This article was downloaded by: *[Morbelli, Marta A.]*
On: *25 September 2010*
Access details: *Access Details: [subscription number 926605072]*
Publisher *Taylor & Francis*
Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK

Grana
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713648917

Spore wall ultrastructure of Polypodiaceae from north-western Argentina

Marta A. Morbelli[a]; Gabriela E. Giudice[b]
[a] Cátedra de Palinología, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina [b] Cátedra de Morfología Vegetal, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina

Online publication date: 04 September 2010

To cite this Article Morbelli, Marta A. and Giudice, Gabriela E.(2010) 'Spore wall ultrastructure of Polypodiaceae from north-western Argentina', Grana, 49: 3, 204 — 214

To link to this Article: DOI: 10.1080/00173134.2010.513418

URL: http://dx.doi.org/10.1080/00173134.2010.513418

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: http://www.informaworld.com/terms-and-conditions-of-access.pdf

This article may be used for research, teaching and private study purposes. Any substantial or systematic reproduction, re-distribution, re-selling, loan or sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

Grana, 2010; 49: 204–214

Taylor & Francis
Taylor & Francis Group

Spore wall ultrastructure of Polypodiaceae from north-western Argentina

MARTA A. MORBELLI[1] & GABRIELA E. GIUDICE[2]

[1]*Cátedra de Palinología, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina,* [2]*Cátedra de Morfología Vegetal, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina*

Downloaded By: [Morbelli, Marta A.] At: 18:37 25 September 2010

Abstract

The spore wall ultrastructure of *Campyloneurum*, *Microgramma*, *Pecluma*, *Phlebodium*, *Pleopeltis* and *Serpocaulum* (Polypodiaceae) from north-western Argentina has been studied using transmission electron microscopy (TEM). The exospore is 0.4–3 µm thick, two-layered and variously ornamented in all taxa. The exospore surface is distinctive, but in general ultrastructure the exospore is similar in all species studied. The structural elements of the exospore consist of cavities in the inner part as well as channels with a radial orientation and channels at both sides of the laesura. Variation in the exospore surface was observed in spores at different stages of maturation. The perispore is darkly contrasted and 0.04–2 µm thick. Three different structure types were recognised, including fibrillar, multilamellar and lacunose. Scattered globules and spherules were always present on the perispore surface. The structural variability of the perispore was surveyed within complete sporangia. We concluded that the observed variability may be related to the stage in spore maturation and, consequently, to the stages in perispore differentiation. As the exospore ultrastructure is similar and interpreted as related to functional activity in the studied material, it cannot be used for systematic delimitations at this generic or specific level.

Keywords: *Polypodiaceae, sporoderm ultrastructure, exospore, perispore, Argentina*

The spores of Polypodiaceae ferns from north-west Argentina (*Campyloneurum*, *Microgramma*, *Pecluma*, *Phlebodium*, *Pleopeltis* and *Serpocaulum*) show general uniform morphology in light microscopy (LM) and scanning electron microscopy (SEM), but with some variation in surface ornamentation (Giudice et al., 2004). However, in these taxa, it is sometimes extremely difficult to understand the sporoderm structure and to discern whether a perispore is present or not based on LM and SEM alone.

Several previous studies of sporoderm structure of Polypodiaceae indicate some variation in spore wall structure, but generally with the presence of a perispore. Spores of *Polypodium serratum* Aubl. were described as having a "blechnoid" exospore constituting the spore ornamentation, and a perispore constituting a continuous thin layer adhered to the exospore surface (Lugardon, 1974). Within the genus *Polypodium*, Tryon and Lugardon (1991) observed a sporoderm with a two-layered exospore where the outer stratum forms the surface contours, while the generally thin perispore is sometimes folded or echinate with captive globules. In other Polypodiaceae such as *Lepisorus*, *Dictymia* and *Microsorum*, perispores are multilamellate and granulate (Tryon & Lugardon, 1991).

The spores of 51 species of *Pyrrosia* (Polypodiaceae) were analysed under SEM by Van Uffelen and Hennipman (1985). They show a wide diversity in sporoderm sculpture: the authors recognised five spore types, mainly based on their perispore characteristics.

Hennipman (1990) analysed several species of Polypodiaceae using SEM and transmission electron microscopy (TEM). The study was focused on the sporoderm structure and exospore channels. Additional

Correspondence: Marta A. Morbelli, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina. E-mail: *marta_morbelli@hotmail.com*

(Received 4 February 2010; accepted 1 August 2010)

ISSN 0017-3134 print/ISSN 1651-2049 online © 2010 Collegium Palynologicum Scandinavicum
DOI: 10.1080/00173134.2010.513418

Downloaded By: [Morbelli, Marta A.] At: 18:37 25 September 2010

studies of sporogenesis and spore wall differentiation in Polypodiaceae were carried out by Van Uffelen (1992, 1997). The author differentiated surface patterns and made a connection of these patterns with the different stages in exospore development.

The main aim of this study is to understand sporoderm organisation and complexity of the spore wall ultrastructure in the six Polypodiaceae genera from north-western Argentina by also studying the spores by means of TEM. The study includes nine species: *Campyloneurum lorentzii* (Hieron.) Ching, *Microgramma squamulosa* (Kaulf.) de la Sota, *Pecluma oranense* (de la Sota) de la Sota, *Pecluma filicula* (Kaulf.) M. G. Price, *Phlebodium pseudoaureum* (Cav.) Lellinger, *Pleopeltis macrocarpa* (Bory ex Willd.) Kaulf., *Pleopeltis pinnatifida* Gilles ex Hook. & Grez, *Pleopeltis pleopeltidis* (Fée) de la Sota and *Serpocaulon lasiopus* (Klotzsch) A. R. Sm. The systematic applicability of these characters was then tested. The sporoderm structure is finally compared to previous reports for spores of other Polypodiaceae as well as of other Filicopsida.

Materials and methods

For this study, herbarium material from the Museo de Ciencias Naturales de La Plata (LP) was used; the samples, numbered as "MP", are filed at the Laboratorio de Palinología, Facultad de Ciencias Naturales y Museo de La Plata, Universidad Nacional de La Plata.

Complete sporangia, their *in situ* spores, and single mature spores were included in the analysis. Dry material from herbarium specimens was hydrated following the technique suggested by Rowley and Nilsson (1972) using phosphate buffer and alcian blue. The material was fixed with 2% glutaraldehyde + 1% alcian blue in phosphate buffer for 12 hours and post-fixed with 1% OsO_4 in water + 1% alcian blue. The spores were dehydrated in an acetone series and then embedded in Spurr's soft mixture. Sections (3 μm thick) were stained in toluidine blue and studied under LM. Ultrathin sections were stained in 1% uranyl acetate for 15 minutes followed by lead citrate for three minutes. Transmission studies were conducted with a Zeiss T-109 transmission electron microscope.

