



FROND ANATOMY OF TANDILIA RANGE FERNS FROM ARGENTINA: IDENTIFYING DIAGNOSTIC TRAITS AND ECOLOGICAL ADAPTATIONS

ANATOMÍA DE FRONDA DE HELECHOS SERRANOS DEL SISTEMA DE TANDILIA, ARGENTINA: IDENTIFICACIÓN DE CARACTERES DIAGNÓSTICOS Y ADAPTACIONES ECOLÓGICAS

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SUMMARY

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Background and aims: The Tandilia Range in the Pampean Plain of Argentina is a key center of fern diversity in the region. However, anatomical information about the main species is scarce. The aim of the present study was to characterize and compare the leaf blade anatomy and petiole anatomy of six species of native ferns from the Tandilia Range and identify diagnostic features to develop an identification key and recognize ecological adaptations.

M&M: *Anemia tomentosa*, *Blechnum auriculatum*, *Doryopteris triphylla*, *Haukia crotalophoroides*, *Rumohra ponceana*, and *Physematum montevidense* were collected. Cross-sections of frond were made. Measurements of some epidermal characters were carried out, and comparisons between species were performed via generalized linear mixed models.

Results: The epidermal cells of the pinnae in most of the studied species presented walls with sinuous-wavy edges. Anomocytic were the most frequent stomatal type. Glandular trichomes in *A. tomentosa*, *B. auriculatum*, *D. triphylla*, *R. ponceana* and *P. montevidense* were identified. The presence of multiple epidermis, circumendodermal band, epidermal papillae, conical stegmata, and aerophores in the petiole base were detected in some of the species.

Conclusions: This is the first anatomical characterization of native ferns from the Tandilia Range. These findings provide valuable information for species identification and may support future ecological research.

KEY WORDS

Anatomy, Argentina, leaves, native ferns, petioles, Tandilia Range.

RESUMEN

Introducción y objetivos: El sistema serrano de Tandilia, constituye un importante centro de diversidad de helechos en la región. Sin embargo, la información anatómica sobre las principales especies es escasa. El objetivo del presente estudio fue caracterizar y comparar la anatomía foliar de seis especies de helechos nativos del sistema serrano de Tandilia e identificar rasgos diagnósticos para desarrollar una clave de identificación y reconocer adaptaciones ecológicas.

M&M: Se recolectaron individuos de *Anemia tomentosa*, *Blechnum auriculatum*, *Doryopteris triphylla*, *Haukia crotalophoroides*, *Rumohra ponceana* y *Physematum montevidense*. Se realizaron cortes transversales a mano alzada de lámina foliar y de la base del pecíolo. Se efectuaron mediciones de caracteres epidérmicos y las comparaciones entre especies se llevaron a cabo mediante modelos lineales generalizados mixtos.

Resultados: En la mayoría de las especies, las células epidérmicas de las pínulas presentaron paredes con contornos sinuoso-ondulados y se observaron estomas de tipo anomocítico. Se identificaron tricomas glandulares en *A. tomentosa*, *B. auriculatum*, *D. triphylla*, *R. ponceana* y *P. montevidense*. En algunas especies se detectó la presencia de epidermis múltiple, banda circunendodérmica, papilas epidérmicas, estegmatas cónicos y aeróforos en la base del pecíolo.

Conclusiones: Esta es la primera caracterización anatómica de helechos nativos del sistema serrano de Tandilia. Estos resultados pueden contribuir a la identificación de las especies y servir como base para futuras investigaciones ecológicas.

PALABRAS CLAVE

Anatomía, Argentina, helechos nativos, hojas, pecíolos, Sistema serrano de Tandilia.

INTRODUCTION

Ferns and lycophytes are a group widely represented in Argentina, with approximately 400 species (Arana *et al.* 2011). The fern diversity of Buenos Aires Province is distributed in elevated areas, especially in the Tandilia and Ventania Ranges (Frangi, 1975; Alonso *et al.*, 2009; D'Alfonso *et al.*, 2011; Echeverría *et al.*, 2017). In particular, the Tandilia Range offers a high array of microsites with different microclimatic conditions, which provides habitats for different species. In this context, a recent study on the composition, biogeographic affinity, and ecological patterns of ferns in this region identified a total of 22 species (Sottile *et al.*, 2024). Some of the most frequently cited species in the rock outcrop communities of the Tandilia System include *Adiantum raddianum* C. Presl., *Anemia tomentosa* (Savigny) Sw., *Blechnum auriculatum* Cav., *B. laevigatum* Cav., *Cheilanthes hieronymi* Herter, *C. micropteris* Sw., *Doryopteris triphylla* (Lam.) Christ, *Elaphoglossum gayanum* (Fée) T. Moore, *Pellaea ternifolia* (Cav.) Link, *Polystichum montevidense* Rosenst., *Pteridium esculentum* (G.Forst.) Cockayne, *Rumohra ponceana* Arana, M. L. Luna & Giudice, *Serpocaulon gilliesii* (C.Ch.) A. R. Sm., and *Woodsia montevidensis* Hieron. (Frangi, 1975; Echeverría *et al.*, 2017; Arana *et al.*, 2021; Wraage, 2022).

The use of plants with medicinal properties has been known since ancient times. In Argentina, several works provide information on this subject, including medicinal floras from Córdoba (Barboza *et al.*, 2006) and Mendoza (Roig, 2002), as well as regional floristic contributions (Martínez Crovetto, 1981a, b). Among ferns, species such as *Anemia tomentosa* and *Rumohra adiantiformis* are mentioned for their medicinal properties, with the latter reported in the province of Buenos Aires for its antibacterial, astringent, emmenagogue, and diaphoretic properties, among others (Barboza *et al.*, 2009).

Anatomical studies are essential tools for species identification, especially those with medicinal or culinary uses (Cutler & Botha, 2007). In particular, studies of epidermal tissue

can make significant contributions to controlling the adulteration of medicinal plant sales due to the high diagnostic value of cell types for identification (Altamirano & Yajía, 2017). Luján *et al.* (2011) conducted an epidermal analysis of the vegetative and reproductive organs of 28 medicinal fern and lycophyte taxa growing in Córdoba (Argentina), with the aim of providing additional information for the adequate quality control of ferns sold in that province. Furthermore, anatomical studies can contribute to understanding plant adaptations according to the ecological group to which they belong, where significant differences can be observed between plants more associated with shady environments and those growing in areas with higher sun exposure (Ivanova, 2014).

