Morphological and anatomical adaptations to dry, shady environments in *Adiantum reniforme* var. *sinense* (Pteridaceae)

Di Wu[1], Linbao Li[1], Xiaobo Ma[1], Guiyun Huang[1] and Chaodong Yang[2]

[1] Rare Plants Research Institute of Yangtze River, Three Gorges Corporation, Yichang, China
[2] Engineering Research Center of Ecology and Agriculture Use of Wetland, Ministry of Education, Yangtze University, Jingzhou, China

ABSTRACT

The natural distribution of the rare perennial fern *Adiantum reniforme* var. *sinense* (Pteridaceae), which is endemic to shady cliff environments, is limited to small areas of Wanzhou County, Chongqing, China. In this study, we used brightfield and epifluorescence microscopy to investigate the anatomical structures and histochemical features that may allow this species to thrive in shady, dry cliff environments. The *A. reniforme* var. *sinense* sporophyte had a primary structure and a dictyostele. The plants of this species had an endodermis, sclerenchyma layers and hypodermal sterome, reflecting an adaption to dry cliff environments. Blades had a thin cuticle and isolateral mesophyll, suggesting a tolerance of shady environments. These characteristics are similar to many sciophyte ferns such as *Lygodium japonicum* and *Pteris multifida*. Thus, the morphological and anatomical characteristics of *A. reniforme* var. *sinense* identified in this study are consistent with adaptations to shady, dry cliff environments.

Subjects Conservation Biology, Plant Science
Keywords Endodermis, Dictyostele, Sclerenchyma layer, Suberin lamellae, Thin cuticle

Submitted 14 April 2020
Accepted 24 August 2020
Published 30 September 2020

Corresponding authors
Guiyun Huang,
huang_guiyun@ctg.com.cn
Chaodong Yang,
546728708@qq.com

Academic editor
Victoria Sosa

Additional Information and Declarations can be found on page 10

DOI 10.7717/peerj.9937

INTRODUCTION

Adiantum reniforme var. *sinense* (Pteridaceae, subfamily Vittarioideae) is a rare cliff-dwelling perennial pteridophyte, with a natural distribution limited to small areas of Wanzhou County, Chongqing, China. This plant has been used in Chinese medicine for more than 100 years (*Lin, 1980*; *Zhang & Wu, 2013*; *Rothfels & Schuettpelz, 2014*; *PPG, 2016*; *Pryer et al., 2016*). *A. reniforme* is of immense botanical interest due to its intercontinental distribution; *A. reniforme* is found in the Azores, *A. reniforme* var. *sinense* in China and *A. reniforme* var. *asarifolium* in south-central Africa (*Lin, 1980*; *Zhang & Wu, 2013*; *Wang et al., 2015*). The Chinese variants of this species have low genetic diversity (*Pan, Ji & Chen, 2005*; *Liu, Gituru & Chen, 2007*; *Wang et al., 2015*). In China, the natural habitat of this plant was lost due the construction of Three Gorges Dam, which was completed in 2012. Since this time, *A. reniforme* var. *sinense* has been conserved ex situ in the germplasm resource nursery managed by the China Three Gorges Corporation and the Wuhan Botanical Garden (*Pan, Ji & Chen, 2005*; *Liao et al., 2007*; *Zhou, Jiang & Huang, 2008*; *Wu, 2012*). Due to its endangered status, narrow distribution, ex situ conservation, and low genetic diversity, *A. reniforme* var. *sinense* is listed as a class II

How to cite this article Wu D, Li L, Ma X, Huang G, Yang C. 2020. Morphological and anatomical adaptations to dry, shady environments in *Adiantum reniforme* var. *sinense* (Pteridaceae). **PeerJ 8:e9937 DOI 10.7717/peerj.9937**

protected fern in China (*Lin, 1980*; *Xu, Zhen & Jin, 1987*; *Fu & Jin, 1992*; *Pan, Ji & Chen, 2005*; *Liu, Gituru & Chen, 2007*; *Zhang et al., 2013*; *Wang et al., 2015*).

Pteridophytes have evolved various morpho-anatomical features to adapt to terrestrial, xeric, epiphytic, rupicolous and aquatic environments (*Wylie, 1949*; *Zhang et al., 2013*; *Neira et al., 2017*; *Sârbu et al., 2017*; *Wetzel et al., 2017*); this group is thus taxonomically, evolutionarily, and phylogenically diverse (*Kato & Imaichi, 1997*; *Li et al., 2013*; *Vasco, Moran & Ambrose, 2013*; *Plackett, Di Stilio & Langdale, 2015*; *Harrison & Morris, 2017*; *Huiet et al., 2018*). Pteridophyte rhizomes have species-or group-specific stele, including the dictyostele of the Monachosorideae and the Polypodiaceae (*Jeffreys, 1903*; *Wardlaw, 1944*; *Wu et al., 1992*; *Srivastava & Chandra, 2009*; *Deroin & Rakotondrainibe, 2015*; *Nopun et al., 2016*; *Becari-Viana & Schwartsburd, 2017*). The adventitious roots of pteridophytes possess a primary xylem and phloem in the stele, a cortex with an endodermis and/or lacking an exodermis with Casparian bands, and lignified cortical walls (*Chapple & Peterson, 1987*; *Damus et al., 1997*; *Schneider, 1997*). The leaves have an endodermis, a sclerenchyma layer, and a cuticle as apoplastic barriers (*Ribeiro, Santos & Moraes, 2007*; *De los Ángeles Lagoria et al., 2018*; *Mahley et al., 2018*; *Palacios-Rios et al., 2019*). Moreover, the morphologies of sun and shade plants are obviously different (*Boardman, 1977*; *Nasrulhaq-Boyce & Mohamed, 1987*; *Givnish, 1988*; *Santos-Silva, Mastroberti & De Araujo Mariath, 2011*), the leaves of shade plants are large, with large cells, few mesophyll tissues, and decreased stomatal and vein densities (*Ribeiro, Santos & Moraes, 2007*; *Zhang & Wu, 2013*; *Neira et al., 2017*; *Dematteis et al., 2019*; *Shah et al., 2019*; *Baer, Wheeler & Pittermann, 2020*). In ferns, gymnosperms, and angiosperms, the endodermis or circumendodermal band and the exodermis act as barriers, which restrict water-solute exchange, reduce oxygen loss after submersion, and terrestrial environments (*Ogura, 1972*; *Lersten, 1997*; *Enstone, Peterson & Ma, 2003*; *Hernandez-Hernandez et al., 2012*; *Geldner, 2013*; *Xiang et al., 2019*; *Yang et al., 2011*, *2014*, *2019a*, *2019b*, *2019c*, *2020*; *Zhang et al., 2017*; *Zhang, Yang & Seago, 2018*).

Phylogenetic and ontogenetic relationships within *Adiantum* have historically been based on anatomical characteristics, particularly the presence of dictyostele in the leaves (*Wylie, 1949*; *Imaichi, 1988*; *Huiet et al., 2018*). However, recent molecular genetic analyses have suggested that *A. reniforme* var. *sinense* is synonymous with *A. nelumboides*, in opposition to classical morphological taxonomy (*Lin, 1980*; *Zhang et al., 2013*; *Wang et al., 2015*). In addition, although *A. reniforme* var. *sinense* has been well studied with respect to optimal spore culture conditions, structural sporophyte anatomy and photosynthetic capacity have received little attention (*Wu et al., 2010*, *2011*; *Liao et al., 2007*).

Here, we aimed to investigate the structural and histochemical features of the *A. reniforme* var. *sinense* sporophyte to determine whether these features were adaptations to dry cliff environments. We also sampled the leaves of *A. reniforme* var. *sinense* sporophytes in the sun and shade to identify the morphological and anatomical traits that indicated adaptations to shady environments; the leaves exhibited the same traits observed in other species. Evidence of such adaptive characteristics might help to explain the ability of *A. reniforme* var. *sinense* to grow in shady, dry cliff environments. Our results may also inform future studies of the ex situ conservation, taxonomy, evolution and phylogeny of this rare plant and its relatives.

