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Morphology and ultrastructure of *Sphaeropteris* spores (Cyatheaceae) from the Neotropics

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ABSTRACT

Spores of species of *Sphaeropteris* genus from America were studied with TEM and SEM. Six species were quoted as growing in America (cf. Tryon, 1971; Windisch, 1977): *Sphaeropteris brunei* (Christ) Tryon, *Sphaeropteris cuatrecasacansii* Tryon, *Sphaeropteris gardneri* (Hook.) Tryon, *Sphaeropteris horrida* (Liebm.) Tryon, *Sphaeropteris insignis* (D. C. Eaton) Tryon and *Sphaeropteris quindiuensis* (Karst.) Tryon. The aims are to characterize the species through their spore morphology and sporoderm ultrastructure. Based on these results it speculates about the relationships of these taxa within the family Cyatheaceae. It was find out with SEM, three kinds of surfaces can be recognized. It was find out with TEM that the exospore and perispore have two layers. The perispore is composed of an inner layer with three strata and the outer layer has two strata. The palynological characteristics were important in the identification of a natural taxonomic group.

1. Introduction

There are about 120 species of *Sphaeropteris* (Tryon and Tryon, 1982) distributed mainly in Asia and Oceania. However, six of them grow in America (Tryon, 1971; Windisch, 1977): *Sphaeropteris brunei* (Christ) Tryon, *Sphaeropteris cuatrecasasii* Tryon, *Sphaeropteris gardneri* (Hooker) Tryon, *Sphaeropteris horrida* (Liebmann) Tryon, *Sphaeropteris insignis* (D. C. Eaton) Tryon and *Sphaeropteris quindiuensis* (Karsten) Tryon. The main features of the genus are, the scales of the petiole structurally conform (Tryon, 1970; Lellinger, 2002) and echinate spores (Korall et al., 2007).

Holttum (1963) proposed the first classification of Cyatheaceae based on the presence of scales at the petiole bases and included the species with settiferous scales in *Cyathea* subg. *Sphaeropteris*. Tryon (1970) reconsidered the group of species with conform scales (= settiferous) and raised the status of *Sphaeropteris* from subgenus to genus. Finally, Lellinger (1987) circumscribed the genus *Sphaeropteris*, including the Tryon species of the Old World, and six species of the "neotropical group *S. horrida*".

New phylogenetic studies, based on morphologic, molecular and paleontologic data (Conant et al., 1994, 1995, 1996; Korall et al., 2006), confirmed the circumscription of the genus *Sphaeroptetheris* according to Lellinger. The spore morphology also supports that phylogenetic hypothesis (Korall et al., 2007)

Former observations of spores were made with light microscope and described as having a rugulate-striate pattern and echinulate processes on the spore surface of *Sphaeropteris cooperi* (under *Cyathea*) Erdtman and Sorsa (1971).

Gastony and Tryon (1976) analyzed the spores of *Sphaeropteris* with SEM, described two different patterns of ornamentation: (1) spores with pointed projections on the surface, present in paleotropical species and those of the neotropical group allied to *Sphaeropteris horrida*; (2) spores with threads in a dense network present in the rest of the neotropical species.

Liew and Wang (1976) also studied spores with SEM and described those of *Sphaeropteris* and some *Alsophila* species from Taiwan as echinate and established relationships based on the spore morphology. The authors proposed the evolutionary trend *Sphaeropteris-Alsophila-Nephelea*, in which the presence of echinae was considered as primitive and the presence of ridges was an evolved characteristic.

Tryon and Tryon (1982) considered three types of spore ornamentation in Neotropical species of *Sphaeropteris* and found that most species have a perispore with fibers of particulate material and the exospores having variable surfaces. The second type of spores has a granular perispore on a foraminated exospore. The third spore type, has an echinate perispore with short projections, present in the group of species allied to *Sphaeropteris horrida*. Braggins and Large (1990) described the ornamentation of spores of *Sphaeropteris medullaris* (under *Cyathea*) with LM and SEM as having abundant echinae on the distal side, which are rare or absent on the proximal side.

Few papers deal with the sporoderm ultrastructure in Cyatheaceae. Lugardon (1971, 1974) was the first author in using TEM in this group in sections of *Sphaeropteris cooperi* and *Sphaeropteris medullaris* spores, both from Oceania. He described a blechnoid exospore and a two-layered perispore, with a deep layer composed of three strata.

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Tryon and Lugardon (1991) described and provided TEM and SEM illustrations of *Sphaeropteris* spores and recognized two subgenera. The spores of the subgenus *Sphaeropteris* that have echinae arranged on the surface of low ridges; while those of the subgenus *Scleropteris* have a smooth to verrucate surface, with rodlets like those present in *Cyathea*.

Marquez et al. (2010) described the morphology and ultrastructure of *Sphaeropteris gardneri* from Brazil. They characterized the perispore ornamentation as formed of short spinulate ridges. With TEM, the exospore has two layers and the perispore is complex with two layers, the outer layer with threads and the inner layer with three strata.

