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ORIGINAL ARTICLE

Spore morphology and wall ultrastructure of *Trachypteris* species (Pteridaceae)

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Abstract *Trachypteris* is a small genus consisting of four species native to America and Madagascar: *Trachypteris induta*, *T. pinnata*, *T. gilliana*, and *T. drakeana*. The spores of the genus were studied using light microscopy and scanning and transmission electron microscopy. They are trilete, triangular to globose, with equatorial diameter of 29–58 μm and polar diameter of 26–53 μm. The exospore is 0.5–1.1 μm thick, plane, and two-layered. The perispore is 0.3–6.8 μm thick and two-layered. Depending on the species, two different ornamentations were observed: cristated with partially fused cristae, and ridged with partially fused ridges, forming an incomplete reticulum. Globules immersed in the perispore were occasionally observed. The systematic value of the *Trachypteris* spores is discussed, and their morphology and ultrastructure are compared with those of other related cheilanthoid ferns. The palynological characteristics presented here may be useful for phylogenetic studies within the Pteridaceae, and particularly within the cheilanthoid ferns.

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Introduction

The genus *Trachypteris* André ex H. Christ is a part of the Pteridaceae, subfamily Cheilanthoideae. The cheilanthoid ferns comprise about 400 species, grouped in 20 genera (Schuettpelz et al. 2007). They grow in a variety of habitats, with many species adapted to seasonally xeric habitats (Tryon et al. 1990; Gastony and Rollo 1995). This group is clearly related to other groups of Pteridaceae by their chromosome numbers and spore characteristics.

Trachypteris represents a specialized genus of unclear relationship within the cheilanthoid ferns (Tryon and Tryon 1982). It is characterized as being composed of terrestrial or rupestral plants with stem decumbent to erect, with broad brownish or sometimes pink, nearly concolorous scales, monomorphic or dimorphic fronds, densely covered with scales abaxially, areolate venation without included veinlets, sporangia borne in an exindusiate soral band on and between the veins (Tryon et al. 1990).

This genus comprises four species with a particular distribution. Three of them are from South America: *Trachypteris induta* (Maxon) R.M. Tryon & A.F. Tryon, endemic to Peru; *T. pinnata* (Hook. f.) C. Chr., which grows in the Andean region from Ecuador to Northwest Argentina and also in the Galapagos Islands, and *T. gilliana* (Baker) Svenson, native to Minas Gerais and Bahia, Brazil. The species *T. drakeana* (Jeanp.) C. Chr. grows in Madagascar (Tryon and Tryon 1982; Ramos Giacosa et al. 2008). Previously, *T. gilliana* has not been critically evaluated, and the genus was treated as comprising only three species by Tryon and Tryon (1982). Concerning *T. induta*,

this species was described as *Saffordia induta* but has so many common features that there seems to be no basis for recognition as a genus (Tryon and Tryon 1982).

In spite of the fact that this genus consists of few species, no contributions about all of the taxa were found. *Trachypteris* was mentioned in catalogs by Lawesson et al. (1987) and Jørgensen and León-Yánez (1999), in floristic works such as those by Tardieu-Blot (1958), de la Sota (1977), Tryon and Tryon (1982), and Tryon and Stolze (1989), and in biogeographic studies by Moran and Smith (2001).

Concerning palynological contributions, Tryon and Tryon (1973) established morphological patterns of the sporoderm in the cheilanthoid ferns and included *Trachypteris induta* (as *Saffordia induta*) within the cristate type. They observed a clear cristate sporoderm in this species and agreed with Christensen's (1938) point of view on close relations of the species with *Doryopteris*.

Haufler and Gastony (1978) studied *Bommeria* (Pteridaceae) spores by light microscopy (LM) and scanning electron microscopy (SEM) and compared them with spores of other genera within the family. The authors mentioned that *T. pinnata* and *T. induta* spores are globose to subglobose and their perispore is made up of large cristate projections.

Using SEM, Tryon and Tryon (1982) illustrated the spores of *T. induta* and *T. pinnata* from Peru and Galapagos Islands, respectively. Tryon and Lugardon (1991) illustrated the spores of *T. induta*, *T. drakeana*, and *T. pinnata* by SEM.

Ramos Giacosa et al. (2001) studied the spores of *T. pinnata* from Argentina using LM and SEM and characterized them as being triangular to globose with a cristate perispore, the cristae being partially fused.

Ramos Giacosa et al. (2008) reported that the spores of *T. pinnata* analyzed by LM and SEM are valuable to differentiate this species from *T. gilliana* from Brazil.

The spore morphology of the Pteridaceae is an important taxonomic characteristic, as was demonstrated by previous studies regarding other cheilanthoid ferns such as *Bommeria* (Haufler and Gastony 1978), *Cheilanthes* (Morbelli and Ponce 1997; Ponce et al. 2007), *Doryopteris* (Giudice et al. 2000), *Argyrochosma* (Morbelli et al. 2001), *Adiantopsis* (Piñeiro et al. 2006), *Notholaena* (Morbelli et al. 2001), and *Pellaea* (Piñeiro et al. 2001). Tryon and Tryon (1973) showed that most groups within the cheilanthoids were related by basic sporoderm patterns.

Nevertheless, a palynological study of *Trachypteris* as a whole has not been carried out yet. None of the sporoderm ultrastructures of the species within the genus have been analyzed.

The aim of this work is to analyze the spore morphology and wall ultrastructure of *Trachypteris* to improve knowledge of the spores within the genus, and to compare them with other spores of related cheilanthoid ferns from South America.

Materials and methods

Spores were obtained from herbarium specimens from the following institutions (abbreviations according to Holmgren et al. 1990): GH, LIL, LP, P, PACA, RB, and SI.

The spores were studied using light (LM), scanning (SEM) and transmission (TEM) electron microscopy. For LM, the spores were treated with hot 3% sodium carbonate for 2 min in order to preserve the perispore (Morbelli 1980) and acetolyzed according to the method of Erdtman (1960).

For SEM, the material was treated with hot 3% sodium carbonate, washed, dehydrated, suspended in 96% ethanol, and then transferred to acetate plates. After drying, they were coated with gold.

