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Spore morphology and ultrastructure of Dennstaedtiaceae from Paranaense Phytogeographic Province I.: genus *Dennstaedtia*

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ABSTRACT

The spore morphology and wall structure of *Dennstaedtia* species from the Phytogeographic Paranaense Province: *Dennstaedtia cicutaria*, *D. cornuta*, *D. dissecta*, *D. globulifera*, *D. obtusifolia* were studied using light microscopy (LM), scanning electron microscopy (SEM) and transmission electron microscopy (TEM). The spores are trilete, brown, triangular in polar view and plane-hemispheric to plane-convex in equatorial view. The exospore is homogeneous, with two layers. The perispore has an alveolar structure and is composed of one or two layers. The outer perispore surface bears the sculpture, which has elements of varied shapes (verrucae, ridges, reticles), an different sizes and fusion. This variation allows characterize species or groups of species. Three different types of perispore ornamentation can be found: 1. Verrucate with verrucae covered with rodlets; 2. Verrucate-rugate with verrucae and smooth ridges; 3. Reticulate. The spores constitute an important source of characters with a systematic value for the genus *Dennstaedtia* and they are a useful tool for the identification of herbarium samples.

1. Introduction

This work is part of a larger project in which the morphology and ultrastructure of the spores of the family Dennstaedtiaceae in the Paranaense phytogeographic province of the Neotropical region (Cabrera and Willink, 1973) are studied.

Dennstaedtiaceae is a fern family, containing approximately 170 pantropical and, occasionally, boreal species, or species from temperate regions (Tryon and Stoltze, 1989). The delimitation of subordinate taxa is still under discussion due to the great diversity of genera that are usually included in the family. While some authors divided them into three independent families: Dennstaedtiaceae, Hypolepidaceae and Lindsaeaceae (Ching, 1940; Nayar, 1970; Pichi Sermolli, 1970, 1977), others grouped them within a single Dennstaedtiaceae family which was, in turn, divided into subfamilies (Holttum, 1947, 1949; Crabbe et al., 1975; Lovis, 1977; Kramer and Green, 1990) or tribes (Tryon and Tryon, 1982). In more recent molecular studies (Hasebe et al., 1994, 1995; Wolf et al., 1994; Pryer et al., 2004; Schuettpelz and Pryer, 2007; Christenhusz et al., 2011), the monophyletic group made up of Dennstaedtiaceae and Hypolepidaceae *sensu* Pichi Sermolli (1970) has been identified as Dennstaedtiaceae *sensu stricto*. This work follows the classification suggested by Smith et al. (2006) in which the Dennstaedtiaceae *s.s.* are included (except for the genus *Saccoloma*), since, up to now, it is the only analysis that takes into account the morphological as well as the molecular analyses previously carried out for the family.

The genus *Dennstaedtia* has a long-creeping rhizome usually covered with hairs and big laminae with marginal sori protected by a double purse-shaped indusium (an inner "true" indusium, and an outer one formed by the reflexed leaf margin). There are about 45 species distributed along tropical and warm-temperate regions (Kramer and Green, 1990).

In America, this genus is mainly found in wet mountain forests, forest openings, and secondary vegetation areas, even though there are differences in habitat between tropical and northern species (Tryon and Tryon, 1982). Eleven species were identified by Tryon (1960) when reviewing the genus in the continent. However, more recent studies (Mickel and Smith, 2004) reveal show that 20 species occur in this region.

According to different floristic and taxonomic surveys (Hassler, 1928; Tryon, 1960; Moran and Riba, 1995; Peña Chocarro et al., 1999; Prado, 2004; Figueiredo and Salino, 2005; Sakagami, 2006; Ponce et al., 2008; Salino and Almeida, 2008; Tressens et al., 2008; Schwartsburd, 2010; Costa Assis and Salino, 2011; Yañez et al., 2012) the following species have been identified for the field of study: *D. cicutaria* (Swartz) Moore, *D. cornuta* (Kaulfuss) Mettenius, *D. dissecta* (Swartz) Moore, *D. globulifera* (Poiret) Hieronymus, and *D. obtusifolia* (Willdenow) Moore.

Only a few palynological studies have been carried out on the genus *Dennstaedtia*. The first observations were made with a transmitted light microscope (LM) by Erdtman (1957), who described the surface of the spores of *Dennstaedtia punctilobula* (Michaux) Moore as granulate, with a wall consisting of three layers. In subsequent works, the morphology of the spores of Pteridaceae *sensu* Copeland (1947) was studied by Nayar and Devi (1968) also using LM and four *Dennstaedtia* species were included. These spores showed a verrucate ornamentation

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determined by the exine, with different levels of fusion in between the verrucae.