In the present contribution the spores of *Sphaeropteris* from the Neotropics will be studied with light microscope and TEM and SEM in order to characterize the spore morphology, and to get to understand the complex ultrastructure of the sporoderm. Then, the different patterns found within the Cyatheaceae will be compared with the aim of establishing possible relationships within the family.

2. Material and methods

Spores were obtained from herbarium specimens of the following Institutions: Instituto Anchietano de Pesquisas, São Leopoldo, Rio Grande do Sul, Brazil (PACA), Harvard University, Cambridge, Massachusetts, U.S.A. (GH), the Smithsonian Institution, Washington DC, USA (US), Muséum National d'Histoire Naturelle, Paris, France (P) and Museo de Ciencias Naturales de La Plata, La Plata, Buenos Aires, Argentina (LP). Spores of several untreated chemically specimens were studied with light microscopy (LM), scanning electron microscopy (SEM) and transmission electron microscopy (TEM).

For LM observations an Olympus BH2 was used, values of polar diameter, equatorial diameter, exospore and perispore thickness were obtained by LM observations and sizes were based on measurements of 25 spores in each sample. The exospore and perispore thicknesses were also measured from TEM photomicrographs.

For SEM studies 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. The observations were performed with a JEOL JSMT-100 SEM at 15 kV and about 20 spores were examined per sample.

For TEM studies herbarium specimens were hydrated with buffer plus alcian blue (AB), then the material was fixed with 1% glutaraldehyde (GA) + 1% AB in phosphate buffer for 12 h and postfixed with 1% OsO_4 in water plus 1% AB for 2 h (Rowley and Nilsson, 1972).

The spores were dehydrated in an acetone series and then embedded in Spurr's soft mixture. Thick sections were stained with toluidine blue and observed with LM. Ultra-thin sections were stained with 1% uranyl acetate for 15 min followed by lead citrate for 3 min. The observations were made with a Zeiss M-10 TEM at 80 kV and taking into account about 10–15 spores in each sample.

The spores of the type material of the following species were analyzed: *Sphaeropteris cuatrecasasii, Cuatrecasas 22423* (US) **Holotype**; *Sphaeropteris gardneri, Regnell 577* (P) **Isotype**.

2.1. Studied material

Sphaeropteris brunei (Christ) Tryon

Costa Rica: Cartago, Trinidad, Turrialba volcano, 1/05/1965, *Lent 559* (GH).

Sphaeropteris cuatrecasasii Tryon

Colombia: Valle del Cauca, Sobre Las Brisas entre El Tabor y Alto de Mira, 22/10/1946, *Cuatrecasas 22423* (US).

Sphaeropteris gardneri (Hooker) Tryon

Brazil: Santa Catarina, Mun. Papanduva, Serra do Espigao, 20/04/1962, *Reitz & Klein 12656* (PACA); Biguaçu, Antinha, 04/03/1943, *Reitz 232* (PACA); Ilhota, Morro de Baú, 21/01/1953, *Reitz 5170* (PACA). Minas Gerais, Caldas, 1855, *Regnell 577* (P).