Table 1 Spore morphological data of *Trachypteris* species. Dimensions in μm

Taxa	Shape in equatorial view	Shape in polar view	Equatorial diameter	Polar diameter	Laesurae length	Ornamentation	Exospore ultrastructure	Perispore ultrastructure
T. drakeana	Plane–convex hemispheric	Triangular to globose	46–56	40–48	17–25	Cristate–reticulate	Two-layered	Two-layered: P1, P2; P1: one/three strata
T. gilliana	Convex hemispheric	Triangular to globose	29–41	31–40	14–22	Ridged distally, microreticulate proximally	Two-layered	Three-layered
T. induta	Convex hemispheric	Globose	46–58	39–50	17–25	Cristate–reticulate	Two-layered	Two layered: P1, P2; P1: three strata
T. pinnata	Convex hemispheric	Triangular to globose	39–58	26–53	12–23	Cristate–reticulate	Two-layered	Two layered: P1, P2; P1: three strata

For TEM studies, dry material from herbarium specimens was hydrated following the technique by Rowley and Nilsson (1972), by use of phosphate buffer and Alcian blue (AB). Then, the material was fixed with glutaraldehyde + 1% Alcian blue in phosphate buffer for 12 h and postfixed with 1% OsO_4 in water plus 1% Alcian blue. The spores were dehydrated in an acetone series and then embedded in Spurr soft mixture. Sections (3 μm thick) were stained with Toluidine blue and observed by LM. Ultrathin sections were stained with 1% uranyl acetate for 15 min followed by lead citrate for 3 min.

The observations were made using an Olympus BH2, a JEOL JSMT-100 scanning electron microscope, and a Zeiss T-109 transmission electron microscope.

Results

Trachypteris

The palynological characteristics of the analyzed taxa are summarized in Table 1. The spores are trilete, with triangular to globose outline in polar view. The equatorial diameter is 29–41 μm, and the polar diameter is 26–53 μm. In equatorial view, the proximal face is plane–convex or convex, and the distal face is hemispheric. The laesurae are 12–25 μm long, and they usually are covered with cristae along their whole extension.

The perispore is cristate, with partially fused cristae, or ridged with partially fused ridges, forming an incomplete reticulum.

Trachypteris drakeana (Figs. 1–4, 19–22)

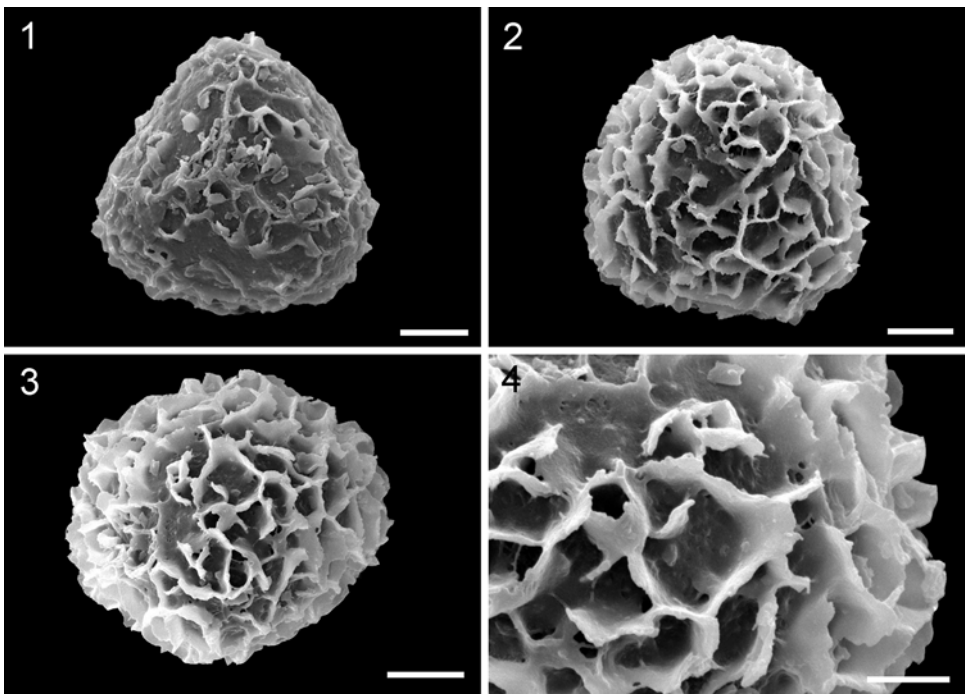
The spores are trilete with triangular to globose outline in polar view. The equatorial diameter is 46–56 μm, and the polar diameter is 40–48 μm. In equatorial view, the proximal face is plane–convex and the distal face is hemispheric. The laesurae are 17–25 μm long.

Observed by SEM (Figs. 1–4), the perispore is cristate. The cristae have an irregular margin and a few threads at their base. The cristae are partially fused, forming an incomplete reticulum. The proximal face is less ornamented than the distal face; the cristae are scattered, low and less in height (Fig. 1).

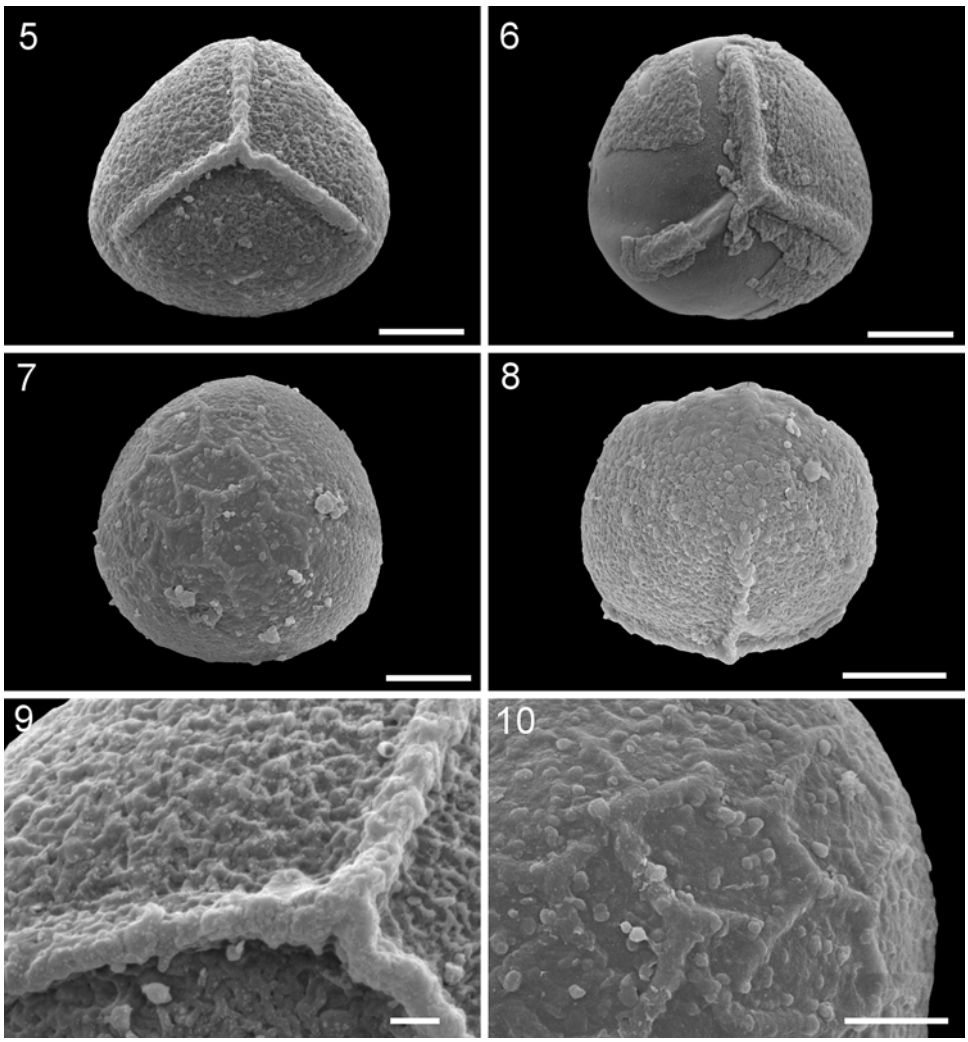
When analyzed by TEM (Figs. 19–22), the exospore is 0.5–1.1 μm thick and two-layered: the inner layer is 0.1–0.2 μm, and the outer layer is 0.5–0.9 μm thick and less contrasted than the inner one. Radial channels with dark content are observed in the outer layer. These channels are abundant and located next to and at both sides of the commissure (Fig. 19).