The hills range of Buenos Aires Province possess diverse microhabitats, in which fern species with different anatomical adaptations can be observed (Ponce, 1982). Given the importance of this group of plants in ethnomedicine (Luján *et al.*, 2011), it is essential to provide basic and adequate scientific knowledge for the correct identification of species, such as the morphoanatomical characteristics of vegetative organs and reproductive structures, to advance the understanding of native ferns in the Tandilia Range. Although floristic studies have been conducted on ferns in the southeastern region of the province, this group has not been studied from an anatomical perspective. Therefore, the objective of this study was to characterize and compare the frond anatomy of six native fern species from the Tandilia Range, *Anemia tomentosa*, *Blechnum auriculatum*, *Doryopteris triphylla*, *Haukia crotalophoroides* (Walter) Li Bing Zhang & Liang Zhang, *Rumohra ponceana*, and *Physematum montevidense* (Spreng.) Shmakov (ex *Woodsia montevidensis*) and identify diagnostic features to develop an identification key and recognize ecological adaptations. These results will contribute to the generation of basic information about species from this area and could be used in histochemical and phytochemical studies for the location and identification of secondary metabolites present in fronds with potential medicinal value.

MATERIAL AND METHODS

Study area

The Tandilia Range or Tandilia Hill System extends in the southeast of the Province of Buenos Aires, Argentina, from Olavarria to the city of Mar del Plata (Fig. 1). Its approximate length is 350 km long by 50 km wide. It appears as a series of hills arranged in a line, among which isolated hills rise with consolidated rocks emerging at their summits, reaching a maximum height of 500 m (Frangi, 1975; D'Alfonso *et al.*, 2011). In hills, different geomorphological units can be differentiated, each with different soil and microclimatic characteristics (Martinez, 2011). The climate of the study area is temperate, with a mean annual precipitation of 940.6 mm and a mean annual temperature of 13.8°C, with a mean of 20°C during the hottest month (January) and a mean of 7.3°C during the coolest month (July).

Collection and processing of material

One complete mature specimen of each native species, *Anemia tomentosa* (Anemiaceae), *Blechnum auriculatum* (Blechnaceae),

Doryopteris triphylla (Pteridaceae), *Haukia crotalophoroides* (Ophioglossaceae), *Rumohra ponceana* (Dryopteridaceae), and *Physematum montevidense* (Woodsiaceae), was collected from the summit of Sierra de los Padres (37° 56' 26" S, 57° 47' 38" W, 150 m a.s.l.), a site south of the Tandilia Range (Fig. 1). The species *A. tomentosa*, *R. ponceana*, and *H. crotalophoroides* were collected from sites with full sun exposure, while *D. triphylla* and *P. montevidense* were collected from small, shady ledges, and *B. auriculatum* was collected from exposed but shady sites. The specimens were preserved, identified, and later deposited in the MDQ Herbarium of Vascular Plants at the "Instituto de Investigaciones Marinas y Costeras" (IIMyC, FCEyN/UNMdP-CONICET). Additionally, fronds from three different individuals of the six species were collected in the field and immediately fixed in FAA (formalin, acetic acid, and alcohol in a 90:5:5 ratio).

Epidermal studies were carried out through clarifications from fresh and fixed leaves according to and Arambarri (2018). Additionally, freehand cross-sections were obtained from



Fig. 1. Study area. **A-B:** Representative images of the sampling area. **C:** *Doryopteris triphylla*. **D:** *Anemia tomentosa*. References= ▲ Mar del plata; * Olavarria.

the leaf blade and the base of the petioles. For detailed anatomical observations, portions of the leaf blade and petiole of some species were dehydrated through a graded ethanol series, embedded in paraffin, sectioned with a rotary microtome according to D'Ambrogio de Argueso (1986). The clarifications were stained with aqueous safranin, and the cross-sections were stained with 0.1% aqueous toluidine blue. Next, the preparations were mounted in glycerin-gelatin and observed under an Olympus CX21 light microscope. The adaxial and abaxial epidermises and their associated structures were described and characterized. Measurements of stomata and epidermal cells were performed on both epidermal surfaces when stomata were present on both sides of the leaf blade; otherwise, measurements were restricted to the stomata-bearing surface. The stomatal types were classified according to Van Cotthem (1970) and Sen & De (1992). The trichomes were characterized using cross-sections and cleared tissues and classified according to Payne (1978), Theobald *et al.* (1979), and Di Fulvio & Dottori (1995). Furthermore, stomatal size and epidermal cell length and width were estimated according to Dematteis *et al.* (2019) in 10 random fields from three leaflets of different individuals of each species fixed in FAA. Additionally, stomatal density per mm² was calculated. Original photomicrographs and drawings were edited using Adobe Illustrator 2019.

Study material. *Anemia tomentosa* (Savigny) Sw. ARGENTINA. Prov. Buenos Aires: *Dpto. General Pueyrredón*, Sierra de los Padres, (37° 56' 26" S, 57° 47' 38" W), 08-III-2024, *O'Connor 01016* (MDQ Herbarium). *Blechnum auriculatum* Cav. ARGENTINA. Prov. Buenos Aires: *Dpto. General Pueyrredón*, Sierra de los Padres, (37° 56' 26" S, 57° 47' 38" W), 08-III-2024, *O'Connor 01019* (MDQ Herbarium). *Doryopteris triphylla* (Lam.) Christ. ARGENTINA. Prov. Buenos Aires: *Dpto. General Pueyrredón*, Sierra de los Padres, (37° 56' 26" S, 57° 47' 38" W), 08-III-2024, *O'Connor 01020* (MDQ Herbarium). *Haukia crotalophoroides* (Walter) Li Bing Zhang & Liang Zhang. ARGENTINA. Prov. Buenos Aires: *Dpto. General Pueyrredón*, Sierra de los Padres, (37° 56' 27" S, 57° 47' 41" W), 04-IX-2018, *Sottile 00409* (MDQ Herbarium). *Rumohra*

ponceana Arana, Luna & Giudice. ARGENTINA. Prov. Buenos Aires: *Dpto. General Pueyrredón*, Sierra de los Padres, (37° 56' 26" S, 57° 47' 38" W), 08-III-2024, *O'Connor 01017* (MDQ Herbarium). *Physematium montevidense* (Spreng.) Shmakov. ARGENTINA. Prov. Buenos Aires: *Dpto. General Pueyrredón*, Sierra de los Padres, (37° 56' 26" S, 57° 47' 38" W), 08-III-2024, *O'Connor 01018* (MDQ Herbarium).