The first studies for the family were carried out by Lugardon (1971, 1974) using a scanning electron microscope (SEM) and a transmission electron microscope (TEM). In these studies, the spores of *Dennstaedtia bipinnata* (Cavanilles) Maxon were analyzed. The exospore was described as blechnoide, run through by channels, and the perispore consisting of only one compact layer, which, in turn, forms the verrucate surface. The presence of perispore and exospore in species of the genus was also observed by Erdtman and Sorsa (1971) by SEM.

Some regional works on the species of *Dennstaedtia* were carried out from a palynological point of view. According to these descriptions, the spores of the genus are gemmate (Tschudy and Tschudy, 1965) verrucate (Murillo and Bless, 1974; Belling and Heusser, 1975; Devi, 1977; Graf-Meier, 1985) or granulate to reticulate (Huang, 1981).

In 1982 the spores of Dennstaedtiaceae – mainly those of the New World – were studied by Tryon and Tryon using SEM, and in their analysis, morphological types related to the geographical distribution of the species were identified. A similar analysis was carried out by Tryon and Lugardon (1991), in which differences were found in the perispore ornamentation among paleotropical and neotropical species, and among tropical and temperate American representatives.

In Giudice et al., 2006 described the morphology and ultrastructure of the Dennstaedtiaceae from north-west Argentina using LM, SEM and TEM. In the analyzed species of *Dennstaedtia*, the exospore was two-layered: the outer one presented a smooth margin with cavities and channels running through; while the perispore consisted of one or two layers, being the outer one always ornamented.

There was only one palynological study of the genus in the area (Lorscheitter et al., 2002), in which the spores of Dennstaedtiaceae from Rio Grande do Sul were analyzed using SEM. The species of *Dennstaedtia* were described as having a laevigate exospore and a verrucate perispore, with irregular verrucae scattered all over the surface, which may fuse and form ridges.

According to Mickel (1973), it was necessary to perform comparative studies of the spores of Dennstaedtiaceae using electron microscopic techniques since the analysis of their morphological characters could be useful for the classification of the genera and subgenera. Tryon (1986) came to the same conclusion.

The main goal of this work is to broaden the palynological knowledge of *Dennstaedtia* through the study of the morphology and ultrastructure of the spore wall of species found in the phytogeographical Paranaense province. These data are useful for the correct circumscription of species. In addition, this information allows comparisons with other taxa of other regions at generic level. It offers a hypothesis about the role of the sporoderm that is studied in different stages of development and also contributes to a more accurate paleobotanical nomenclature.

2. Material and methods

2.1. Studied material

Spores were obtained from herbarium specimens from the following institutions: BA (Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina), BHCB (Universidade Federal de Minas Gerais, Minas Gerais, Brasil), CTES (Instituto de Botánica del Nordeste, Corrientes, Argentina), LP (Museo de Ciencias Naturales de La Plata. La Plata, Argentina), MO (Missouri Botanical Garden. Missouri, Saint Louis, USA), HB (Herbarium Bradeanum, Rio de Janeiro, Brasil), PACA (Instituto Anchietano de Pesquisas, Rio Grande do Sul, Brasil), SP (Instituto de Botânica, São Paulo, Brasil), SI (Instituto de Botánica Darwinion. San Isidro, Argentina) y UPCB (Universidade Federal do Paraná. Curitiba, Brasil). Additionally, fresh material collected by the authors in successive field trips to Misiones province (Argentina) during the months of February and March 2010–2012 were studied. The collected material is kept in the Herbarium of the Museo de La Plata (LP).

The letters MP, in the list of specimens investigated indicate the reference number of each palynological sample filed in the Laboratorio de Palinología, Facultad de Ciencias Naturales y Museo de La Plata (La Plata, Argentina).

2.2. Methods

The spores were studied using Light microscope (LM), scanning electron microscope (SEM) and Transmission electron microscope (TEM).

For LM spores were studied without previous chemical treatment since the perispore does not survive acetolysis treatment (Erdtman, 1960), and they were mounted in gelatin glycerin jelly slides. For each specimen, 25 spores were selected randomly, and the polar diameter (A), major and minor equatorial diameters (B and C) and thickness of perispore and exospore were measured (Nayar, 1964) (Fig. 1). The observations were performed with an Olympus BH2 LM microscope and photographs were taken with a Nikon Coolpix S10 digital camera.

For SEM the spores was treated with hot 3% sodium carbonate, washed, dehydrated, suspended in 96% ethanol and then transferred to acetate plates (Morbelli, 1980). After drying, they were coated with gold. To fracture the sporoderm, some spores were placed in an ultrasonic bath for 10 s. The observations were made with a Jeol JSMT-100 electron microscope of the microscopy service of Facultad de Ciencias Naturales y Museo de La Plata (La Plata).