The perispore is 0.3–4.8 μm thick and is composed of two layers: P1 and P2. The P1 layer has one or three strata in the same spore. If three strata are present, they have an inner layer 0.1–0.2 μm thick of irregular surface. The middle stratum is 1–1.9 μm thick; rods show continuity with the outer and inner stratum. The outer stratum is 0.3–0.5 μm thick when measured in spaces without crests.

Small cavities and globules are present (Figs. 19–21) in the outer stratum, in the rods of the middle stratum, and in the inner stratum.



Figs. 1–4 SEM micrographs of spores of *Trachypteris drakeana*. **1** Proximal view of a spore with triangular to globose outline. **2** Distal view. The perispore is cristated. **3** Equatorial view of a spore. **4** Detail of the cristated perispore. The cristae have an irregular margin and are partially fused, forming an incomplete reticulum. *Scale bars* **1–3**: 10 μm, **4**: 5 μm



Figs. 5–10 SEM micrographs of spores of *Trachypteris gilliana*. **5** Proximal view of a spore with triangular to globose outline. **6** Proximal view of a spore. In some regions of the spore, the perispore was removed and the smooth exospore is evident. **7** Distal view. The perispore is ridged. Some ridges are fused, forming an incomplete reticulum. **8** Equatorial view. The proximal face is convex, and the distal face is hemispheric. **9** Detail of the proximal surface. The perispore is microreticulate. **10** Detail of the distal surface. The ridges are fused, leaving a wide, polygonal luminae. The background has small verrucae. *Scale bars* **5–8**: 10 µm, **9**: 2 µm, **10**: 5 µm

P2 layer is, in some cases, difficult to see; it is 20 nm, thin, and less contrasted than P1, and it covers the outer and inner surfaces of P1 (Fig. 20).

Trachypteris gilliana (Figs. 5–10, 23–28)

The spores are trilete, with triangular to globose outline in polar view. The equatorial diameter is 29–41 µm, and the polar diameter is 31–40 µm. In equatorial view, the proximal face is convex and the distal face is hemispheric. The laesurae are 14–22 µm long and reach the equator.

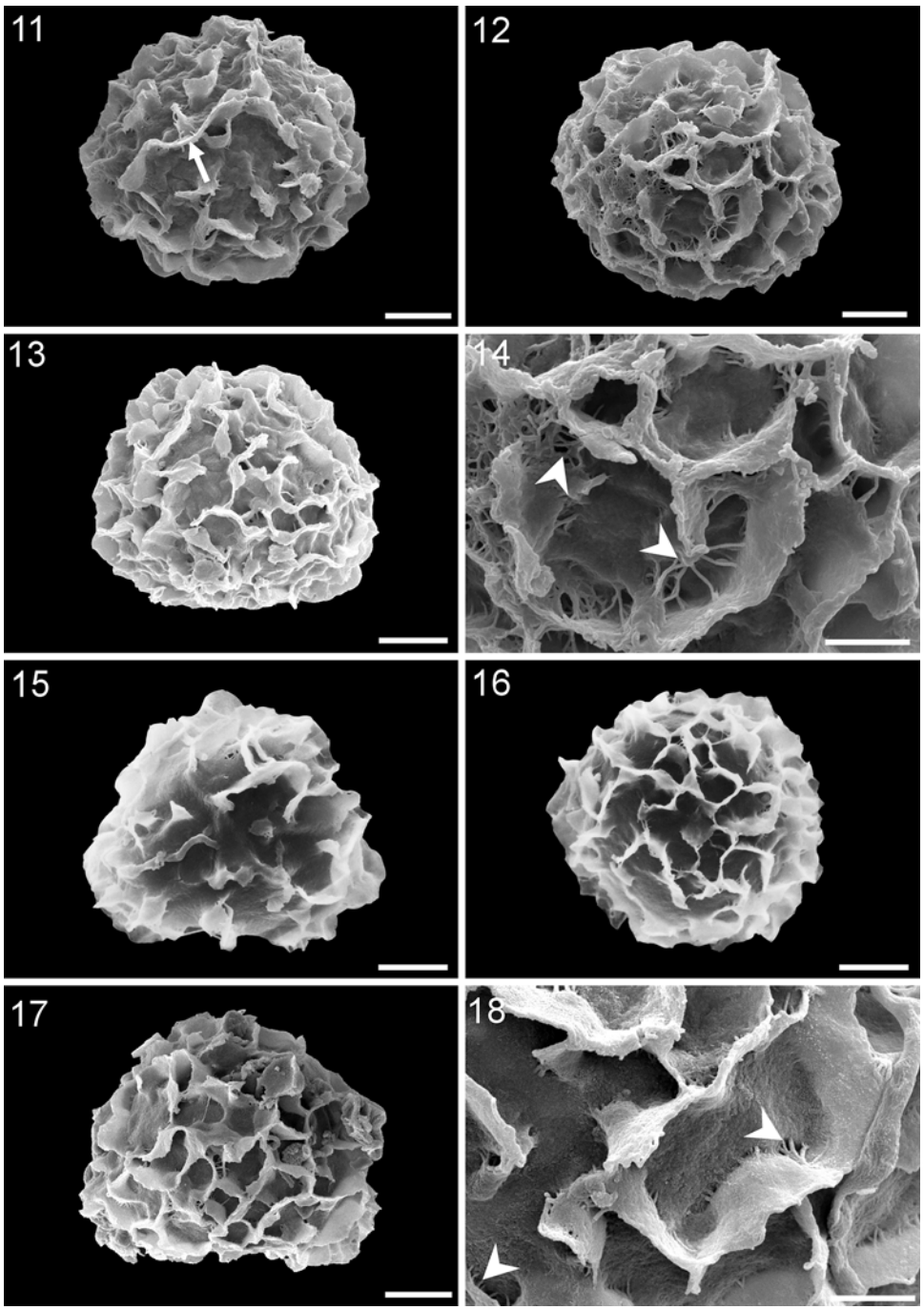
Observed by SEM (Figs. 5–10), the perispore is ridged, with partially fused ridges forming an incomplete reticulum and with scattered verrucae disposed distally. The proximal face is microreticulate with scattered verrucae.