Data analysis

Generalized linear mixed models (GLMMs) with a gamma distribution and log link function were used, with sample identification as a random factor, to evaluate differences between species in relation to the length and width of epidermal cells, the thickness of epidermal cell walls, the area of epidermal cells, and the length and width of stomata. A GLMM with a Poisson distribution and log link function was also performed, with sample identification as a random factor, to evaluate the difference in stomatal density between species. The appropriate contrasts were made using Tukey's test. Statistical analyses were performed in R software version 4.3.1 (R Core Team, 2023). A significance level of $P < 0.05$ was considered for all analyses.

RESULTS

Leaf blade anatomy

Epidermal cells on both the adaxial and abaxial surfaces show sinuous-wavy edges in *Anemia tomentosa*, *Blechnum auriculatum*, *Doryopteris triphylla*, *Rumohra ponceana*, and *Physematium montevidense* (Fig. 2). *Haukia crotalophoroides* is the only species with epidermal cells possessing straight to slightly curved walls in both the adaxial and abaxial epidermis. Different types of stomata are observed on the abaxial epidermis and are at the same level as the epidermal cells in *A. tomentosa* (Table 1; Fig. 2A, G), *B. auriculatum* (Table 1; Fig. 2B, G), *D. triphylla* (Table 1; Fig. 2C, G), *R. ponceana* (Table 1; Fig. 2E, G), and *P. montevidense* (Table 1; Fig. 2F, G). In *A. tomentosa*, some stomata are elevated above the level of epidermal cells. In contrast, *H. crotalophoroides* is the only species with only one type of stomata (anomocytic) and is present in

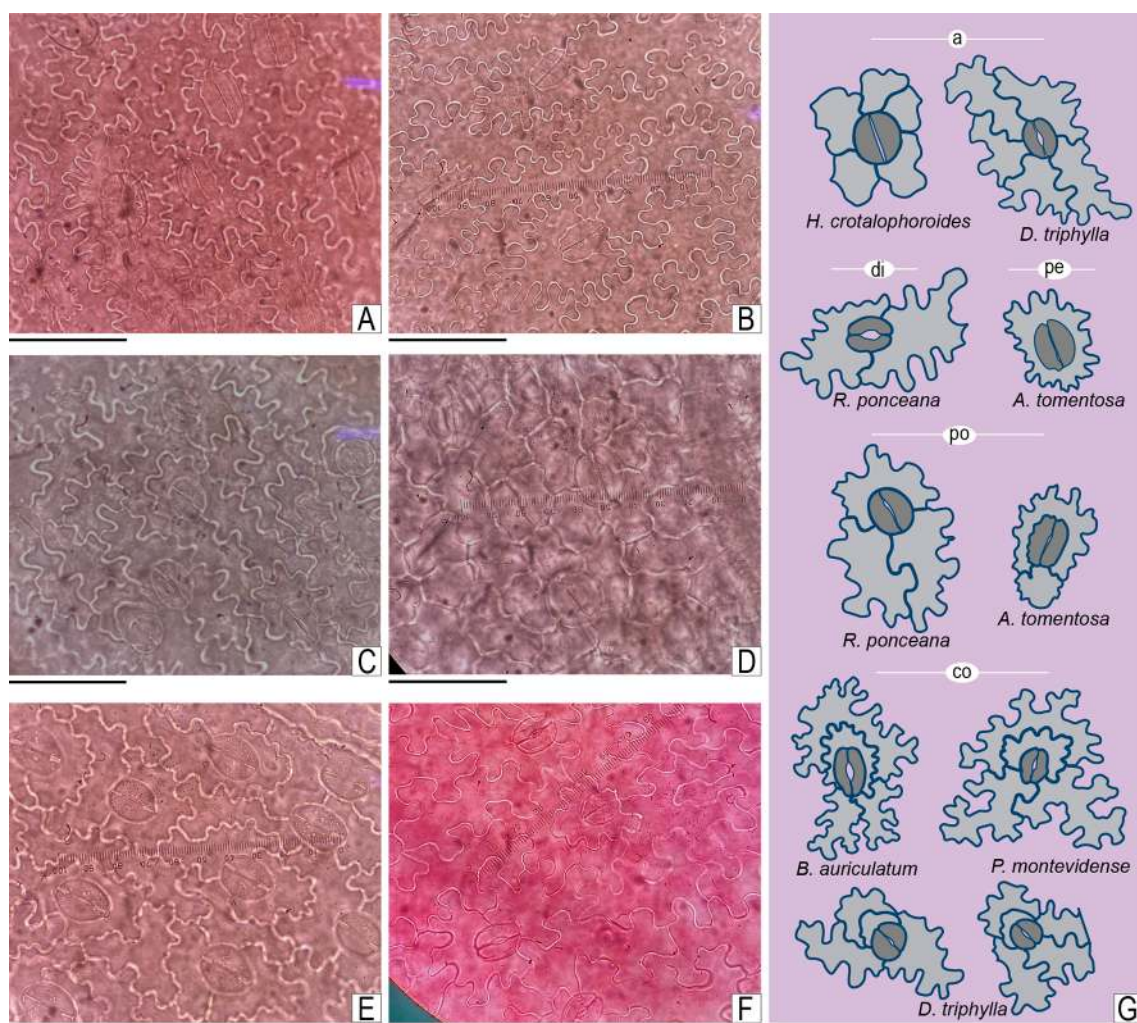


Fig. 2. Leaf blade segments clearing, abaxial surface. **A:** *Anemia tomentosa*. **B:** *Blechnum auriculatum*. **C:** *Doryopteris triphylla*. **D:** *Haukia crotalophoroides*. **E:** *Rumohra ponceana*. **F:** *Physematum montevidense*. **G:** Diagrams of the different stomatal types. Abbreviations= a: Anomocytic. di: Diacytic. pe: Pericytic. po: Polocytic. co: Copolocytic. Scale bars=100 μ m.

both epidermis (Table 1, Fig. 2D, G). Notably, in copolocytic stomata, the subsidiary cells envelop guard cells differently according to the species (Fig. 2G).

Eglandular and glandular trichomes are observed in the studied species, except in *H. crotalophoroides*, whose leaf blades are glabrous (Fig. 3). Uniseriate eglandular trichomes, composed of 3 to 7 cells, are described in *A. tomentosa* (Fig. 3A), and 3 to 8 cells are described in *P. montevidense* (Fig. 3B) in both epidermises. In total, three types of glandular

trichomes were identified: unicellular with an elongated head (nonstipitate) (Fig. 3C), unicellular stipitate (Fig. 3D-F), and bicellular globose (Fig. 3G, H). In *A. tomentosa*, bicellular globose trichomes are found only on the abaxial epidermis, whereas unicellular trichomes with an elongated, nonstipitate head are present on both epidermises. In *B. auriculatum*, *P. montevidense* and *R. ponceana*, unicellular glandular trichomes with a stipitate globose head are observed on both epidermises. In *D. triphylla*, stipitate bicellular globose glandular trichomes are present but rare.