Results

A major result of this study is that all representatives of the six genera occurring in north-western Argentina are similar in exospore ultrastructure, whereas three types of perispore ultrastructure have been recognised. The perispore structure varies along the surface of the same spore. Globules, plates, scales, papillate processes and other interesting structures are sometimes present at different levels of the perispore.

Characteristics of the exospore

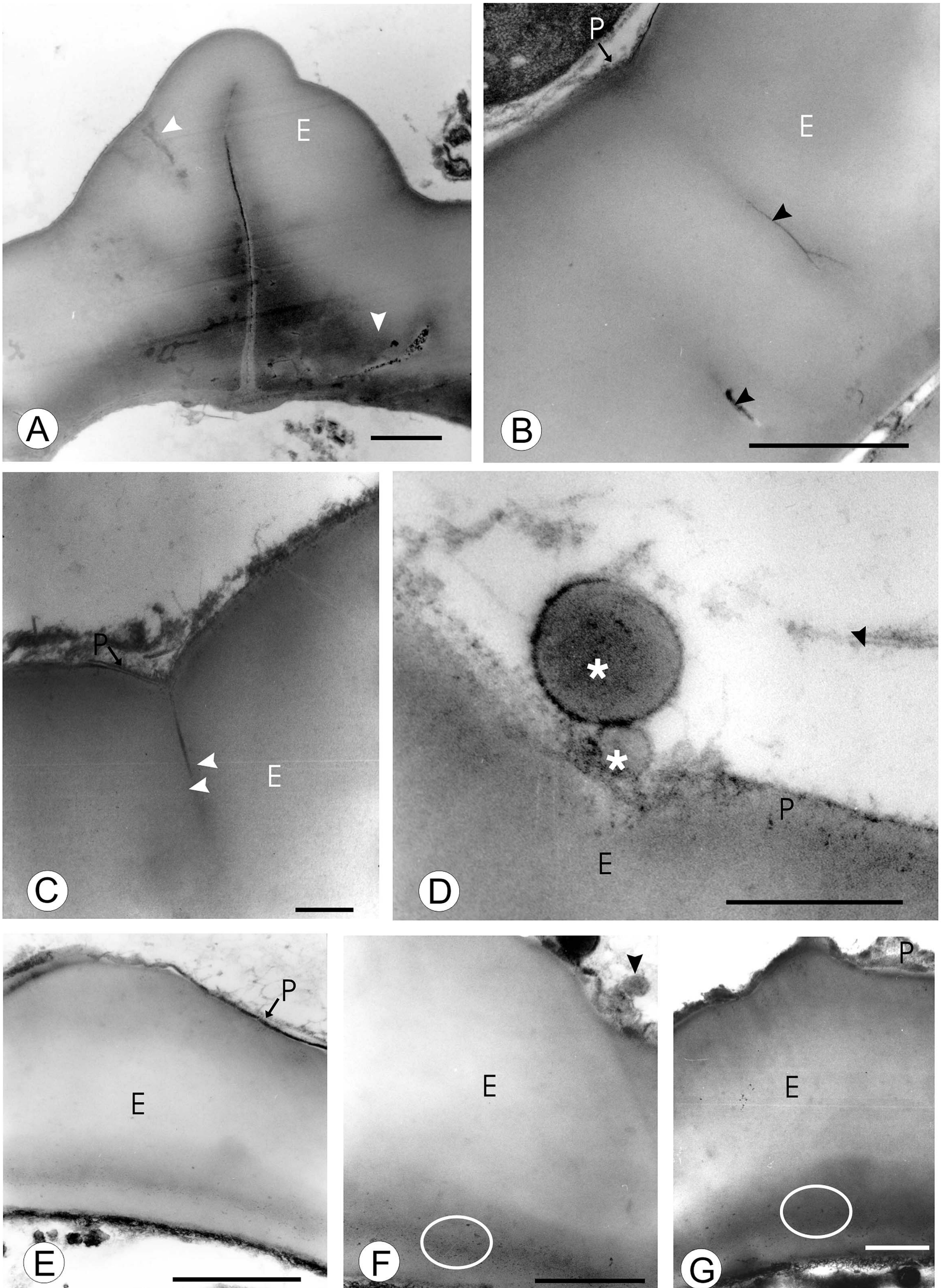
In all analysed species, the exospore is 0.4–3 μm thick, less dense to the electrons than the perispore, and double-layered with a massive structure. The exospore layers can be differentiated by their thickness, contrast and structure. Small cavities filled with dark contents are present in the inner part of the outer exospore in *Microgramma squamulosa*, *Pleopeltis macrocarpa*, *P. pinnatifida* and *Serpocaulon lasiopus* (Figures 1E, F, 3G, 4C). In most samples, the inner layer is difficult to discern, thin and highly contrasted in comparison to the outer one, as for example in *P. pinnatifida* (Figure 4A–C).

A section of the exospore through the laesura documents that it is thicker at the top of the structure and that a complex system of channels is associated with the commissure in the middle and basal regions. This is the case, for example, in *Campyloneurum lorentzii* and *Serpocaulon lasiopus* (Figures 1A–D, 6A).

→

Figure 1. Spore wall ultrastructure of *Campyloneurum lorentzii* and *Microgramma squamulosa*. **A–D.** *Campyloneurum lorentzii*: **A.** Section through the laesura. The exospore is thick and continuous on the upper part of the laesura. Channels with contrasted contents are evident in the middle and inner parts of the exospore (*arrowheads*). A thin, darkly contrasted layer of perispore covers the exospore surface. The inner part of the exospore is darkly contrasted at the laesura base; **B.** Section through the sporoderm with portions of channels with a radial orientation and a contrasted content (*arrowhead*). One of the channels is ramified. A thin perispore is on the surface; **C.** Outer and middle parts of the exospore. A narrow space is in the area of contact between adjacent verrucae (*arrowhead*). The perispore has a different thickness and complexity along the spore surface; **D.** Detail of the wall surface with two globules (*asterisks*) of different sizes in contact with the perispore. The perispore is thin and darkly contrasted and has an outer layer with a discontinuous sequence of osmiophilic granules on the left. There are also threads and short pieces of membranes (*arrowhead*) over the spore surface. **E–G.** *Microgramma squamulosa*: **E.** The exospore is thick and apparently double-layered with broad elevations. The perispore has variable degrees of thickness, being thin and darkly contrasted on the right and thick and differently contrasted and structured on the left; **F.** Small globules are seen on the perispore surface (*arrowhead*). Cavities filled with dark material are present in the inner part of the exospore (*circle*); **G.** Accumulations of perisporal material give an uneven aspect to the surface. Cavities filled with dark contrasted material are present in the inner part of the exospore (*circle*). Abbreviations: (E) = exospore, (P) = perispore. Scale bars – 1 μm (A, C, E), 500 nm (B), 250 nm (D, F, G).