For TEM, *Densstaedtia globulifera*, *D. dissecta* and *D. cicutaria* were selected as these are representative of the morphological types observed in the genus. Dry material from herbarium specimens was hydrated following the technique proposed by Rowley and Nilsson (1972) that consist of the use of a buffer plus alcian blue (AB), then the material was fixed with 2% glutaraldehyde (GA) + 1% alcian blue in phosphate buffer for 12 h, rinsed with phosphate buffer + AB, and post-fixed with 1% OsO4 in water plus 1% AB for 1 h.

Living material was fixed with 1% GA + 0.0025% ruthenium red (RR) in phosphate buffer washed in phosphate buffer + RR, then post-fixed with 1% OsO4 in water plus 0.0025% RR in a phosphate buffer.

The spores were dehydrated in an acetone series and then mounted in Spurr's embedding medium. Three-micrometer 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 1 min.

The observations were performed with Zeiss M-10 microscope of the microscopy service of Laboratorio Nacional de Investigación y Servicios de Microscopía Electrónica, LANAIS-MIE (Ciudad Autónoma de Buenos Aires).

2.3. Terminology

Nayar (1964), Kremp (1965), Tryon and Lugardon (1991), Punt et al. (1994, 2007), Lellinger (2002) were used for describing morphology and ultrastructure of spores.

2.4. Studied material

Dennstaedtia cicutaria (Swartz) Moore. Observed with LM, SEM and TEM.

Argentina: San Pedro, Parque Provincial Moconá, 23/04/1993, *Guillén et al. 135* (CTES). Brazil: Rio Grande do Sul, Sao Leopoldo, s/d, *Dutra* 234 (SI), MP 4204; Santa Catarina, Blumenau, Passo Mansa, 1906, *Rosenstock* 173 (SI), MP 4205; Paraná, Guaraqueçaba, Reserva Natural Salto Morato, 19/12/1999, *Gatti & Gatti 574* (UPCB), MP 4209; Jacareí, 16/07/1914, *Dusén 15288* (MO), MP 4211; Morretes, 13/05/1977, *Dombrowsky s/n* (PACA 77666).

Dennstaedtia cornuta (Kaulfuss) Mettenius Observed with LM and SEM.

Brazil: Minas Gerais, Parque Natural do Ribeirão do Campo, 30/05/2003, *Salino et al. 8749* (BHCB), MP 4222; Lambari, Parque Estadual de

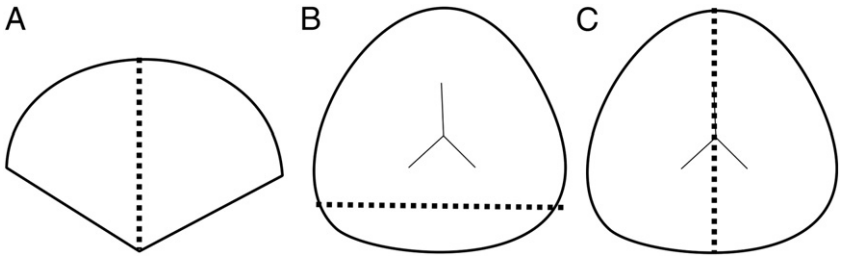


Fig. 1. Diagrams of spores diameters (dashed lines). A. Polar diameter. B. Major equatorial diameter. C. Minor equatorial diameter.

Nova Baden, 13/07/2007, *Salino et al. 12539* (BHCB), MP 4225 Paraná, Ponta Grossa, Parque Estadual de Vila Velha, 21/08/2004, *Schwartsburd et al. 322* (UPCB), MP 4221; Rio de Janeiro, Teresópolis, 28/03/1997, *Almeida-Neto 122* (HB).

Dennstaedtia globulifera (Poiret) Hieronymus Observed with LM, SEM and TEM.

Argentina: Misiones, General Manuel Belgrano, Parque Provincial Urugua-í, 12/10/2011, *Yañez & García 98* (LP) MP 4213; Guaraní, 23/01/1993, *Tressens 4636* (LP) MP 4193; San Pedro, Reserva de Biosfera Yabotí, 12/2010, *Yañez & Macluf 70* (LP), MP 4202; 14/03/2011, *Yañez & Marquez 86* (LP) MP 4203; Brazil: Rio Grande do Sul, Ipeas, 24/01/1973, *Krapovickas et al. 22918* (LP), MP 4192.

Dennstaedtia dissecta (Swartz) Moore. Observed with LM, SEM and TEM.