Table 1. Epidermal characters and measurements made from clarified fronds (mean ± standard deviation).						
Character	<i>Anemia tomentosa</i>	<i>Blechnum auriculatum</i>	<i>Doryopteris triphylla</i>	<i>Haukia crotalophoroides</i>	<i>Rumohra ponceana</i>	<i>Physematum montevidense</i>
Epidermal cell length (µm)	105,61±22,33	175,69±36,77	98,93±16,50	76,97±16,55	113,67±23,18	110,23±24,44
Epidermal cell width (µm)	28,24±15,21	36,14±9,70	35,84±13,00	39,49±6,28	32,05±11,73	35,74±19,83
Epidermal cell wall thickness (µm)	1,40±0,42	0,84±0,18	1,78±0,46	0,83±0,18	2,23±0,51	0,87±0,18
Epidermal cell area (µm²)	2847,53±530,61	6815,98±1563,30	3423,96±752,00	2398,82±622,22	3307,04±768,22	4140,50±1287,06
Stomata length (µm)	51,67±5,22	50,67±4,04	40,25±4,57	65,25±5,23	46,58±2,41	35,50±5,10
Stomata width (µm)	37,50±2,46	30,08±2,75	34,42±4,08	55,33±5,52	37,00±2,01	26,92±2,84
Stomata density (n°/mm²)	64,19±13,44	71,06±11,56	45,19±15,19	28,75±8,44	74,56±14,50	57,50±11,06

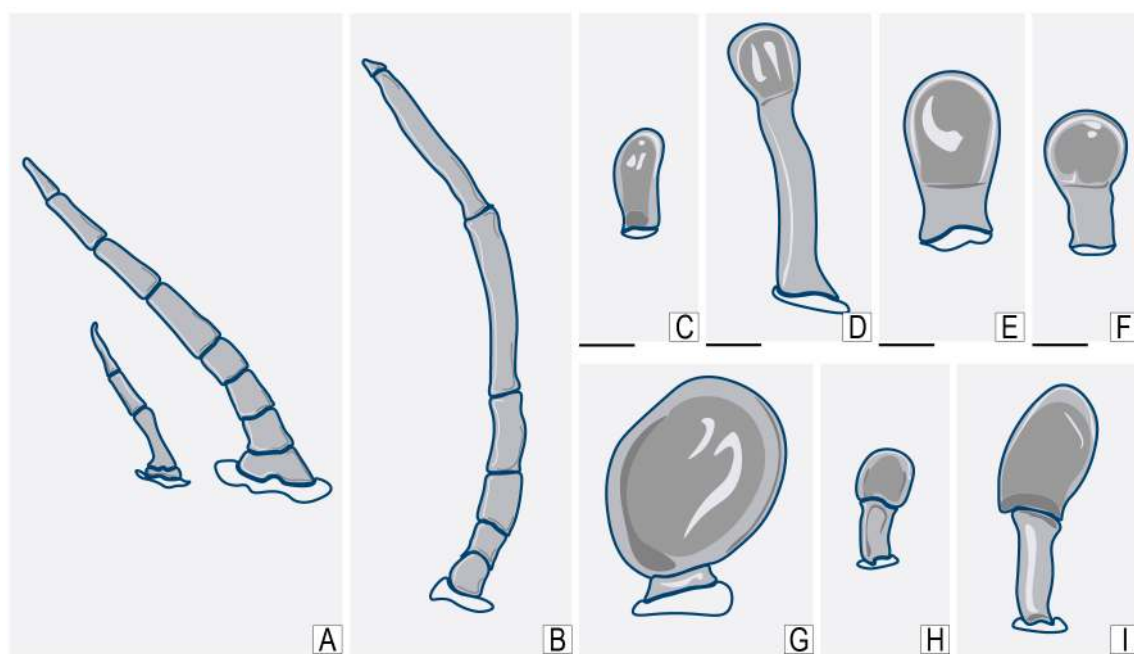


Fig. 3. Trichome diversity. **A, C, G:** *Anemia tomentosa*. **B, F:** *Physematium montevidense*. **D, I:** *Blechnum auriculatum*. **E:** *Rumohra ponceana*. **H:** *Doryopteris triphylla*. **A-B:** multicellular eglandular trichomes. **C-I:** Glandular trichomes. **C:** Unicellular elipsoid head nonstipitate. **D-F:** Unicellular, stipitate globular head. **G-H:** Bicellular, stipitate globular head. **I:** Bicellular, elipsoid head. Scale bars= A-B: 100 µm; C-I: 25 µm.

Cross-sections of the leaf blade (Fig. 4) show a single-layered epidermis in *A. tomentosa*, *B. auriculatum* (with papillose cells in the adaxial epidermis), *D. triphylla*, *H. crotalophoroides*, and *P. montevidense*. In *R. ponceana*, both the adaxial and abaxial epidermis are double layered. The adaxial epidermis contains cells with primary walls, whereas the abaxial epidermis contains cells with thickened lignified walls, as revealed by toluidine blue staining (Fig. 4E). Below the adaxial epidermis and at the central vein level, sclerenchyma is present in *A. tomentosa*, *B. auriculatum*, *D. triphylla*, and *P. montevidense*. This tissue is also observed on the reflexed margins of *D. triphylla* leaves. Additionally, in *A. tomentosa*, conical stegmata with silica deposits occur only in adaxial epidermal regions aligned with the vascular bundles.

With the exception of *H. crotalophoroides*, the mesophyll of the remaining species exhibits a dorsiventral organization, comprising 1 to 4 layers of palisade parenchyma and 1 to 6 layers of spongy parenchyma, the latter displaying distinct intercellular spaces in certain species (Fig. 4A-C, E). Furthermore, these species possess amphicribal

median veins bounded by 1 to 3 layers of pericycle and a single endodermal layer (Fig. 5A-C, E-F); a parenchymatous sheath surrounds the endodermis, whereas *R. ponceana* exhibits a circumendodermal band (Fig. 5E). Conversely, *H. crotalophoroides* features a slightly loose homogeneous parenchyma consisting of 6 to 12 layers (Fig. 4D), the median vein lacks both a pericycle and an endodermis, and the phloem does not surround the xylem as observed in the other species (Fig. 5D).

