diplazium cristatum*. Alate-folded. **V-X**: *Diplazium lilloi*. Alate-folded. Scale bar: 10 μm.

Aperture: monolete; Color: brown; Shape in equatorial view: Plane/convex; Amb: ellipsoidal/subcircular; Ornamentation: Alate-folded, short folds, echinulate margin, surface perforated between and on folds.

Asplenium harpeodes: Fig. 2A-C

Aperture: monolete; Color: brown; Shape in equatorial view: Plane/convex; Amb: ellipsoidal/subcircular; Ornamentation: Alate-folded, short folds, echinulate margin, surface perforated between and on folds.

Asplenium inaequilaterale: Fig. 2D-F

Aperture: monolete; Color: brown; Shape in equatorial view: Plane/convex; Amb: ellipsoidal; Ornamentation: Alate-folded, long folds, echinulate margin, surface perforated between folds.

Asplenium lorentzii: Fig. 2G-I; 7A-C

Aperture: monolete; Color: brown; Shape in equatorial view: Plane/convex; Amb: ellipsoidal/subcircular; Ornamentation: Alate-folded, short folds, echinulate margin, surface perforated between and on folds.

Asplenium monanthes: Fig. 2J-L

Aperture: monolete; Color: brown; Shape in equatorial view: Plane/convex; Amb: ellipsoidal; Ornamentation: Alate-folded, long folds, echinulate margin, surface perforated between folds.

Asplenium serra: Fig. 2M-O

Aperture: monolete; Color: brown; Shape in equatorial view: Plane/convex; Amb: ellipsoidal; Ornamentation: Reticulate mesh supported by spines or bacula.

Asplenium squamosum: Fig. 2P-R

Aperture: monolete; Color: light brown; Shape in equatorial view: Plane/convex; Amb: ellipsoidal/subcircular; Ornamentation: Alate-folded, long folds, echinulate margin, surface perforated between folds.

ATHYRIACEAE

Diplazium cristatum: Fig. 2S-U; 7D-E

Aperture: monolete; Color: brown; Shape in equatorial view: Plane/convex; Amb: Ellipsoidal/subcircular; Ornamentation: Alate-folded.

Diplazium lilloi: Fig. 2V-X

Aperture: monolete; Color: light brown; Shape in equatorial view: Plane/convex; Amb: Ellipsoidal/subcircular; Ornamentation: Alate-folded.

BLECHNACEAE

Austroblechnum squamipes: Fig. 3A-C

Aperture: monolete; Color: brown; Shape in equatorial view: Plane/convex; Amb: Ellipsoidal; Ornamentation: psilate.

Blechnum laevigatum: Fig. 3D-F

Aperture: monolete; Color: Light brown; Shape in equatorial view: Concave/convex; Amb: Oblong to ellipsoidal; Ornamentation: psilate.

Blechnum occidentale: Fig. 3G-I

Aperture: monolete; Color: brown; Shape in equatorial view: Plane/convex; Amb: ellipsiodal; Ornamentation: psilate.

Cranfillia caudata: Fig. 3J-L

Aperture: monolete; Color: brown; Shape in equatorial view: Plane/convex; Amb: ellipsoidal; Ornamentation: folded.

Lomariocycas moritziana: Fig. 3M-O

Aperture: monolete; Color: light brown; Shape in equatorial view: Plane/convex; Amb: ellipsoidal; Ornamentation: folded, narrow and low folds.

Parablechnum cordatum: Fig. 3P-R

Aperture: monolete; Color: brown/dark brown; Shape in equatorial view: Plane/convex; Amb: ellipsoidal; Ornamentation: folded.

CYATHEACEAE

Alsophilla odonelliana: Fig. 3S-U

Aperture: trilete; Color: yellow; Shape in equatorial view: Conic-convex/convex; Amb: Triangular, concave to straight sides and rounded angles; Ornamentation: cristate.

CYSTOPTERIDACEAE

Cystopteris diaphana: Fig. 3V-X

Aperture: monolete; Color: dark brown; Shape in equatorial view: Plane/convex; Amb: ellipsoidal; Ornamentation: echinate.

DENNSTAEDTIACEAE

Mucura globulifera: Fig. 4A-C

Aperture: trilete; Color: brown; Shape in equatorial view: plane/convex; Amb: Triangular, concave sides and rounded angles; Ornamentation: Verrucate-reticulate.

Hypolepis poeppigii: Fig. 4D-F; 7I-K

Aperture: monolete; Color: yellowish; Shape in equatorial view: plane/convex; Amb: ellipsoidal; Ornamentation: Baculate-cristate.

DRYOPTERIDACEAE

Bolbitis serratifolia: Fig. 4G-I

Aperture: monolete; Color: brown; Shape in equatorial view: Plane/hemisferic; Amb: globose; Ornamentation: folded.

Ctenitis submarginalis: Fig. 4J-L

Aperture: monolete; Color: light brown; Shape in equatorial view: Plane/convex; Amb: ellipsoidal; Ornamentation: folded, short and subglobose folds.

Dryopteris patula: Fig. 4M-O

Aperture: monolete; Color: dark brown; Shape in equatorial view: Plane/convex; Amb: Ellipsoidal; Ornamentation: Folded, coarse folds fusionated partially.