Downloaded By: [Morbelli, Marta A.] At: 18:37 25 September 2010



In non-apertural areas, radial channels, simple or ramified, and usually filled with dark contents, were observed in the exospore of *Campyloneurum lorentzii* and *Pleopeltis macrocarpa* (Figures 1A, B, 3F). In *Phlebodium pseudoaureum*, some channels are fused and some are open to the exospore surface and in contact with the inner surface of the perispore (Figure 3E).

The surface of the outer exospore is smooth and extensively waved, forming typical verrucae that characterise most of the studied species (i.e. *Pecluma oranense*, Figure 2D–F); whereas the exospore surface shows tubercles, is thicker and has truncated outgrows that constitute these typical tubercles (i.e. in *Phlebodium pseudoaureum*, Figures 2D–F, 3A, B).

In mature spores of most species, the verrucae are laterally fused (i.e. in wall sections of *Campyloneurum lorentzii* (Figure 1C), *Pecluma oranense* (Figure 2E) and *Pleopeltis pleopeltidis* (Figure 5B)). The former spaces between exospore verrucae are evident as a narrow space, short radially orientated cavities or a sequence of dark spots.

Characteristics of the perispore

The perispore is generally 0.04–2 μm thick, darkly contrasted and one-layered in section. The thickness of the perispore varies in the same spore from a thin plate to a thick lacunate layer, as for example in *Pecluma filicula* (Figure 2A, B). The perispore covers the surface of the exospore verrucae and fills the spaces between verrucae as in *P. oranense* (Figure 2D–F). Scattered elements with a massive structure and a round or polygonal shape of 200–400 nm in diameter are also evident on the spore surfaces in the same species (Figure 2B, C). A fibrillar structure consisting of a framework of tiny, fused fibres characterises both species as well (Figure 2E, F, 5G, *Peltolepis*). Massive dark spots occur in the areas where the fibres join (see e.g. in *P. oranense*, Figure 2D, E).

Short portions of tripartite lamellae are present in the inner part of the perispore (Figures 3C, 4B, C). Its structure is variable along the surface of the same spore, being single-layered, massive and darkly contrasted in some areas, while it consists of superimposed tripartite lamellae of 60–90 nm thick in other spores, as seen in *Phlebodium pseudoaureum* (Figure 3B, C). In *Pleopeltis macrocarpa*, the perispore is composed of one to several basal lamellae with contrasted edges (Figure 3F, H). On the exospore occurs a dark extensive plate with a similar structure to that of the inner part of the perispore (see e.g. in *Pleopeltis pinnatifida*, Figure 4B, C). According to the plane of sectioning, short portions of tripartite lamellae are also evident in the inner part of the perispore (Figure 4C). A similar stratification was observed in some "globules" (Figure 4A).

In all analysed species the spores have "globules" on the perispore surface. These are different in size and "grouping". They occur either single or grouped (Figures 1D, F, 4A, 5A, 6D) and consist of a core with the same structure as the exospore, covered with a layer that has a similar structure to that of the perispore. Additionally, short papilla-like processes were observed in spores of *Pleopeltis pinnatifida* both on the perispore and in the equivalent structure on the globules (Figure 4A).

Discussion and conclusions

The presence of microchannels at the base of the laesurae and on the sides of its commissure, the presence of channels radially oriented traversing the exospore throughout, as well as the presence of small cavities lined tangentially with respect to the inner part of the exospore can all be regarded as characteristic for the exospore morphology in the analysed species. They constitute basic functional features not only present in Polypodiaceae, but also in the exospores of most other fern spores.

By analysing the spore content of closed sporangia, we have also noticed that the thickness and sculpture of the exospore vary depending on the stage in spore maturation. In mature spores, the number of layers that form the exospore can be difficult to define since layers are better appreciated in young spores, and especially in the base of the laesurae. This appreciation was considered an important characteristic since some authors like Hennipman (1990) used characteristics such as

Downloaded By: [Morbelli, Marta A.] At: 18:37 25 September 2010

→

distance from the surface and they are linked to the perispore surface by perisporal strands. **D–F.** *Pecluma oranense*: **D.** Section through the proximal sporoderm that shows two exospore verrucae. Part of the laesura is at the bottom left corner. Channels associated with the laesura are evident in the inner part of the exospore (*arrowhead*). The perispore is more contrasted than the exospore and it is composed of a network of contrasted slender threads and a sequence of osmiophilic granules. The perispore covers the exospore following the verrucae surface; **E.** The section shows a thick massive exospore with wide elevations and a radial cavity which is still visible between two verrucae (*arrowhead*).The perispore shows a complex network (arrow) lying on the exospore surface. The perispore also fills the spaces between processes; **F.** Detail of the perispore in (**E**) with a complex network filling the space between verrucae. The surface of the exospore with small verrucae (*arrowheads*) is obscured by the thick layer of the perispore. Abbreviations: (E) = exospore, (L) = laesura, (P) = perispore. Scale bars – 1 μm (B, C, E, F), 500 nm (A, D).