The average values and deviations for epidermal cell size, area, and wall thickness in both the adaxial and abaxial epidermis, as well as stomatal length, width, and density, are presented for the studied species, are detailed in Table 1. Significant differences were found in all analyzed variables (Tables S1 and S2). The highest stomatal density was observed in *R. ponceana* and *B. auriculatum*, whereas the lowest stomatal density was detected in *H. crotalophoroides* (Table S3). The longest and widest stomata were measured in *H. crotalophoroides*, whereas the smallest were measured in *P. montevidense* (Tables S4 and S5). The greatest epidermal cell length and area were

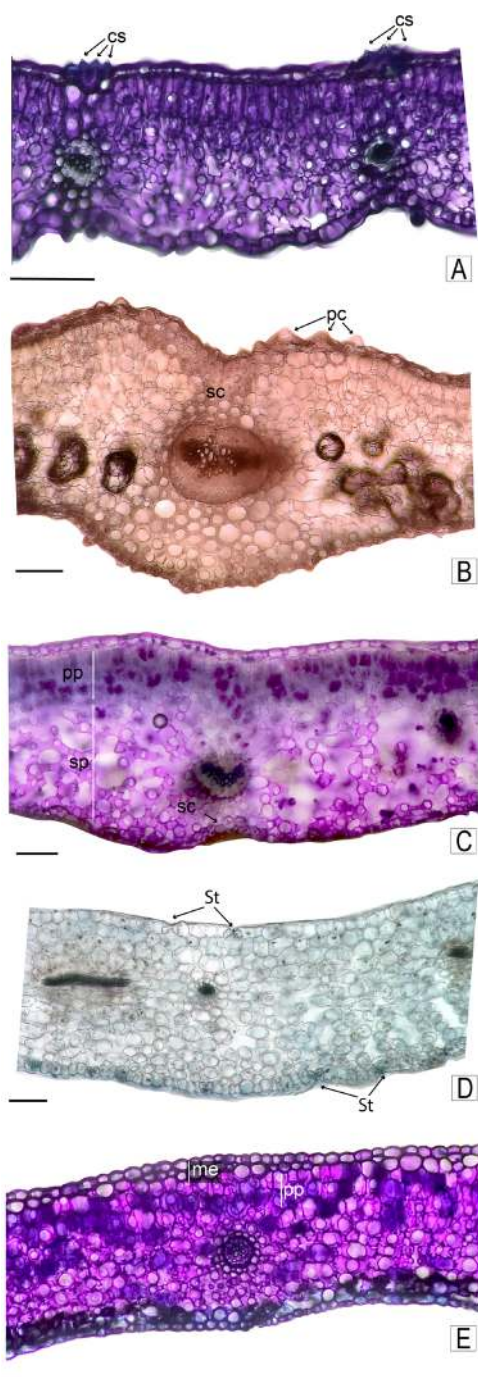


Fig. 4. Leaf blade cross sections. **A:** *Anemia tomentosa*. **B:** *Blechnum auriculatum*. **C:** *Doryopteris triphylla*. **D:** *Haukia crotalophoroides*. **E:** *Rumohra ponceana*. Abbreviations= pc: papillose cells; me: multiple epidermis; sc: sclerenchyma; cs: conical stegmata; pp: palisade parenchyma; sp: spongy parenchyma; st: stomata. Scale bars= 100 μ m.

observed in *B. auriculatum*, and the smallest were observed in *H. crotalophoroides* (Tables S6 and S8). In terms of epidermal cell width, the greatest value was found in *H. crotalophoroides*, and the lowest value was found in *A. tomentosa* (Table S7). Finally, the thickest epidermal cell walls were found in *R. ponceana*, with the thinnest in *H. crotalophoroides*, *B. auriculatum*, and *P. montevidense* (Table S9).

Petiole anatomy

A one-layered epidermis was observed in all the studied species (Fig. 6). In *A. tomentosa*, this tissue exhibits conical stegmata and the same types of eglandular trichomes described for the leaf blade (Fig. 6A). In *B. auriculatum*, some papillose epidermal cells and bicellular glandular trichomes with an elliptical head are present (Fig. 6B, 3I), whereas in *P. montevidense*, the same eglandular and glandular trichomes as those in the leaf blade are observed. No trichomes were observed on the petioles of *R. ponceana*, *D. triphylla*, and *H. crotalophoroides*.

In five species, the cortex consists of sclerenchymatous tissue (sterome) that ranges from 1-18 layers, followed by 3-9 layers of parenchyma cells (Figs. 6-7), which exhibit thickened walls in *D. triphylla* (Figs. 6C, 7D-E) and correspond to chlorenchyma in *R. ponceana* and *P. montevidense* (Fig. 7H, J). In the cortical tissue of *H. crotalophoroides*, compact isodiametric parenchyma cells are observed (Fig. 6D). The vascular bundles in the petioles of all the species except in *H. crotalophoroides* are amphicribal (Fig. 6), consisting of a central vascular bundle in *A. tomentosa*, *D. triphylla* y *P. montevidense* (Fig. 6A, C, F), two in *B. auriculatum* (Fig. 6B), four in *H. crotalophoroides* (Fig. 6D) and eight vascular bundles surround a pith of parenchymatous cells in *R. ponceana*, (Fig. 6E). Again, with the exception of *H. crotalophoroides*, which features a simplified vascular cylinder (Fig. 7F), each vascular bundle is surrounded by 1 to 3 layers of pericycle and a single layer of endodermis (Fig. 7A-E, G-K), with a circumendodermal band being present in *R. ponceana* (Fig. 7G, I).

In the petiole base, aerophores (interruptions of tissues starting from the epidermis, passing through sclerenchyma and parenchyma tissues) are identified as zigzag spaces in *A. tomentosa* and *B. auriculatum* (Fig. 7C) and as strips of parenchyma in *R. ponceana* (Figs. 6E; 7G, H).

Identification key

An identification key is presented based on some characters of the epidermis of the leaf blade of the species.