Sphaeropteris horrida (Liebmann) Tryon

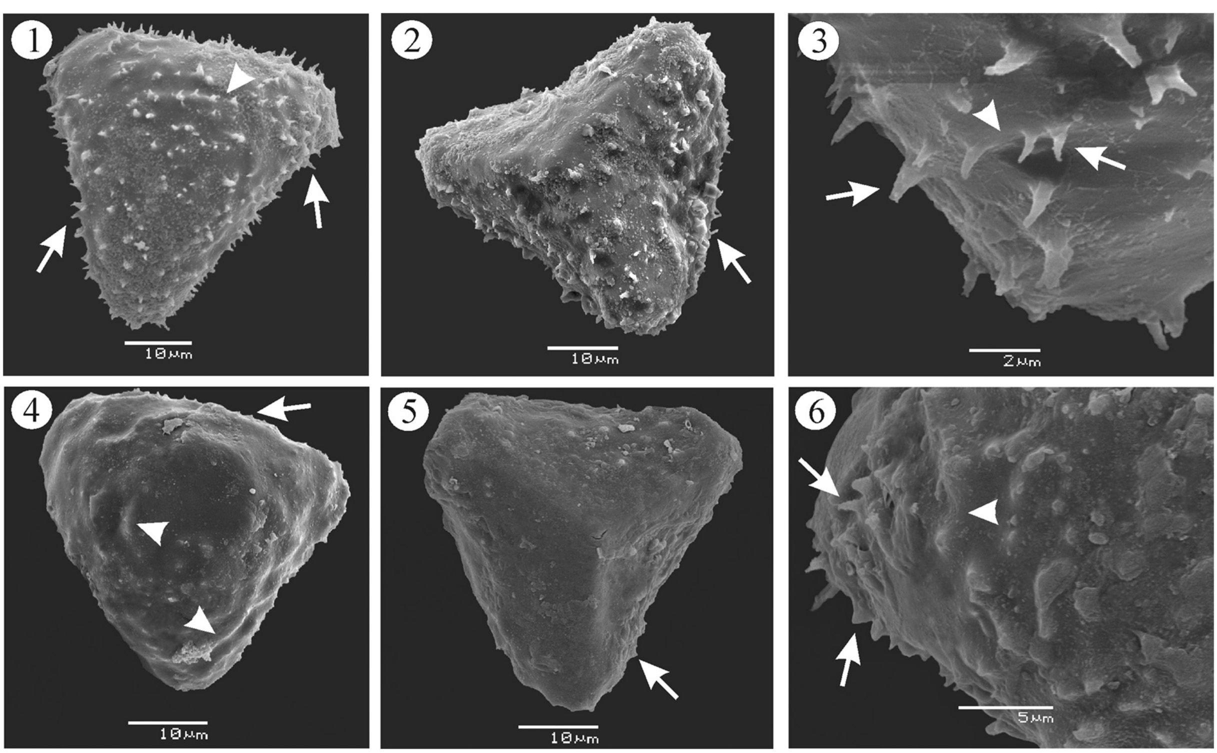

Plate I. SEM pictures of spores of *Sphaeropteris brunei* and *Sphaeropteris cuatrecasasii*. 1–3: *S. brunei*. 1) Distal view, the ornamentation is composed of spines (arrows) and ridges (arrowhead); 2) proximal view, with spines (arrows) and low ridges; 3) detail of the distal surface of a spore, with large spines (arrows) and low ridges (arrowhead). 4–6: *S. cuatrecasasii*. 4) Distal view, the ornamentation is composed of ridges (arrowheads) of different sizes; 5) proximal view with few short spines and mall verrucae and the area over the laesurae is laevigate; 6) the spore surface has ridges, with low spines (arrows) on the margin. Scale bars: 1, 2, 4, 5 = 10 µm; 3 = 2 µm; 6 = 5 µm.