MATERIALS AND METHODS

Plant sourcing and collection

Adiantum reniforme var. *sinense* specimens were cultivated at the Chinese Germplasm Resource Nursery of the Three Gorges Corporation (Ichang, Hubei, China). Several sporophytes were collected in October 2019. From each plant, we collected approximately 10 roots, eight rhizomes, five leaves growing in the sun (intensity of illumination about 4,840 lux; humidity 51.6%) and five leaves growing in the shade (intensity of illumination about 805.5 lux; humidity 49.5%). Freshly collected samples were immediately fixed in formaldehyde-alcohol-acetic acid (FAA) (*Ruzin, 1999*).

Microstructure and histochemistry

Root tissues were then sectioned freehand, using a two-sided razor blade, under a stereoscope (JNOEC JSZ6, China). Root sections were cut at 5, 10 and 20 mm from the root tip. Rhizomes were cut into two sections: young (~10 mm from the tip; white surface coloration) and mature (~30 mm from the tip; brown surface). Petioles were also cut into young (white surface) and mature (black surface) sections. Blades were cut in the center to determine tissue thickness. Sections were divided into three sets such that each set contained 3–6 sections (obtained from different specimens) representing each distance from the root tip; the young and mature rhizomes; the young and mature petioles; and the blade centers and margins.

Each set of sections was stained with one of three stains: 0.1% (w/v) Sudan red 7B (SR7B) to test for suberin in the cell walls (*Brundrett, Kendrick & Peterson, 1991*); 0.1% (w/v) berberine hemisulfate-aniline blue (BAB) to test for Casparian bands and lignin in the cell walls (*Brundrett, Enstone & Peterson, 1988*; *Seago et al., 1999*); and 0.05% (w/v) toluidine blue O (TBO) to visualize tissue structures (*Feder & O'Brien, 1968*; *Peterson, Peterson & Melville, 2008*). All specimens were washed with sterile water 2–3 times, mounted with sterile water, and then examined using bright-field microscopy under a Leica DME microscope (Germany). Specimens were photographed with a digital camera and a micrometer (Nikon E5400, Japan). Specimens stained with BAB were viewed under ultraviolet light on an Olympus IX71 epifluorescence microscope with excitation filter G 365 nm, absorption filter barriers U-WB (blue light), dichromatic mirror DM 500, compensation excitation filter BP 450–480, and compensation absorption filter BA 515, BAB-stained specimens were photographed with a digital camera and a micrometer (RZ200C-21; Ruizhi Cop., China) (*Yang et al., 2011*).

Blade data collection and statistical analyses

The length and width of leaf area was measured with a centimeter ruler. Tissue thickness data was collected from sections stained by SR7B, BAB and TBO as discussed in the above section. We sectioned the leaflet at the blade margin to measure the density of the fine veins. We also sectioned the leaflet at the blade center (not along the blade margin) to measure the stoma and cell number and size of tissue density and epidermal features. All sections included five blade samples that remained unstained and were mounted with sterile water. Specimens were observed under a Leica DME microscope with a micrometer. Differences between the morphological and anatomical traits from sunny and shady blades were analyzed with the paired-samples *T*-test using SPSS (version 13.0; SPSS Inc., Chicago, IL, USA).

RESULTS

The stele within the adventitious roots had diarch symmetry with protoxylem poles (Figs. 1A–1I). At 5 mm from the root tip, we observed faint Casparian bands in the endodermis of the inner root cortex, a thin-walled sclerenchyma layer around the endodermis, and a rhizodermis on the root surface (Figs. 1A and 1B). At 10 mm from the root tip, lateral roots emerged from the stele, and the stele had prominent protoxylem and protophloem (Figs. 1C–1F). In addition, the endodermis had complete suberin lamellae with a few passage cells, and the sclerenchyma layer had thicker walls (except for the idioblasts) opposite the passage cells and the protoxylem (Figs. 1C–1F). At 20 mm from the root base, the stele had primary xylem and phloem tissues, as well as deep suberin lamellae in the endodermis; the sclerenchyma layer was thick-walled (Figs. 1G–1I).

Both young and mature rhizomes had a dictyostele surrounded by sclerenchyma layers. The dictyostele included petiole vascular bundles with a prominent central protoxylem (Figs. 2A–1H). Each vascular bundle had an endodermis with Casparian bands (Figs. 2B, 2D, 2E and 2G), which became suberized at maturity (Figs. 2D, 2E, 2G and 2H). The rhizomes had a parenchymatous cortex; the rhizome surface had a thin cuticle and brown scale leaves (Figs. 2A, 2C, 2F and 2I). The petiole vascular bundles originated from the rhizomes (Figs. 2A–2E).

Young and mature petioles had a single vascular bundle with a central endodermis, a cortex, a peripheral sclerenchyma layer and an epidermis (Figs. 3A–3C). At maturity, the endodermis had Casparian bands and suberized lamellae (Fig. 3B). The petiole surface had a thin cuticle (Fig. 3C). Table 1 shows the morpho-anatomical characteristics of the blades: leaf area, tissue thicknesses, tissue densities, and epidermal features. The leaf blades from both sunny and shady environments had an epidermis, isolateral mesophyll tissue, and a dichotomous vein with a sclerenchyma layer (Figs. 3D–3I; Table 1); the endodermis of the dichotomous vein had Casparian bands and suberized lamellae (Figs. 3E, 3F, 3H and 3I). The stoma was only present on the abaxial epidermis (Figs. 3J and 3K); the shady blades had fewer and larger stoma compared to the sunny blades (Table 1). The thin cuticle was slightly thicker on the adaxial and abaxial on the sunny blades compared to shady blades (Figs. 3D–3I; Table 1). The surface of the leaf blade had a hypodermal sterome (Figs. 3D–3I). Lastly, the mesophyll was thicker in the middle of the sunny blades than the shady blades (Figs. 3D–3I; Table 1).

DISCUSSION

We observed various morphological and anatomical characteristics that were likely to support the successful colonization of dry and shady environments by *A. reniforme* var.