Downloaded By: [Morbelli, Marta A.] At: 18:37 25 September 2010

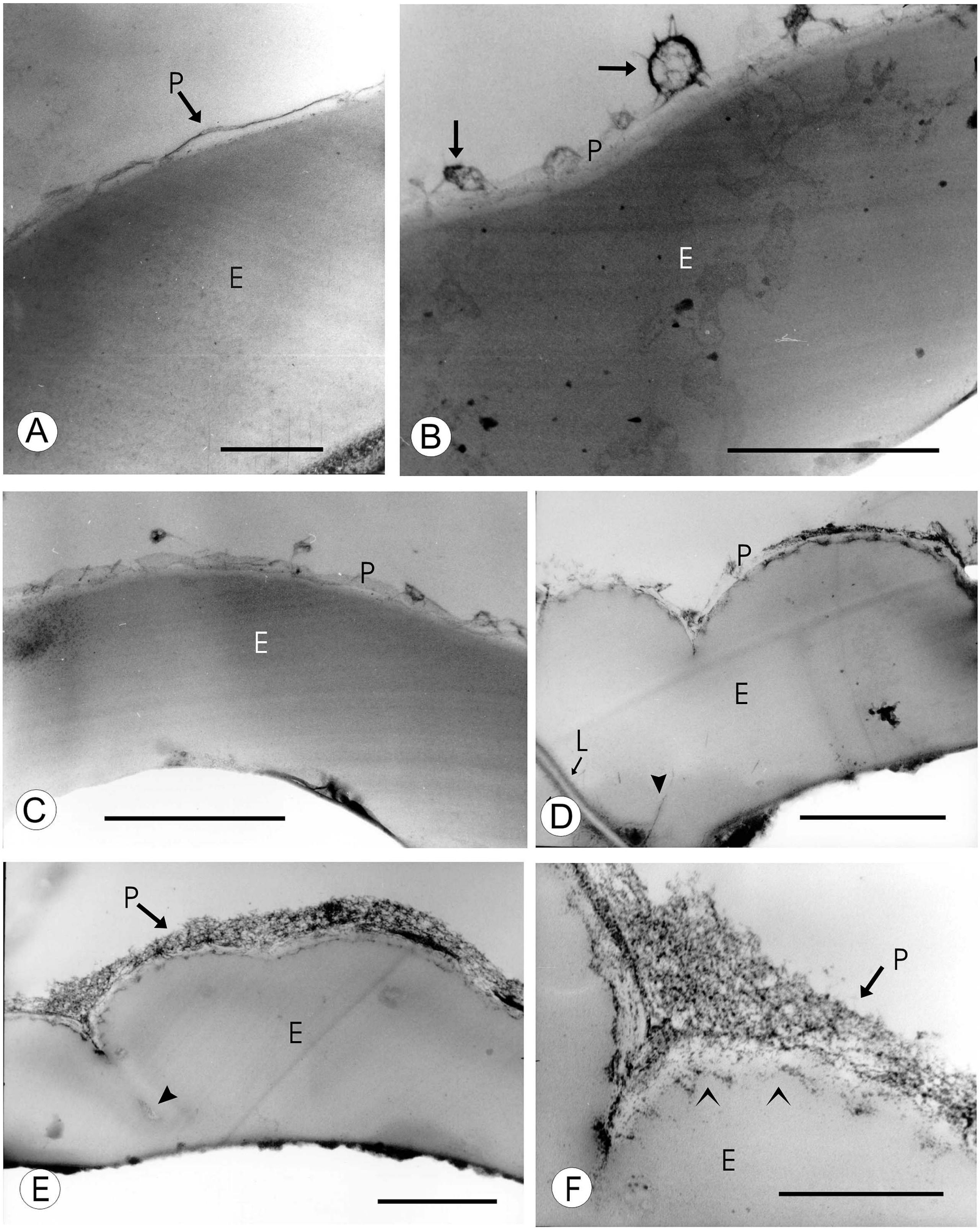


Figure 2. Spore wall sections of *Pecluma filicula* and *Pecluma oranense*. **A–C.** *Pecluma filicula*: **A.** The exospore is thick and massive. The perispore consists of a thin contrasted layer (*arrow*); **B.** The exospore is thick. The perispore is less contrasted than the exospore and consists of a thin continuous layer, with a sequence of irregular elements linked by perisporal strands. They have a less contrasted centre made up of a fine contrasted network (*arrows*). One element has long spines along its surface; **C.** The exospore is thick and massive and the perispore seems to be formed by short thin lamellae, including a sequence of irregular elements darkly contrasted. Similar bodies are at a considerable

Downloaded By: [Morbelli, Marta A.] At: 18:37 25 September 2010

exospore thickness, sculpture, presence of channels at the base and on the sides of the apertural region, to define exospore types within the Polypodiaceae. Our observations of sporoderm structure in spores of some Polypodiaceae are in agreement with those obtained by Lugardon (1974). This author stated that leptosporangiate isosporate Pteridophyta (with the exception of Gleicheniaceae) share a similar type of exospore.

The outer exospore in all analysed taxa forms sculptural elements, which are either verrucae or tubercles. Large, wide cavities with a radial orientation occur between two sculptural processes in mature spores of *Campyloneurum lorentzii*, *Pecluma oranense* and *Pleopeltis pinnatifida*. They are here interpreted as remnants of the former spaces between sculptural processes in immature spores. Similar structures were mentioned by Van Uffelen (1993) for *Pecluma singerii* who interpreted these cavities as being related to transport and storage during exospore differentiation and growth.

Small cavities in the inner part of the exospore are present in spores of *Microgramma squamulosa*, *Pleopeltis macrocarpa* and *Pleopeltis pinnatifida*. Lugardon (1974) stated that cavities with similar characteristics constitute a stratum named "strate fissure". This is located in the inner stratum of the exospore. Spores with a perispore constituting several superimposed lamellae occur in sections of whole sporangia of *Phlebodium pseudoaureum*.

One or more extensive lamellae were also observed on the exospore surface of spores of *Phlebodium*, *Pleopeltis* and *Serpocaulon*. In our interpretation, these structures correspond to the initial steps of perispore differentiation. A similar view was presented by Van Uffelen (1997) for *Microgramma*. Hennipmann (1990), Tryon and Lugardon (1991) and Van Uffelen (1992) interpreted these structures similarly in other genera of Polypodiaceae.

The short portions of lamellae in the inner part of the perispore of *Serpocaulon* and *Microgramma* are similar to those structures described and illustrated in spores of several other genera of Polypodiaceae and in other families of Filicophyta. These were named "scales" by Tryon and Lugardon (1991, p. 333, figures 122.12 and 122.15). Similar short portions of membranes with a radial orientation were also evident within the perispore of *Pleopeltis pinnatifida*; some of them were covered by perispore-derived projections of varied shapes. We interpret masses of perisporal material linked to the exospore surface of *Pecluma filicula* by strands, as those named "blobs" in *Microgramma ciliata* (Willd.) Alston by Van Uffelen (1992).

