

The Structure of Petioles in *Pteris* (Pteridaceae)

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ABSTRACT.—We studied the petiole structure of twelve American species of *Pteris*: *P. ciliaris*, *P. cretica*, *P. deflexa*, *P. denticulata*, *P. ensiformis*, *P. exigua*, *P. inermis*, *P. multifida*, *P. mutilata*, *P. quadriaurita*, *P. tristicula* and *P. vittata*, using both light and scanning electron microscopy. We found that petioles are characterized externally by the presence of an adaxial groove and two dorsal-lateral ventilation areas. Internally, petioles are monostelic V-, U- or inverted- Ω -shaped axes. The vascular system is surrounded by one endodermis cell layer and 1–3 pericycle strata. We propose a classification of the vascular bundles into four types considering their shape, the shape of the xylem ends, the number of protoxylem zones and the presence of parenchyma bands in the xylem.

KEY WORDS.—*Pteris*, vascular bundles, petioles, ventilation areas

The paraphyletic genus *Pteris* (Schuettpelz and Pryer, 2007; Prado *et al.*, 2007) includes about 200 mainly pantropical species (Prado and Windisch, 2000). In the American continent there are about 60 species (Tryon and Tryon, 1982). In this paper we report the structure of vascular bundles of the petioles of twelve *Pteris* species, native or naturalized in the Americas: *P. ciliaris* D.C. Eaton, *P. cretica* L., *P. deflexa* Link, *P. denticulata* Sw., *P. ensiformis* Burm.f., *P. exigua* O.G. Martínez and J. Prado (Martínez and Prado, 2011), *P. inermis* (Rosenst.) de la Sota, *P. multifida* Poir., *P. mutilata* L., *P. quadriaurita* Retz., *P. tristicula* Raddi and *P. vittata* L.

Many authors consider the structure of vascular bundles significant in identifying different taxonomic groups, including Ogura (1972), White (1974), Lin and De Vol (1977, 1978), Graçano *et al.* (2001), Hernández *et al.* (2006), Hernández-Hernández *et al.* (2007), Srivastava (2008a, 2008b), among others. Ogura (1972) describe the structure of petioles in *Pteris* as being made only by one stele along their entire course, or several at the base that at some point meet. Lin and De Vol (1977) present a key to Taiwan ferns on the basis of petiole structure, and they provide diagnostic value to the number and shape of vascular bundles, sclerenchyma distribution, presence and number of adaxial grooves, ventilation areas and indument. Lin and De Vol (1978) describe the petiole structure of nine *Pteris* species (including *P. multifida*) and recognize “V”, “U” or “ Ω ”-shaped vascular bundles. Graçano *et al.* (2001) indicate that the petiole vascular bundles of *P. denticulata* and *P. leptophylla* Sw. are “U”-shaped, and assume an inverted Ω shape in *P. propinqua* J. Agardh. Bondada *et al.* (2006) report that the petiole in *P. vittata* has a “U”-shaped vascular bundle. In all cases, the xylem is described with the ends folded of the “hippocampus” type.

There have been no prior anatomical studies of most of the species treated in this work, so we expect our results will add to the anatomical and phylogenetic knowledge about this genus.

MATERIALS AND METHODS

The studies were conducted on herbarium material provided by the following institutions: BA, BM, CTES, G, K, LP, LPB, MCNS, NY, P, S, SI, SP, UNR, US and Z. Living specimens were collected in Argentina and were deposited in the MCNS Herbarium.

For anatomical studies, we considered three areas of the petiole: basal (next to the rhizome), middle (half of the petiole) and distal (next to the blade). Histological sections were made with a rotary microtome and freehand, stained with Safranin-Fast Green and mounted in Canada balsam. The histochemical tests used to detect cutin and suberin, lignin and tannins were Sudan III and fluoroglucine Fe_3Cl with CaCO_3 , respectively (D'Ambrogio Argüeso, 1986). To observe xylem we macerated using the Jeffrey technique (Jeffrey, 1917).

Observations, illustrations and photographs were done with a light Zeiss Standard 16 microscope and a scanning electron microscope of the JEOL JSM 6480LL model, belonging to the Universidad Nacional de Salta (Argentina). Samples for SEM observations were subjected to an increasing alcohol series, and then dried to critical point with CO_2 . The metallization was carried out with a thin gold-palladium coating. For the schemes, the conducting tissues are represented by Metcalfe and Chalk (1950), as suggested by Martínez (2003). Illustrations were made with the aid of a camera lucida.