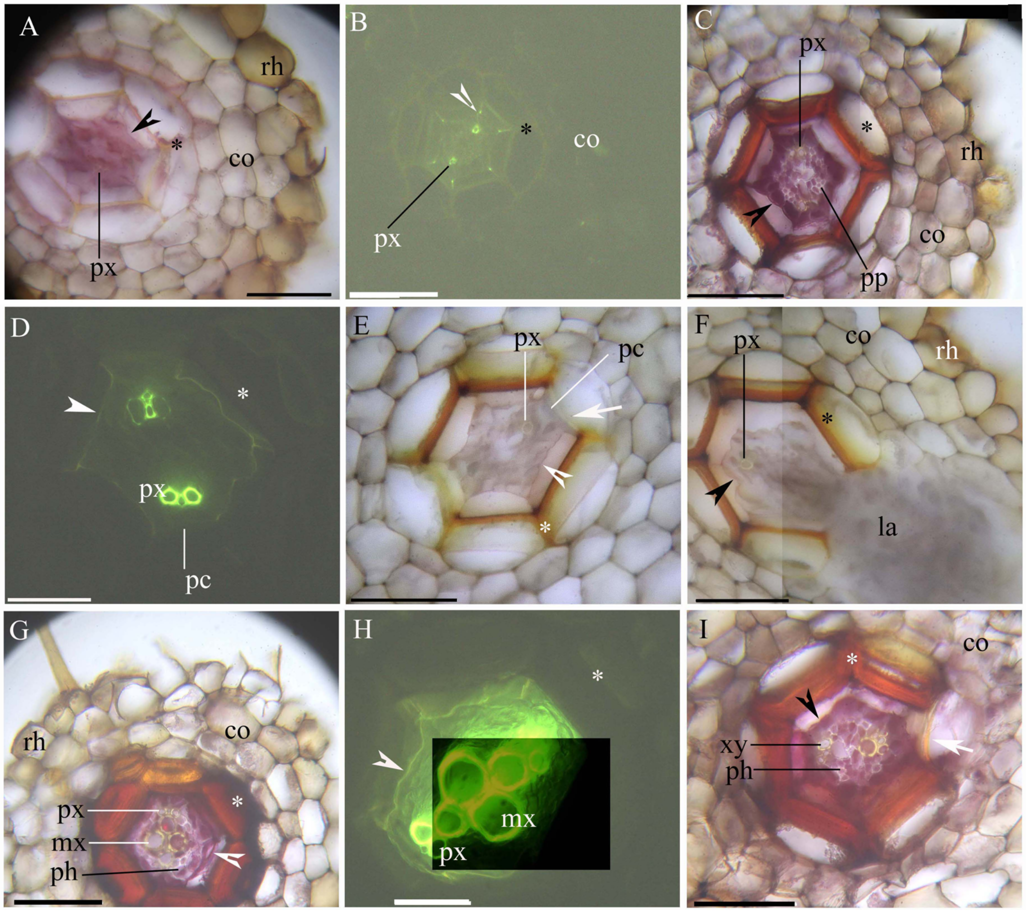

Figure 1 **(A–I) A Photomicrographs of the adventitious roots of *Adiantum reniforme* var. *sinense* (70–130 mm long); scale bars = 50 µm.** (A) A total of 5 mm from root tip. Protoxylem, endodermis (arrowhead), sclerenchyma layer (*), cortex, rhizodermis. Staining: Berberine sulfate-aniline blue (BAB); (B) A total of 5 mm from root tip. Protoxylem, endodermis (arrowhead), sclerenchyma layer (*), cortex. Staining: BAB; (C) A total of 10 mm from root tip. Protoxylem, protophloem, suberized endodermis (arrowhead), sclerenchyma layer (*), cortex, rhizodermis. Staining: Sudan red 7B (SR7B); (D) A total of 10 mm from root tip. Protoxylem, suberized endodermis (arrowhead), passage cells, sclerenchyma layer (*). Staining: BAB; (E) A total of 10 mm from root tip. Protoxylem, endodermis (arrowhead), passage cells, sclerenchyma layer (*), idioblast (arrow), cortex. Staining: SR7B; (F) A total of 10 mm from root tip. Protoxylem, suberized endodermis (arrowhead), sclerenchyma layer (*), cortex, lateral root, rhizodermis. Staining: SR7B; (G) A total of 20 mm from root tip. Protoxylem, metaxylem, primary phloem, suberized endodermis (arrowhead), sclerenchyma layer (*), cortex, rhizodermis. Staining: SR7B; (H) A total of 20 mm from root tip. Protoxylem, metaxylem, suberized endodermis (arrowhead), sclerenchyma layer (*). Staining: BAB; (I) A total of 20 mm from root tip. Primary xylem, primary phloem, suberized endodermis (arrowhead), sclerenchyma layer (*), idioblast (arrow), cortex. Staining: SR7B; Abbreviations: co, cortex; la, lateral root; mx, metaxylem; pc, passage cells; ph, primary phloem; pp, protophloem; px, protoxylem; rh, rhizodermis; xy, primary xylem. Full-size DOI: 10.7717/peerj.9937/fig-1

sinense. For example, in *A. reniforme* var. *sinense*, the adventitious roots, the rhizomes, and the leaf axes all had an endodermis with the following histochemical features; Casparian bands and suberin lamellae surrounded by sclerenchyma layers. These characteristics tend to vary distinctly across tissues and organs in almost all other vascular plants (*Ogura, 1972*; *Fahn, 1990*; *Lersten, 1997*; *Enstone, Peterson & Ma, 2003*; *Evert, 2006*;

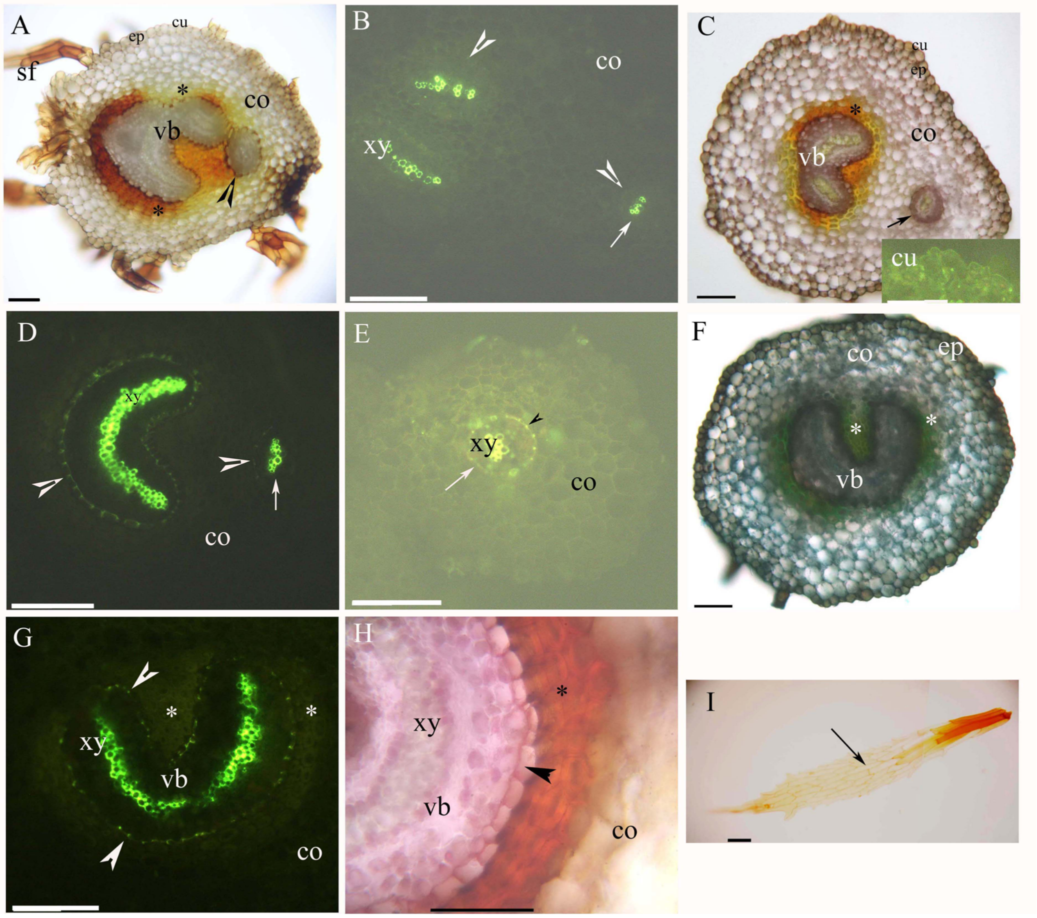

Figure 2 **(A–I) Photomicrographs of the young (A and B) and mature (C–I) rhizomes of *A. reniforme* var. *sinense* (40–60 mm long); scale bars = 50 μm.** (A) Vascular bundles, immature sclerenchyma layer (*), petiole vascular bundles (arrowhead), cortex, epidermis, cuticle, scale leaves. Staining: Sudan red 7B (SR7B); (B) Primary xylem, endodermis (arrowhead), petiole vascular bundles (arrow), cortex. Staining: Berberine sulfate-aniline blue (BAB); (C) Vascular bundles, sclerenchyma layer (*), petiole vascular bundles (arrow), cortex, epidermis, cuticle. Staining: SR7B. Inset: young cuticle. Staining: BAB; (D) Primary xylem, suberized endodermis (arrowhead), petiole vascular bundles (arrow), cortex. Staining: BAB; (E) Petiole vascular bundles (arrow), primary xylem, suberized endodermis (arrowhead), cortex. Staining: BAB; (F) Vascular bundles, sclerenchyma layer (*), cortex, epidermis. Staining: TBO; (G) Vascular bundles, primary xylem, suberized endodermis (arrowhead), sclerenchyma layer (*), cortex. Staining: BAB; (H) Vascular bundles, primary xylem, suberized endodermis (arrowhead), sclerenchyma layer (*), cortex. Staining: SR7B; (I) Scale leaves (arrow). Unstained. Abbreviations: co, cortex; cu, cuticle; ep, epidermis; sf, scale leaf; vb, vascular bundles; xy, primary xylem. Full-size DOI: 10.7717/peerj.9937/fig-2