Argentina: Misiones, General Manuel Belgrano, 23/02/1971, *Palacios 1296* (LP) MP 4190; San Antonio, 03/12/1957, *Capurro 1279* (BA). Brazil: Paraná, Serra do Mar, 17/03/1914, *Dusén 14678* (SI) MP 4210; Telemaco Borba, Parque Ecológico Klabin, 18/01/2005, *Sakagami & Sakagami 229* (UPCB) MP 4212; Rio de Janeiro, Itatiaia, Parque Nacional do Itatiaia, 09/01/2008, *Labiak et al. 4410* (UPCB) MP 4208; Santa Catarina, Dionisio Cerqueira, 29/12/1956, *Smith et al. 9629* (SI) MP 4207; Blumenau, 02/04/2008, *Schwartsburd & Ceolin 1627* (SP).

Dennstaedtia obtusifolia (Willdenow) Moore. Observed with LM.

Brazil: Minas Gerais, Nova Lima, 24/09/1995, *Salino 2227* (BHCB); Paraná, Serra do Mar, 17/03/1914, *Dusén 14678* (SI).

3. Results

The species of *Dennstaedtia* studied have trilete spores, triangular in polar view, with straight to concave sides and rounded corners (Plates I; II, 1–2, 5–6; III, 1, 3, 7). In equatorial view the spores are plane-hemispheric, except in *Dennstaedtia cicutaria*, where the spores can be convex-hemispheric (Plate I, 2). The laesurae are straight extending 3/4 of the way to the spore equator (Plates II, 1, 5; III, 1, 5–6). With LM the exospore is light brown and the perispore is brown to dark brown. The exospore is 0.1–0.9 μm thick and the perispore is 0.1–6 μm thick. The difference in the thickness of the perispore is due to the ornamentation elements. Spheroid bodies are visible on the surface (Table 1).

3.1. Spore morphology

Dennstaedtia cicutaria (Plates I, 1–3; II, 1–4)

The sculpture is verrucate, with circular to polygonal elements of 2.3–4.7 μm in diameter, distributed at random. In proximal view, lines of verrucae at both side of the laesurae were observed (Plate II, 1).

The surface of the verrucae is composed of rodlets about 1 μm long, which are fused at the base or at the distal edges (Plate II, 2, 3). Sometimes, the rodlets are fused and form spines (Plate II, 3–4). Among the verrucae narrow links were observed (Plate II, 4).

Dennstaedtia cornuta (Plates I, 4–6; II, 5–7)

The ornamentation of spores is rugate. It is composed by irregular verrucae of 0.5–2 μm long, which usually are fused forming ridges of 1 × 2–9 μm (Plate II, 5, 6). The proximal face and the sides of the spores show verrucae and short ridges distributed at random, and, sometimes, the end of the laesurae is covered by elements of the ornamentation (Plate II, 5). On distal face, the ornamentation elements are larger and sinuous ridges, arranged in a compact way, forming a labyrinth. Last longer ridges can be fused and form a fine reticulum (Plate II, 6). The surface of verrucae and ridges is microverrucose (Plate II, 7).

Dennstaedtia globulifera (Plates I, 7–9; III, 1–4)

The ornamentation of the spores is verrucate and ridged. Verrucae of different size are fused forming width ridges of 1–5 × 3–12 μm, broadly conical with rounded or flattened edge.

Laesurae are crassimarginate, the ridges are arranged parallel to them. (Plate III, 1, 4). Verrucae of 1–3 μm in diameter are seen on equator (Plate III, 2). The distal surface shows ridges more or less straight, which are fused forming an incomplete reticulum with large lumina (Plate III, 3). The higher degree of fusion of the ridges was observed at the corners, which may be completely covered (Plate III, 2), and with LM the perispore is shown thicker. The surface of the ornamentation elements is smooth or microgranulate, and shows dispersed spheroid bodies (Plate III, 4).

Dennstaedtia obtusifolia and *Dennstaedtia dissecta* (Plates I, 10–12; III, 5–7)

The spore surfaces of both species are quite similar, with heterometric verrucae (1–3 μm) and ridges of 1–2 × 2–10 with rounded or flattened edges (Plate III, 5, 7). The elements of the ornamentation are single and distributed at-random on the spore surface, except near the laesura, where some ridges are parallels and cover them (Plate III, 6). The surface of the ornamentation is smooth or microgranulate, and spheroid bodies can be seen (Plate III, 5, 6).

3.2. Ultrastructure of the sporoderm

With TEM, the exospore is two-layered in the studied species. The inner layer (iE) is 10–60 nm thick, low electrodensity and homogeneous structure (Plate IV, 1, 2, 3). The outer layer (oE) is 100–900 nm, and is constituted of two strata: the inner stratum (oE2) with short channels, fissures and cavities; and the outer stratum (oE1) with irregular margin and a homogeneous structure (V, 1, 3). In oE1 there are cavities and channels filled with an electrondense substance. The channels are ramified forming a network (Plate IV, 1). These channels are frequent in the laesurae and connected with the channels present in oE2 (Plate V, 3) and with the perispore (Plates IV, 1; V, 1).