Analyzed by TEM (Figs. 23–28), the exospore is 0.5–1 µm thick and two-layered. The inner layer is 20–60 nm thick, and the outer one is 0.5–1 µm thick and less contrasted than the inner layer. A few radial channels are observed, especially in the outer layer. These channels have dark content; in some cases, they ramify and reach the inner exospore layer (Figs. 25–26).

The perispore is 0.4–0.7 µm thick and has two layers: P1 and P2. The inner layer (P1) is composed of three strata. The inner stratum is 20–40 nm thick and is adhered to the exospore. The middle stratum is 0.2–0.4 µm thick and gives shape to the elements of the ornamentation. The outer stratum is 20–80 nm thick, more contrasted than the inner and medium strata, and its surface is irregular (Fig. 24). P2 layer is 20–40 nm thick, less contrasted than P1, and it covers the outer surfaces of P1 layer (Fig. 24).

In section, the distal ridges (Fig. 10) have a complex central structure, in which dilated tubules are observed; they are circular in section with their axis oriented in the same direction of the ridges (Figs. 27, 28). They also show bright contrast.

On the surface, scattered spherules with a similar structure and contrast to that of the perispore are observed (Fig. 24).



Figs. 11–18 SEM micrographs of spores of *Trachypteris induta* and *T. pinnata*. **11–14** *T. induta*. **11** Proximal view of a globose spore. The laesurae are usually covered by the cristae (*arrow*). **12** Distal view of a cristate spore. **13** Equatorial view. The proximal face is convex, and the distal face is hemispheric. **14** Detail of the cristate perispore. The cristae are fused, partially forming an incomplete reticulum. In their base, they have a network of threads, in some cases at high density (*arrowheads*). **15–18** *T. pinnata*. **15** Proximal view of a spore with triangular to globose outline. **16** Distal view of a cristate spore. **17** Equatorial view. The proximal face is convex, and the distal face is hemispheric. **18** Detail of the perispore. The cristae are fused, partially forming an incomplete reticulum. In the base of the cristae, some networks of threads are evident (*arrowheads*). *Scale bars* **11–13**, **15–17**: 10 μm, **14**, **18**: 5 μm

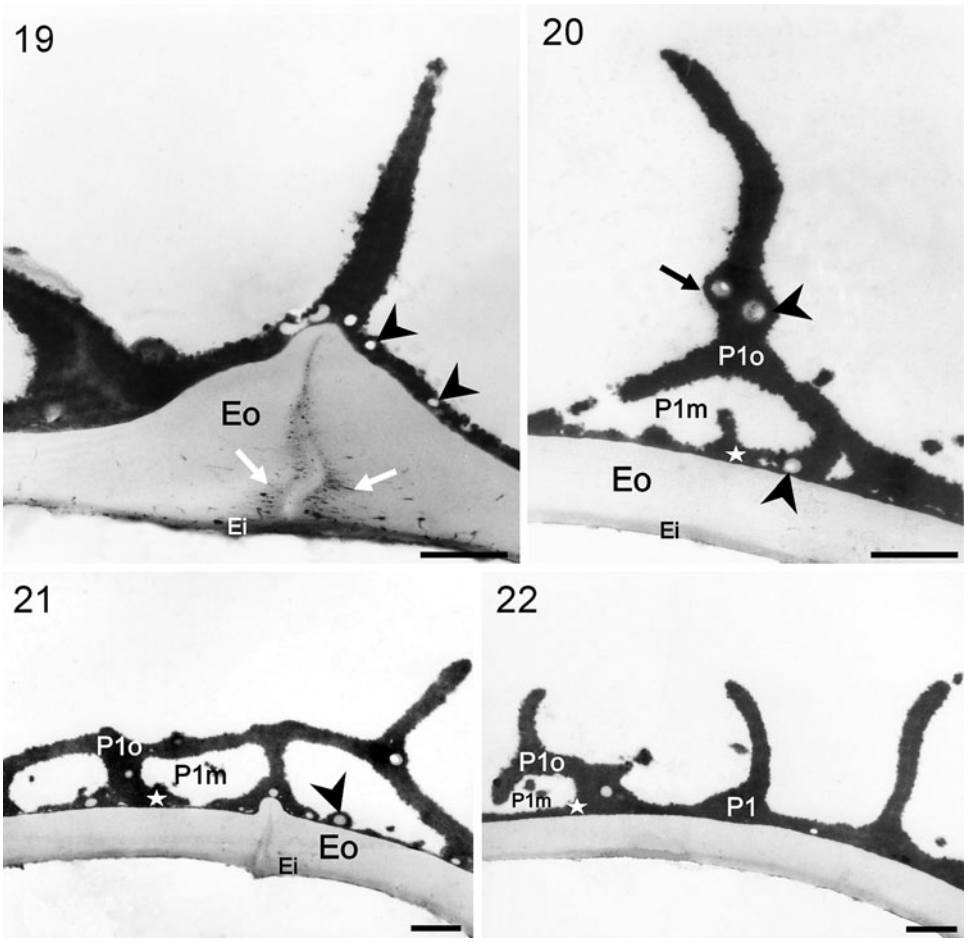
Trachypteris induta (Figs. 11–14, 29–34)

The spores are trilete, with globose outline in polar view. The equatorial diameter is 46–58 μm, and the polar diameter is 39–50 μm. In equatorial view, the proximal face is convex and the distal face is hemispheric. The laesurae are 17–25 μm long. A high continuous crista along each of them is frequently found.