MATERIAL STUDIED. *P. ciliaris*.—CUBA. East: without locality, 150 m, 9/VI/1915, Ekman 5364 (S); Santiago de Cuba: 1843-4, Linden 1924 (P). HAITI. South: Jérémie, Massif de la Hotte, western group, 800 m, 22/VII/1948, Ekman 10403 (G); Idem, 700 m, 25/XII/1926, Ekman 7415 (BM).

P. cretica.—ARGENTINA. **Salta**: Dpto. Capital, Quebrada de San Lorenzo, 1500 m, 10/III/2002, Martínez 913 (MCNS). MEXICO. **Distrito Federal**: Cañada de Contreras, 2800 m, 30/IV/1966, Rzedowski 22 217 (LP). PERU. **Amazonas**: Chachapoyas, 5/VI/1962, Wurdack 776 (K).

P. deflexa.—ARGENTINA. **Jujuy**: Dpto. Manuel Belgrano, camino a Tiraxi, 9 km of RN 9, 10/XII/1998, Morrone 3202 (CTES). **Salta**: Dpto. Santa Victoria, Parque Nacional Baritú, Abra de Minas, S 22° 27.4' W64°44.4', 1400 m, 10/VIII/2009, Martínez *et al.* 1831 (MCNS). **Tucumán**: Dpto. Monteros, Qda. del Portugués, 1550 m, Martínez 703, 30/XI/1999 (MCNS).

P. denticulata.—ARGENTINA. **Jujuy**: Dpto. Ledesma, Parque Nacional Calilegua, camino a Valle Grande, 20/IV/2002, Martínez 914 (MCNS). **Misiones**: Dpto. Candelaria, Candelaria, 8/IX/1993, Arbo *et al.* 6007 (LP). BOLIVIA. **Santa Cruz**: Valle Grande, S18°48' W63°49', 1000 m, 24/V/1996, Kessler *et al.* 6043 (LPB); CUBA. **Oriente**: Pinar de Yigüe, 500 m. 29/III/1915, Ekman 5138 (S).

P. ensiformis.—UNITED STATES OF AMERICA. **California**: Los Angeles, 20/XI/2002, Hoshizaky s.n. (MCNS 1814). JAPAN. **Hong Kong**: Tai Po Kau Forest Reserve, 21/XI/1980, Kramer *et al.* 8225 (Z). TAIWAN. **Satun**, E100°10' N 6°42', 100 m, 27/VIII/1995, Larsen *et al.* 46081 (NY).

P. exigua.—ARGENTINA. **Jujuy**: Dpto. Ledesma, camino Calilegua-San Francisco, 17/III/2009, Martínez y Chambi 1802 (MCNS), **Salta**: Dpto. Capital,

Quebrada Los Berros, 1500 m, 11/IV/2002, Martínez 881 (MCNS), **Tucumán:** Dpto. Burruyacu, Cerro Nogalito, 12/VI/1929, Venturi 8879 (SI).

P. inermis.—ARGENTINA. **Jujuy:** Dpto. Ledesma, camino a Valle Grande, 22/II/1972, Cabrera *et al.* 22384 (LP), Parque Nacional Calilegua, RP 83 S 23°41,9' W 64° 52,8', 1365 m, 17/III/2009, Martínez y Chambi 1778 (MCNS). **Salta:** Dpto. Capital, Quebrada de San Lorenzo, S 24°43.1 'W 65°30.5', 10/VII/2010, Martínez y Chambi 1919 (MCNS).

P. multifida.—ARGENTINA. **Chaco:** Dpto. Primero de Mayo: Colonia Benítez, IV/1983, Romero 1 (LP). **BOLIVIA. Santa Cruz de la Sierra:** Biocentro Gembé, 400 m, 02/IV/2010, Martínez 1872 (MCNS). **CUBA. La Habana:** Guanabacoa 7/XII/1921, Ekman 13543 (S).

P. mutilata.—CUBA. La Habana: Lomas de la Jaula, 11/VI/1914, Ekman 1313 (S). **HAITI.** West: Gonave Island, VIII/1927, Eyerdam 247 (CA). **PUERTO RICO.** Rio Abajo State Forest, N 18°20,3' W 66°42,0', 4/VI/1999. Acevedo-Rodriguez 10657 (US).