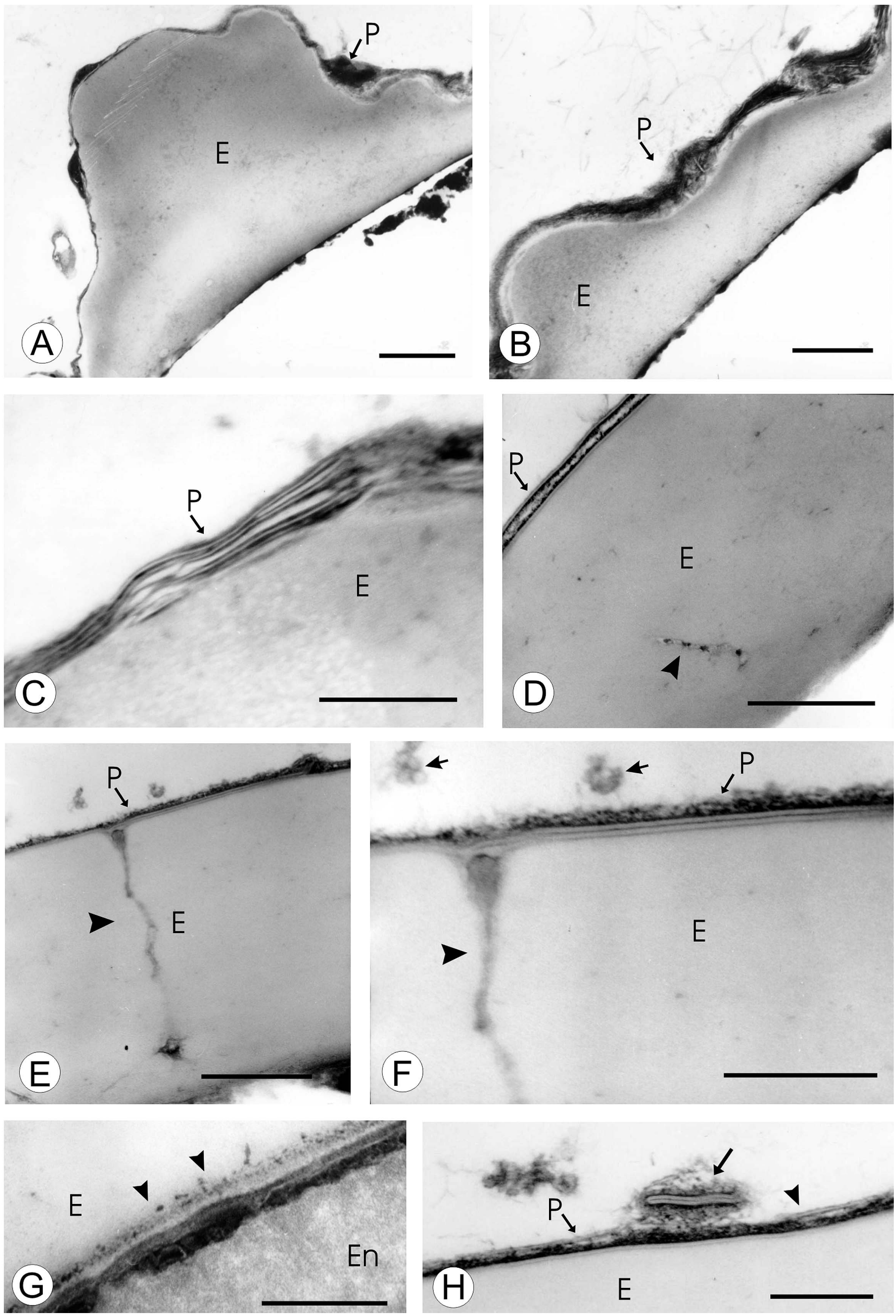
Flattened bodies formed of tripartite membranes with a central white line, framed by fibrous material, were also found on the perispore surface, with a structure similar to that of the perispore in *Pleopeltis macrocarpa*.

In the material included in our study, the perispore generally varies in thickness along the surface of the same spore. The structural variations of the perispore, observed in different spores within the same sporangium, were interpreted as different stages in spore maturation and which are characterised by different levels of differentiation, but not as "different types" of perispore structure. The perispore structure of the species studied here seems to have the typical characteristics of a perispore derived from the activity of an amoeboid tapetum. A similar observation was made by Van Uffelen (1997) in studies of spore wall development of Polypodiaceae. Morbelli (1977) reported that the Polypodiaceae

→

Figure 3. Spore wall sections of *Phlebodium pseudoaureum* and *Pleopeltis macrocarpa*. **A–C.** *Phlebodium pseudoaureum*: **A.** Section through the sporoderm that cuts across a sculptural process of the exospore. The perispore is darkly contrasted and has a different thickness on the exospore surface of the same spore; **B.** The exospore has low and blunt processes. The perispore is darkly contrasted and has a different thickness and structure along the exospore surface; **C.** Part of the exospore surface with several superimposed perisporal lamellae. **D–H.** *Pleopeltis macrocarpa*: **D.** Section with a thick exospore. A channel (*arrowhead*) filled with a dark content is evident in the inner part of the exospore. The perispore is darkly contrasted and three-stratified. It is composed of an inner lamella on the exospore surface, a middle stratum with spaced slender radial filaments, and an outer stratum consisting of a lamella similar to that of the basal stratum; **E.** A channel (*arrowhead*) with a radial orientation is evident. It is ramified in the inner part of the exospore and it is wider in the outermost part. The perispore in this case is composed of two basal laminae and a dark contrasted outer layer of short interwoven threads; **F.** Detail of (**E**) with the outer part of the exospore and the perispore. Within the exospore, the outermost part of the channel (*arrowhead*) is seen; it is wider than its inner part and it is filled with an apparently amorphous content. Both sides of the channel are connected to the innermost basal lamella. A perispore outer layer is composed of short slender contrasted intermixed threads. Two spherules (*arrows*) are connected to the perispore surface by structural threads; **G.** Detail of the inner part of the exospore with an aligned series of cavities filled with dark contents (*arrowheads*). The endospore can be seen below. An inner dark layer is in the boundary between the exospore and the endospore; **H.** The perispore is composed of an extensive basal lamella and a dark layer of thin interwoven fine elements which are darkly contrasted. Another lamella is superimposed at the top of the perispore (*arrowhead*). A tripartite membrane with central white line, framed by fibrous material, is on the perispore surface (*arrow*) with a structure similar to that of the perispore. Abbreviations: (E) = exospore, (En) = endospore, (P) = perispore. Scale bars – 1 μm (A), 500 nm (B, D, E), 250 nm (C, F, G, H).