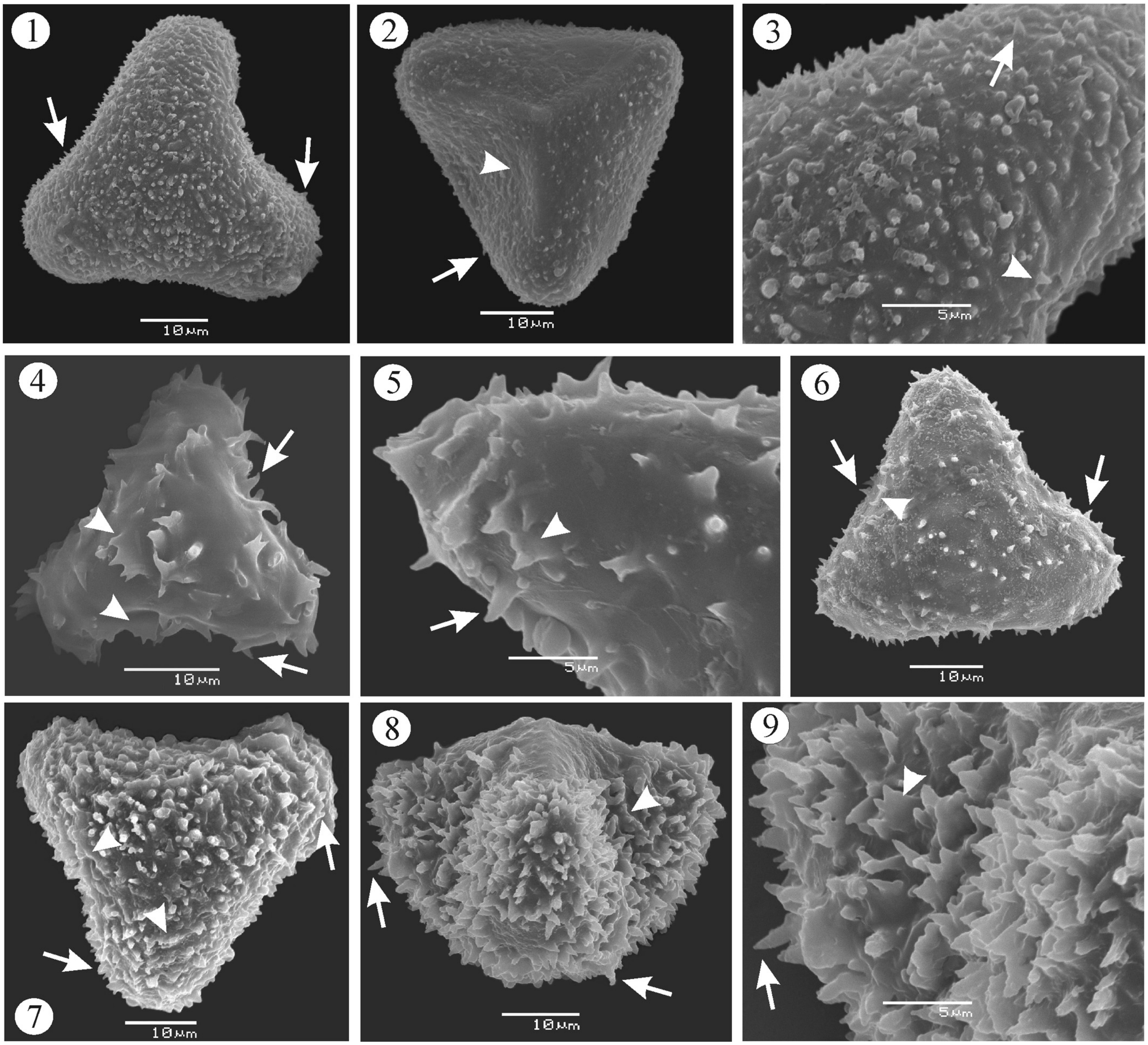

Plate II. SEM pictures of spores of *Sphaeropteris horrida*, *Sphaeropteris insignis*, *Sphaeropteris gardneri* and *Sphaeropteris quindensis*. 1–3; *S. horrida*. 1) Distal view, the ornamentation is composed of spines (arrows) distributed at random; 2) proximal view, with many spines (arrow) and some ridges (arrowhead); 3) detail of the distal spore surface with spinules (arrows) and low ridges (arrowhead). 4–5: *S. insignis*. 4) Distal view, the surface is composed of short crests (arrowhead) with high spines on their margins (arrow); 5) detail of the surface with crest (arrowhead) and spines (arrow). 6) Distal view of *S. gardneri* spores, spines (arrow) and ridges (arrowhead). 7–9: *S. quindensis*. 7) Distal view and 8) equatorial view with crest (arrowhead) and spines (arrows), it can observed the laesurae with smooth low ridges without spines; 9) detail of the spore surface with crest (arrowhead) and spines (arrow). Scale bars: 1, 2, 4, 6, 7, 8 = 10 µm; 3, 5, 9 = 5 µm.

Mexico: Oxaca, Putla, 11/10/1969, *Mickel & Hellwig 4003* (LP); Veracruz, Sierra de Chiconquiaco, 1/1/1982, *Perez García* et al. *47* (LP).

Sphaeropteris insignis (D. C. Eaton) Tryon

Cuba: Santa Clara, Buenos Aires, Trinidad Hills, 11/09/1929, *Jack 7271* (GH); *Morton 4161* (P). **Jamaica**: St. Andrew, New Haven Gap, 2-10/09/1906, *Underwood 3221* (P).

Table 1
Morphological data of the spores of Shpaeropteris from the Neotropics.

Species	Equatorial diameter 1	Equatorial diameter 2	Polar diameter	Ornamentation	Exospore thickness	Perispore thickness
Sphaeropteris brunei	44.8-(46.5)-49.8	48.1-(49.8)-52.3	33.2-(34.9)-37.4	Large low ridges. High spines	2–2.8	3.1–3.7
Sphaeropteris cuatrecasasii	39.8-(41.5)-43.2	41.5-(44.8)-46.5	31.5-(33.2)-35.7	Large low ridges. Low conic spines	2–2.6	1.5–2.6
Sphaeropteris gardneri	42.3-(45.6)-49	44-(49.8)-52.3	34-(36.5)-39.8	Large low ridges. High spines	2–3.2	1.2–2.6
Sphaeropteris horrida	45.6-(48.1)-49.8	46.5-(49.8)-51.5	31.5-(33.2)-37.4	Short low ridges. Low conic spines	2.7–3	1.8–2.2
Sphaeropteris insignis	36.5-(40.2)-47.2	39.8-(44)-49.8	26.6-(33.2)-37.4	High cristate ridges. High spines	2–2.5	1.7–2.8
Sphaeropteris quindiuensis	44.8-(48.1)-49.8	46.5-(51.5)-54.8	33.2-(36.5)-40.7	Low cristate ridges. Low spines	2.5–3.2	2.4–3.1

Dominican Republic: Barahona, Noche Buena Berg, 09/1911, *Fuertes 1058* (P).

Sphaeropteris quindiuensis (Karsten) Tryon

Colombia: Quindío, 1851–1857, *Triana s/n* (P)

3. Results

3.1. Morphology

Spores of the group of species allied to *Sphaeropteris horrida* are trilete, triangular in polar view, with straight to concave sides (Plates I, 1, 5; Plate II, 1, 6, 7); plane-hemispherical (Plate II, 8) to concave-hemispherical in equatorial view (Plate II, 2). The laesurae are straight and generally reach the equator. The equatorial diameter is 36.5–49.8 μm, and the polar diameter is 26.6–40.7 μm. The exospore is 2–3.2 μm thick, psilate, and the perispore is 1.2–3.7 μm thick (Table 1).

The SEM shows that the perispore ornamentation is composed of ridges with an echinate margin; difference in the height and length of the ridges and spines were observed.

In *Sphaeropteris brunei* (Christ) Tryon (Plate II, 1, 2, 3; Plate VI, 2, 5) and *Sphaeropteris gardneri* (Hooker) Tryon (Plate II, 6; Plate VI, 9, 12), ridges are parallel to spore sides and distributed at random towards the distal pole. The spines on the ridge margins are conic, 1.2–1.9 μm high and can be fused at their bases.

In *Sphaeropteris cuatrecasasii* Tryon ridges are long, wide, and low (Plate I, 4, 5, 6; Plate VI, 7, 10); they are arranged parallel to the spore sides, and more evident in the distal face. The echinae on the ridges are mostly conical and extremely low, although they may be higher in the equatorial region (Plate I, 6).