Yang et al., 2011, *2014*, *2019a*, *2019b*, *2019c*, *2020*; *Zhang et al., 2017*; *Zhang, Yang & Seago, 2018*; *Crang, Lyons-Sobaski & Wise, 2018*; *Xiang et al., 2019*). Displaying alike to *A. reniforme* var. *sinense*, the terrestrial species *Asplenium* sp. and the epiphytic *Pleopeltis macrocarpa* possess an endodermis and a sclerenchyma layer around the vascular bundles throughout the plant (*Wetzel et al., 2017*; *De los Ángeles Lagoria et al., 2018*).

The endodermis and the sclerenchyma layers support and protect the bodies of vascular plants such as ferns, gymnosperms, and angiosperms (*Fahn, 1990*; *Lersten, 1997*; *Enstone, Peterson & Ma, 2003*; *Evert, 2006*; *Yang et al., 2011*, *2014*, *2019a*, *2019b*, *2019c*,

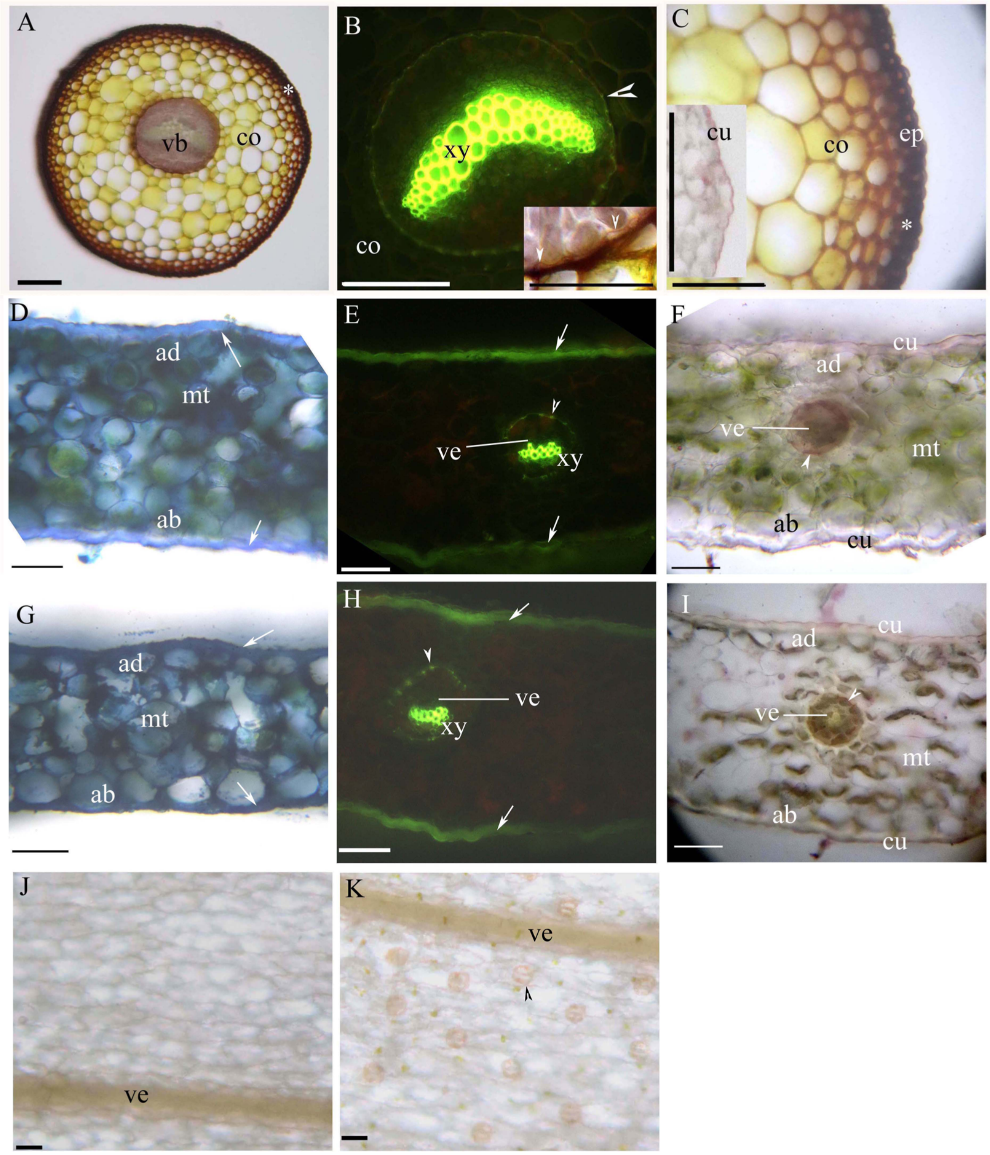

Figure 3 (A–K) Photomicrographs of the mature petioles (A–C), sunny leaves (D–F) and shady leaves (G–K) of *A. reniforme* var. *sinense*; scale bars = 50 μm. (D–I) Show the leaf blade adaxial side up. (A) Vascular bundles (arrowhead), cortex, peripheral sclerenchyma layer (*). Staining: Sudan red 7B (SR7B); (B) Primary xylem, suberized endodermis (arrowhead), cortex. Staining: Berberine sulfate-aniline blue (BAB). Inset shows the suberized endodermis (arrowhead). Staining: SR7B; (C) Cortex, peripheral sclerenchyma layer (*), epidermis. Inset shows the cuticle of a young petiole. Staining: SR7B; (D) Isolateral mesophyll tissue, hypodermal sterome (arrow), adaxial epidermis, abaxial epidermis. TBO; (E) Vein, primary xylem, suberized endodermis (arrowhead), hypodermal sterome (arrow). Staining: BAB; (F) Vein, isolateral mesophyll tissue, suberized endodermis (arrowhead), adaxial epidermis, abaxial epidermis, cuticle. Staining: SR7B; (G) Isolateral mesophyll tissue, hypodermal sterome (arrow), adaxial epidermis, abaxial epidermis. TBO; (H) Vein, primary xylem, suberized endodermis (arrowhead), hypodermal sterome (arrow). Staining: BAB; (I) Vein, isolateral mesophyll tissue, suberized endodermis (arrowhead), adaxial epidermis, abaxial epidermis, cuticle. Staining: SR7B; (J) Adaxial surface lack stomata, vein. Unstaining; (K) Abaxial surface contain stomata (arrowhead), vein. Unstaining; Abbreviations: ad, adaxial epidermis; ab, abaxial epidermis; co, cortex; cu, cuticle; ep, epidermis; mt, isolateral mesophyll tissue; vb, vascular bundles; ve, vein; xy, primary xylem.