The perispores of *Dennstaedtia globulifera* and *D. dissecta* are single-layered, more electrondense than the exospore and they show a highly variable thickness, due to it forms the elements of the ornamentation (Plates IV, 1, 3; VI, 1). The perispores are thin on the apertural crest (Plate V, 1). The perispore is alveolar at structural level, with alveoli of different shape and size, which can be filled with an electrondense substance (Plate IV, 1, 3). The structure is more lax and diffuse towards the margin, like frayed (Plates IV, 1; V, 1, 2; VI, 1).

In *Dennstaedtia cicutaria* the perispore is verrucose and is two layered: the inner (iP) and the outer (oP) (Plate VII, 1). At structural level iP is alveolar, with empty cavities (Plate VII, 1, 3). The outer layer (oP)

is thin, homogeneous, discontinuous and lining the outside surface iP (Plate VII, 2). The verrucae are formed by iP and have a narrow base that widen to form the body of them, and sometimes are connected by processes like "bridges" of different thickness (30–700 nm) (Plate VII, 3–4). The margin of verrucae shows projections (Plate VII, 2).

In both *Dennstaedtia dissecta* and *D. cicutaria* spheroid bodies were observed within the perispore (Plates V, 2; VI, 2; VII, 4).

4. Discussion

The spore ornamentation of *Dennstaedtia* species that grow in the Paranaense province consists of verrucae which may fuse to form ridges and reticles of variable length and thickness. These observations go along with the descriptions made by Nayar and Devi (1968), Erdtman and Sorsa (1971), Murillo and Bless (1974), Lorscheitter et al. (2002), and Giudice et al. (2006), and with the morphology found in other species of the genus, such as *Dennstaedtia hirsuta* (Swartz) Mettenius ex Miquel, *D. scabra* (Wallich ex Hooker) Moore, *D. scyens* (Blume) Moore, and *D. smithii* (Hooker) Moore in Taiwan (Huang, 1981), *D. punctilobula* (Michaux) Moore in North America (Belling and Heusser, 1975) and *D. arborescens* (Willdenow) Ekman et Maxon in Bolivia (Graf-Meier, 1985).

In all cases, the perispore constitutes the verrucae, in contradiction with the descriptions made by Murillo and Bless (1974), Nayar and Devi (1968) and Devi (1977), in which the ornamentation was formed by the exospore, and the perispore being absent. However, was Devi (1977) who observed "an outer skin-like layer of the exine bearing the ornamentation (? perine) which often cracks and peels off during acetolysis".

According to the observations made by means of LM and SEM, and bearing in mind the elements of the ornamentation, the studied taxa can be grouped into the following types: 1 — verrucate. Verrucae ornamented with rodlets, 2 — verrucate-rugate, the elements of the ornamentation being smooth or rugate, and 3 — reticulate.

The first type is found in the spores of *Dennstaedtia cicutaria* where the verrucae have their surfaces ornamented. The elements covering the verrucae were described as spines by Tschudy and Tschudy (1965), and from their point of view, this type of ornamentation is distinctive among the *Dennstaedtia* from Venezuela. As we see it, these elements are, in fact, rodlets which, only in certain cases, can fuse to form spines. Under LM, the rodlets are seen as dark spots on the verrucae giving them a dark-brown color, which differs from the light-brown verrucae present in the rest of the species.

The results obtained by Tryon and Tryon (1982) in samples of *Dennstaedtia cicutaria* from Panama, do not match the data gathered in this work. In their description, the spores have compact, smooth verrucae which may be fused into rugae. Although Tryon and Lugardon (1991) agree with the latter description, in ultrastructural analysis, they indicate the presence of rodlets on the perispore surface. SEMs of *D. cicutaria* published by Tryon and Tryon (1982) and Tryon and Lugardon (1991), are from Panama and very different from those observed in this work. Since the aim of this study was to include populations of *D. cicutaria* growing in The Paranaense Province. However, due to the differences observed in the spores, would be interesting to carry out a review of *D. cicutaria* in order to determine whether the specimens from both regions belong to the same species. This conclusion was added to the manuscript.