Downloaded By: [Morbelli, Marta A.] At: 18:37 25 September 2010



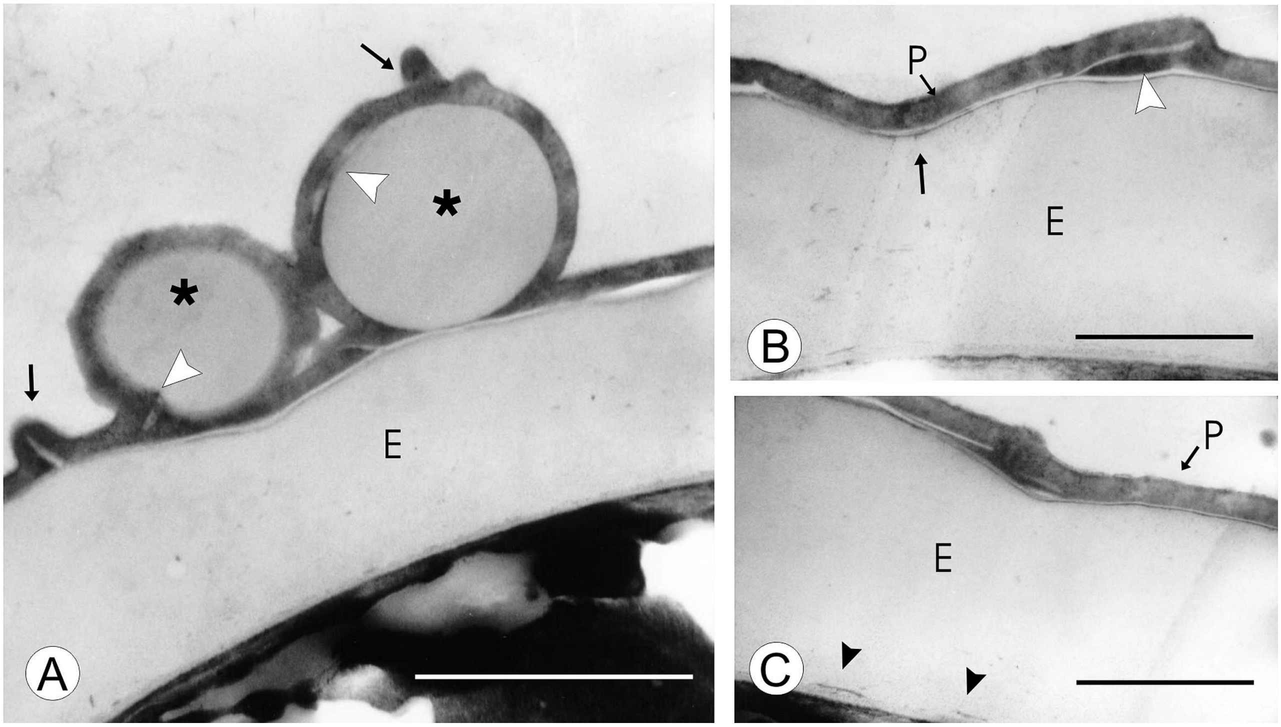


Figure 4. Spore wall section of *Pleopeltis pinnatifida*. **A.** The exospore is lightly contrasted and its margin has broad elevations with a smooth surface. A thin darkly contrasted layer lies on the outer surface of the exospore. The perispore is darkly contrasted and homogeneous. Short portions of membranes with a radial orientation are evident within the perispore and they form projections (*arrows*). Two globules (*asterisks*) are present on the perispore. Short pieces of membranes (*white arrowheads*) are also seen in the globule on the right at the base of its perisporal cover. A radial projection of the perispore (*arrow*) is also present. **B.** Detail of the sporoderm between two elevations of the exospore. A thin dark extensive plate (*arrow*) is evident on the exospore. The perispore is darkly contrasted; a piece of membrane is evident in the centre along an elevation (*white arrowhead*). **C.** Section with a sequence of cavities filled with dark contents (*arrowheads*) in the inner part of the exospore. On the left of this section portions of membranes are evident in the inner part of the perispore. Abbreviations: (E) = exospore, (P) = perispore. Scale bars – 1 μm (A), 500 nm (B, C).

Downloaded By: [Morbelli, Marta A.] At: 18:37 25 September 2010

sensu lato have a tapetum with two layers according to Manton (1950), Smith (1955) and Foster and Gifford (1959). Consequently, we suggest that the inner tapetal layer functions as plasmodial, while the function of the outer one would be secretory.

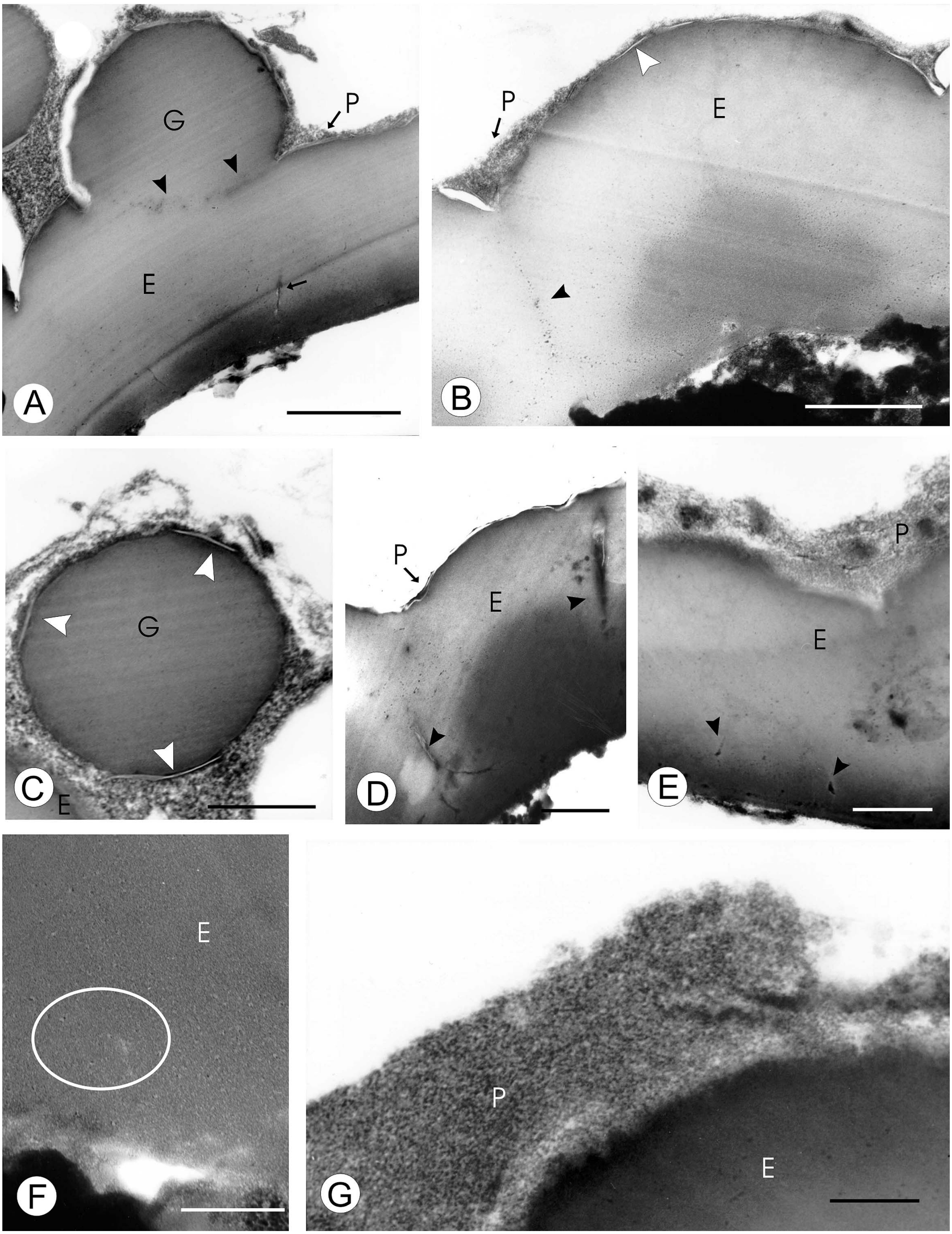
Due to the similar exospore structure in all the studied species we suggest that perispore stratification and ultrastructure change according to the stage of maturation. Future studies on spore development would therefore provide the valuable information required for a better understanding of wall structure and differentiation of these taxa.