1. Adaxial and abaxial epidermal cells with straight to slightly curved anticlinal walls; trichomes absent. 2
Haukia crotalophoroides
- 1'. Adaxial and abaxial epidermal cells with sinuous to wavy anticlinal walls; trichomes present. 2
2. Adaxial and abaxial epidermis bearing both glandular and uniseriate eglandular trichomes 3
3. Adaxial epidermis with conical stegmata aligned with the vascular bundles; two types of glandular trichomes on the leaf blade: bicellular with globose heads and unicellular with elongated non-stipitate heads. 3
Anemia tomentosa
- 3'. Adaxial epidermis without conical stegmata; one type of glandular trichomes on the leaf blade: unicellular with a stipitate globose head. 3
Physematium montevidense
- 2'. Adaxial and abaxial epidermis bearing only glandular trichomes. 4
4. Adaxial and abaxial epidermis with papillae. 4
Blechnum auriculatum
- 4'. Adaxial and abaxial epidermis without papillae. 5
5. Adaxial and abaxial epidermis containing unicellular glandular trichomes with a stipitate globose head. 5
Rumohra ponceana
- 5'. Adaxial and abaxial epidermis containing bicellular glandular trichomes with stipitate globose head. 5
Doryopteris triphylla

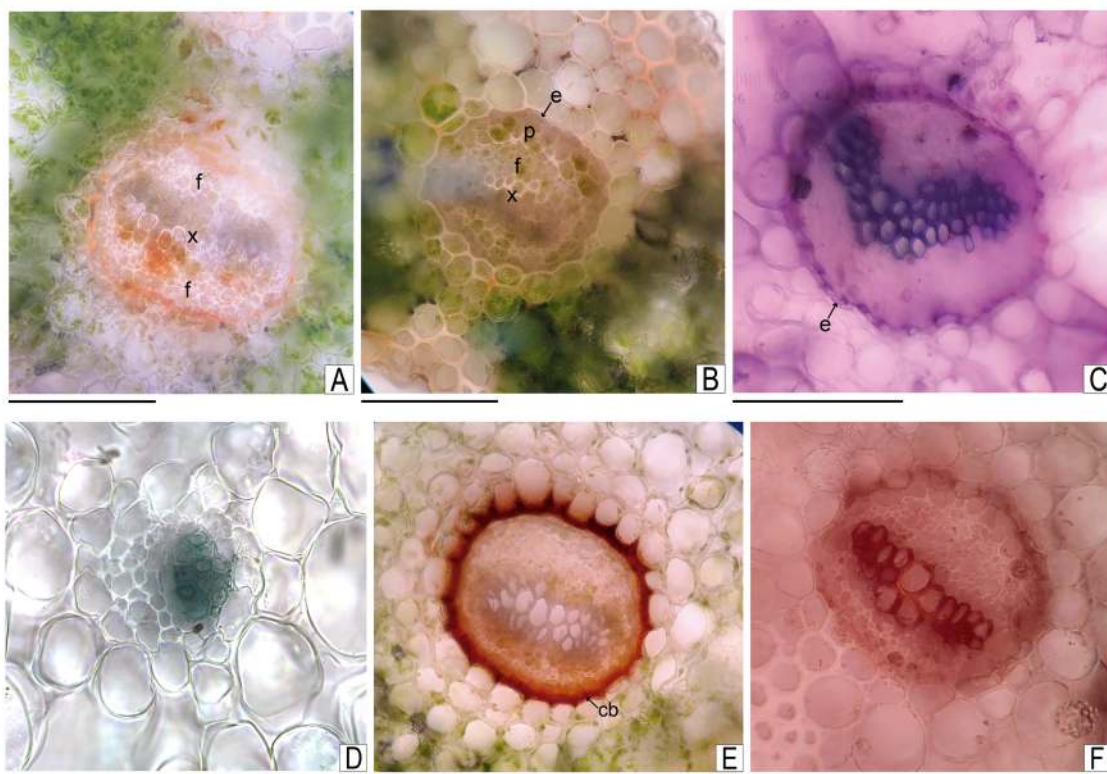


Fig. 5. Close-up of central vascular bundles in pinna cross-sections. **A:** *Anemia tomentosa*. **B:** *Blechnum auriculatum*. **C:** *Doryopteris triphylla*. **D:** *Haukia crotalophoroides*. **E:** *Rumohra ponceana*. **F:** *Physematium montevidense*. Abbreviations= e: endodermis; p: pericycle; f: phloem; x: xylem; cb: circumendodermal band. Scale bars= 100 µm.

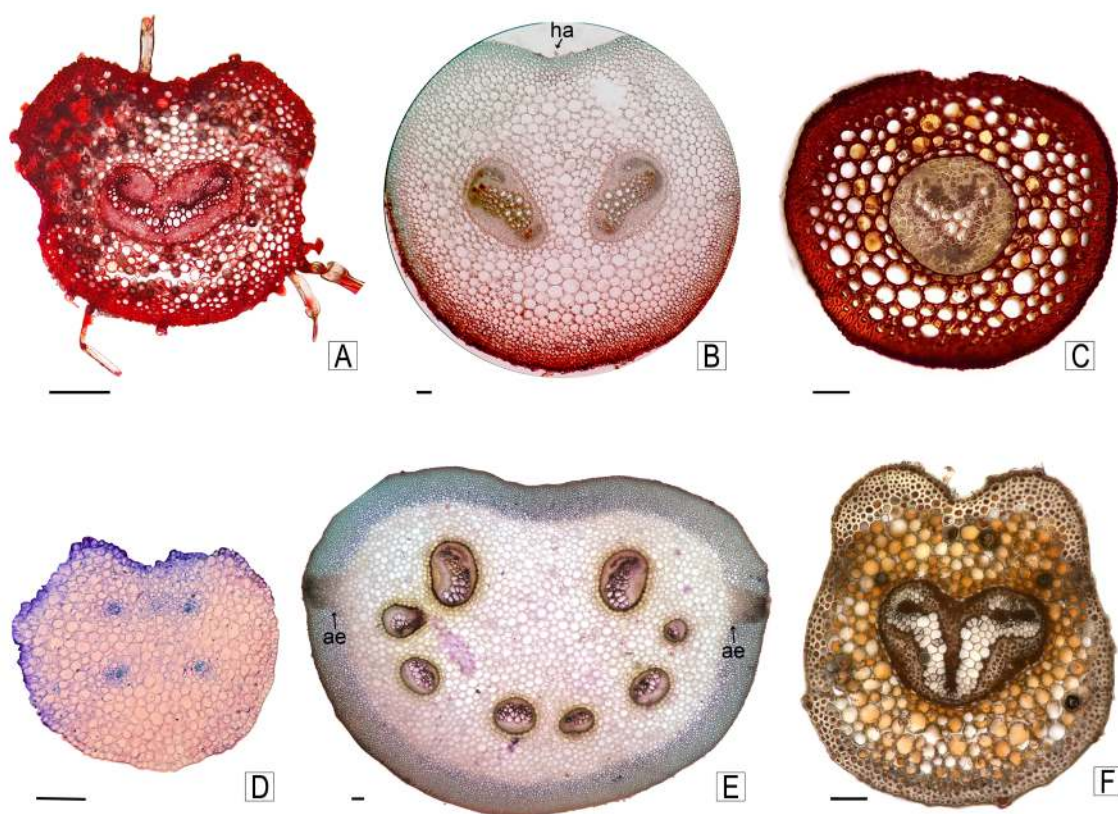


Fig. 6. Petiole base cross-sections of **A:** *Anemia tomentosa*. **B:** *Blechnum auriculatum*. **C:** *Doryopteris triphylla*. **D:** *Haukia crotalophoroides*. **E:** *Rumohra ponceana*. **F:** *Physematium montevidense*. Abbreviations= ae: aerophores; ha: hair. Scale bars= 100 μ m.