The ornamentation of spores of *Sphaeropteris horrida* (Liebmann) Tryon (Plate II, 1, 2, 3; Plate VI, 3, 6) is composed of many short ridges, distributed at random in the whole surface; the margins of the ridges bear also small conical spines.

The surface pattern of sporoderm of *Sphaeropteris insignis* (D. C. Eaton) Tryon (Plate II, 4, 5; Plate VI, 1, 4) has short and high cristate ridges, which are distributed at random. The spines on the margins are high (more than 3 μm), straight or curved.

Sphaeropteris quindiuensis (Karsten) Tryon (Plate II, 7, 8, 9; Plate VI, 8, 11) has densely packed, short, low ridges covering the whole spore surface, and are arranged parallel to the sides and angles. Several spines on the margins of the ridges are conical or flat and reach up to less than 2 μm. Ridges were not observed on the laesurae.

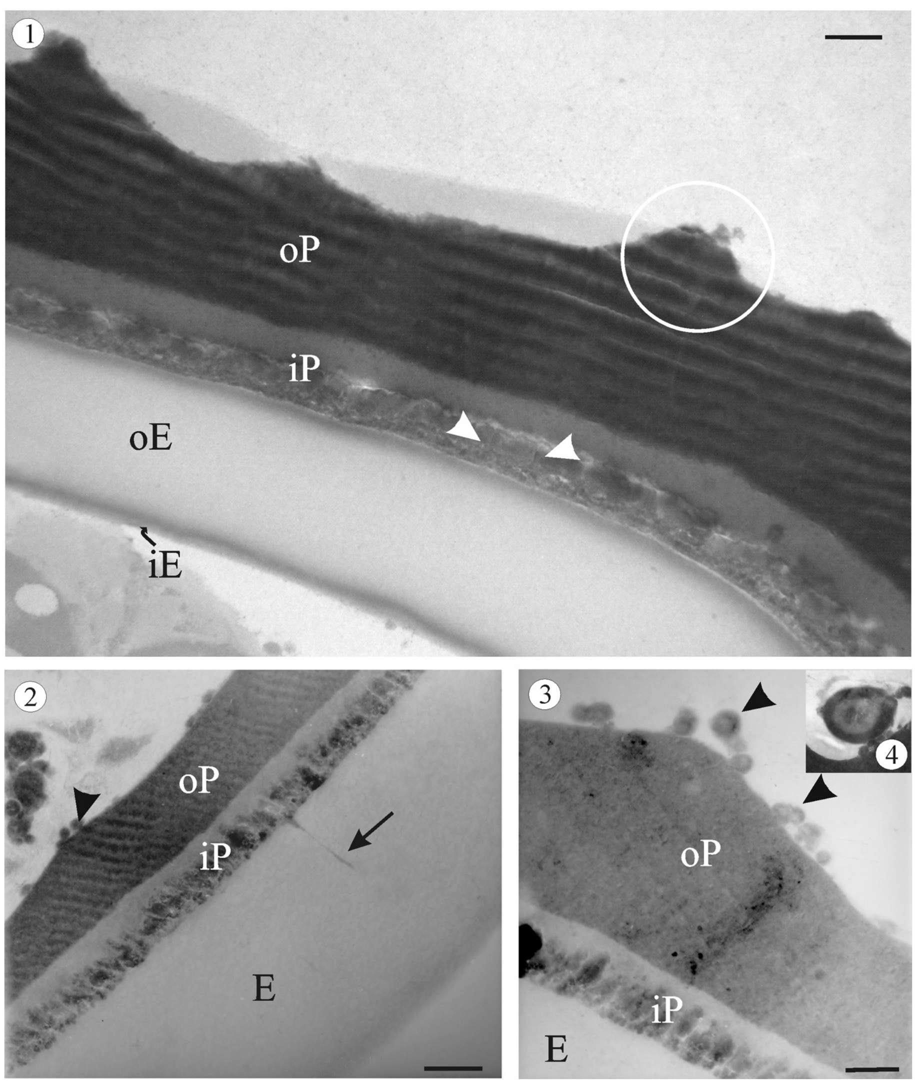

Plate III. TEM sections through the sporoderm of *Sphaeropteris horrida* and *Sphaeropteris gardneri*. 1) In *S. horrida*, the exospore has two layers, the inner exospore (iE) is darker than the outer exospore (oE) the inner perispore (iP) has three strata with inner channels (arrowheads); the outer perispore (oP) has one layer which bears spines on its surface (circle). 2); 3), *S. gardneri*. In both pictures, the exospore (E) has inner channels (arrow); the inner perispore (iP) has three typical strata; and the outer perispore (oP) has spherules on the margin (arrowheads). 4) *S. gardneri*. Detail of a globule. Scale bar = 0,5 μm.

