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To cite this article: Gonzalo J. Márquez, Marta A. Morbelli & Gabriela E. Giudice (2010) Spore morphology and ultrastructure of *Cyathea* (Cyatheaceae, Pteridophyta) species from southern South America, *Grana*, 49:4, 269-280, DOI: 10.1080/00173134.2010.517270

To link to this article: https://doi.org/10.1080/00173134.2010.517270

Published online: 15 Oct 2010.
Spore morphology and ultrastructure of *Cyathea* (Cyatheaceae, Pteridophyta) species from southern South America

GONZALO J. MÁRQUEZ¹, MARTA A. MORBELLI¹ & GABRIELA E. GIUDICE²

¹Cátedra de Palinología, Facultad de Ciencias Naturales y Museo, UNLP, La Plata, Argentina, ²Cátedra de Morfología Vegetal, Facultad de Ciencias Naturales y Museo, UNLP, La Plata, Argentina

Abstract
Spore sculpture and wall structure of eight *Cyathea* (Cyatheaceae) species from southern South America were studied using light microscopy (LM), scanning electron microscopy (SEM) and transmission electron microscopy (TEM) techniques. Two layers, i.e. an inner and an outer layer, were observed in the perispore. The inner layer has two strata: the inner stratum is attached to the exospore and composed of rodlets tangentially oriented to the spore surface and randomly intermixed; the outer stratum consists of a three-dimensional network of rodlets with either free or fused distal edges forming spinules. The outer layer is thin, darkly contrasted and covers the rodlets. In most cases, the exospore has two layers and a pitted surface. In *Cyathea arovirens*, the exospore surface is smooth, while in *C. delgadii* and *C. myriotheca* it is verrucate. The homogeneity of perispore features within the genus *Cyathea* is evident, while exospore features are heterogeneous. The exospore has different kinds of surface-structures that are of potential interest for assessing evolutionary trends within the group.

Keywords: Spores, morphology, ultrastructure, Cyathea, southern South America, Cyatheaceae

Introduction
The tree fern genus *Cyathea* includes about 150 species that are mainly distributed in the New World and islands across the Pacific Ocean (Korall et al., 2007). The environments of greatest diversification are the humid montane forests and the cloud forests (Tryon & Tryon, 1982). The species have an arborescent habit, abaxial leptosporagiate sori, and marginate scales without an apical seta on the petiole (see Tryon, 1970, p. 7).

The first modern classification of the Cyatheaceae was based on features of the petiole scales, and only one genus, i.e. *Cyathea* s. l., including all the scaly tree ferns, was included (Holttum & Sen, 1961). In later studies, Tryon (1970) and Tryon and Tryon (1982) identified six genera of scaly tree ferns: *Alsophila*, *Cnemidaria*, *Cyathea*, *Nephelea*, *Sphaeropteris* and *Trichiopteris*. Lellinger (1987) redefined the circumscription of *Cyathea* based on the scaly features and spores, and included *Cyathea sensu* Tryon, *Trichiopteris* and most American species of *Sphaeropteris* within this genus, but excluding the *S. horrida* group.

Phylogenetic analyses over the last two decades (Conant et al., 1994, 1995, 1996; Korall & Taylor, 2006; Korall et al., 2007; Schuettelpelz & Pryer, 2007) have identified three evolutionary lineages within the scaly tree ferns: *Alsophila*, *Cyathea* and *Sphaeropteris*. In this paper, we adapt the genus concept *Cyathea sensu* Lellinger (1987), with the addition of the genus *Hymenophyllopsis* (Christenhusz, 2009).

Several authors have described the spores of *Cyathea* (under different circumscriptions) as trilette with a smooth, verrucate or perforated exospore and a pilose perispore (Harris, 1955; Holttum & Sen, 1961; Erdtman & Sorsa, 1971; Murillo & Bless, 1974; Barth, 1975; Gastony & Tryon, 1976; Tryon, 1976; Barrington, 1978; Tryon & Tryon, 1982; Esteves & Felipe, 1985; Lellinger, 1987; Simabukuro...
et al., 1998). Recently, Moran et al. (2008) transferred *Polypodium myriotrichum* to *Cyathea myriotricha* and described its spores as verrucose, covered with rodlets.