P. quadriaurita.—ARGENTINA. **Jujuy:** Dpto. Ledesma, Parque Nacional Calilegua, ruta provincial 83, Mesada Las Colmenas, Martínez y Guerra 1993, 24/VIII/2010 (MCNS). **Salta:** Dpto. Orán, Los Naranjos, a orillas del río San Andrés, 1150 m, Martínez y Prada 1746, 18/06/2008 (MCNS); Rio Pescado, 8 km de Arazayal, 25/X/1970, Vervoorst y Cuezso 7804 (BA).

P. tristicula.—ARGENTINA. **Corrientes:** Ituzaingó, Arroyo Garapé y río Paraná, 45 km E de Ituzaingó, Tressens *et al.* 408, 23–24/10/1974 (LP). **Salta:** Dpto. Orán, Río Blanquito a los Naranjos, S 23°41.7' W 64°51.9', 610 m, Martínez y Prada 1697, 17/VI/2008 (MCNS). **BRAZIL.** Rio de Janeiro, São Carlos, Fazenda Canchim, ca. 8 km. NE of São Carlos, 22/VI/1961, Eiten *et al.* 3182 (SP).

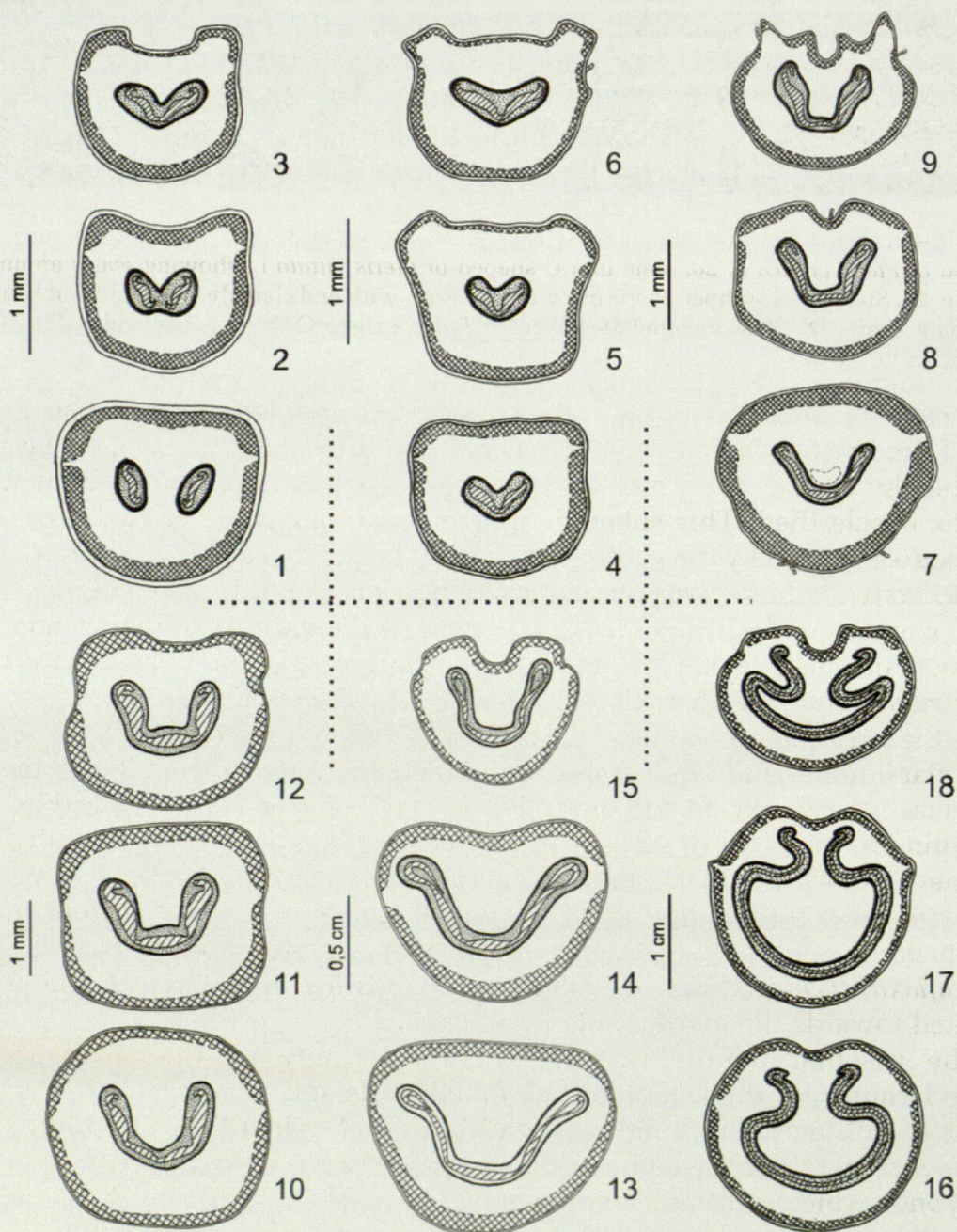
P. vittata.—ARGENTINA. **Entre Ríos:** Dpto. Rosario del Talar, Acebal, Sorarú 39, 31/III/1963 (LP). **Jujuy:** Dpto. Ledesma, Libertador General San Martín, 600 m, Martínez 1399, 13/V/2007 (MCNS). **Santa Fe:** Facultad de Ciencias Agrarias, Universidad Nacional de Rosario, Lewis 1585, 25/III/1983 (UNR 4624).