Observed by SEM, the perispore is cristate (Figs. 11–14). The cristae are partially fused, forming an incomplete reticulum. The cristae have an irregular margin, and a network of threads appears in their bases. In some cases, the threads are present at high density (Fig. 14).

Analyzed by TEM (Figs. 29–34), the exospore is 0.7–1 μm thick. It comprises two layers: the inner layer is 0.1 μm thick, and the outer layer is 0.5–0.9 μm thick and smooth. In the inner layer, small cavities with dark content are evident.

The perispore is 3.2–6.8 μm thick including the cristae, and 0.7–0.8 μm thick between cristae. It is two-layered: P1



Figs. 19–22 Spores of *Trachypteris drakeana* by TEM. **19** Section through a laesurae. Several channels with dark content are visible on both sides of the laesura (*white arrows*). The inner exospore layer (Ei) shows higher contrast than the outer exospore (Eo). Cristae are observed on the laesura. In the inner stratum of the perispore, small cavities are observed (*arrowheads*). **20**, **21** Section through the sporoderm. The exospore inner layer (Ei) is more contrasted than the exospore outer layer (Eo). The perispore is composed of two layers: P1 and P2. P1 layer has three strata: the inner stratum (P1i) is adhered to the exospore (*white star*), the middle stratum (P1m) is made up of rods. The outer stratum (P1o) has the cristae. A few globules and cavities (*arrowheads*) are present in all the strata. P2 layer (*black arrows*) is thin, less contrasted than P1, and covers the outer surfaces of P1. **22** In this section of the sporoderm, the P1 layer of the perispore has one or three strata. *Scale bars* **19**–**22**: 1 μm

and P2. The inner layer (P1) consists of three strata. The inner stratum is 0.1–0.2 μm thick and has an irregular surface. The middle stratum is 0.3–1.5 μm thick with a large number of threads oriented in several directions, and it shows continuity with the outer and inner stratum. The threads are circular in transversal section and composed of helicoidally curved subunits (Fig. 34). In this stratum, chambers are located in one or several levels. The chambers in the inner part have threads which are also circular in section and show continuity with the different levels of chambers. The cristae are frequently ramified and fused with the neighboring cristae. The outer stratum is 0.3–0.6 μm thick.

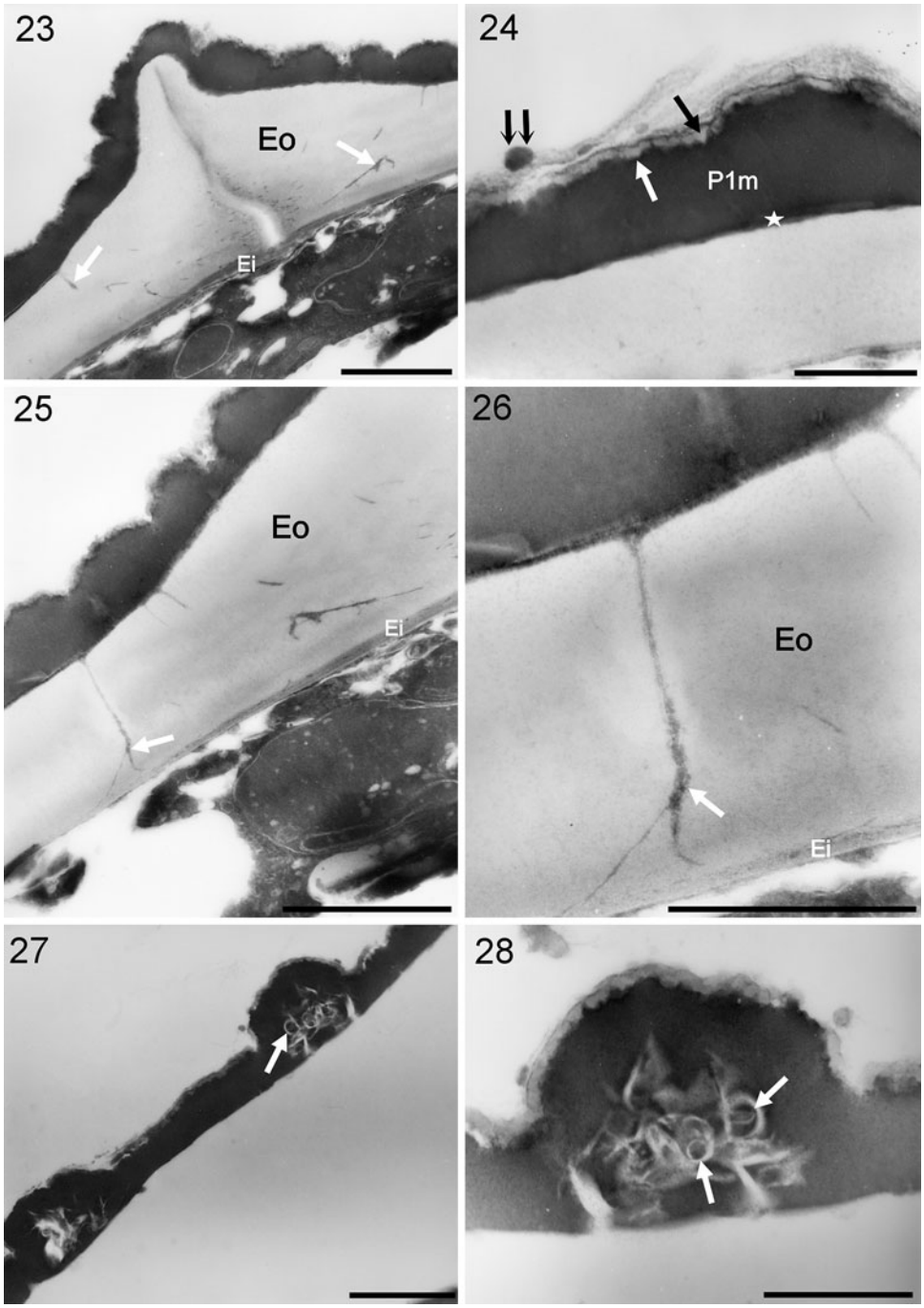
P2 layer is 20–40 nm thick, less contrasted than P1, and covers all free surfaces of it (Fig. 33).