Scanning electron microscopy (SEM) studies of *Trichipteris* spores by Gastony (1979) revealed a perispore of intermixed slender filaments and great morphological variation in exospore morphology. Similarly, Tryon and Lugardon (1991) showed that in spores of *Cyathea, Trichipteris, Sphaeropteris* subg. *Sclerophyteris* and in some species of *Alsophila* and *Nephelea* the perispore is formed by rods. It is now clear that there is close similarity in spore morphology and structure among species of the *Trichipteris, Cyathea* and the *Sphaeropteris aterrima* group. Analyses of the pteridophytes spores of Rio Grande do Sul, Brazil, by Lorscheitter et al. (1999) evidenced that the spores of *C. atrovirens, C. corcovadensis, C. delgadii* and *C. phalerata* have a thin perispore with dense rodlets attached to it.

In this contribution, the spore morphology and wall ultrastructure of eight *Cyathea* species were analysed as part of the palynological studies on *Cyatheaceae* from southern South America (Márquez, 2009; Márquez et al., 2007, 2008, 2009). Analyses were performed using light microscopy (LM), SEM and transmission electron microscopy (TEM) techniques. The aim of this paper is to characterise each species according to its palynological features and evaluate the systematic, phylogenetic, developmental, and functional significance of these features.

**Materials and methods**

**Material**

Spores were obtained from herbarium specimens stored at the following institutions: Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (Buenos Aires, Argentina), Instituto de Botánica del Nordeste (Corrientes, Argentina), Museo de Ciencias Naturales de La Plata (La Plata, Argentina), Instituto Anchietano de Pesquisas (São Leopoldo, Brasil), Instituto de Botánica Darwinion (San Isidro, Argentina), Universidade de São Paulo (São Paulo, Brasil), the Smithsonian Institution (Washington, USA), and Universidade Federal do Paraná (Curitiba, Brasil).

Terms suggested by Tryon and Lugardon (1991) were used to describe spore surface and structure, while terms proposed by Nayar and Devi (1966) were applied to the description of spore shape in equatorial view. The letters MP on the list of specimens investigated indicate the reference number of each sample filed in the Laboratorio de Palinología, Facultad de Ciencias Naturales y Museo de La Plata.

**Techniques**

For LM investigations, the spores were studied without any chemical treatment. Polar and equatorial diameter as well as exospore and perispore thickness were measured (25 spores for each specimen). For SEM investigations, the material was treated with hot 3% sodium carbonate, washed, dehydrated, suspended in 96% ethanol and then transferred to acetate plates. After drying, the material was coated with gold. For TEM investigations, dry material from herbarium specimens of *Cyathea atrovirens, C. corcovadensis* and *C. delgadii* was hydrated with buffer + alcin blue (AB). The material was subsequently fixed with 1% glutaraldehyde (GA) + 1% AB in phosphate buffer for 12 hours, rinsed with phosphate buffer + AB, and post-fixed with 1% OsO$_4$ in water plus 1% AB (Rowley & Nilsson, 1972).

Living material of *Cyathea atrovirens* was fixed with 1% GA + 0.0025% ruthenium red (RR) in phosphate buffer, washed in phosphate buffer + RR, then post-fixed with 1% OsO$_4$ in water + 0.0025% RR in phosphate buffer. The spores were dehydrated in an alcohol series and then embedded in Spurr medium mixture. Sections (3 µm thick) were stained with toluidine blue and studied under LM. Ultra-thin sections were stained with 1% uranyl acetate for 15 minutes followed by lead citrate for three minutes. For the investigations an Olympus BH2 light microscope, a Jeol JSMT-100 scanning electron microscope, and a Zeiss M-10 transmission electron microscope were used.

![Spores of Cyathea atrovirens and C. corcovadensis by means of SEM. A–D. C. atrovirens spores: A. Proximal view, showing the surface covered by rodlets; B. Proximal view of a spore devoid of perispore; the exospore surface is smooth, the perforations are evident near the laesurae; C. Fracture through the perispore in the place where the laesurae join; the arrow indicates the perforations next to the laesurae; D. Surface in detail, where interwoven rods have their tips either free or fused forming spinules (circle). E-J. C. corcovadensis spores: E. Detail of the distal surface with perispore; large interwoven rodlets, with their tips free are visible; F. Proximal view, with superficial rods; G. Proximal view of a spore devoid of perispore that shows the perforated surface of the exospore (arrow); H. Detail of the spore in (G), where superficial perforations (arrow) and those close to the laesurae (arrowhead) are visible; I. Detail of the perispore rodlets with a smooth surface; J. Detail of perispore rods with irregular surfaces. Scale bars – 10 µm (A, B, F, G), 2 µm (C, D, E), 1 µm (H, I, J).](image-url)
Figure 2. Spores of *Cyathea delgadii*, *C. myriotricha* and *C. phalerata* by means of SEM. A-C. *C. delgadii* spores: A. Proximal view; the surface is verrucate and it is covered with a network of rodlets; B. Equatorial view of a spore with perispore; C. Detail of a spore surface devoid of perispore; the exospore is verrucate and has perforations located in the base of the verrucae (arrow). D-E. *C. myriotricha* spores:
Results