Species of the genus *Taenitis* (*Taenitis hookeri* (Christensen) Holttum and *T. requiniana* (Gaudin) Copeland) and *Cyathea* (*Cyathea caracasana* (Klotzsch) Domin, *C. divergens* Kunze and *C. delgadii* Sternberg) also show ornamented tubercles and verrucae. However, unlike *Dennstaedtia cicutaria*, the outer exospore constitutes the elements of the ornamentation, and the perispore forms rodlets which cover, not only the tuberculate and verrucate areas, but also the psilate exospore (Tryon and Lugardon, 1991: 262–265; Marquez, 2012). Therefore, the study of the sporoderm ultrastructure would be required in order to consult the spores as potential source of characteristics of phylogenetic value.

The second type of ornamentation is observed in *Dennstaedtia dissecta* and *D. obtusifolia*: the spores have verrucae and psilate or rugate ridges, scattered at random all over the surface. Several authors disagree on the taxonomic delimitation of these species, and there is controversy over whether they belong to the same taxon (Stolze, 1981; Tryon and Stolze, 1989; Moran and Riba, 1995; Costa Assis and Salino, 2011) or whether they are independent entities (Tryon, 1960, 1964; Sehnem, 1972; Tryon and Tryon, 1982; Navarrete and Øllgaard, 2000; Kieling-Rubio and Windisch, 2002). The spore ornamentation does not justify the division of these taxa. Lorscheitter et al. (2002) came to the same conclusion.

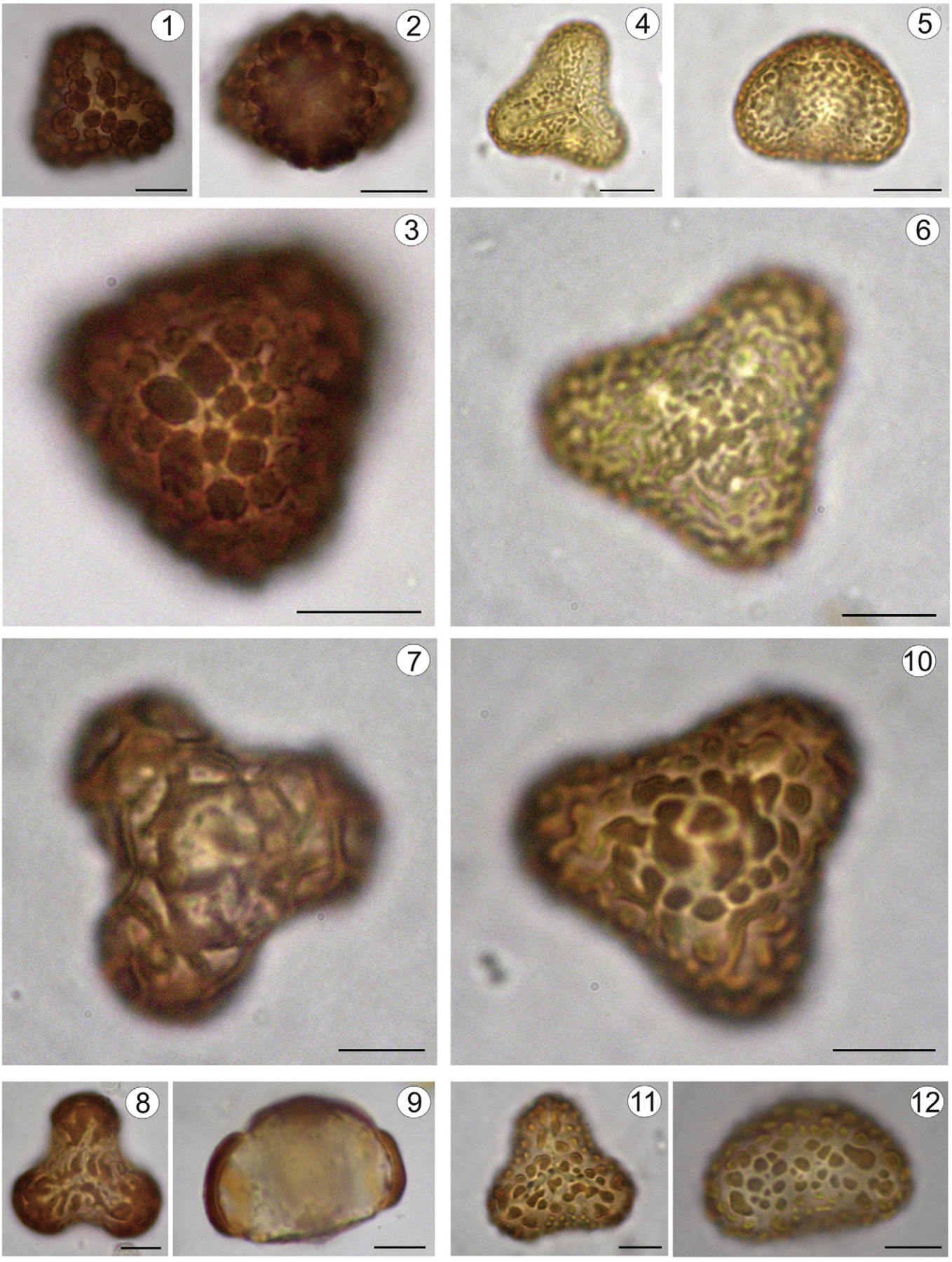
The type of ornamentation present in *Dennstaedtia cornuta* is similar to that observed in *D. dissecta* and *D. obtusifolia*. However, in the case of this particular species, the space between verrucae and ridges is narrower and, on distal face, the fusion of the ridges defines its rugate pattern.