RESULTS

Externally, the petioles are green, yellow with macules or brown, always with a dark base. Their length varies between 1/2–2/3 of the total length of the fronds. The petioles of the fertile fronds are longer than those of the sterile fronds. The diameter in the middle ranges from 1 mm in *P. ensiformis* up to 20 mm in *P. deflexa*.

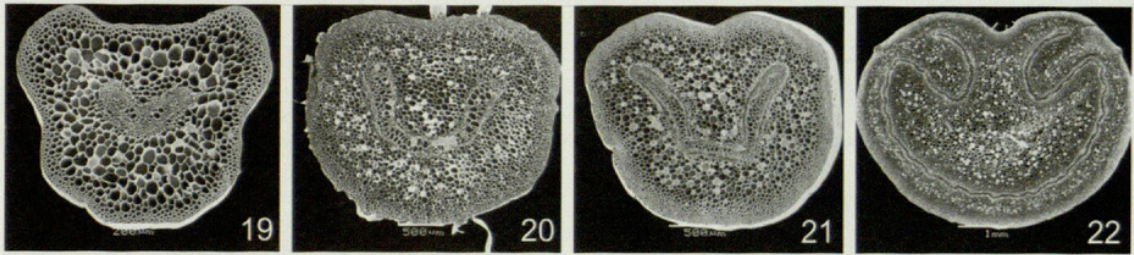
In cross section, petioles (Figs. 1–18) have bases with triangular or tetragonal boundaries (Figs. 1, 4, 7, 10, 13, 16), and subcircular middle (Figs. 2, 5, 8, 11, 14, 17) to upper sections (Figs. 3, 6, 9, 12, 15, 18) with a simple groove on the adaxial side. This groove runs lengthwise over the entire axis including the rachis, with a considerable depth from the lower basal third, and, as in the base, it is usually slightly concave. Two continuous white lines parallel to this groove, one on each side, are ventilation areas.

The indumentum of petioles consists of scales and trichomes. Scales are common in the base, similar to the rhizomatic structure; they are basifixed,



FIGS. 1-18. Petioles cross-section. 1-3. *Pteris cretica* L. 4-6. *Pteris ensiformis* Burm.f., 7-9. *Pteris denticulata* Sw. 10-12. *Pteris vittata* L., 13-15. *Pteris quadriaurita* Retz., 16-18. *Pteris deflexa* Link. 1, 4, 7, 10, 13, 16. Basal section, close to the rhizome. 2, 5, 8, 11, 14, 17. Middle section of petioles. 3, 6, 9, 12, 15, 18. Upper section, near the blade. grid = sclerenchyma, thick line = endodermis + pericycle, dotted = phloem, parallel lines = xylem.

brown, deltoid, subulate, linear-lanceolate, sub-opaque, colored in all taxa except *P. ciliaris*, which presents discolored scales and a sclerotic middle area of more intense color. Trichomes are simple, translucent to whitish, 2-4-cell, except *P. multifida* with 5-9-cell, and usually deciduous; thus the petioles of mature plants are glabrous except in the region of the longitudinal groove.