Dryopteris wallichiana: Fig. 4P-R

Aperture: monolete; Color: brown; Shape in equatorial view: Plane/convex; Amb: Ellipsoidal; Ornamentation: Folded, narrow folds fusionated partially.

Elaphoglossum crassipes: Fig. 4S-U

Aperture: monolete; Color: brown; Shape in equatorial view: Plane/convex; Amb: Ellipsoidal; Ornamentation: Folded, narrow folds fusionated partially.

Elaphoglossum gayanum: Fig. 4V-X

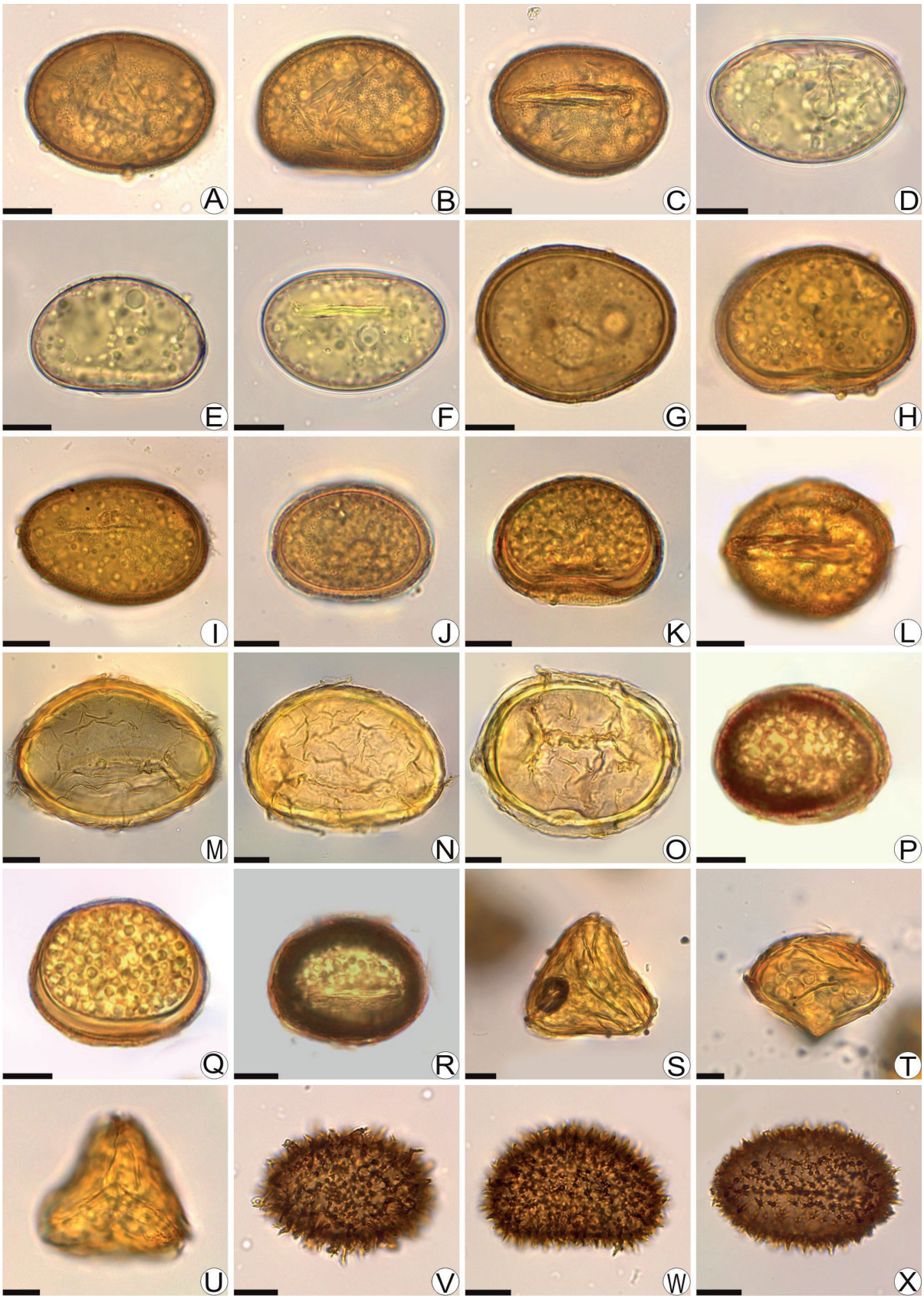

Figure 3. A-C: *Austroblechnum squamipes*. Psilate. **D-F**: *Blechnum laevigatum*. Psilate. **G-I**: *Blechnum occidentale*. Psilate. **J-L**: *Cranfillia caudata*. Folded. **M-O**: *Lomariocycas moritziana*. Folded, with narrow and low folds. **P-R**: *Parablechnum cordatum*. Folded. **S-U**: *Alsophila odonelliana*. Cristate. **V-X**: *Cystopteris diaphana*. Echinate. Scale bar: 10 µm.