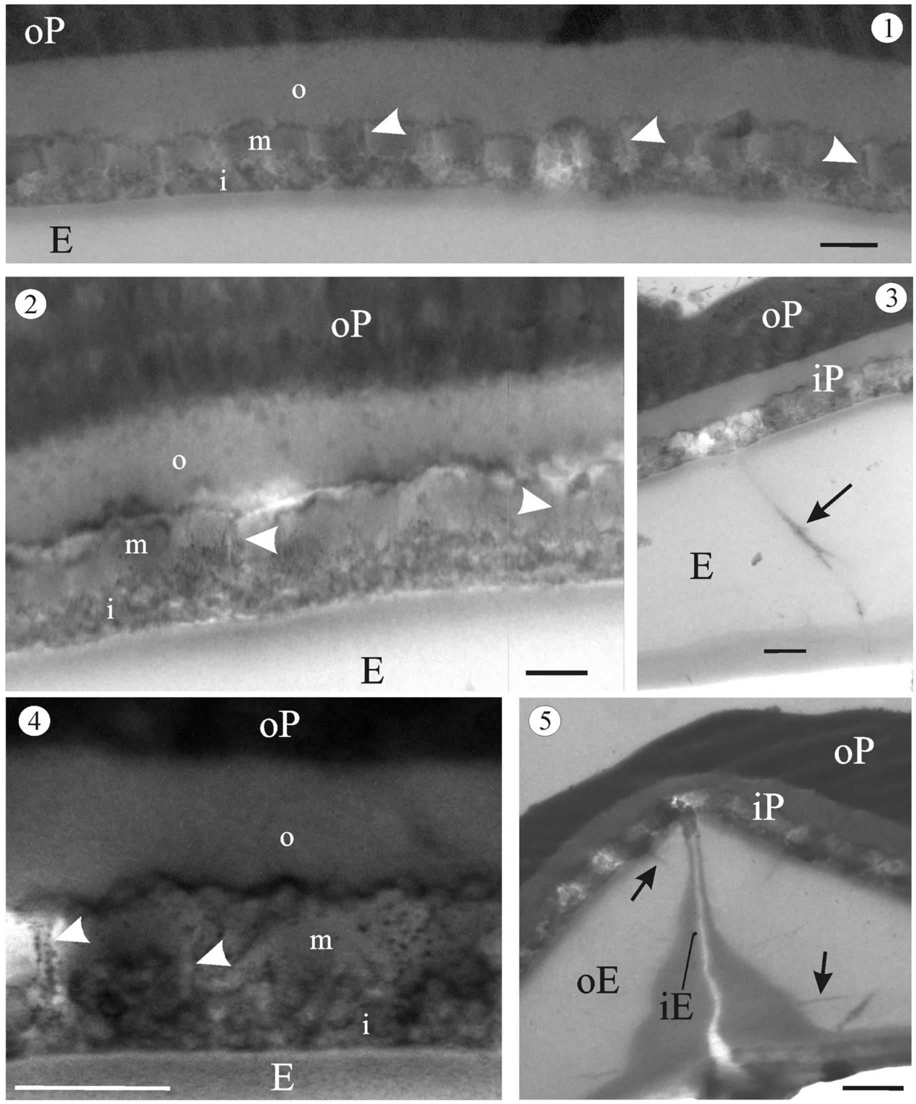

Plate IV. TEM section through the sporoderm of *Sphaeropteris horrida*. 1); 2) Sections showing the inner perispore with three strata: the inner stratum (i), the circular sections of threads looking like they consist of alveolar material; the medium stratum (m) stratum, with channels (arrowheads) connected with the adjacent stratum; and the outer stratum (o) composed of an homogeneous material. 3) A channel cross through the exospore (E) continuing into the inner perispore (iP) and the base of the exospore. 4) Three strata of the inner perispore: the inner stratum (i), the medium stratum (m) and the outer stratum (o). 5) Section at the level of the laesurae. Channels (arrows) are in contact with the inner exospore (iE), and continue to the laesurae base; those present in the outer exospore (oE) continue into the inner perispore (iP). oP: outer perispore; E: exospore. Scale bars: 1, 2, 3, 4 = 200 nm; 5 = 500 nm.

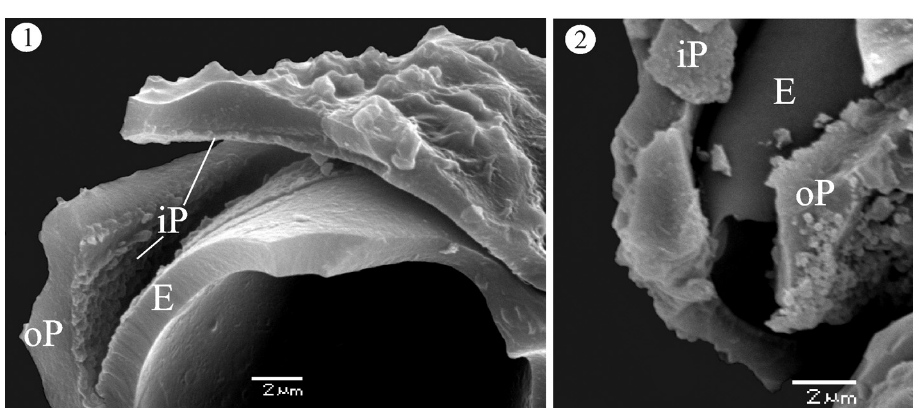

Plate V. Fractured sporoderm of *Sphaeropteris insignis* and *Sphaeropteris cuatrecasasii*. 1) In *S. insignis* the outer perispore (oP) is detached from the exospore (E) by the inner perispore (iP). 2) Parts of the sporoderm of *S. cuatrecasasii*; exospore (E), inner perispore (iP) and outer perispore (oP). Scale bars = 2 μm.