FIGS. 19–22. SEM photograph of monostelic petioles, in the middle of the shaft. **19.** Stele in V-shaped of *Pteris cretica* L. **20.** Stele in a U-shaped of *Pteris vittata* L. showing scales around the petiole. **21.** Stele in a U-shaped *Pteris quadriaurita* Retz. with ends largely elongated and bent over the main shaft. **22.** Stele inverted Ω -shaped of *Pteris exigua* O.G. Martínez and J. Prado with trichomes in the longitudinal groove.

In cross section (Fig. 19–22), petioles show a cortex formed -from the outside in- of a monostratified epidermis covered by a thick cuticle, and 2–18 layers of sclerenchyma and parenchyma (Fig. 23). In large plants as *P. deflexa* the whole cortex is sclerified. This subepidermal supporting tissue has two gaps along the petiole formed by the ventilation areas. The presence of tannins is common in the cortex, which gives the mature petioles a brown to dark color.

In young and fragile petioles, of 1 mm in diameter, ventilation areas are substomatal chambers, while in the robust petioles these areas are composed of parenchymatous tissue, with few intercellular spaces (Fig. 24).

In the medulla, depending on the cross section area, there are one or two vascular bundles. In *P. cretica* and *P. multifida*, there are two bundles on the base that fuse in the lower third of the petiole by the V-shaped abaxial ends (Fig. 1–3). The nine remaining species have monostelic petioles along the entire shaft.

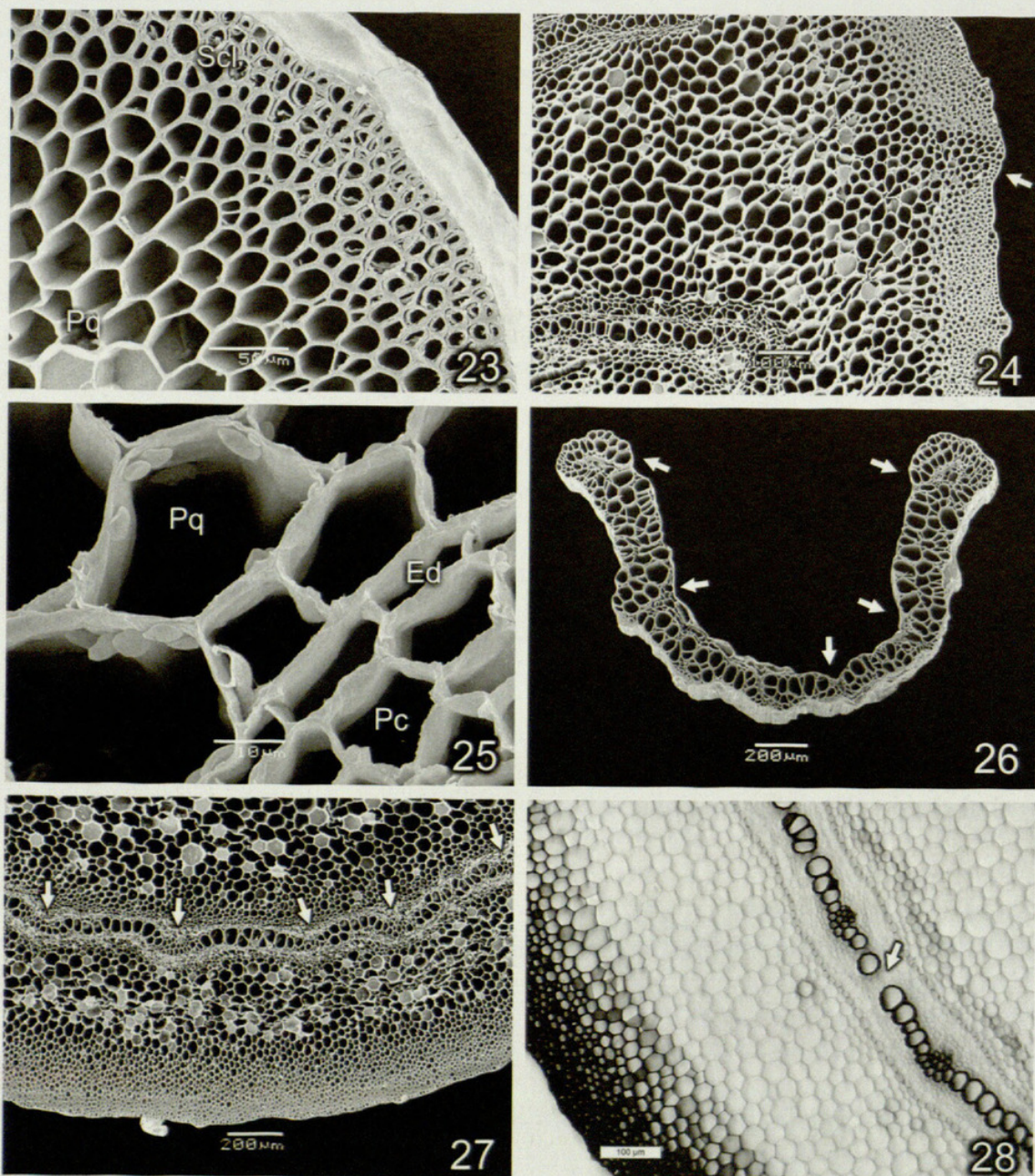
The stele is “V”-shaped (Fig. 19) in *P. ensiformis*, *P. ciliaris*, *P. cretica*, *P. multifida* and *P. mutilata*, “U”-shaped (Figs. 20, 21) in *P. vittata* and *P. denticulata*, *P. tristicula*, *P. quadriaurita*, and “inverted Ω -shaped” (Fig. 22) in *P. deflexa*, *P. exigua* and *P. inermis*. The opening of the vascular bundle is located towards the adaxial side in all cases.