The verrucate and rugate ornamentation of the three species previously described is similar to the ornamentation in the genus *Loxoma* (Loxomataceae) (Tryon and Lugardon, 1991 pág. 211). Likewise, some genera of the family Pteridaceae, such as *Anogramma* (Ramos Giacosa et al., 2001, 2004), *Pteris* (Martínez and Morbelli, 2009), *Pityrogramma* (*Pityrogramma tartarea* (Cavanilles) Maxon) (Giudice and Morbelli, 1998), *Cheilanthes* (*Cheilanthes vellea* (Aiton) Domin) and *Cryptogramma* (Tryon and Lugardon, 1991: 154, 176) share this same pattern; the difference is that the verrucae and the ridges are formed by the exospore. In

Plate I. Spores of *Dennstaedtia* species from Paranaense Phytogeografic Province with LM. Figs. 1–3. *Dennstaedtia cicutaria*. 1. Spore in proximal view. 2. Spore in equatorial view. 3. Spore in distal view. The ornamentation is verrucate. Figs. 4–6. *Dennstaedtia cornuta*. 4. Spore in proximal view. 5. Spore in equatorial view. 6. Spore in distal view. The ornamentation is rugate. Figs. 7–9. *Dennstaedtia globulifera*. 7. Spore in distal view. 8. Spore in proximal view. 9. Spore in equatorial view. The ornamentation is reticulate. 10. Spore in distal view of *Dennstaedtia dissecta*. The ornamentation is verrucate-ridged. 11–12 *Dennstaedtia obtusifolia*. 11. Spore in proximal view. 12. Spore in equatorial view. The ornamentation is verrucate-ridged. Scale bar = 10 μm.

Plate II. Spore of *Dennstaedtia cicutaria* and *Dennstaedtia cornuta* with SEM. Figs. 1–4. *Dennstaedtia cicutaria*. 1. Spore in proximal view. The ornamentation is formed of verrucae with rodlets on their surfaces (arrows). The verrucae partially cover the laesura ends (circle). Scale bar = 10 μm. 2. Spore in distal view. The ornamentation is formed of verrucae with rodlets on their surfaces (arrows). Groups of verrucae fused through perispore processes are evident (circle). Scale bar = 5 μm. Figs. 3–4. A detail of the distal surface. The rodlets that cover the verrucae sometimes are fused at their bases (incomplete circle) or tips (complete circle). Are seen also several rodlets fused forming spines, with broad bases and acute tips (arrows). The verrucae are fused for narrow perispore processes (arrowheads). Scale bar = 2 μm. Figs. 5–7. *Dennstaedtia cornuta*. 5. Spore in proximal view. The ornamentation is formed of verrucae and short ridges distributed at-random (arrows). The ornamentation elements cover partially the lesurae ends (circle). Scale bar = 5 μm. 6. Spore in distal view. The ornamentation is rugate. There are also large fused sinuous ridges packed placed (arrows). Scale bar = 10 μm. 7. Distal face in detail. The ridges have a granulate surface (circle) and form a poorly defined reticule with narrow luminae (arrow). Spheroidal bodies are seen scatteredly distributed on the surface (arrowheads). Scale bar = 2 μm. (See on page 6)