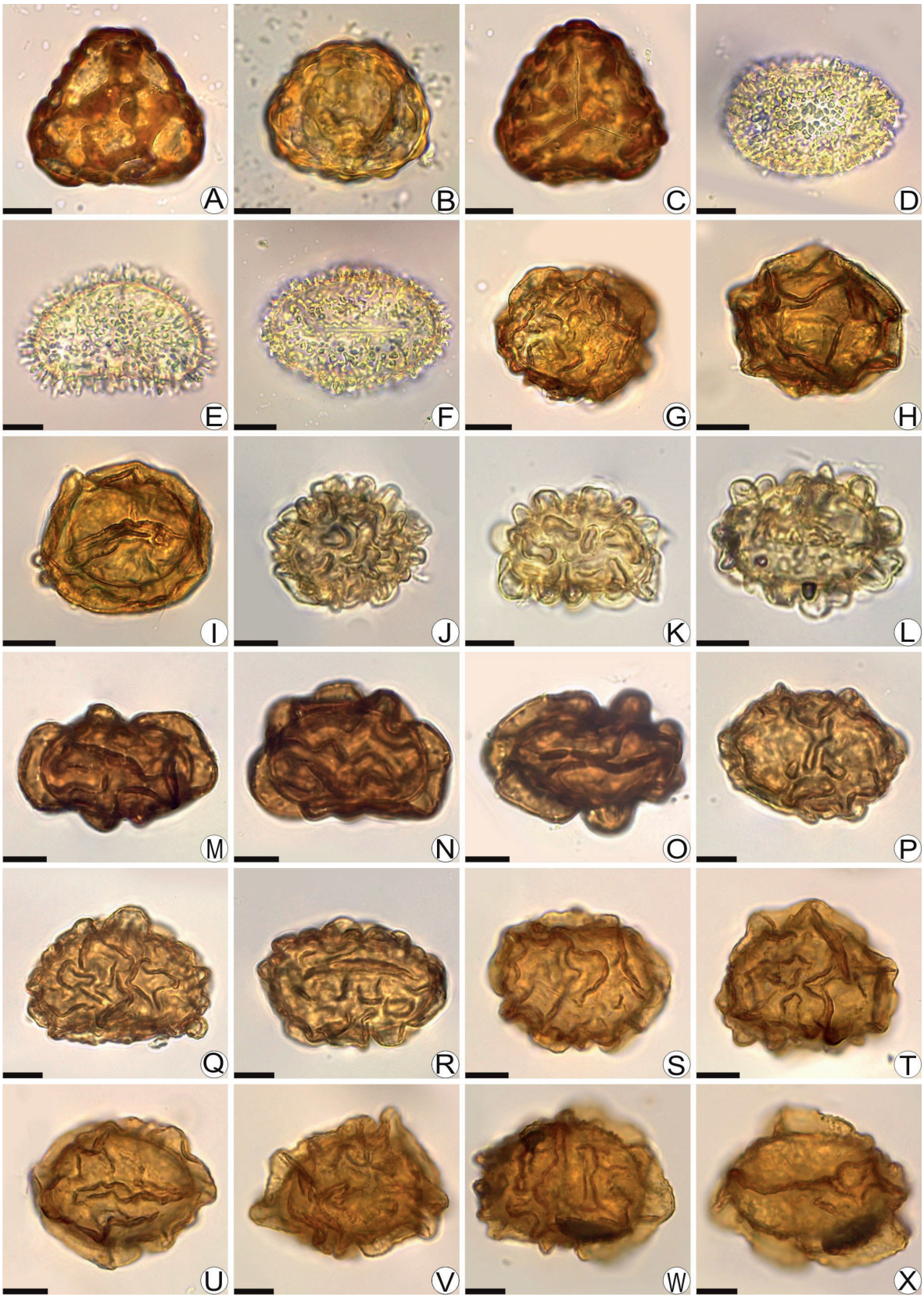

Figure 4. A-C: *Mucura globulifera*. Verrucate-reticulate. **D-F**: *Hypolepis poeppigii*. Baculate-cristate. **G-I**: *Bolbitis serratifolia*. Folded. **J-L**: *Ctenitis submarginalis*. Folded, with short and subglobose folds. **M-O**: *Dryopteris patula*. Folded, coarse folds fusionated partially. **P-R**: *Dryopteris wallichiana*. Folded, narrow folds fusionated partially. **S-U**: *Elaphoglossum crassipes*. Folded, narrow folds fusionated partially. **V-X**: *Elaphoglossum gayanum*. Folded, narrow echinulate surface. Scale bar: 10 µm.

Aperture: monolete; Color: brown; Shape in equatorial view: Plane/convex; Amb: Ellipsoidal; Ornamentation: Folded, narrow echinulate surface.

Elaphoglossum hybridum: Fig. 5A-C

Aperture: monolete; Color: brown; Shape in equatorial view: Plane/convex; Amb: Ellipsoidal; Ornamentation: Folded, narrow folds fusionated partially.

Elaphoglossum sellowianum: Fig. 5D-F; 7F-H

Aperture: monolete; Color: brown; Shape in equatorial view: Plane/convex; Amb: Ellipsoidal; Ornamentation: Folded, narrow folds fusionated partially.

Elaphoglossum spathulatum: Fig. 5G-I

Aperture: monolete; Color: dark brown; Shape in equatorial view: Plane/convex; Amb: Ellipsoidal/subcircular; Ornamentation: Folded, narrow echinulate surface.

Elaphoglossum yungense: Fig. 5J-L

Aperture: monolete; Color: brown; Shape in equatorial view: Plane/convex; Amb: Ellipsoidal/subcircular; Ornamentation: Folded, narrow folds fusionated partially.