The vascular bundle is surrounded externally by the monostratified endodermis with thickening on the radial walls and a pericycle consisting of (1–)2–3 cell layers surrounding the phloem and xylem (Fig. 25). Morphologically, the xylem is characterized by having curved ends in *P. vittata* or long bent ends which sometimes make contact with the main axis in *P. denticulata*, *P. tristicula* and *P. quadriaurita*. Around the vascular bundles, strands of fibers consist of 4–12 cells, which are isolated in small plants or together in a continuous or discontinuous ring depending on the age of plants.

Depending on the shape of the vascular strands and xylem structure, we propose a classification of the vascular bundles in four possible types:

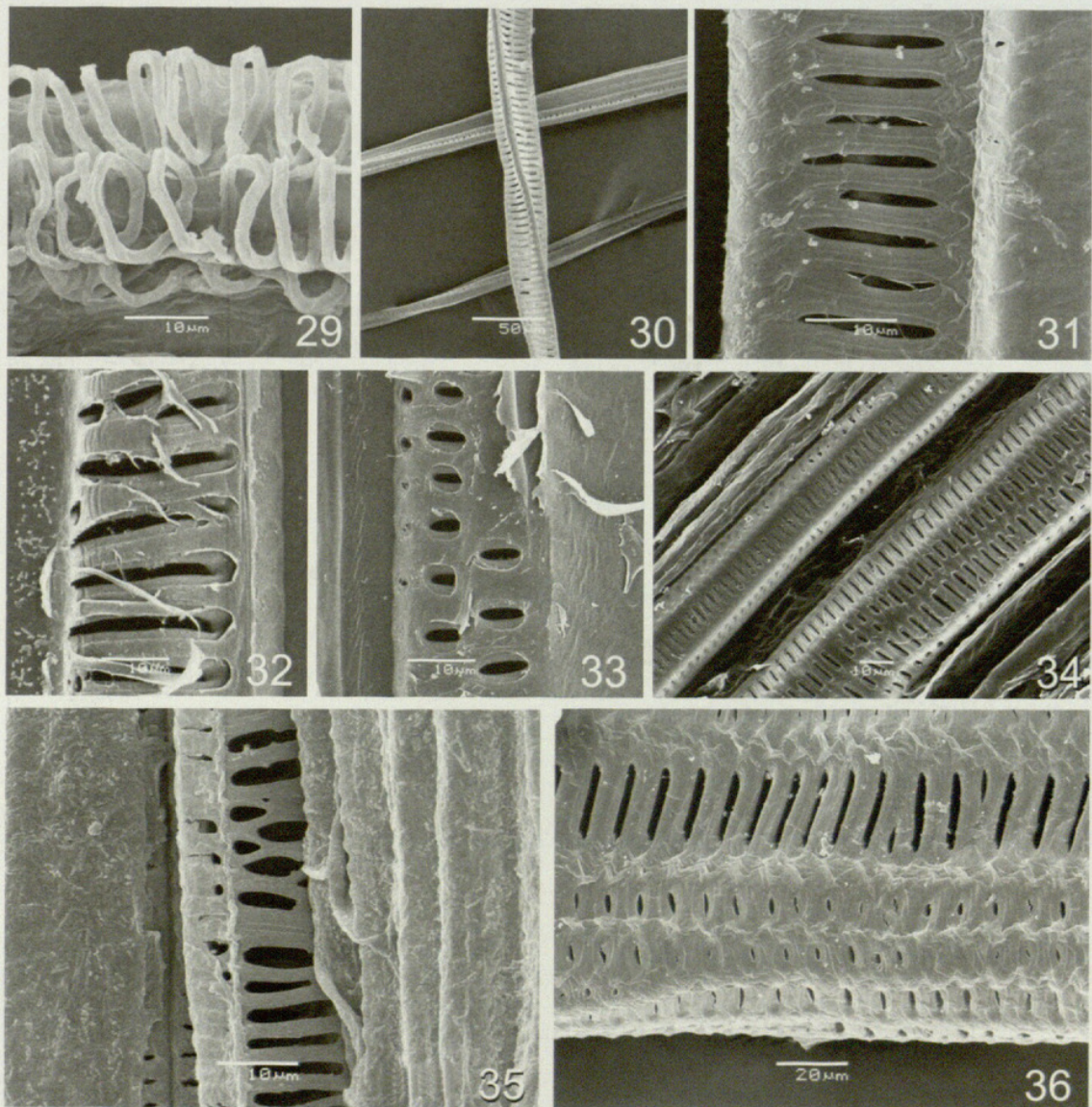
Type I. V-shaped (Fig. 19), with the ends of the xylem folded in a short hook, with three protoxylem areas: *P. ciliaris*, *P. cretica*, *P. ensiformis*, *P. multifida* and *P. mutilata*.