Trachypteris pinnata (Figs. 15–18, 35–40)

The spores are trilete, with triangular to globose outline in polar view. The equatorial diameter is 39–58 μm, and the polar diameter is 26–53 μm. In equatorial view, the proximal face is convex and the distal face is hemispheric. The laesurae are 12–23 μm long and usually covered by cristae which make their visualization difficult.

Observed by SEM, the perispore is cristate. The cristae have an irregular margin and present a network of threads in their bases (Figs. 15–18). The cristae are partially fused, forming an incomplete reticulum.

Analyzed by TEM (Figs. 35–40), the exospore is 0.5–0.7 μm thick. It comprises two layers: the inner layer is 60–80 nm thick, and the outer one is 0.5–0.6 μm thick and

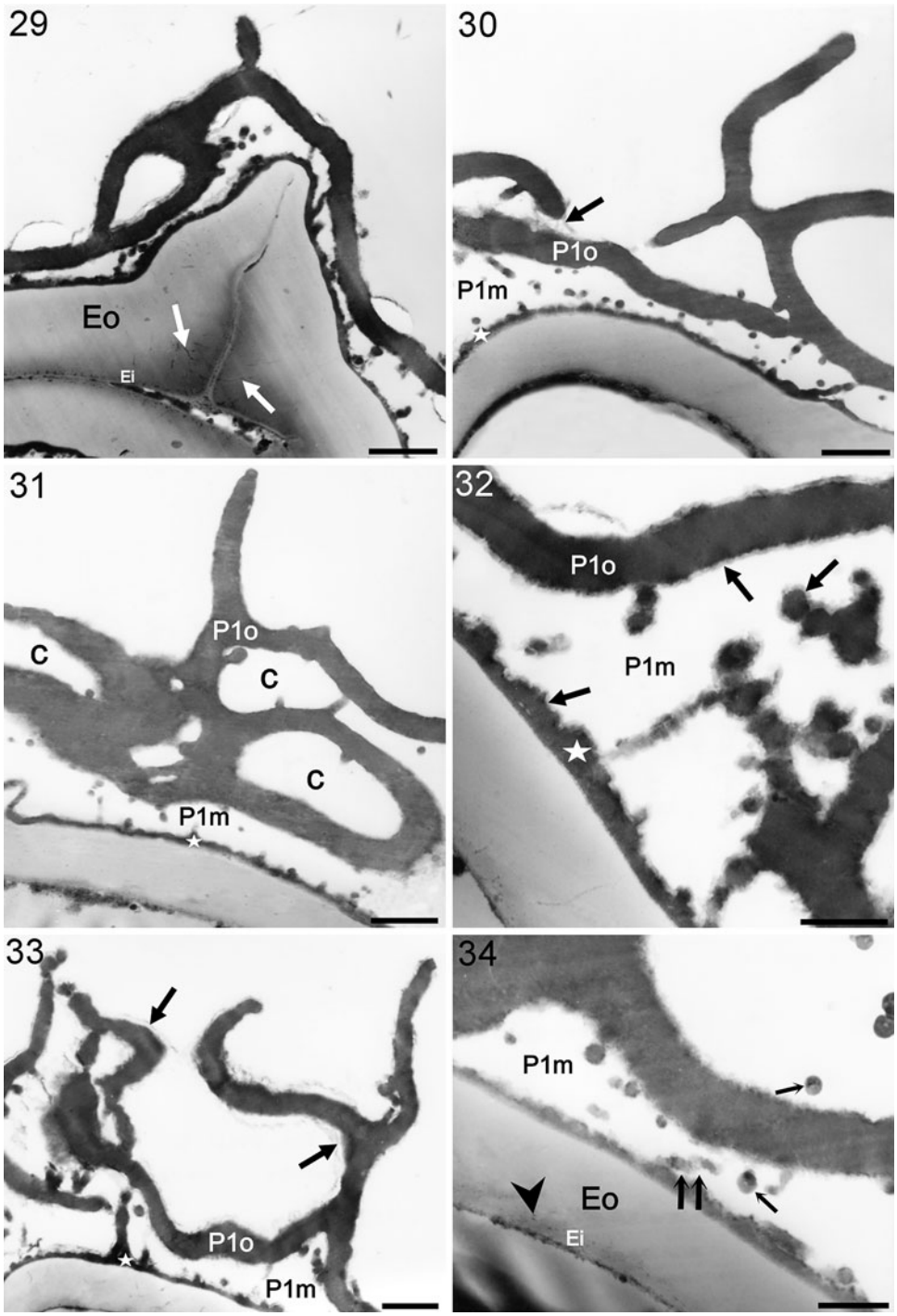


Figs. 23–28 Spores of *Trachypteris gilliana* by TEM. **23** Section through the sporoderm at the laesura level. The exospore consists of two layers. The inner exospore layer (Ei) shows higher contrast than the outer exospore (Eo). Channels with dark content are visible on both sides of the laesura (*arrows*). **24** The perispore consists of two layers: P1 and P2. P1 layer has three strata: the inner stratum (*star*) is adhered to the exospore, the middle stratum (P1m) is compact and forms the elements of the ornamentation. The outer stratum (*white arrow*) is more contrasted and thin. P2 layer (*black arrow*) is less contrasted than P1 and covers the outer surfaces of P1. A spherule is attached to the perispore surface (*double arrow*). **25**, **26** The exospore has channels (*arrows*) with dark content; in some cases they are ramified and reach the inner layer of the exospore (Ei). **27**, **28** The ridges observed in Fig. 10 have a central complex structure. Dilated tubules, which are circular in transverse section, are observed (*arrows*). *Scale bars* **23**, **25**: 1 μm, **24**, **26**: 0.5 μm, **27**: 1 μm, **28**: 0.5 μm

smooth. Radial channels are present in the outer layer, some of them in connection with the perispore (Figs. 37, 38).

The perispore is 4–6 μm thick including the cristae, and 0.6–1 μm thick between cristae. It is two-layered. The inner layer (P1) is composed of three strata. The inner stratum is 0.1–0.2 μm thick and has an irregular surface. The middle stratum is 0.2–2 μm thick, with a lax camerate structure of threads. A few threads show continuity with inner and outer layers. The outer stratum without the cristae is 0.2–0.5 μm thick. A few globules are observed in the inner perispore and on the outer surface of the spores (Figs. 39, 40).

P2 layer is 20–30 nm thick and more contrasted than P1. It covers all the free surfaces of the layer (P1) (Figs. 36–39).