Megalastrum adenopteris: Fig. 6A-C; 7L-N

Aperture: monolete; Color: brown; Shape in equatorial view: Plane-concave/convex; Amb: ellipsoidal; Ornamentation: Folded, reticulate surface.

Megalastrum fugaceum: Fig. 6D-F

Aperture: monolete; Color: light brown; Shape in equatorial view: Plane/convex; Amb: Oblong; Ornamentation: echinate.

Polystichum montevidense: Fig. 6G-I

Aperture: monolete; Color: dark brown; Shape in equatorial view: Plane/convex; Amb: ellipsoidal; Ornamentation: Alate-folded, echinulate surface.

Polystichum platyphyllum var. Platyphyllum: Fig. 6J-L

Aperture: monolete; Color: brown; Shape in equatorial view: Plane/convex; Amb: ellipsoidal; Ornamentation: Folded, short and subglobose folds.

EQUISETACEAE

Equisetum bogotense: Fig. 6M-N

Aperture: alete; Color: brown greenish; Shape in equatorial view: globose; Amb: globose; Ornamentation: Psilate with elaters.

Equisetum giganteum: Fig. 6O-P

Aperture: alete; Color: brown greenish; Shape in equatorial view: globose; Amb: globose; Ornamentation: Psilate with elaters.

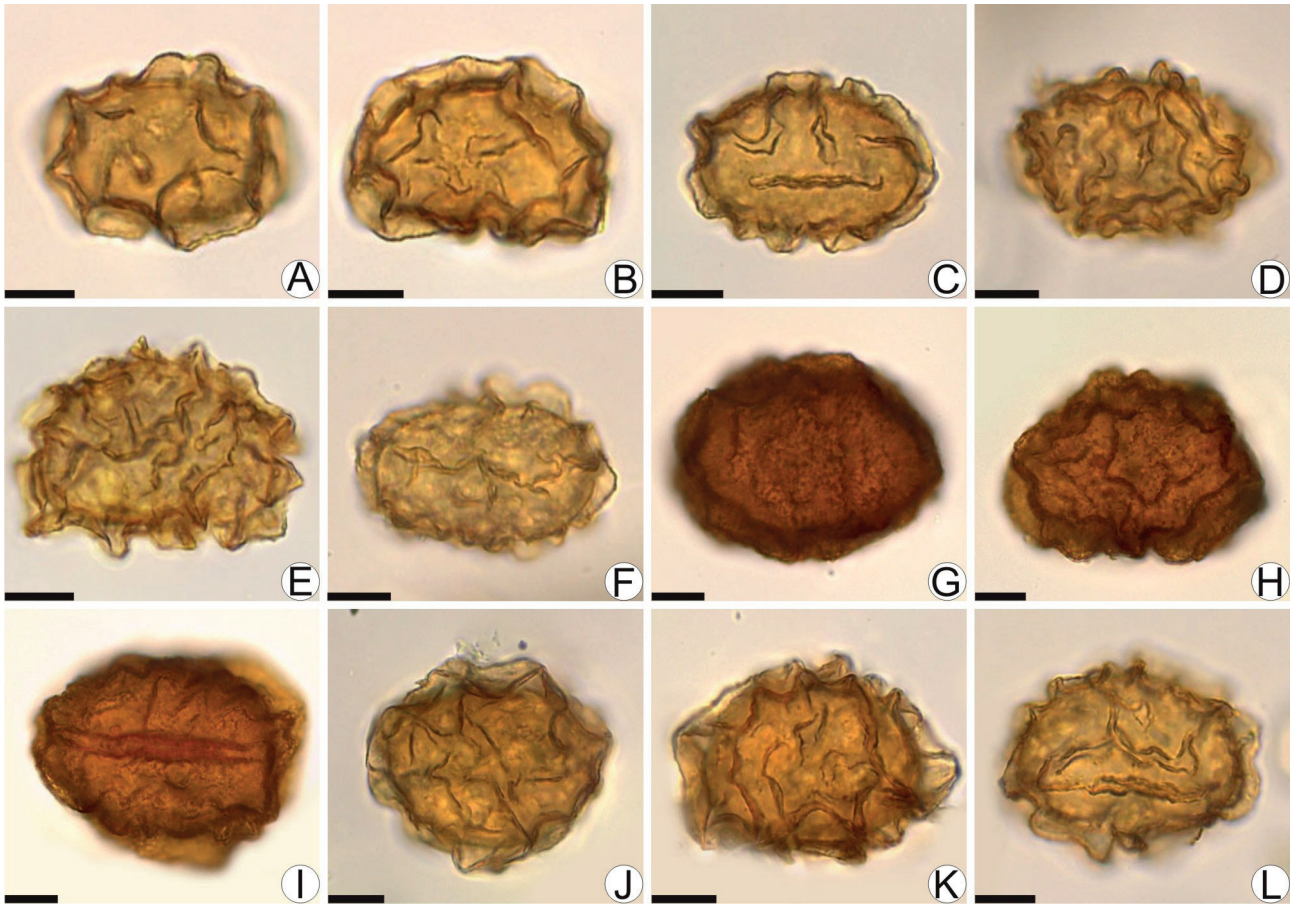

Figure 5. A-C: *Elaphoglossum hybridum*. Folded, narrow folds fusionated partially. **D-F**: *Elaphoglossum sellowianum*. Folded, narrow folds fusionated partially. **G-I**: *Elaphoglossum spathulatum*. Folded, narrow folds echinulate surface. **J-L**: *Elaphoglossum yungense*. Folded, narrow folds fusionated partially. Scale bar: 10 μm.