3.2. Ultrastructure

With TEM, two layers were recognized in the exospore (Plate III, 1; Plate IV, 5): the inner layer (iE) is thin and has high electron-density while the outer layer (oE) is thicker than iE and has lower electron-density. Both layers have channels filled with an electron-dense substance, evidenced mainly through the laesurae bases; it is also present throughout the entire wall (Plate IV, 3, 5). These channels continue into the perispore inner stratum (Plate III, 2; Plate IV, 5) and were also observed as branched in the inner part of exospore (Plate IV, 3).

The perispore is a much more complex layer than the exospore and two layers can be distinguished an inner layer (iP) and an outer layer

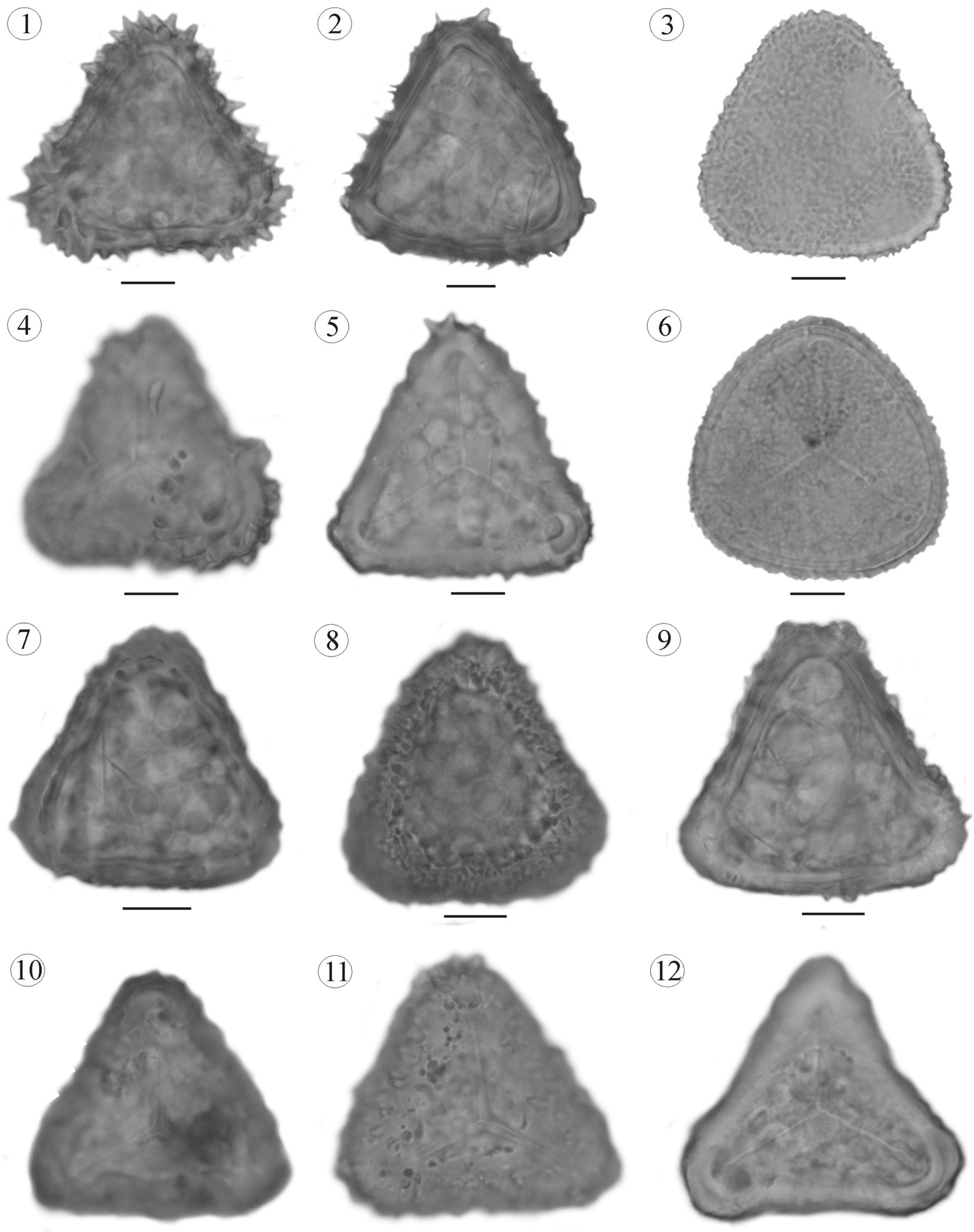

Plate VI. Light-microscopic pictures of spores of neotropical *Sphaeropteris* species 1 and 4: *Sphaeropteris insignis.* 1) distal view; 4) proximal view. 2 and 5: *Sphaeropteris brunei.* 2) distal view; 5) proximal view. 3 and 6: *Sphaeropteris horrida.* 3) distal view; 6) proximal view. 7 and 10: *Sphaeropteris cuatrecasasii.* 7) distal view; 10) proximal view. 8 and 11; *Sphaeropteris quindiuensis.* 8) distal view; 11) proximal view. 9 and 12: *Sphaeropteris gardneri.* 9) distal view; 12) proximal view. Scale bars = 10 μm.