Acknowledgements

The authors thank Ing. Luis Zimmermann of the TEM Unit, Instituto de Biología Celular, Facultad

→

Figure 5. Spore wall section of *Pleopeltis pleopeltidis*. **A.** A section that shows a thick and compact exospore. A channel with a radial orientation (*arrow*) is visible in the inner part of the exospore. There is a darkly contrasted, lacunose perispore on the exospore surface. A globule is fused to the exospore. There is a sequence of cavities (*arrowheads*) in the area of fusion of the globule to the exospore. Part of another globule (top left) is on a perispore expansion. **B.** Section with a thick exospore and an uneven lacunose perispore. The outer exospore forms the ornamentation processes. A sequence of cavities (*arrowheads*) bifurcating in the inner part of the exospore is along the area of junction between processes. Short pieces of membranes are evident at the inner part of the perispore (*arrowhead*). **C.** Detail of a globule on the perispore surface. Pieces of membranes (*arrowheads*) are in the inner part of the perispore that surrounds a central area of the globule. Lamellae with similar characteristics are shown on the globule surface. Part of the exospore is seen at the bottom left corner. **D.** Section with a thick exospore with radial channels (*arrowheads*) with a contrasted content. The perispore is thin and darkly contrasted. **E.** Section that shows a thick compact exospore. Parts of two channels are seen in the inner part of the layer (*arrowheads*). The perispore is thick and composed of thin threads and spaced concentrations of dense material. **F.** Detail of the inner exospore with a lacunose area (*circle*). **G.** Detail of the outer portion of the sporoderm. The perispore is thick and lacunose. Abbreviations: (E) = exospore, (G) = globule, (P) = perispore. Scale bars – 1 μm (A, B), 500nm (C, D, E), 250 nm (F, G).