Spore identification key

1. Alete spores, with elaters 2
1'. Monolete or trilete spores, without elaters 3
2. Spores smaller than 40 µm ..... *Equisetum bogotense*
2'. Spores larger than 40 µm ..... *Equisetum giganteum*
3. Trilete spores 4
3'. Monolete spores 7
4. Parallel and wide ridges separated by narrow grooves 5
4'. Verrucae or narrow cristae 6
5. Ridges with echinulate surface, without baculae ..... *Anemia australis*
5'. Parallel and narrow ridges with high baculae ..... *Anemia herzogii/Anemia phyllitidis*
6. Cristate and yellowish spores ..... *Alsophila odonelliana*
6'. Verrucate and brownish spores ..... *Mucura globulifera*
7. Echinate, baculate or psilaxte spores 8
7'. Folded or reticulate spores 12
8. Psilate ornamentation 9
8'. Echinate or baculate ornamentation 10
9. Light brown spores ..... *Blechnum laevigatum*
9'. Dark brown spores ..... *Austroblechnum squamipes/Blechnum occidentale*
10. Ornamentation formed by baculae that can fuse and form short ridges, spores yellowish ..... *Hypolepis poeppigii*
10'. Ornamentation formed by echinae that cannot fuse, spores brown 11
11. Light brown spores, MAED up to 34 µm ..... *Megalastrum fugaceum*
11'. Dark brown spores, MAED greater than 39 µm ..... *Cystopteris diaphana*
12. Reticulate mesh supported by spines or bacula, spores brown ..... *Asplenium serra*
12'. Folded ornamentation 13
13. Short, subglobose and inflated folds 14
13'. Alate or narrow folds, never inflated or subglobose folds 15
14. Light brown spores ..... *Ctenitis submarginalis*
14'. Brown to dark brown spores ..... *Polystichum platyphyllum* var. *platyphyllum*
15. Alate folds with perforations between and on folds 16
15'. Other type of folds without perforations 19
16. Short folds with echinulate margin ..... *Asplenium argentinum/ Asplenium gilliesii/ Asplenium harpeodes/ Asplenium lorentzii*
16'. Long folds, with echinulate or smooth margin 17
17. Echinulate margin 18
17'. Smooth margin, MAED can exceed 50 µm ..... *Asplenium auritum/Asplenium cuspidatum*
18. Light brown spores ..... *Asplenium inaequilaterale/ Asplenium claussenii/ Asplenium squamosum*
18'. Brown to dark brown spores ..... *Asplenium monanthes*
19. Folds with echinulate surface 20
19'. Folds without echinulate surface 22
20. Light brown spores ..... *Elaphoglossum gayanum/ Diplazium cristatum*
20'. Dark brown spores 21
21. High and narrow folds, alated type, with MAED 34-48 µm ..... *Polystichum montevidense*
21'. Low and narrow folds, not alated type, with MAED 42-63 µm ..... *Elaphoglossum spathulatum*
22. Folds full fused to form complete reticles 23
22'. Folds partially fused without forming complete reticles 24
23. Heterobrochate reticles, with small brochi or lumina of different sizes ..... *Megalastrum adenopteris*
23'. Homobrochate reticles, with big brochi or lumina of similar sizes ..... *Parablechnum cordatum*
24. Coarse and wide folds, dark brown spores ..... *Dryopteris patula*
24'. Folds never coarse and wide, brown to light brown spores 25
25. High and compressed folds, notoriously alate type, up to 10 µm high ..... *Diplazium lilloi*
25'. Narrow and low folds, if high they never exceed 7 µm ..... *Bolbitis serratifolia/ Cranfillia caudata/ Dryopteris wallichiana/ Elaphoglossum crassipes/ Elaphoglossum hybridum/ Elaphoglossum sellowianum/ Elaphoglossum yungense/ Lomariocycas moritziana*