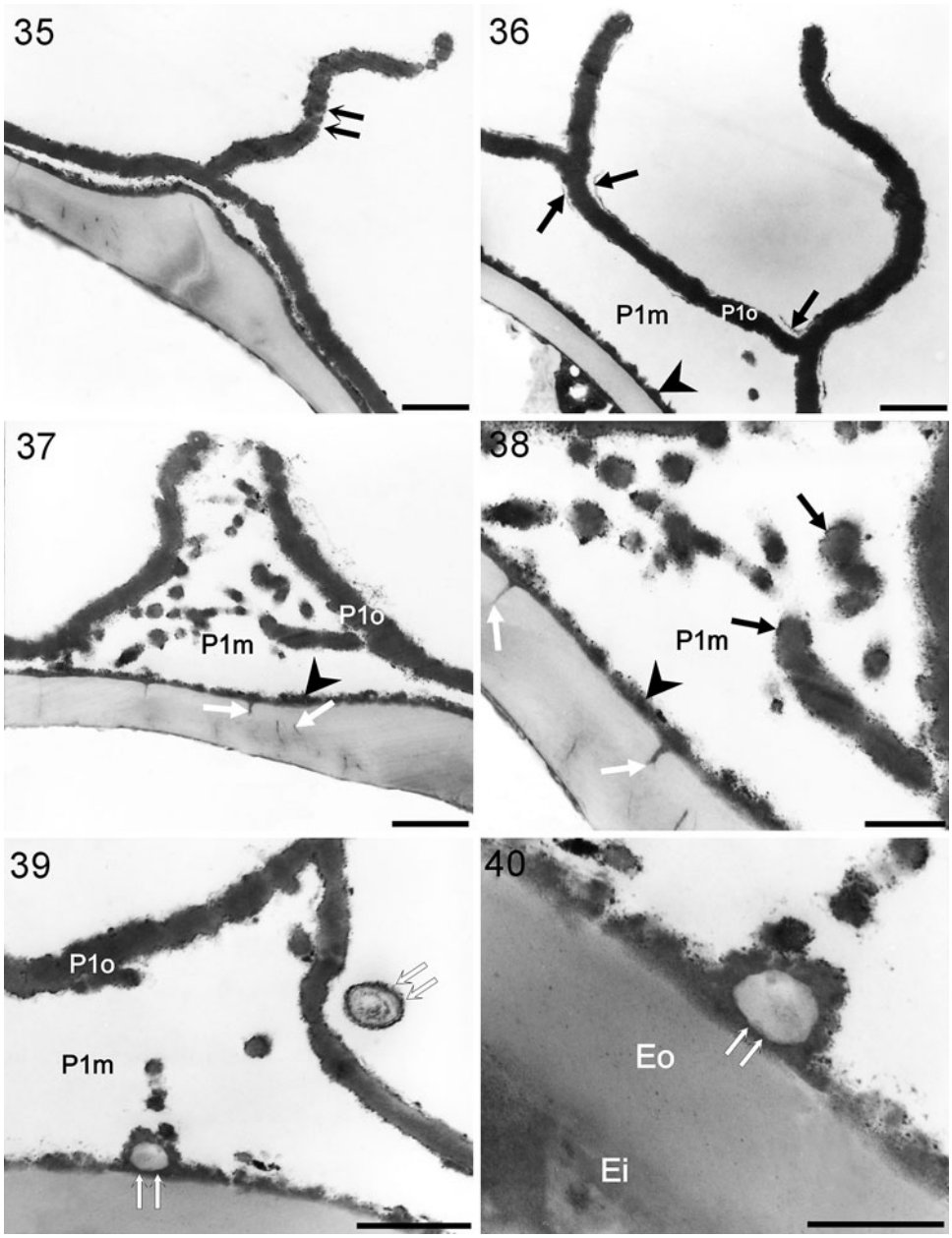
Figs. 29–34 Spores of *Trachypteris induta* by TEM. **29** Section through a laesura. Channels with dark content are visible on both sides of the laesura (*arrows*). The exospore has two layers: an inner one which is less contrasted (Ei) and an outer one (Eo). **30–33**. The perispore is made up of two layers: P1 and P2. P1 layer has three strata: the inner stratum (*star*) is adhered to the exospore, the middle stratum (P1m) is composed by threads oriented in several directions. The outer stratum (P1o) has the cristae. In some cases, chambers (C) located in several levels are observed like in Fig. 31. P2 layer (*black arrows*) is less contrasted than P1 and covers all the free surfaces of P1. **34** The two layers of the exospore are evident. Some cavities with dark content (*arrowheads*) are observed in the inner layer. The threads of the perispore are circular in transverse section (*arrows*). One helicoid (*double arrow*) is observed in the middle stratum of the perispore (P1m). *Scale bars* **29–31**, **33**: 1 μm, **32**, **34**: 0.5 μm

Discussion and conclusions

Until now no comparative studies have been carried out on *Trachypteris*. Moreover, the sporoderm ultrastructure had not been studied and, consequently, was unknown for the genus.

The spores of *Trachypteris* are triangular to globose with a plane exospore in all the species analyzed. The spores of *T. drakeana*, *T. induta*, and *T. pinnata* have similarities when observed by both light microscopy and SEM. In these species, the perispore is cristated; the cristae are partially fused and have threads in variable frequency at the cristae basis.

The spores of *T. gilliana*, have striking differences in morphology in comparison with other species of the genus, as mentioned by Ramos Giacosa et al. (2008). Their distal ornamentation is ridged, and the ridges are partially fused, forming an incomplete reticulum and scattered verrucae.



Figs. 35–40 Spores of *Trachypteris pinnata* by TEM. **35** Section through the sporoderm at the laesura level. A crista (*double arrow*) is observed on the laesura. **36–38** In the exospore, some radial channels with dark content are present (*white arrows*). The perispore is two layered: the inner layer (P1) is composed of three strata. The inner stratum is adhered to the exospore and has an irregular surface (*arrowheads*). The middle stratum (P1m) has threads that show continuity with the inner and outer layer. P2 layer (*black arrows*) is more contrasted than P1 and covers all the free surfaces of the P1 layer. The structural threads are visible in longitudinal and transverse section. **39** Section through the sporoderm. Globules (*double arrows*) are immersed in the inner stratum of P1 layer and on the outer surface of the spores. **40** The exospore has an inner layer (Ei) and an outer layer (Eo). Detail of the globule in **39** (*double arrow*). Its center has the same structure and contrast as the exospore. *Scale bars* **35–37**, **39**: 1 μm, **38**, **40**: 0.5 μm

The proximal face is microreticulate with scattered verrucae. These differences can be seen even when the spores are observed by light microscopy. When the spore diameters of all the species of the genus are comparatively analyzed, it becomes evident that *T. gilliana* has the smallest spores.