Full-size DOI: 10.7717/peerj.9937/fig-3

Table 1 **Blades morphological and anatomical traits and environmental data.**

Morphological traits	Sunny (mean ± SE)	Shady (mean ± SE)
Leaf area		
Length (cm)	4.64 ± 0.31	4.70 ± 0.28
Width (cm)	3.88 ± 0.36	4.16 ± 0.36
Thickness (μm)	208.96 ± 23.77	189.60 ± 10.06
Tissue thickness		
Adaxial cuticle (μm)	1.5 ± 0.41	1.22 ± 0.23
Abaxial cuticle (μm)	0.54 ± 0.11	0.30 ± 0.10*
Mesophyll (μm)	153.60 ± 15.18	129.40 ± 11.17*
Adaxial epidermis (μm)	13.06 ± 4.16	10.64 ± 2.60
Abaxial epidermis (μm)	15.36 ± 4.90	13.42 ± 1.39
Adaxial hypodermal sterome (μm)	11.14 ± 2.50	10.62 ± 2.75
Abaxial hypodermal sterome (μm)	5.38 ± 2.50	6.24 ± 0.83
Tissue density		
Adaxial epidermis (n mm^{2})	282.40 ± 25.83	281.20 ± 22.79
Abaxial epidermis (n mm^{2})	188.60 ± 27.82	171.40 ± 10.29
Abaxial stomatal (n mm^{2})	45.80 ± 4.82	29.80 ± 3.11*
Marginal of fine veins (n mm)	1.90 ± 0.20	2.04 ± 0.33
Epidermal features		
Adaxial epidermis length (μm)	88.00 ± 23.32	88.80 ± 2.28
Adaxial epidermis width (μm)	40.00 ± 5.66	44.80 ± 7.29
Abaxial epidermis length (μm)	129.60 ± 39.35	105.20 ± 15.85
Abaxial epidermis width (μm)	43.20 ± 7.16	47.00 ± 4.69
Abaxial stomatal length (μm)	36.80 ± 4.38	38.40 ± 3.58
Abaxial stomatal width (μm)	30.40 ± 3.58	36.80 ± 4.38*

Note:

* A significant difference according to T-test ($P < 0.05$).

2020; *Crang, Lyons-Sobaski & Wise, 2018*; *Zhang et al., 2017*; *Zhang, Yang & Seago, 2018*; *Xiang et al., 2019*). The presence of these structures suggested that *A. reniforme* var. *sinense* would survive in dry cliff environments (*Chapple & Peterson, 1987*; *Lersten, 1997*; *Yang et al., 2011*, *2014*, *2019a*, *2019b*, *2019c*, *2020*; *Neira et al., 2017*; *Wetzel et al., 2017*; *Zhang et al., 2017*; *Zhang, Yang & Seago, 2018*; *De los Ángeles Lagoria et al., 2018*; *Xiang et al., 2019*).

Many pteridophytes have an endodermis and a sclerenchyma layer in the adventitious roots, including the terrestrial species *Platycerium bifurcatum* (*Chapple & Peterson, 1987*), *Asplenium* sp. (*Schneider, 1997*; *Leroux et al., 2011*; *Wetzel et al., 2017*), *Lycopodium obscururn*, *Selaginella* sp. (*Damus et al., 1997*), *Pteris vittata* (*Bondada, Tu & Ma, 2006*; *Sridhar et al., 2011*), *Pleopeltis* sp. (*Hernandez et al., 2013*; *De los Ángeles Lagoria et al., 2018*) and *Doryopteris triphylla* (*Neira et al., 2017*). The roots of these plants had several additional similarities to those of *A. reniforme* var. *sinense*. For example, the endodermis of *Platycerium bifurcatum* deposited suberin lamellae (*Chapple & Peterson, 1987*); idioblasts were identified in the sclerenchyma layer in the *Platycerium bifurcatum* and *Pleopeltis* *macrocarpa* (Chapple & Peterson, 1987; De los Ángeles Lagoria et al., 2018); the roots of *Selaginella* sp. had an exodermis and lignified cortical walls (Damus et al., 1997); the roots of *Platycerium bifurcatum*, *Pleopeltis* sp., and *Doryopteris triphylla* had two or more sclerenchyma layers (Chapple & Peterson, 1987; Hernandez et al., 2013; Neira et al., 2017; De los Ángeles Lagoria et al., 2018); and the rhizodermis of *Asplenium* sp. had helical thickenings (Wetzel et al., 2017). Compared to these species, *A. reniforme* var. *sinense* roots weakly adapted to dry environments (Chapple & Peterson, 1987; Damus et al., 1997; Hernandez et al., 2013; Neira et al., 2017; Wetzel et al., 2017; De los Ángeles Lagoria et al., 2018).

In *A. reniforme* var. *sinense*, the rhizomes had a dictyostele and an endodermis surrounded by sclerenchyma layers and a thin cuticle. The rhizome structures presented similarities to terrestrial ferns such as *Onoclea sensibilis* (Wardlaw, 1944), *Polypodium* sp. (Srivastava & Chandra, 2009), *Pteris vittata* (Sridhar et al., 2011), *Ceradenia* sp. (Deroin & Rakotondrainibe, 2015), *Blotiella lindeniana* (Becari-Viana & Schwartsburd, 2017) and *Doryopteris triphylla* (Neira et al., 2017). In contrast, epiphytic and xerophytic species, such as *Asplenium* sp., *Pleopeltis macrocarpa* and *Niphobolus adnascens*, had peripheral sclerenchyma layers under the epidermis. Thus, these plants were more adapted to xerophytic environments than shady *A. reniforme* var. *sinense* (Pande, 1935; Wetzel et al., 2017; De los Ángeles Lagoria et al., 2018).

The petioles of *A. reniforme* var. *sinense* had a central endodermis and a peripheral sclerenchyma layer underneath the epidermis, which is similar to other ferns (Hernandez-Hernandez et al., 2012), including *Anemia* (Ribeiro, Santos & Moraes, 2007), *Pteris* (Bondada, Tu & Ma, 2006; Martínez & Vilte, 2012; Sridhar et al., 2011; Palacios-Rios et al., 2019), *Davallia* (Ummu-Hani et al., 2013), *Blechnum* (Noraini et al., 2014), *Asplenium* (Wetzel et al., 2017), *Doryopteris triphylla* (Neira et al., 2017) and *Pleopeltis macrocarpa* (De los Ángeles Lagoria et al., 2018). In *Asplenium* species, the petiole endodermis was surrounded a sclerenchyma layer (Wetzel et al., 2017), whereas in *Doryopteris triphylla*, the petiole epidermis had a thick cuticle at the surface (Neira et al., 2017).

The blades of *A. reniforme* var. *sinense* had suberized endodermises, with Casparian strips around the vein and a hypodermal sterome (Mahley et al., 2018). These structures were like those of *Anemia* sp. (Ribeiro, Santos & Moraes, 2007; Mahley et al., 2018), indicating that *A. reniforme* var. *sinense* adapted to terrestrial environments. The blades of *A. reniforme* var. *sinense* had isolateral mesophyll, which was also identified in *Coptis chinensis*, *Doryopteris pentagona*, *Lygodium japonicum, Pteris multifida*, *Nephrolepis cordifolia*, *A. capillus-veneris* and *Pteris ensiformis* cv. *victoriae* (Yuan, Zhang & Shang, 2007; Zhang & Wu, 2013; Dematteis et al., 2019). Blades with isolateral mesophyll are a shared feature among the sciophytes (Yuan, Zhang & Shang, 2007; Zhang & Wu, 2013; Dematteis et al., 2019). The blades of *A. reniforme* var. *sinense* had thin cuticles, which is like to other shade ferns such as *Lygodium japonicum, Pteris multifida*, *Nephrolepis cordifolia*, *A. capillus-veneris, Pteris ensiformis* cv. *victoriae* and *Doryopteris pentagona* (Zhang & Wu, 2013; Dematteis et al., 2019). The thin cuticles of the *A. reniforme* var. *sinense* blades suggested that this species was adapted to shady environments, in contrast to sunny or xeromorphic ferns, such as *Cheilanthes glauca* and *Doryopteris triphylla*, which have thick cuticles (*Zhang & Wu, 2013*; *Neira et al., 2017*; *Dematteis et al., 2019*; *Shah et al., 2019*). In *A. reniforme* var. *sinense*, the shaded blades had fewer mesophyll tissues and lower stomatal densities than the unshaded blades, showing that this species displays environmental adaptive plasticity (*Givnish, 1988*; *Ribeiro, Santos & Moraes, 2007*; *Santos-Silva, Mastroberti & De Araujo Mariath, 2011*; *Neira et al., 2017*; *Dematteis et al., 2019*; *Shah et al., 2019*; *Baer, Wheeler & Pittermann, 2020*).