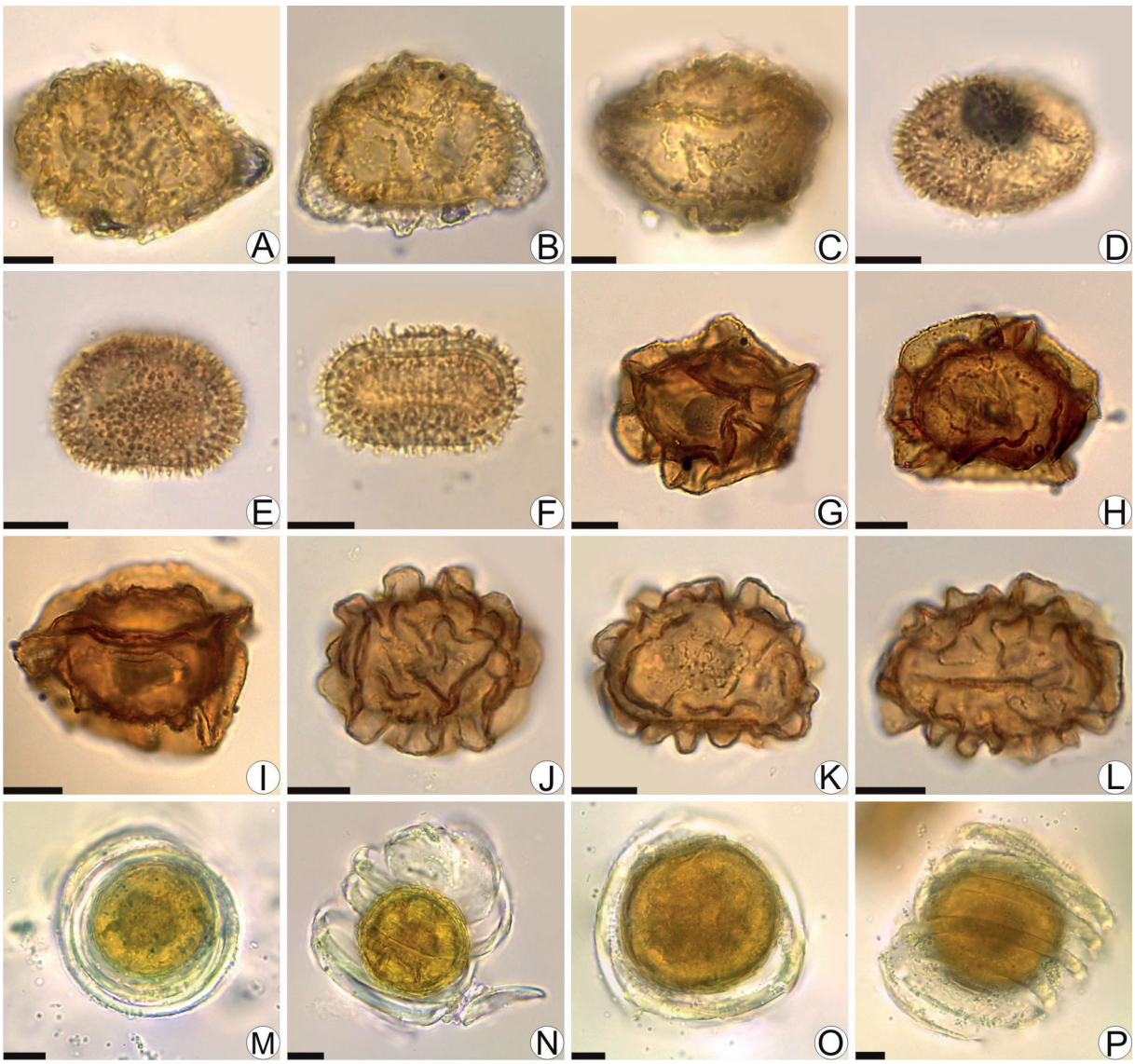

Figure 6. A-C: *Megalastrum adenopteris*. Folded, reticulate surface. **D-F**: *Megalastrum fugaceum*. Echinate. **G-I**: *Polystichum montevidense*. Alate-folded, echinulate surface. **J-L**: *Polystichum platyphyllum* var. *platyphyllum*. Folded, short and subglobose folds. **M-N**: *Equisetum bogotense*. Psilate with elaters. **O-P**: *Equisetum giganteum*. Psilate with elaters. Scale bar: 10 μm.

Discussion

ANEMIACEAE

The ornamentation observed here for the genus *Anemia* is the same that Ramos Giacosa *et al.* (2012) observed. These authors analyzed the same three species that we analyzed here but they did not illustrate them with LM. The only difference found is in the longer size of equatorial diameter of *A. phyllitidis* var. *phyllitidis* (42-55 vs. 54-74μm). The authors cited material from Jujuy (Yungas Biogeographic Province) but also from Misiones (Paranaense Biogeographic Province), so the difference could be due to this geographical disjunction.

ASPLENIACEAE

Ganem (2018) and Ganem *et al.* (2013b; 2014) analyzed and illustrated with SEM the spores of *Asplenium* from Argentina. They recognized a folded perispore with variability in the density of perforations and the margin of the folds that may be smooth, jagged, or echinulate. We agree with the authors that the spores of the genus present a folded perispore and that the folds are alate type, except *A. serra* wich has a reticulate perispore. However, regarding the margin of the folds, we did not make a difference between jagged or echinulate, since the LM magnification (1000x) did not allow us to differentiate between teeth and echinulae.

Regarding the relationship between the perispore and the size of the plants, in this study it is observed that the epiphytic species present particular spores, dark brown in color with long folds and a smooth margin (*A. auritum* and *A. cuspidatum*) or reticulated mesh (*A. serra*), which agrees with Ganem (2018).