Type II. U-shaped, with two forms: type II-a (Figs. 20, 26) with shortly curved xylem ends and with five to six protoxylem areas observed in *P.*



FIGS. 23–28. Cross section of petioles photographed with SEM and light microscope. **23.** Cortex of *Pteris cretica* L., showing epidermis, sclerenchyma (Scl) and parenchyma (Pq). **24.** Cortex of *Pteris tristicula* Raddi, the arrow points to the ventilation area. **25.** Middle zone of the petiole in *Pteris denticulata* Sw., pointing parenchyma with chloroplasts (Pq), endodermis composed of a layer of rectangular cells (Ed), and pericycle (Pc) with more or less isodiametric cells. **26.** Xylem of *Pteris vittata* L., the arrows indicate protoxylem areas. **27.** Part of the vascular bundle of *Pteris deflexa* Link, the arrows point to protoxylem areas. **28.** Detail of xylem interrupted by a parenchyma band in *Pteris inermis* (Rosenst.) de la Sota.

vittata, and type II-b (Fig. 21) with the ends long extended, sometimes joined to the main axis, with four protoxylem areas: *Pteris denticulata*, *P. quadriaurita* and *P. tristicula*.



FIGS. 29–36. SEM photographs of tracheids. **29.** Helical thickening in the protoxylem of *Pteris denticulate* Sw. **30.** Tracheids with scalariform thickening in *Pteris mutilata* L. Detail of the pits **31.** *Pteris mutilata* L. **32–33.** *Pteris cretica* L. **34–35.** *Pteris deflexa* Link. **36.** *Pteris inermis* (Rosenst.) de la Sota.

Type III. Inverted-Ω-shaped (Figs. 22, 27), with more than ten protoxylem areas and the xylem interrupted by parenchyma bands (Fig. 28): *Pteris deflexa*, *P. exigua* and *P. inermis*.

The xylem is mesarch, with protoxylem of helical to ringed walls (Fig. 29). The metaxylem has elongated to lenticular pits (Figs. 30–36).

DISCUSSION

The external morphological characters of the *Pteris* petioles, such as a central channel and two lines covering the ventilation areas, have also been

observed in *Asplenium*, *Christella*, *Dennstaedtia*, *Microlepia*, *Pteridium*, and others by Lin and De Vol (1978). The brown to purple coloration of petioles, a color also frequent in *Adiantum*, *Cheilanthes* and *Pytirogramma*, among others, is attributed to the presence of tannins.