CONCLUSION

The adventitious roots, petioles, and rhizomes of *A. reniforme* var. *sinense* had several structures that adapted to dry environments, including an endodermis, sclerenchyma layers, and hypodermal sterome (*Chapple & Peterson, 1987*; *Neira et al., 2017*; *Wetzel et al., 2017*; *De los Ángeles Lagoria et al., 2018*). However, like many shade-adapted ferns (*Evert, 2006*; *Yuan, Zhang & Shang, 2007*; *Zhang & Wu, 2013*; *Crang, Lyons-Sobaski & Wise, 2018*), this plant also had a thin cuticle and isolateral mesophyll, which suggested a tolerance of shady environments. In contrast, epiphytic and xerophytic ferns, which are more adapted to xeric environments but also do not tolerate shade, have roots with an exodermis, many sclerenchyma layers, and helical thickenings (*Chapple & Peterson, 1987*; *Damus et al., 1997*; *Neira et al., 2017*; *Wetzel et al., 2017*; *De los Ángeles Lagoria et al., 2018*); rhizomes with peripheral sclerenchyma layers (*Wetzel et al., 2017*; *De los Ángeles Lagoria et al., 2018*); and leaves with thick cuticles (*Neira et al., 2017*). Thus, the anatomical structures of the sciophyte *A. reniforme* var. *sinense* identified herein were consistent with adaptations to dry and shady environments.

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

This work was supported by the China Three Gorges Corporation (2019H210).
The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures

The following grant information was disclosed by the authors:
China Three Gorges Corporation: 2019H210.

Competing Interests

Di Wu, Linbao Li, Xiaobo Ma and Guiyun Huang are employed by Three Gorges Corporation that have no conflicts of interest. The authors have no conflicts of interest to declare.

Author Contributions

- Di Wu conceived and designed the experiments, performed the experiments, prepared figures and/or tables, and approved the final draft.
- LinBao Li performed the experiments, authored or reviewed drafts of the paper, and approved the final draft.

- Xiaobo Ma performed the experiments, analyzed the data, prepared figures and/or tables, and approved the final draft.
- Guiyun Huang conceived and designed the experiments, analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.
- Chaodong Yang conceived and designed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.

Data Availability

The following information was supplied regarding data availability:

The raw data is in Figs. 1–3 and a Supplemental File.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.9937#supplemental-information.

REFERENCES

Baer A, Wheeler JK, Pittermann J. 2020. Limited hydraulic adjustments drive the acclimation response of *Pteridium aquilinum* (L.) Kuhn to variable light. *Annals of Botany* **125(4)**:691–700 DOI 10.1093/aob/mcaa006.

Becari-Viana I, Schwartsburd PB. 2017. Morpho-anatomical studies and evolutionary interpretations of the rhizomes of extant dennstaedtiaceae. *American Fern Journal* **107(3)**:105–123 DOI 10.1640/0002-8444-107.3.105.

Boardman NK. 1977. comparative photosynthesis of sun and shade plant. *Annual Review of Plant Physiology* **28(1)**:355–357 DOI 10.1146/annurev.pp.28.060177.002035.

Bondada B, Tu C, Ma L. 2006. Surface structure and anatomical aspects of Chinese brake fern (*Pteris vittata*; Pteridaceae). *Brittonia* **58(3)**:217–228 DOI 10.1663/0007-196X(2006)58[217:SSAAAO]2.0.CO;2.

Brundrett MC, Enstone DE, Peterson CA. 1988. A berberine-aniline blue fluorescent staining procedure for suberin, lignin, and callose in plant tissue. *Protoplasma* **146(2–3)**:133–142 DOI 10.1007/BF01405922.

Brundrett MC, Kendrick B, Peterson CA. 1991. Efficient lipid staining in plant material with Sudan red 7B or Fluorol yellow 088 in polyethlene glycol-glycerol. *Biotechnic & Histochemistry* **66(3)**:111–116 DOI 10.3109/10520299109110562.

Chapple CCS, Peterson RL. 1987. Root structure in the fern *Platycerium bifurcatum* (Cav.) C. Chr. (Polypodiaceae). *Botanical Gazette* **148(2)**:180–187 DOI 10.1086/337646.

Crang R, Lyons-Sobaski S, Wise R. 2018. *Plant anatomy: a concept-based approach to the structure of seed plants*. First Edition. Switzerland: Springer.

Damus M, Peterson RL, Enstone DE, Peterson CA. 1997. Modifications of cortical cell walls in roots of seedless vascular plants. *Botanica Acta* **110(2)**:190–195 DOI 10.1111/j.1438-8677.1997.tb00628.x.

De los Ángeles Lagoria M, Avila G, Neira DA, Rodríguez AM, Ríos NF, Prado J, Hernández MA. 2018. Morphoanatomical and histochemical characteristics of the epiphytic fern *Pleopeltis macrocarpa* (Polypodiaceae). *Brazilian Journal of Botany* **41(3)**:739–750 DOI 10.1007/s40415-018-0474-8.

Dematteis B, Solís SM, Yesilyurt JC, Meza Torres EI. 2019. Comparative anatomy in four cheilanthoid ferns. *Boletin de la Sociedad Argentina Botanica* **54(2)**:203–214 DOI 10.31055/1851.2372.v54.n2.24365.

Deroin T, Rakotondrainibe F. 2015. Comparative rhizome anatomy of some species of *Ceradenia* LE Bishop and *Zygophlebia* LE Bishop (Polypodiaceae, formerly Grammitidaceae) from Madagascar. *Modern Phytomorphology* **7**:5–12.

Enstone DE, Peterson CA, Ma F. 2003. Root endodermis and exodermis: structure, function, and responses to the environment. *Journal of Plant Growth Regulation* **21(4)**:335–351 DOI 10.1007/s00344-003-0002-2.

Evert RF. 2006. Esau's plant anatomy: meristems, cells, and tissues of the plant body—their structure, function, and development. Third Edition. Hoboken: Wiley-Interscience.

Fahn A. 1990. *Plant anatomy*. Fourth Edition. Oxford: Pergamon Press.

Feder N, O'Brien TP. 1968. Plant microtechnique: some principles and new methods. *American Journal of Botany* **55(1)**:123–142 DOI 10.1002/j.1537-2197.1968.tb06952.x.

Fu LK, Jin JM. 1992. *China plant red data book-rare and endangered plant*. Beijing: Science Press.

Geldner N. 2013. The endodermis. *Annual Review of Plant Biology* **64(1)**:531–558 DOI 10.1146/annurev-arplant-050312-120050.

Givnish TJ. 1988. Adaptation to sun and shade: a whole plant perspective. *Australian Journal of Plant Physiology* **15(2)**:63–92 DOI 10.1071/pp9880063.

Harrison CJ, Morris JL. 2017. The origin and early evolution of vascular plant shoots and leaves. *Philosophical Transactions of the Royal Society B: Biological Sciences* **373(1739)**:20160496 DOI 10.1098/rstb.2016.0496.

Hernandez MA, Teran L, Mata M, Martinez OG, Prado J. 2013. Helical cell wall thickenings in root cortical cells of Polypodiaceae species from Northwestern Argentina. *American Fern Journal* **103(4)**:225–240 DOI 10.1640/0002-8444-103.4.225.

Hernandez-Hernandez V, Terrazas T, Mehltreter K, Angeles G. 2012. Studies of petiolar anatomy in ferns: structural diversity and systematic significance of the circumendodermal band. *Botanical Journal of the Linnean Society* **169(4)**:596–610 DOI 10.1111/j.1095-8339.2012.01236.x.