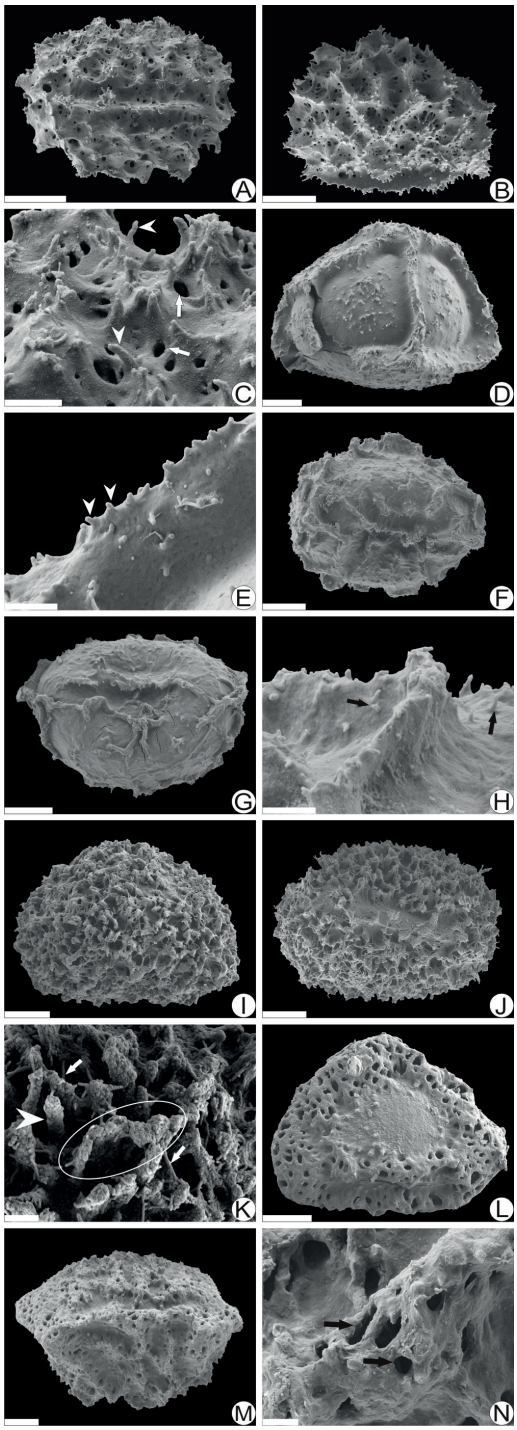

Figure 7. A-C: *Asplenium lorentzii*. **A**) Proximal view. **B**) Ecuatorial view. **C**) Perispore surface. The arrowheads show echinulae and the arrows the perforations. **D-E**: *Diplazium cristatum*. **D**) Equatorial view. **E**) Perispore surface. The arrowheads show echinulae. **F-H**: *Elaphoglossum sellowianum*. **F**) Distal view. **G**) Proximal view. **H**) Perispore surface. The arrows show echinulae. **I-K**: *Hypolepis poeppigii*. **I**) Equatorial view. **J**) Proximal view. **K**) Perispore surface. The arrowead show bacula. The baculae is formed by threads (arrows). The ellipse shows crest. **L-N**: *Megalastrum adenopteris*. **L**) Equatorial view. **M**) Proximal view. **N**) Perispore surface. Perforation-like opening formed by the dense reticulum (arrows).Scale bar: A-B, D, F-G, I-J, L-M: 10 µm; E, H, K, N: 2 µm; C: 0.2 µm.

ATHYRIACEAE

Spores of *Diplazium* species growing in Argentina have not been illustrated with LM or SEM until now. Other American species have been analyzed with SEM by Tryon and Lugardon (1991) and those analyzed by these authors presented a minimum size of the MAED 16 µm smaller than those analized here. However, the ornamentation of *D. lilloi* and *D. cristatum* described here coincides with what was mentioned by these authors, in which they have prominent wing-like folds.

BLECHNACEAE

Melo da Silva *et al.* (2019) illustrated *A. squamipes* from Brazil with LM and SEM. They describe it with psilate ornamentation, just as we have observed it here.

L. moritziana from Jujuy was illustrated with SEM and LM by Ramos Giacosa (2019). He affirms that the spores of this species present a folded ornamentation, and the folds partially merge, forming an incomplete reticle. Here we observe that the spores present low and narrow rugulate folds, which can fuse patially, as mentioned this author. An even more noticeable difference with the spores analyzed by Ramos Giacosa (2019) is that ours presented a MAED up to 25 µm lower (49-70 vs. 82-95µm). This variation could be due to hybridization and polyploidy issues, which are very recurrent throughout the family, and do not provide a useful tool to differentiate subfamilies or genera, much less at a specific level (Melo da Silva *et al.* 2021).

According to Melo da Silva *et al.* (2019) the Brazilian specimens of *Cranfillia caudata* have narrow and smooth ridges that form thin reticles. Passarelli *et al.* (2010) described Argentinian specimens of *C. caudata* (= *Blechnum sprucei*) with a folded perispore. Here it has been observed that have very low rugulae, even almost imperceptible, but there are no ridges or folds that could form reticles. The closest thing to what we observed is what Ramos Giacosa *et al.* (2009), where with SEM they illustrate spores that have a few folds and a smoothly rugulate surface.

Parablechnum cordatum (= *Blechnum cordatum*) was illustrated by Ramos Giacosa *et al.* (2009) with SEM and by Melo da Silva *et al.* (2019) with SEM and LM. The spores analyzed here do not agree with the description mentioned by these authors, probably due to a failure in the acetolysis. Spores of various colors were found with the same degree of maturation and without evidence of folds, but of very low rugulas, barely perceptible. Although in the equatorial view a supralesural fold can be seen, as affirm Contreras-Duarte *et al.* (2006).