Downloaded By: [Morbelli, Marta A.] At: 18:37 25 September 2010

Downloaded By: [Morbelli, Marta A.] At: 18:37 25 September 2010

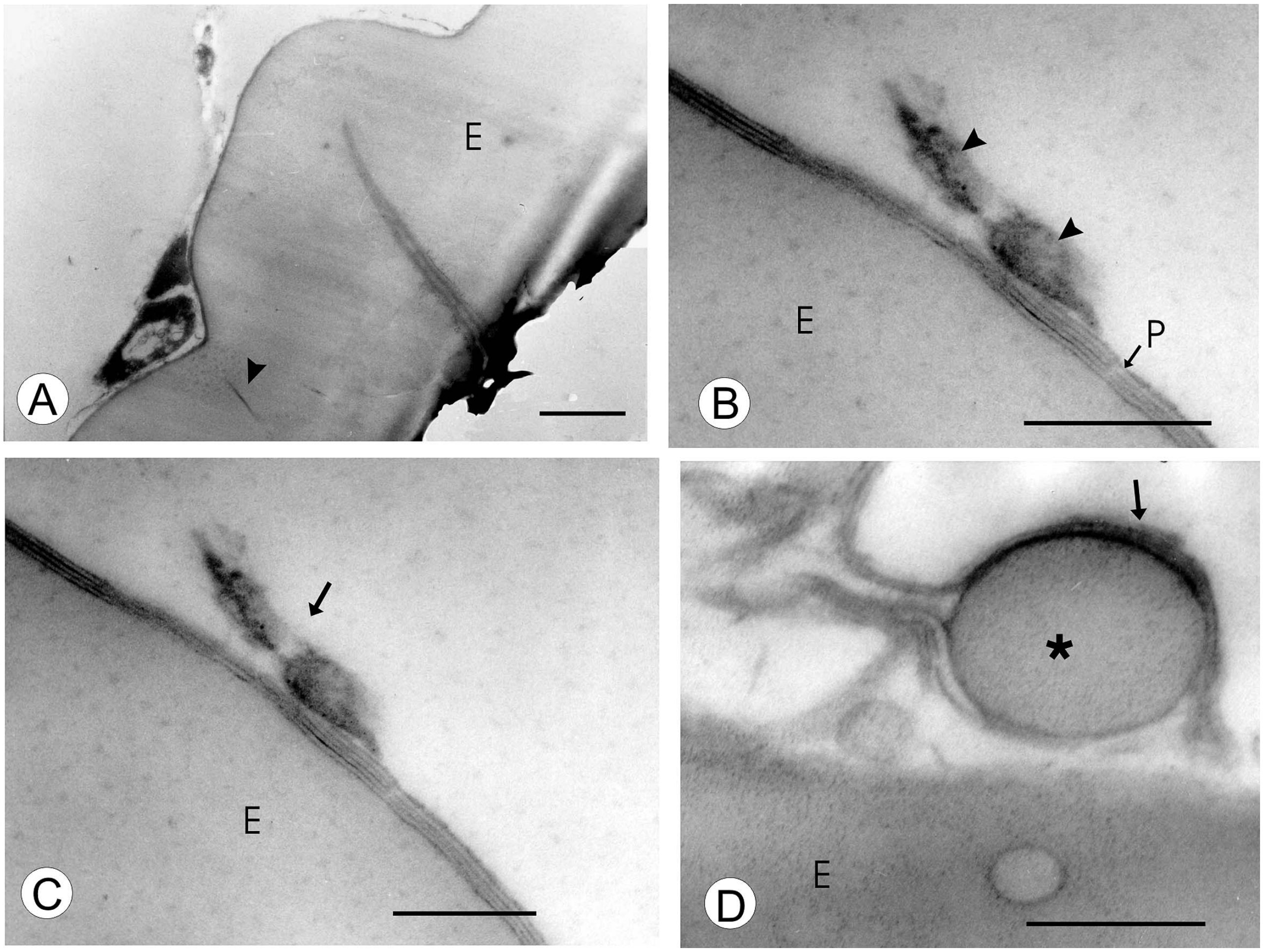


Figure 6. Spore wall section of *Serpocaulon lasiopus*. **A.** Section of the sporoderm through out the laesura. The exospore is thick at the laesura. Part of a channel with a radial orientation is visible on the left (*arrowhead*). The perispore is not completely developed. It consists of a tiny thin layer. There are two concentrations of dark perisporal material on a depression and they are linked by structural units to the perispore surface. **B.** Detail of the outer part of the exospore and the basal part of the perispore in an early stage. It consists of several superimposed extensive lamellae. A thin layer with a different structure is present on the outermost lamella. Two masses of perisporal material are at a certain distance on the perispore (*arrowheads*). Structural threads can be seen between the masses of perisporal material and the basal lamella. **C.** In this section, the exospore is thick and its outer part forms broad elevations. The perispore is thin. A spherule is next to the perispore (*arrow*). **D.** Section that shows the outer part of the exospore. Several aspects are indicative of an early stage in perispore differentiation. A globule (*asterisk*) is on the exospore surface. It has the same structure as the sporoderm. Structural threads run from the globule to the exospore surface. The lamellae and perisporal material partially cover the globule on the exospore surface (*arrow*). Abbreviations: (E) = exospore, (P) = perispore. Scale bars – 1 μm (A, C), 250 nm (B, D).

de Medicina de la Universidad de Buenos Aires, and Isabel Farías, Instituto de Neurobiología, Buenos Aires, for her valuable assistance in some technical aspects of sample processing and sectioning. This work was supported by grants from the National Council of Scientific and Technological Research (CONICET), Buenos Aires, for PIP 5044, from the Universidad Nacional de La Plata for Projects 363 and 451, and from National Agency of Scientific and Technologic Promotion, Buenos Aires, for PICT 12758.

Specimens investigated

Campyloneurum lorentzii Argentina: Jujuy, Capital, Quebrada Yala, Cabrera y Kiesling 25227 (LP), MP 3953.

Microgramma squamulosa Argentina: Salta, Ruta Nac. 9, Pampa Grande, Calandra s/n° (LP), MP 3903.

Pecluma filicula Argentina: Salta, Oran, Aguas Blancas, Quebrada El Nogal, Palací 92 (LP), MP 3911.

Pecluma oranense Argentina: Jujuy, Capital, Cerro Labrado, de la Sota 4310 (LP), MP 3909.

Phlebodium pseudoaureum Argentina: Jujuy, Capital, Cabrera 8178 (LP), MP 3906.

Pleopeltis macrocarpa Argentina: Salta, Santa Victoria, Los Toldos, Martinez et al. 653 (LP), MP 3891.

Pleopeltis pinnatifida Argentina: Salta, Santa Victoria, Hurrel 51 (LP), MP 3852.

Pleopeltis pleopeltidis Argentina: Jujuy, Ledesma, Abra de las Cañas, de la Sota 4428 (LP), MP 3917.

Serpocaulum lasiopus Argentina: Salta, Guachipas, Estancia Pampa Grande, Hawkes et al. 3976 (LP), MP 3887.

References

Foster, A. A. & Gifford, E. M. (1959). *Comparative morphology of vascular plants*. San Francisco, CA: Freeman and Co.

Giudice, G. E., Morbelli, M., Piñeiro, M. R., Copello, M. & Erra, G. (2004). Spore morphology of the Polypodiaceae from northwestern Argentina. *American Fern Journal*, *94*, 9–27.

Hennipman, E. (1990). The significance of the SEM for character analysis of spores of Polypodiaceae (Filicales). In D. Claugher (Ed.), *Scanning electron microscopy in taxonomy and functional morphology. Systematics Association Special Volume 41* (pp. 23–44). Oxford: Clarendron Press.

Lugardon, B. (1974). La structure fine de l'exospore et de la périspore des filicinées isosporées. II. Filicales. Commentaires. *Pollen et Spores*, *16*, 161–226.

Manton, I. (1950). *Problems of cytology and evolution in the Pteridophyta*. Cambridge: Cambridge University Press.

Morbelli, M. A. (1977). Presencia de Corpúsculos de Ubisch en las esporas de las Pteridofitas. *Obra del Centenario del Museo de La Plata (Botánica)*, *3*, 237–247.

Rowley, J. & Nilsson, J. (1972). Structural stabilisation for electron microscopy of pollen from herbarium specimens. *Grana*, *12*, 23–30.

Smith, G. S. (1955). *Cryptogamic botany. Bryophytes and Pteridophytes. Volume II*. Tokyo: Kogakusha Co.

Tryon, A. & Lugardon, B. (1991). *Spores of Pteridophyta. Surface, wall structure, and diversity based on electron microscope studies*. New York: Springer Verlag.

Van Uffelen, G. A. (1992). Sporogenesis in Polypodiaceae (Filicales). II. The genera *Microgramma* Presl. and *Belvisia* Mirbel. *Blumea*, *36*, 515–540.

Van Uffelen, G. A. (1993). Sporogenesis in Polypodiaceae (Filicales). III. Species of several genera. Spore characters and their value in phylogenetic analysis. *Blumea*, *37*, 529–561.

Van Uffelen, G. A. (1997). The spore wall in Polypodiaceae: development and evolution. In R. J. Johns (Ed.), *Holttum memorial volume* (pp. 95–117). Kew: Royal Botanic Gardens.

Van Uffelen, G. A. & Hennipman, E. (1985). The spores of *Pyrrosia* Mirbel. (Polypodiaceae), a SEM study. *Pollen et Spores*, *27*, 155–198.

Downloaded By: [Morbelli, Marta A.] At: 18:37 25 September 2010