General morphology

The spores of the Cyathea species studied here are trilete, triangular in polar view, with generally concave sides and rounded corners (Figures 1A, F, 2A, G, 3A, I). They are plane-hemispheric to convex-hemispheric in equatorial view (Figures 2B, I, 3B). Laesurae are straight and generally never reach the equator (Figures 1B, 2A, J, 3H, I). Spores are 29.0–55.6 μm in equatorial diameter and 21.6–48.1 μm in polar diameter. The exospore is 1.2–3.7 μm thick, psilate, perforate or verrucate, and the perispore is 0.3–0.6 μm thick (Table I).

Perispore

The perispore is thin, 0.3–0.6 μm thick and appears dark brown when seen in LM. The spore surface bears a tri-dimensional network of rodlets with either free or fused distal edges, forming small spinules of variable sizes (Figures 1D, E, 2F, 3C). The surface of the rodlets is smooth or irregular (Figure 1I, J). Spores of Cyathea hirsuta and C. leucofolis (Figure 3E–H) were devoid of perispore or only had a fine deposition of perispore.

TEM studies of the perispore (P) show two clearly discernible layers, the inner layer (P1) and the outer layer (P2). The inner layer is composed of two strata, an inner and an outer stratum (iP1 and oP1) (Figure 4). The inner stratum is 20–90 nm thick with an undulate margin and is made up of slender, randomly fused threads, 10 nm in diameter (Figure 5C, D). In SEM, the surface of the inner stratum is granular (Figure 4D). The outer stratum is 50–500 nm thick and consists of small rods, c. 100 nm in diameter, circular in section, with a central channel, 10–20 nm in diameter (Figures 4C, F, 5C, D, 6). Basal rods are oriented tangentially to the spore surface, the more distal ones are perpendicular to the surface (Figure 5C, D) and may be fused at their tips to form spinules (Figure 5C). The substructure of the rods forming the oP1 layer is complex. Each rod is an independent unit with subunits helicoidally arranged around the central channel. These subunits consist of small threads, 10–20 nm in diameter (Figure 6). Finally, the outer perispore layer (P2) is thin and has a high electrodensity. It is attached to the outer P1 layer (Figure 5C, D).

Exospore

The exospore is 1.2–3.4 μm thick and appears yellowish when seen under LM. In Cyathea delgadii, the thickness of the exospore is variable due to the presence of verrucae. It is 2.9–3.7 μm thick in the verrucae, and 1.6–2.4 μm thick in between them. The exospore surface is variable. In C. corcovadensis, C. hirsuta, C. leucofolis and C. villosa, the surface is characterised by perforations of variable size (Figures 1G, H, 3C, E, G, H). Fractured surfaces and ultrathin sections show that the perforations are fovea, about 100 nm in depth (Figure 4A–C, F). In C. atrorvires, the entire exospore surface is psilate (Figures 1B, 5A, C, D), while the surface is proximally psilate and distally perforated in C. phalerata (Figure 2J, K). In C. delgadii and C. myriotricha, the exospore is verrucate (Figure 2A–F), which fuse and form complex structures, similar to short muri (Figure 2C, D). Verrucae have a parallel orientation at the laesurae, but are differently oriented at the surface of the laesurae (Figure 2A, E). The surface of the verrucae is smooth with perforations at their bases (Figure 2C). A common feature of all the studied species is the presence of perforations in the laesurae margins (Figures 1C, H, 2J, 3G, H).

The exospore consists of two layers (Figures 4C, E, F, 5A): the inner layer (iE) is thin with distinctly high electrodensity at the laesura base (Figure 4F) and the outer layer (oE) is lighter to electrons and thicker, the oE/iE relationship being 4:1. The ultrastructure of both exospore layers is massive, homogeneous and quite difficult to discern. Radial channels and cavities with a contrasted content are present all along the exospore, but they are more evident in the inner part of the outer exospore (Figure 5A, B) and in the middle and inner sides of the commissurae of each laesura (Figure 4F).