(oP) (Plate III, 1, 2, 3; Plate IV, 3, 5; Plate V). The inner layer (iP) has three clearly differentiated strata. The inner stratum (i) has short densely packed threads distributed parallel or oblique to the inner surface. The middle stratum (m) is composed of threads spaced apart; perpendicularly arranged to the adjacent surfaces. The threads are fused by their ends to the inner and outer strata and immersed in a homogeneous substance. The outer stratum (o) is homogeneous and its inner surface has a high electron-density (Plate IV, 1, 2, 4). The outer layer (oP) is homogeneous, with zebra-like bands throughout its length (Plate III, 1, 2); however, at higher magnifications, the structure is scarcely distinguishable (Plate III, 3; Plate IV, 2, 3). Sharp projections of the perispore can be distinguished in the outer margin of (oP) (Plate III, 1, *circle*), and spherical elements can be observed on its surface, which are less electron-dense in the center than in its outer periphery (Plate III, 2, 3, 4).

4. Discussion

The spore ornamentation of American *Sphaeropteris* species is characterized by the presence of ridges with an echinate margin. This observation is coincident with previous descriptions by Gastony and Tryon (1976), Liew and Wang (1976), Tryon and Tryon (1982), Braggins and Large (1990), Tryon and Lugardon (1991), and Marquez et al. (2010). Nevertheless, the ridges of the individual species show important differences with regard to their height, length, and shape, and the shape and size of the spines on their margins. Three morphologically distinctive features were found among the analyzed taxa: (1) low ridges and few conic spines (*Sphaeropteris cuatrecasasii*), (2) high cristate ridges, with high spines (*Sphaeropteris insignis*); and (3) ridges with different kinds of spines (*Sphaeropteris brunei, Sphaeropteris gardneri, Sphaeropteris horrida,* and *Sphaeropteris quindiuensis*).

With TEM, the exospore is blechnoid (cf. Lugardon, 1971, 1974) and the perispore is complex, composed of two layers of which the inner layer has three strata. This observation agrees with those of Tryon and Lugardon (1991) for species from Oceania and Polynesia, and Marquez et al. (2010) for one species from Brazil, which appears to have a complex stratification that is a characteristic feature of the genus.

Analyzing the spores of different ferns, few kinds of spores appear to have perispores as complex as those of *Sphaeropteris*. As discussed by Marquez and Morbelli (2015), the spores of the genera *Alsophila* and *Sphaeropteris* (Cyatheaceae) show a clear affinity; both have the same three strata in (**iP**), and ultrastructural differences in (**oP**).

Comparing the TEM images shown here on Plate III, 1, 2 and Plate IV, 1, 5 with those of Lugardon (1971, plate 45, 1974, p. 193, plate XI) and Tryon and Lugardon (1991, p. 351, plate 84), the presence of zebra-like bands appears to be a consistent feature in the outer perispore layer (**oP**) in the genus. At higher magnifications, the ultrastructure is homogeneous, and therefore, it is here concluded that these bands could be due to an artifact, probably produced by the resistance that this layer offers during sectioning.

According to Marquez and Morbelli (2015), the elements that comprise the perispore would be made out of threads, with an inner channel; each thread is composed of small coiled units. The presence of channels piercing the perispore is quite interesting, since it could provide important data for the discussion on sporoderm function before, during, and after spore development. The channels observed in all layers and strata in the perispore and exospore show connections that form a tridimensional network into the sporoderm, which provide continuity to the outer medium with the inner part (protoplast) of the spore.

There is no evidence about the function of sporoderm channels in ferns, nor the internal chemical composition, although it was studied in Lycophyta and Selaginellaceae (Morbelli and Rowley, 1993; Morbelli, 1995; Rowley and Morbelli, 1995; Rowley and Morbelli, 2009). Future studies on spore development, treated with different substances (e.g., lanthanum cf. Rowley, 1973) in order to identify the specific chemical substances present in these channels could shed some light on some of these questions.

When I started the study of spores of the American species genus *Sphaeropteris*, I was unsure about the circumscription of two very closely related species. In the original description of *Sphaeropteris cuatrecasasii*, Tryon (1971) characterized both, this species and *Sphaeropteris brunei,* as being very similar. The most important feature in which they differ is the presence of reddish squamulae in the petiole of *S. cuatrecasasii*. The morphology of the spores (smaller and with lower spines in *S. cuatrecasasii*) provides new evidence that reinforces the hypothesis for recognizing these forms as two different species.

Finally, it should be highlighted that the spore morphology and wall ultrastructure of *Sphaeropteris* show a wide homogeneity, reinforcing the cohesion of the species allied to *Sphaeropteris horrida* and underscoring the importance of the palynological characteristics for the identification of natural taxa more evident.

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