DISCUSSION

Leaf blade anatomy

The most frequent stomatal type in all the species studied was anomocytic, followed by the polocytic and copolocytic types. This finding is consistent with Luján *et al.* (2011), who reported that the most common types in an epidermal study of 28 species of ferns and lycophytes from Córdoba (central Argentina) were anomocytic and polocytic. Similarly, Dematteis *et al.* (2019) and Polentarrutti *et al.* (2026) reported the predominance of these stomatal types in *D. triphylla*. However, Lujan *et al.* (2011) reported a greater variety of stomatal types for *Anemia tomentosa* than those observed in the present study, including desmocytic, diacytic, and hypocytic types. Falczuk *et al.* (1996) also analyzed several species growing in the Córdoba hills (central Argentina), including *Woodsia*

montevidensis (= *Physematium montevidense*), and reported anomocytic stomata that align with the results of the present study. However, they did not observe polocytic or copolocytic types, which were found in the plants analyzed in the present work. These results indicate differences in the types of stomata within the same species depending on the environment, and this is important to consider given that stomatal type is regarded as a taxonomic trait in ferns (Van Cotthem, 1970). Nevertheless, classifications of stomatal types in ferns can vary among authors, so further detailed research is needed to precisely determine these differences. Regarding stomatal position, elevated stomata were found only in *A. tomentosa*, which is in line with the observations of Ponce (1982).

Glandular trichomes observed in *A. tomentosa*, *R. ponceana*, and *P. montevidense* were previously reported by Ponce (1982). Luján *et al.* (2011), on

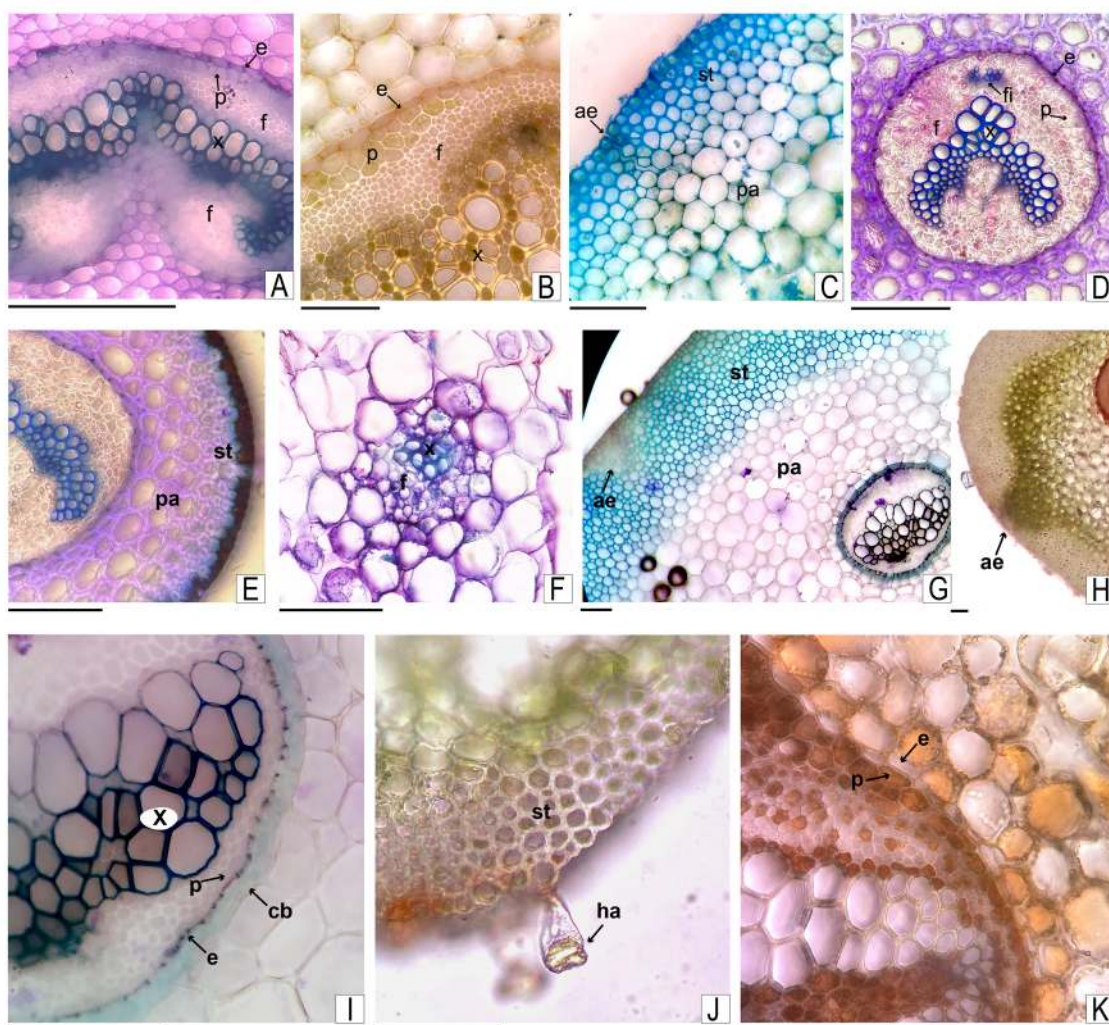


Fig. 7. Detail of petiole bases cross-sections. **A:** *Anemia tomentosa*. **B-C:** *Blechnum auriculatum*. **D-E:** *Doryopteris triphylla*. **F:** *Haukia crotalophoroides*. **G-I:** *Rumohra ponceana*. **J-K:** *Physematum montevidense*. Abbreviations= e: endodermis; p: pericycle; f: phloem; x: xylem; ha: hair; st: stereome; fi: fibres; pa: parenchyma; ae: aerophores cb: circumendodermal band. Scale bars= 100 μ m.

the other hand, described only one type of glandular trichome for *A. tomentosa* individuals. Neira *et al.* (2017) described the same types of trichomes as those observed in this work for *D. triphylla*. The observed variation in trichome types among species also reinforces their taxonomic and diagnostic significance, in agreement with the findings of Luján *et al.* (2011).