The number of steles is an important characteristic for rapid identification of different taxonomic groups. Lin and De Vol (1978) characterized Pteridaceae by the presence of two vascular bundles in the base of petioles that fuse upwards. This has been found in two species, *P. cretica* and *P. multifida*, whose xylem bundles join by the abaxial ends in the lower basal third of the shaft. Ogura (1972) finds such development of the vascular bundle in *Onoclea*, *Woodsia* and *Athyrium*, and calls it the "Onoclea form."

The twelve species studied have a monostelic axis from the middle petiole, although the stele shape varies. According to the classification proposed by Ogura (1972) for the monostelic axes, *P. ensiformis*, *P. ciliaris*, *P. cretica*, *P. multifida* and *P. mutilata* present Hymenophyllaceae type stele, whereas *P. denticulata*, *P. quadriaurita* and *P. tristicula* have Loxoma type vascular strand, and *P. deflexa*, *P. exigua* and *P. inermis* present the Pteris podophylla type. This author also describes two distinct types for the genus *Pteris*, the Loxoma type in *P. longifolia* Wall., *P. tremula* R. Br. and *P. flavellata* Sieb. et Zucc. and the Pteris podophylla type for the same species.

According to the classification suggested in this study, the type I, or V-shaped Hymenophyllaceae type (Ogura 1972), has been mentioned for *Adiantum* (Pteridaceae) and identified by Bidin and Walker (1985) as "saucer" shaped. Ogura (1972) considers this type to be a derivative of the Loxoma type. Lin and De Vol (1978) describe a petiole cross section of *P. multifida* that matches that described here for the species.

The type II, U-shaped or Loxoma type, has been reported for *P. denticulata*, *P. excelsa* Gaudich., *P. leptophylla* Sw., *P. semipinnata* L. and *Pteris vittata* (Lin and De Vol, 1977, 1978; Graçano *et al.*, 2001; Bondada *et al.*, 2006). Ogura (1972) mentioned the existence of modified forms within the Loxoma type, due to the presence of a varying number of protoxylem areas, i.e., five in *P. longifolia* L. and four to eight in *P. tremula* and *P. flavellata*. In this study, we found differences in the number of protoxylem bundles and in the ends of the xylem, so we proposed two different subtypes, II a and b. The first subtype is characteristic of *P. vittata* while the subtype II-b, is characterized by having ends fused to the main shaft, which gives the appearance of rounded ends, and this is likely why Ogura (1972) considered the species of *Pteris* mentioned above to have a xylem devoid of hooks.

The type III, inverted Ω -shaped, has been reported for *P. propinqua* (Graçano *et al.*, 2001) and *P. wallichiana* J. Agardh (Lin and De Vol, 1978). This monostelic type is considered by Ogura (1972) as a simple form derived from a polystelic type comprising several meristeles arranged in a horseshoe, called Saccoloma. Also Gifford and Foster (1996) qualify the monostelic condition of vascular bundles as primitive, and the polystelic condition as specialized. According to this criterion and considering that several interruptions caused by parenchyma bands have been found in the Ω form and the fact that the

numerous protoxylem groups are distributed regularly, we may consider this type to be a derivative form within the genus *Pteris*. The presence of parenchyma in the xylem has been cited in the rhizome of *Astrolepis sinuata* (Lag. ex Sw.) D.M. Benham & Windham (Scheiner and Carlquist, 1997), but no studies describing this feature in petioles have been found.

Potgieter and van Wyk (1992) mention the existence of intercellular pectic projections in the petioles of many ferns, including some *Pteris* species. These structures have not been recorded in the specimens studied, although specific future studies with more precise techniques could detect them. In the same way, the ultrastructural details of the xylem of these species could be studied.

The results of this work show that *Pteris vittata* has different characteristics in the vascular bundles from other species of *Pteris*. Martínez (2010) showed that spore characteristics of *P. vittata* are different from other species of *Pteris*. With the spore differences, these vascular bundle results reaffirm the results of molecular studies by Prado *et al.* (2007), which determined that to achieve monophyly of *Pteris* *P. vittata* should be segregated from other species of *Pteris*.

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