Huiet L, Li FW, Kao TT, Prado J, Smith AR, Schuettpelz E, Pryeri KM. 2018. A worldwide phylogeny of *Adiantum* (Pteridaceae) reveals remarkable convergent evolution in leaf blade architecture. *Taxon* **67(3)**:488–502 DOI 10.12705/673.3.

Imaichi R. 1988. Developmental anatomy of the shoot apex of leptosporangiate ferns—II. Leaf ontogeny of *Adiantum capillus-veneris* (Adiantaceae). *Canadian Journal of Botany* **66(9)**:1729–1733 DOI 10.1139/b88-237.

Jeffreys EC. 1903. IV. The structure and development of the stem in the pteridophyta and gymnosperms. *Philosophical Transactions of the Royal Society B: Biological Sciences* **195(60)**:119–146 DOI 10.1098/rstb.1903.0004.

Kato M, Imaichi R. 1997. Morphological diversity and evolution of vegetative organs in pteridophytes. In: Iwatsuki K, Raven PH, eds. *Evolution and Diversification of Land Plants.* Tokyo: Springer, 27–43.

Leroux O, Bagniewska-Zadworna A, Rambe SK, Knox JP, Marcus SE, Bellefroid E, Stubbe D, Chabbert B, Habrant A, Claeys M, Viane RLL. 2011. Non-lignified helical cell wall thickenings in root cortical cells of *Aspleniaceae* (Polypodiales): histology and taxonomical significance. *Annals of Botany* **107(2)**:195–207 DOI 10.1093/aob/mcq225.

Lersten NR. 1997. Occurrence of endodermis with a casparian strip in stem and leaf. *Botanical Review* **63(3)**:265–272 DOI 10.1007/BF02857952.

Li X, Fang YH, Yang J, Bai SN, Rao GY. 2013. Overview of the morphology, anatomy, and ontogeny of *Adiantum capillus-veneris*: an experimental system to study the development to ferns. *Journal of Systematics and Evolution* **51(5)**:499–510 DOI 10.1111/jse.12034.

Liao JX, Shi HW, Jiang MX, Huang HD. 2007. Leaf traits of natural populations of *Adiantum reniforme var*. sinensis, endemic to the three Gorges region in China. *Photosynthetica* **45(4)**:541–546 DOI 10.1007/s11099-007-0092-3.

Lin YX. 1980. New taxa of *Adiantum* L. in China. *Acta Phytotax Sin* **18**:102.

Liu XQ, Gituru RW, Chen LQ. 2007. Genetic variation in the endangered fern *Adiantum reinforme* var. *sinense* (Adiantaceae) in China. *Annales Botanici Fennici* **44(1)**:25–32 DOI 10.1186/1471-2229-7-15.

Mahley JN, Pittermann J, Rowe N, Baer A, Watkins JE, Schuettpelz E, Wheeler JK, Mehltreter K, Windham M, Testo W, Beck J. 2018. Geometry, allometry and biomechanics of fern leaf petioles: their significance for the evolution of functional and ecological diversity within the Pteridaceae. *Frontiers in Plant Science* **9**:197 DOI 10.3389/fpls.2018.00197.

Martínez OG, Vilte I. 2012. The structure of petioles in *Pteris* (Pteridaceae). *American Fern Journal* **102(1)**:1–11 DOI 10.1640/0002-8444-102.1.1.

Nasrulhaq-Boyce A, Mohamed MAH. 1987. Photosynthetic and respiratory characteristics of Malayan sun and shade ferns. *New Phytologist* **105(1)**:81–88 DOI 10.1111/j.1469-8137.1987.tb00112.x.

Neira DA, Andrada AR, De los Ángeles Páez V, Rodriguez AM, Ríos NF, Martínez OG, Hernández MA. 2017. Anatomical, histochemical and cytogenetic features of *Doryopteris triphylla* (Pteridaceae). *American Journal of Plant Sciences* **8(4)**:907–920 DOI 10.4236/ajps.2017.84061.

Nopun P, Traiperm P, Boonkerd T, Jenjittikul T. 2016. Systematic importance of rhizome stelar anatomy in selected Monilophytes from Thailand. *Taiwania* **61(3)**:175–184.

Noraini T, Amirul-Aiman AJ, Jaman R, Nor-Fairuz AR, Maideen H, Damanhuri A, Ruzi A. 2014. Systematic significance of stipe anatomy in peninsular Malaysian *Blechnum* L. (blechnaceae) species. *Malaysian Applied Biology Journal* **43(2)**:119–125.

Ogura Y. 1972. *Comparative anatomy of vegetative organs of the Pteridophytes*. Berlin: Gebruder Borntraeger, 1–39.

Palacios-Rios M, Galan JMGY, Prada C, Rico-Gray V. 2019. Structure of the petioles and costae of Mexican and Central American species of *Pteris* (Polypodiopsida, Pteridaceae). *Phytotaxa* **401(2)**:101–116 DOI 10.11646/phytotaxa.401.2.2.

Pan L, Ji H, Chen L. 2005. Genetic diversity of the natural populations of *Adiantum reniforme* var. *sinense*. *Chinese Biodiversity* **13(2)**:122–129.

Pande SK. 1935. Notes on the anatomy of a xerophytic fern *Niphobolus adnascens* from the Malay Peninsula. *Proceedings of the Indian Academy of Sciences—Section A Part 3 Mathematical sciences* **1(9)**:556–564 DOI 10.1007/BF03039772.

Peterson RL, Peterson CA, Melville LH. 2008. *Teaching plant anatomy through creative laboratory exercise*. Ontartio: N.P C. Press Ottawa.

Plackett ARG, Di Stilio VS, Langdale JA. 2015. Ferns: the missing link in shoot evolution and development. *Frontiers in Plant Science* **6(544)**:972 DOI 10.3389/fpls.2015.00972.

PPG. 2016. A community-derived classification for extant lycophytes and ferns. *Journal of Systematics and Evolution* **54(6)**:563–603 DOI 10.1111/jse.12229.

Pryer KM, Huiet L, FWei Li, Rothfels CJ, Schuettpelz E. 2016. Maidenhair ferns, *Adiantum*, are indeed monophyletic and sister to shoestring ferns, Vittarioids (Pteridaceae). *Systematic Botany* **41(1)**:17–23 DOI 10.1600/036364416X690660.

Ribeiro MLRC, Santos MG, Moraes MG. 2007. Leaf anatomy of two Anemia Sw. species (Schizaeaceae-Pteridophyte) from a rocky outcrop in Niterói, Rio de Janeiro, Brazil. *Brazilian Journal of Botany* **30(4)**:695–702 DOI 10.1590/S0100-84042007000400014.

Rothfels CJ, Schuettpelz E. 2014. Accelerated rate of molecular evolution for vittarioid ferns is strong and not driven by selection. *Systematic Biology* **63(1)**:31–54 DOI 10.1093/sysbio/syt058.

Ruzin SE. 1999. *Plant microtechnique and microscopy*. New York: Oxford University Press.

Santos-Silva F, Mastroberti AA, De Araujo Mariath JE. 2011. Development of the epidermal cells of the pinnules of *Adiantum raddianum* C. Presl (Pteridaceae): environmental adaptive plastidial characteristics. *American Fern Journal* **101(3)**:172–181 DOI 10.1640/0002-8444-101.3.172.

Sârbu A, Smarandache D, Marinescu AT, Paraschiv AM, Mihai C, Velicu AM. 2017. Anatomical-histological observations conducted on aquatic ferns In the Danube Delta. *Journal of Plant Development* **24**:3–21.

Schneider H. 1997. Root anatomy of Aspleniaceae and the implications for systematics of the fern family. *Fern Gazette* **15**:160–168.