Discussion and conclusions

The spores of Cyathea studied here are characterised by a three-dimensional network of rodlets with free distal edges, several of which are fused forming

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D. Distal view; the surface is verrucate and rodlets are visible between verrucae; E. Proximal view; superficial rods are visible. F. C. delgadii: detail of the distal surface covered with perispore; large rods are loosely intermixed between verrucae; at the verrucae surface are the rodlets intermixed in a compact way. G–K. C. phalerata spores: G. I. Spore surface covered by perispore rodlets, spore in proximal view (G), distal view (H) and equatorial view (I); J–K. Details of the surface in a spore devoid of perispore; J. Detail of the proximal surface of a spore with a smooth exospore; the perforations are restricted to the laesura margins (arrow); K. Detail of the exospore at the distal surface, completely covered with perforations variable in size; note the density of small perforations in the equatorial area (arrow). Scale bars – 10 μm (A, B, D, E, G, H, I), 2 μm (F), 5 μm (C, J, K).
spikes. This is in line with observation for Cyathea spores from other areas (Barth, 1975; Tryon & Lugardon, 1991; Lorscheitter et al., 1999), and the features may be used to support the Cyathea clade as indicated by earlier cladistic studies (Conant et al., 1996; Korall et al., 2007) and the systematic treatments of Barrington (1978), Gastony (1979), Tryon and Tryon (1982), and Holtum and Edwards (1983).

Along with information from acetylation technique with NaOH by Gastony (1974), our TEM and SEM observations clarified that the ornamentation elements are part of the perispore formed from rodlets that are either smooth or with an irregular surface. Both smooth and irregular rodlets may occur on a single spore and may be related to different stages in spore maturation.

In spores of Cyathea leucofolis and C. hirsuta, the perispore is absent or partially deposited. Gastony (1979) reported that these two species in addition lack a perispore or have a not fully developed perispore. However, it would be interesting to study the ontogeny of the spores since there could be failures in perispore deposition.

The homogeneity found in the perispore sculpture and structure of the Cyathea species studied is in agreement with observations made by Gastony (1979), who suggested that spore features might reflect phylogenetic relationships between TrichiOPTeris, Cyathea and the Sphaeropteris aterrima group. The features of the perispore, in addition to the presence of marginate scales without an apical seta at the petiole base, together with results of recent phylogenetic analyses (Conant et al., 1996; Korall et al., 2007), would reinforce the concept for inclusion in the genus Cyathea sensu Lellinger (1987).

Three patterns were identified for the exospore surface: (a) laevigate, present in Cyathea atrorsirens; (b) pitted in either one or both distal and proximal surfaces, present in C. axilaris, C. corcovadensis, C. hirsuta, C. villosa and only on the distal surface, in C. phalerata; and (c) verrucate, present in C. delgadii and C. myriotricha.

Recent studies in Selaginellaceae (Korall & Taylor, 2006), Dryopteridaceae (Moran et al., 2007) and Cyatheaceae (Moran et al., 2008) showed that palynological characteristics are valuable in phylogenetic and systematic analysis of ferns and Lycophytes. Conant et al. (1996) correlated the different types of spores in Cyatheaceae with molecular phylogenetic trees and recognised three basic types of spores among the Cyathea clades: verrucate in the Cyathea divergens group, plain in the Cyathea armata and Cyathea gibbosa groups, and triporate in the Cnemidaria group. We compared the analysis made by Conant et al. (1996) with the spore morphology data provided by Gastony (1979), and identified the Cyathea armata group by the presence of exospore perforations, and the Cyathea gibbosa group by the absence of perforations. Therefore, we deduced that the absence of perforations would be a derived character state.

The exospore surface of the studied species has this variability. It can be inferred that the perforated surface of Cyathea corcovadensis, C. hirsuta, C. leucolepis and C. villosa spores is a plesiomorphic character, and therefore, these species would be placed in basal clades within the genus Cyathea. However, C. atrorsirens and C. phalerata could belong to the most derived groups because they have spores with psilate exospores. Conant et al. (1996) stated that verrucate spores are a derived character because they were only present in the derived C. divergens group. However, Korall et al. (2007) recognised the presence of verrucate spores outside the C. divergens group and suggested that it might represent a plesiomorphic condition within Cyathea. Further phylogenetic studies on spore morphology can clarify the relevance of this character state.