CYATHEACEAE

The type of ornamentation and the measurements of *A. odonelliana* found here are similar to those described by Marquez *et al.* (2009), with large and parallel ridges. In addition, these authors affirm that the edges of the crests are echinulate. We could not observe the latter, since we used LM and they used SEM.

CYSTOPTERIDACEAE

Arana and Mynssen (2015) illustrated with SEM the spores of *C. diaphana* with material from Brazil. In agreement with the authors, the spores analyzed here, with Argentine material, the sculpture and the color are the same, echinate and dark brown.

DENNSTAEDTIACEAE

Martínez *et al.* (2014) illustrated with SEM the spores of *Hypolepis poeppigii* and *Mucura globulifera*. They say that the spores of first species have echinae that are partially fused; while the second has verrucae. Yañez (2015) observed that the spores of *M. globulifera* seen with LM present verrucae that partially merge. These fused verrucae give a darker appearance compared to verrucae that are not fused. The same characteristic has been observed in the photos illustrated by us. The small differences in size (between 5-11µm) could be due to a geographical disjunction since the measurements were taken based on samples from different phytogeographic provinces.

As for the spores of *H. poeppigii* observed here, they present baculae that can fuse laterally forming short ridges, unlike what was observed by Martínez *et al.* (2014). In our SEM illustrations, the baculae are formed by cords that branch and merge with each other and that these cords, in turn, are formed by globose structures, such as spherules. A similar ornamentation was described by Yañez (2015) for other species of the genus *Hypolepis* for northeastern Argentina.

DRYOPTERIDACEAE

Chambi *et al.* (2013) illustrated the spores of *Polystichum motevidense* with SEM, where it can be seen that they present inflated folds, with an equinulate surface, as has been observed here. Likewise, we observed that the echinulate surface and the dark brown color of the spores of this species easily distinguish it from the other species (*P. platypyllum* var. *platypyllum*) that inhabit the CNP (with a surface without equinules and brown color).

The spores of the Argentine species of *Dryopteris* and *Ctenitis* were illustrated with SEM and LM by Gorrer *et al.* (2020; 2022), respectively. The authors mention that *D. patula* spores may present a foveolate surface, seen only with SEM, but this surface has not been observed here with LM. While the spores of the two remaining species of both genera present an ornamentation and color similar to what was said by them.

When Lavalle and Rodríguez (2014) analyzed with SEM six of the seven *Elaphoglossum* species that inhabit in Nortwest Argentina., they described the spore ornamentation of *E. yungense* with reticles and spines. Nevertheless, in the present paper we observed a folded perispore.

Regarding the remaining species analyzed here, we were able to observe that the spore color in *E. spathulatum* is a very important character to differentiate it from the other species.

The spores of the Argentine species of *Megalastrum* have not been illustrated either with SEM or with LM, until now. Arana *et al.* (2016) affirm that the spores of *M. adenopteris* and *M. fugaceum* are equinated. We agree with the ornamentation mentioned by these authors for *M. fugaceum*, but the spores of *M. adenopteris* observed and illustrated here with LM and SEM are folded and have a reticulated surface. EQUISETACEAE

In Argentina, the family has a genus with only two species, *Equisetum bogotense* and *E. giganteum*. The spores of these species have been analyzed with LM and SEM by Piñeiro and Morbelli (2014). Our observations are agree with those of the authors in that the spores of both species are spheroidal, greenish and have two elater ribbons with spatulate ends, located helically around the spore. We noted similarities in the measurements, where *E. bogotense* has smaller spores than those of *E. giganteum*. However, here we could not appreciate with LM the circular apertural mentioned by the authors, so we continue to consider them alete. Also Di Pasquo *et al.* (2016) and Gorrer *et al.* (2021) analyzed the spores of *E. giganteum* with LM from the center-east of Argentina, showing characteristics consistent with those found here.

Conclusion

For the first time, the spores of 27 species are illustrated under a light microscope. Of these 27 species, the spores of five were also illustrated using a scanning electron microscope.

The morphological characteristics of the spores allowed for the identification of 23 species.

The most demanding genera to identify at a specific level are *Asplenium* and *Elaphoglossum,* with some species that are difficult to differentiate by the qualitative or quantitative characteristics of their spores.

The Equisetaceae is the only family that had two species with alete and green (chlorophyllous) spores, but they are differentiated by size, with *E. giganteum* almost 20 µm larger than *E. bogotense*.

In the Dennstaedtiaceae family, both species are differentiated by aperture type, color, and ornamentation, where *H. poeppigii* is monolete, yellowish, and baculate-cristate and *D. globulifera* is trilete, brown, and verrucate.

Only two species are echinate. They belong to two distinct families and are differentiated by color and size. *C. diaphana* (Cystoperidaceae) is dark brown and more than 10µm larger than *M. ciliatum* (Dryopteridaceae), which is brown.

Studying the morphological characteristics of spores allows for the creation of a reference point for paleoenvironmental reconstructions in the Yungas of Northwestern Argentina, particularly in the province of Jujuy. The data set provided here contributes to spore bank analysis, aeropalynological and paleopalynological studies, and taxonomic identifications.

Acknowledgements

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