Seago JL Jr, Peterson CA, Enstone DE, Scholey CA. 1999. Development of the endodermis and hypodermis of *Typha glauca* Godr. and *Typha angustifolia* L. roots. *Canadian Journal of Botany* **77(1)**:122–134 DOI 10.1139/b98-173.

Shah SN, Ahmad M, Zafar M, Ullaha F, Zamana W, Mazumdarf J, Khuramg I, Khana SM. 2019. Leaf micromorphological adaptations of resurrection ferns in Northern Pakistan. *Flora* **255(6)**:1–10 DOI 10.1016/j.flora.2019.03.018.

Sridhar BBM, Han FX, Diehl SV, Monts DL, Su Y. 2011. Effect of phytoaccumulation of arsenic and chromium on structural and ultrastructural changes of brake fern (*Pteris vittata*). *Brazilian Journal of Plant Physiology* **23(4)**:285–293 DOI 10.1590/S1677-04202011000400006.

Srivastava A, Chandra S. 2009. Structure and organization of the rhizome vascular system of four *Polypodium* species. *American Fern Journal* **99(3)**:182–193 DOI 10.1640/0002-8444-99.3.182.

Ummu-Hani B, Noraini T, Maideen H, Damanhuri A, Sin-Rou G, Khatijah H, Ruzi AR. 2013. Taxonomic value of the stipe anatomy in *Davallia* (Davalliaceae) in Peninsular Malaysia. *Malayan Nature Journal* **65(2–3)**:130–144.

Vasco A, Moran RC, Ambrose BA. 2013. The evolution, morphology, and development of fern leaves. *Frontiers in Plant Science* **4**:345 DOI 10.3389/fpls.2013.00345.

Wang AH, Sun Y, Schneider H, Zhai JW, Liu DM, Zhou JS, Xing FW, Chen HF, Wang FG. 2015. Identification of the relationship between Chinese *Adiantum reniforme* var. sinense and Canary Adiantum reniforme. *BMC Plant Biology* **15(1)**:36 DOI 10.1186/s12870-014-0361-9.

Wardlaw CW. 1944. Experimental and analytical studies of pteridophytes: IV. Stelar morphology—experimental observations on the relation between leaf development and stelar morphology in species of *Dryopteris* and *Onoclea*. *Annals of Botany* **8(32)**:387–399 DOI 10.1093/oxfordjournals.aob.a088573.

Wetzel MLR, Sylvestre LDS, Barros CF, Vieira RC. 2017. Vegetative anatomy of *Aspleniaceae newman* from Brazilian Atlantic rainforest and its application in taxonomy. *Flora* **233**:118–126 DOI 10.1016/j.flora.2017.05.010.

Wu JQ. 2012. Key rare and endangered species in Three Gorges Reservoir Area. *China Three Gorges Construction* **5**:26–34.

Wu H, Chen PT, Yuan L, Xu YR, Chen LQ. 2011. Study on the technique of making paraffin section of fern. *Hubei Agricultural Sciences* **50(18)**:3767–3769.

Wu GF, Feng ZJ, Ma WL, Zhou XJ, Lang KC, Hu RL, Wang CJ, Li RG. 1992. *Botany*. Beijing: High Education Press, 128–177.

Wu H, Liu X-Q, Ji H, Chen L-Q. 2010. Effects of light, macronutrients, and sucrose on germination and development of the endangered fern Adiantum reniforme var. sinense (Adiantaceae). *Scientia Horticulturae* **125(3)**:417–421 DOI 10.1016/j.scienta.2010.03.004.

Wylie RB. 1949. Variations in leaf structure among *Adiantum pedatum* plants growing in a rock cavern. *American Journal of Botany* **36(3)**:282–287 DOI 10.1002/j.1537-2197.1949.tb05261.x.

Xiang J, Ming J, Yin H, Zhu Y, Li Y, Long L, Ye Z, Wang H, Wang X, Zhang F, Yang Y, Yang C. 2019. Anatomy and histochemistry of the roots and shoots in the aquatic Selenium hyperaccumulator *Cardamine hupingshanensis* (Brassicaceae). *Open Life Sciences* **14(1)**:318–326 DOI 10.1515/biol-2019-0035.

Xu TQ, Zhen Z, Jin YX. 1987. On the distribution characteristic of the variety *Adiantun reinforme var*. Sinense. *Journal of Wuhan Botanical Research* **5**:247–251.

Yang C, Yang X, Zhang X, Zhou C, Zhang F, Wang Q. 2019a. Anatomical structures of alligator weed (*Alternanthera philoxeroides*) suggest it is well adapted to the aquatic-terrestrial transition zone. *Flora* **253**:27–34 DOI 10.1016/j.flora.2019.02.013.

Yang C, Zhang X, Li JK, Bao MZ, Ni DJ, Seago JL Jr. 2014. Anatomy and histochemistry of roots and shoots in wild rice (*Zizania latifolia* Griseb.). *Journal of Botany* **2014(1)**:1–9 DOI 10.1155/2014/181727.

Yang C, Zhang X, Seago JL Jr, Wang Q. 2020. Anatomical and histochemical features of *Brasenia schreberi* (Cabombaceae) shoots. *Flora* **263**:151524 DOI 10.1016/j.flora.2019.151524.

Yang C, Zhang X, Wang T, Hu S, Zhou C, Zhang J, Wang Q. 2019b. Phenotypic plasticity in the structure of fine adventitious *Metasequoia glyptostroboides* roots allows adaptation to aquatic and terrestrial environments. *Plants* **8(11)**:501 DOI 10.3390/plants8110501.

Yang C, Zhang X, Zhang F, Wang X, Wang Q. 2019c. Structure and ion physiology of *Brasenia schreberi* mucilage hairs in vivo. *Peerj* **7(2)**:e7288 DOI 10.7717/peerj.7288.

Yang C, Zhang X, Zhou C, Seago JL Jr. 2011. Root and stem anatomy and histochemistry of four grasses from the Jianghan Floodplain along the Yangtze River, China. *Flora—Morphology, Distribution, Functional Ecology of Plants* **206(7)**:653–661 DOI 10.1016/j.flora.2010.11.011.

Yuan WJ, Zhang WR, Shang FD. 2007. Study on the anatomical structure of vegetative organs of *Coptis chinensis* and its pertinence to sciophyte conditions. *Journal of Henan University* **37(2)**:184–186 DOI 10.1016/S1872-5791(07)60026-8.

Zhang X, Hu L, Yang C, Zhou C, Yuan L, Chen Z, Seago JL Jr. 2017. Structural features of *Phalaris arundinacea* L. in the Jianghan Floodplain of the Yangtze River, China. *Flora* **229**:100–106 DOI 10.1016/j.flora.2017.02.016.

Zhang GM, Liao WB, Ding MY, Lin YX, Wu ZH, Zhang XC, Dong SY, Prado J, Gilbert MG, Yatskievych G, Ranker TA, Hooper EA, Alverson ER, Metzgar JS, Funston AM, Masuyama S, Kato M. 2013. Pteridaceae. In: Wu ZY, Raven PH, Hong DY, eds. *Flora of China*. Vol. 2–3. Beijing: Science Press and St. Louis Missouri Botanical Garden Press, 169–256.

Zhang ZH, Wu XX. 2013. Study on the anatomy structure of five species of fern leaves and its adaptability to sciophyte environment. *Journal of Huazhong Normal University* **47(6)**:840–843.

Zhang X, Yang C, Seago JL Jr. 2018. Anatomical and histochemical traits of roots and stems of *Artemisia lavandulaefolia* and *A. selengensis* (Asteraceae) in the Jianghan Floodplain, China. *Flora* **239**:87–97 DOI 10.1016/j.flora.2017.11.009.

Zhou SX, Jiang MX, Huang HD. 2008. Spatial pattern of *Adiantum reniform* var. *sinense*, endemic to the Three Gorge Reservoir Region. *Journal of Wuhan Botanical Research* **26**:59–63.