TEM observations of the exospore revealed that inside the outer exospore (oE) is a zone with cavities and ramified channels. This zone was named a ‘fissured stratum’ by Lugardon (1971, 1974), typical for ‘blechnoid’ exospores. In the case of Cyathea delgadii, the outer exospore has a superficial stratum that constitutes the verrucae and is characterised by a high electron density. Nevertheless, ultrastructural differences were not noticed regarding the rest of the layer.
Figure 3. Spores of Cyathea villosa, C. hirsuta and C. leucophyllis by means of SEM. A-C. C. villosa spores: A, B. The rodlets of the perispore cover the whole surface, proximal view (A), equatorial view (B); C. Fracture in the proximal zone that exposes the exospore (E), with perforations; small rods are seen on the perispore surface (P). D-G. C. hirsuta spores: D. Distal view; a granular deposit is visible on the surface; E. Detail of the proximal surface in the place where the laesuræ join; perforations with a thick margin are present on the laesuræ surfaces (arrowheads); F. Detail of the proximal surface; a granular deposit covers the spore surface; G. Detail of the proximal surface of a spore devoid of perispore, in the place where the laesuræ join; note the perforation with a thick margin (arrowhead). H, I. C. leucophyllis spores: H. Detail of the proximal surface of a spore with a perforate exospore; the perforations have larger diameters on the laesuræ margins (arrow); the perforations on the commissure (arrowheads) have a thick margin; I. Proximal view of a spore devoid of perispore. Scale bars – 10 μm (A, B, D, I), 2 μm (E-H), 1 μm (C).
The type of inner perispore structure (including sub-unit structure) is similar to cylindrical units described by Wittborn et al. (1998) for Fagus sylvatica and Lycopodium clavatum. According to these authors, the sub-structural units would also be formed of sub-units that are helichoidally arranged. This hypothesis is reinforced by the size of the structural units and sub-units, their spatial arrangement and a typical striation. The use of more powerful microscopes would provide more accurate information about the fine structure of these elements. Our results support the hypothesis by Rowley (1981, 1988, 1990, 1995) and Rowley and Dahl (1982) that the wall sub-structures of spore/pollen are built by helichoidal sub-structural units. Thus, this contribution differs from the interpretations by Southworth (1986) and Tryon and Lugardon (1991), who considered that the basic sub-structural units of the perispore are granules.

Finally, our results suggest that there is homogeneity within the perispore of the spores in the genus Cyathea. In addition, this ultrastructural analysis provides original data that could be of help for evolutionary estimations and functionality of the sporoderm.

Acknowledgements

The authors specially thank Robbin Moran (New York Botanical Gardens, New York) who provided us with the SEM images of Cyathea myriothricha. The authors thank Luis Zimmermann (Instituto de Biologia Celular, UBA, Buenos Aires), Lic. Rafael Uurrejola (SEM unit of the Facultad de Ciencias Naturales y Museo de La Plata, Isabel Fariás), for help in technical aspects of TEM, Ernesto Krauzuk (Departamento de Flora y Fauna, Misiones), and the herbaria that supplied the studied material. This study was supported by grants from the ANPCyT, National Agency of Science and Technology promotion for PICT 12758 and National University of La Plata for project 11/N 451.

Specimens investigated

Cyathea ararunens (Langsd. & Fisch.) Domín. Argentina: Corrientes, Ituzaingó, Tressens et al. 372 (LP, CTES), MP 4084; idem, Misiones, Geral. Manuel Belgrano, Pantridge s/n (BA 70619 a-b-c), MP 3099; idem, Ignazó, Rodrigues 430 (SI, BA), MP 4078; idem, Guarani, 28/4/1997, Morrone et al. 2135 (SI), MP 4080; idem, San Pedro, P. P. Pinalito, Márquez & Carrón 181 (LP); idem, San Ignacio, P. P. Teyn Cuare, Márquez et al. 230 (CTES, LP); idem, San Antonio, Capacro 935 (BA). Brazil: Rio Grande do Sul, Río Pardo, Jürgens s/n (Rosenthal 257) (SI), Paraguay: San Pedro, Col. Guayaquil, Krapovickas et al. 14822 (SI).