Our observations about spore shape and perispore ornamentation are in agreement with those reported by Haufler and Gastony (1978) for *T. pinnata* and *T. induta*. Similarly, our characteristics of spore shape, ornamentation, and size in these species coincide with those of Tryon and Lugardon (1991).

With respect to palynological contributions, Tryon and Tryon (1973) established sporoderm morphological patterns for the cheilanthoid ferns and included *Trachypteris induta* (as *Saffordia induta*) in the cristate type. However, Ramos Giacosa et al. (2001) considered the spores of *T. pinnata* as cristate–reticulate. In our opinion, the spores of *T. induta*, *T. pinnata*, and *T. drakeana* should be considered as cristate–reticulate, because the cristae are often partially fused, forming an incomplete reticulum.

The exospore is similar in all the species of the genus and consists of two layers. The inner layer is thin and has small cavities filled with contrasted content. The outer layer is thick and less contrasted than the inner one; it has radial channels which are sometimes seen branched and filled with contrasted contents. These channels are

abundant near and at both sides of the commissural area of each laesurae.

The perispore is the wall that has the highest structural differences. In the four species analyzed here, it consists of two layers: P1 and P2. The differences are basically related to the inner layer P1 strata components. Within this structural pattern, there are differences between species. Thus, in *T. pinnata*, P1 layer has the typical structure with three strata: an inner stratum which is thin, a medium one which is wider and presents threads, and an outer one which is thin, with perforations and crests on its surface. On the other hand, in *T. drakeana*, the same layer has two or three strata, like in the previous case, or it can simply have a single stratum.

In *T. induta*, the layer P1 is also made up of three strata but it presents greater complexity since it has multiple levels of chambers with a high number of threads, oriented in several directions. In addition to this, the crests in this species frequently branch and fuse.

In *T. gilliana*, P1 layer has a similar stratification to in *T. drakeana*, *T. induta*, and *T. pinnata*. However, the middle stratum has a compact structure without chambers.

According to the results obtained in this study and in other previous works, carried out by the same authors (Ramos Giacosa et al. 2001, 2008), it can be established that there is no correlation between the palynological characteristics of the different species of *Trachypteris* and other morphological features of the sporophyte, such as the presence/absence of foliar dimorphism or the architecture and division of sterile and fertile blades.

As regards its relationship with other cheilanthoids, *Trachypteris* has a disjunct distribution, similar to that of *Doryopteris* section *Doryopteris* (Tryon and Tryon 1982; Moran and Smith 2001). In accordance with phylogenetic analysis that considered molecular characters (Gastony and Rollo 1995; Schuettpelz et al. 2007), *Trachypteris* would be a sister group of *Doryopteris*. These close relationships are evident also because of similarity of spore morphology in *Doryopteris* and *Trachypteris*. These similarities concern the perispore crest morphology, the rodlet framework at crista bases, and also the sporoderm ultrastructure.

Trachypteris spores also share similarities with those of *Argyrochosma*, analyzed by Morbelli et al. (2001), since they have a cristate to cristate–reticulate perispore with irregular margins. As for the sporoderm ultrastructure, they share a perispore composed of three strata where the middle stratum consists of chambers at multiple levels.

Among the species of the genus *Cheilanthes* (Morbelli and Michelena 1989), *C. micropteris* and *C. pruinata* also have a cristate or cristate–reticulate perispore. Additionally, at the ultrastructural level, they also share similarities with *Trachypteris* in the perispore stratification.

On the other hand, based on the analysis of Schuettpelz et al. (2007), the genus *Adiantopsis*, represented by *Adiantopsis radiata*, would be closely related to *Trachypteris*. However, the palynological studies of Piñeiro et al. (2006) established that *Adiantopsis* spores have an echinate perispore with two levels clearly differentiated. These characteristics differ from those previously mentioned which apply to *Trachypteris*.

According to the data provided in this contribution, it can be concluded that the spore morphology and sporoderm ultrastructure of *Trachypteris* are valuable characteristics and, therefore, they should be taken into account in future taxonomic studies.

The data obtained may be of great value in future analysis in order to find relationships between species of the genus *Trachypteris*. Besides, phylogenetic studies which take into account all the *Trachypteris* species using vegetative morphology and reproductive characters, and studies in which they are combined with molecular characters, will broaden knowledge of the phylogenetic relationships within the cheilanthoids and the Pteridaceae.

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Appendix

Voucher specimens. *Trachypteris drakeana:* Madagascar, Mont Ambohipiraka, Vallée du mananjeba, 3-II-1960, *Humbert & Cours 32.914* (P); Sambirano, 9-II-1964, *Capuron 23.407* (P); *Cours 5637* (P). *Trachypteris gilliana*: Brazil, State of Minas Gerais, Arasenahy, 1880, *Glaziou 13341* (LP); Janvaria, Serra do Barreiro, 8 km. West of Januaria, 30-XII-1953, *Mendes Magalhães 6.096* (RB) MP 4132; State of Bahia, Jequié, *Senhem 16831* (PACA); Serra de Itiuba, 6 km. East of Itiuba, 19-II-1974, *Harley 16.187* (RB). *Trachypteris induta*: Peru, Dpto. Cajamarca, Cumbil-Llama, *López & Sagástegui 5214* (GH); Prov. Contumazá, López, *Sagástegui & Sánchez 3683* (GH); Dpto. La Libertad, Prov. Otuzco, Huaranchal, *Sagástegui 205* (GH). *Trachypteris pinnata*: Argentina: Prov. Salta, Dpto. Orán, Río Bermejo, 25-III-1940,

Ragonese y Covas s/n, (LIL 37811); Dpto. Rosario de la Frontera, 26-II-1905, *M. Lillo 4419* (LIL); Prov. Tucumán: Dpto. Capital, 31-X-1920, *S. Venturi 1020* (SI); Barranca de La Loma (Dique Río Salí), 16-I-1922, *Schreiter 1823* (LIL); Prov. Jujuy: Dpto. San Pedro, *Legname, Figueroa, Schiavone y Cuezo 5367* (LIL). Ecuador, Islas Galápagos, Isla Santa Cruz, 24-VI-1964, *Wiggins 1836* (GH), Iguana Cove, Albermarle Island, 30-XII-1898, *Snodgrass & Heller 17* (GH). Peru, Dpto. Cuzco, Prov. Convención, Rosario mayo, *Vargas 22343* (GH).

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