Distinctive features were observed in the transverse sections of the leaves and petiole bases of several species. In *R. ponceana*, a multilayered

adaxial epidermis (two rows of cells, Fig. 4E) was identified. Torres Boeger *et al.* (2007) refer to the second row of cells in cross-sections of *R. adiantiformis* as subepidermal cells. Some authors debate whether to label this as a multiple epidermis or hypodermis, a distinction that depends on the ontogeny of the tissues, as the epidermis originates from the protoderm and the hypodermis from the fundamental meristem (Martins *et al.*, 2012). Furthermore, a circumendodermal band surrounding the vascular bundles of the leaves and petiole base

was also observed in *R. ponceana*. These bands have been reported for some species in the Dryopteridaceae and Blechnaceae families (Hernández-Hernández *et al.*, 2012). Notably, no such band was observed in *B. auriculatum* (Blechnaceae). The circumendodermal band is associated with biomechanical function and pathogen protection due to its high tannin content (Hernández-Hernández *et al.*, 2012).

Blechnum auriculatum was the only species that exhibited epidermal papillae. These structures have previously been observed in other species of the genus *Blechnum* (Luján *et al.*, 2011) and may be linked to defense against fungal pathogens (Hückelhoven, 2014). Additionally, conical stegmata were observed in the cross-sections of *A. tomentosa*, which were always aligned with vascular bundles. These structures were previously reported for *A. tomentosa* var. *tomentosa* in populations of the Ventania system hills (Ponce, 1982) and for *A. tomentosa* var. *anthriscifolia* by Ribeiro *et al.* (2007). Fernández Honaine *et al.* (2026) suggested that stegmata may provide structural support to the fronds due to the presence of silica.

Another distinctive feature observed in petiole cross-sections is the presence of aerophores, structures that allow gas diffusion through sclerenchymatic and parenchymatic tissues (Vasco *et al.*, 2013; Moran, 2022). These structures were observed in *A. tomentosa*, *B. auriculatum*, and *R. ponceana*, which is consistent with previous reports for *A. tomentosa* and other species in the genus *Blechnum* (Luján *et al.*, 2011). However, no previous studies have reported aerophores in the genus *Rumohra*, although they have been cited for the Dryopteridaceae family in the species *Polybotrya osmundacea* (Moran, 2022).

Relationship between frond anatomy and environmental conditions

Although ferns are generally associated with humid environments, many species exhibit anatomical adaptations that allow them to thrive under relatively dry conditions (Hietz, 2010). Among the species most exposed to solar radiation, *Anemia tomentosa*, *Haukia crotalophoroides*, and *Rumohra ponceana* displayed traits commonly associated with xeric environments. *Anemia tomentosa* exhibited abundant trichomes and stegmata. Zanenga-Godoy & Costa (2003) suggested that stegmata may contribute to reducing transpiration in some

plants. Nevertheless, this species also presented elevated stomata, a feature commonly reported in plants growing under humid conditions (Metcalfe & Chalk, 1979), suggesting a combination of traits associated with contrasting environmental conditions. *H. crotalophoroides* was the only species with straight epidermal cell walls and amphistomatic leaves, a combination of traits commonly associated with high-irradiance environments (Carpenter & Smith, 1975; Graçano *et al.*, 2001; Reyes-López *et al.*, 2015). Nevertheless, it also exhibited the largest stomata and the lowest stomatal density among the species studied, a pattern more commonly reported for plants in shaded and humid environments (Hetherington & Woodward, 2003). In contrast to *H. crotalophoroides*, the remaining species exhibited sinuous epidermal cell walls. In ferns growing on rocky substrates, this feature has been associated with shaded environments (Moraes Neto *et al.*, 2022). *R. ponceana* was the only species with a multilayered epidermis and significantly thicker epidermal cell walls than the other species. Both traits have been described as adaptations that reduce water loss and increase tolerance to drought (Fatima *et al.*, 2018; Dörken *et al.*, 2020; Leshcheniuk & Chipilyak, 2020; Al Shaye, 2023). However, Sottile *et al.* (2024) reported that this species occurs in sites with intermediate water availability. The relatively high stomatal density observed in *R. ponceana* may help explain this apparent discrepancy, as it could facilitate gas exchange under favorable conditions while maintaining structural traits that provide protection against periodic water stress (Franks & Beerling, 2009).

In regard to the parenchyma tissue, a greater development of palisade parenchyma is commonly associated with leaves exposed to high irradiance, as the elongated cells facilitate light penetration and distribution through the mesophyll, thereby enhancing photosynthetic efficiency and photoprotection (Karabourniotis *et al.*, 2021). In contrast, *D. triphylla* exhibited a mesophyll with abundant spongy parenchyma, similar to that described for *D. collina* by Polentarutti *et al.* (2026) in plants growing in humid environments. This pattern differs from the ecological characterization proposed by Sottile *et al.* (2024), who associated *D. triphylla* with lower water availability, suggesting that mesophyll organization in this genus may not be explained solely by moisture conditions.

CONCLUSIONS

This study presents the first anatomical characterization of the leaf blade and petiole of six native fern species from Sierra de los Padres, in the southeastern Tandilia hill system. Among these, the first anatomical description of *Haukia crotalophoroides* in Argentina is detailed, revealing major structural differences compared to the other species studied.

We found that certain easily accessible characters were highly useful for species identification. In *A. tomentosa*, conical stegmata were observed, with epidermal structures with potential roles in support and/or radiation protection, which, owing to their exclusivity in a few species, could represent a taxonomic trait of interest. Another potentially important taxonomic trait is the aerophores, described for the first time in this study for the genus *Rumohra*, as well as the epidermal papillae in *B. auriculatum*. However, trichome morphology and distribution proved to be the most informative epidermal characters, providing reliable diagnostic features that allowed the differentiation of the studied species and constituted key characters in the construction of the dichotomous key.

Finally, some of the results obtained suggest certain relationships between anatomy and xeric conditions, such as the high abundance of trichomes found in *A. tomentosa* or the multilayered epidermis in *R. ponceana*. However, overall, the studied species did not show a uniform set of anatomical traits associated exclusively with either xeric or humid environments. Instead, several species combined characteristics traditionally linked to both conditions, highlighting the complexity of anatomical responses to environmental variation in ferns. These findings suggest that the ecological significance of many anatomical traits may not be straightforward and underscore the need for more detailed eco-anatomical studies integrating anatomical, environmental, and physiological data.

AUTHOR CONTRIBUTIONS

GBH and TO'C contributed to the collection of material, processing of material, anatomical analyses, data measurement, figure and table design, results analysis, discussion, and manuscript

writing. LBP and MEI contributed to the collection of material, processing of material, and data measurement. ACMT contributed to the processing of material, anatomical analyses, results analysis, discussion, and manuscript writing. MFH contributed to the discussion and writing of the manuscript. All the authors commented on previous versions of the manuscript and read and approved the final version.

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