C. corcovadensis (Raddi) Domín. Brazil: Paraná, Pereira 8224 (LP), MP 4105; idem, Curitiba, Krapovickas et al. 23143 (LP), MP 4104; idem, Guaratuba, Dusén 13729 (SI), MP 4102; Santa Catarina, Lagos, Spanigel s/n (Rosenthal 240), (LP), MP 4103.

C. delgadii Sternb. Argentina: Corrientes, Ituzaingó, Meyer 6278 (US 2361678). Brazil: Santa Catarina, Sao Jose, Fernandes 1132 (SPF); Parana, Paranaguá, Fernandes et al. 1117 (SPF), MP 4127; idem, Pirajuara, Fernandes 1115 (SPF).

C. hamata C. Presl. Brazil: Parana, Paranagau, Fernandes 1123 (SPF); Santa Catarina, Rio do Sul, Fernandes 1150 (SPF); idem, Ilha Santa Caterina, Sehnem 786 (PACA); idem, Morro da Iagoa, Sehnem 8398 (PACA).

C. lasiolepis Domín. Brazil: Parana, Morretes, Hatschbach 30390 (PACA); idem, Guaratuba, Krieger 11129 (PACA).

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Figure 4. Spore wall structure (SEM) and ultra-structure (TEM) in species of Cyathea. A, B. C. villena (SEM): fracture of the wall with pointed faveoli (A) at the outer margin (arrows) of the exospore (E), and a perispore (B) detached from the exospore (E); the protruberances (arrowheads) visible in the inner surface of the perispore (P) exactly match the perforation (arrow) bases of the exospore surface. C, D. C. corcovadensis (SEM and TEM): C. TEM image of the inner exospore (IE), the outer exospore (OE) and the perispore (P); note the fovea (circle) in the exospore margin; the perispore was deposited within the foveoli; a roddet of the perispore (arrowhead). D. Fracture of the perispore (EM), where the inner stratum (IP1) of the inner layer of the perispore covers the perforate surface (arrowhead) of the exospore and the outer stratum is formed by roddets. E. C. delgadii (TEM): wall section with large verrucae that are characteristic of this species; this latter consists of two layers: the inner layer (IE) and the outer layer (OE); the perispore (P) covers the exospore surface completely. F. C. corcovadensis (TEM): section of the sporoderm through the laesura; the inner exospore (IE), the outer exospore (OE) and the perispore (P) with roddets (arrowhead) are visible; in the exospore, cavities and straight and fused channels (arrow) are present close to the laesura (L). Note that the exospore is continuous on the commissure. Note the foveoli of the exospore (circle) in another spore, at the bottom left corner of the figure. Scale bars – 2 μm (B), 1 μm (A; D–F), 500 nm (C).

Figure 5. Spore wall ultra-structure in Cyathea species by means of TEM. A. C. delgadii, the inner exospore (IE) and the outer exospore (OE) with a ramified channel (arrow) are visible; roddets constitute the perispore (P) on the surface. B–D. Wall sections of C. ararunens: B. The exospore (E) and the perispore (P) are visible; a radial channel (arrow) is evident within the exospore; in the perispore, the inner stratum is of uniform thickness and the outer stratum is composed of rods; C. A spine formed by fusion of several roddets of the perispore outer stratum (OP1); in the limit between perispore and exospore (E) the less electron-dense inner stratum (IP1) is visible; the outer perispore (P2) is evident as electron-dense layer with a thin cover on the rods; D. Each rod has inner channels in longitudinal and transversal sections (arrowhead) with threads coiled around the channels (arrow); (IP1) inner stratum, (OP1) outer stratum, (P2) outer perispore, (E) exospore. Scale bars – 1 μm (A, B), 500 nm (C), 100 nm (D).
Figure 6. General structure of a perispore thread: a rod of the perispore (here of *Cyathea atrorivera*) with the sub-units (arrows) collared around the inner channel (arrowhead). Scale bar = 100 nm.


*C. phalerata* Mart. Brasil: Parana, Paranaguá, Fernandes & Abreu 1118 (SPF); idem, Ponta Grossa, Krieguer 10818 (SPF); Santa Caterina, Angelina, Fernandes 1133 (SPF); idem, Rio do Sul, Fernandes 1148 (SPF); idem, Ilhota, Fernandes 1140 (SPF), MP 1140.

*C. villosa* Willd. Brazil: Parana, Senges, Hattchbach 26771 (CTES), MP 4125; idem, Furnas, Reitz & Klein 17509 (US).

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