Plate III. Spores of *Dennstaedtia globulifera* and *Dennstaedtia dissecta* with SEM. Figs. 1–4. *Dennstaedtia globulifera*. 1. Spore in proximal view. The ornamentation is verrucate-ridge. The laesurae are crasimarginate (arrows). On the sides, the verrucae and ridges have different degree of fusion (arrow heads). On the corners the ridges form reticules or cover them completely. Scale bar = 10 μm. 2. Spore in equatorial view. The ornamentation is verrucate-reticulate. The verrucae are distributed at-random on the spore sides (arrows). On the angles the ridges fused forming reticules the wide muri and large luminae. Scale bar = 5 μm. 3. Spore in distal view. The ornamentation is reticulate with wide mures (arrows) forming large luminae (arrow heads). The angles are cover by continuous thickenings. Scale bar = 5 μm. 4. Proximal view in detail. Small spheroidal heterometric bodies are distributed on the whole surface (arrows). Scale bar = 2 μm. Figs. 5–7. *Dennstaedtia dissecta*. 5. Spore in proximal view. The ornamentation is verrucate. The verrucae are sparsely distributed at-random on the whole surface. Spheroidal bodies of different sizes are observed to disperse throughout the surface (arrows). Scale bar = 5 μm. 6. Proximal view in detail. Lesurae crassimarginated. The ridges are parallel to the laesurae and cover partially their ends (arrowheads). Sphaeroidal heterometric bodies cover the whole spore surface (arrows). Scale bar = 2 μm. 7. Spore in distal view. The ornamentation is verrucate-ridged. The ridges have variable length and are scattered located (arrows). Scale bar = 10 μm. (See on page 7)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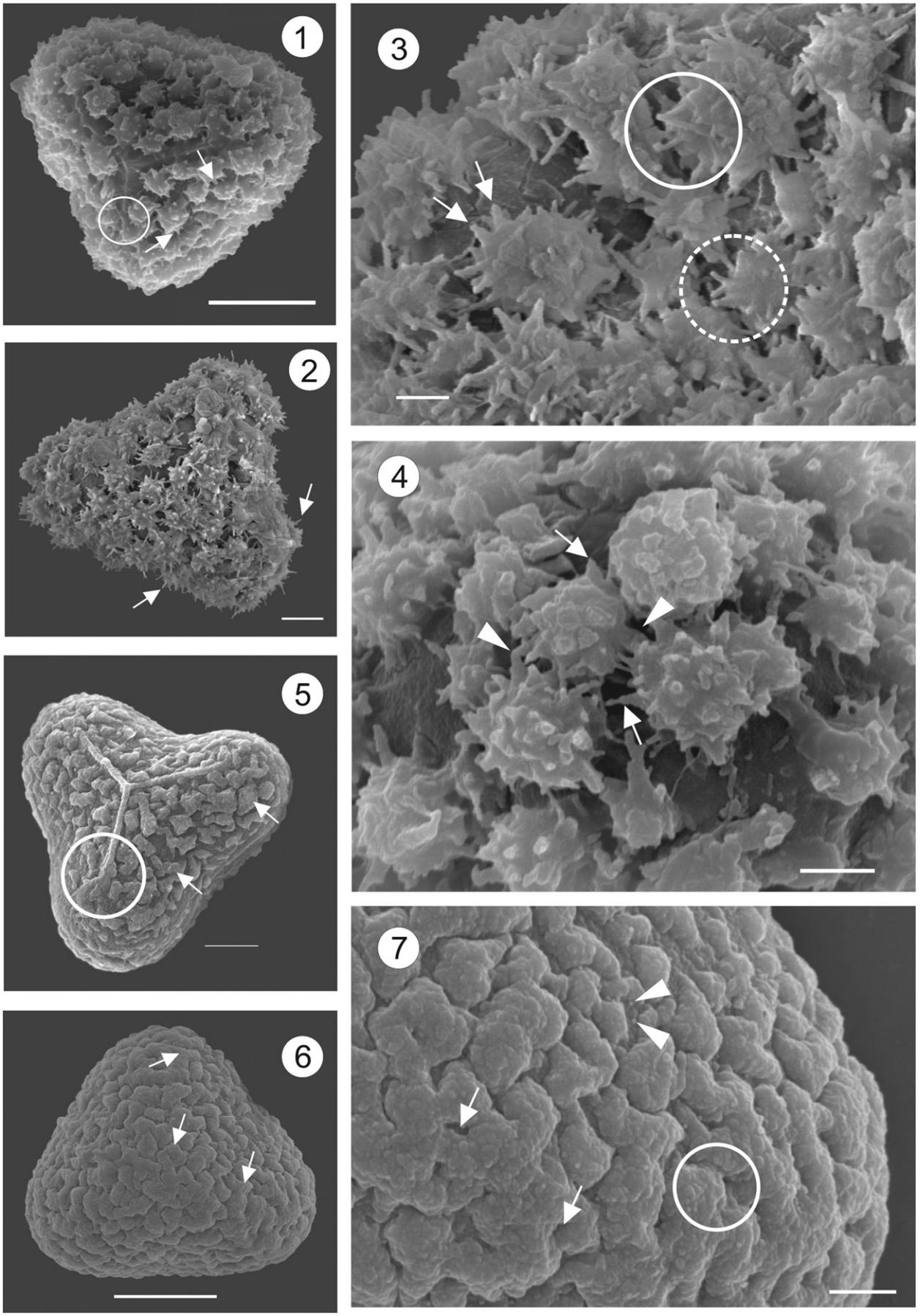


Plate II (*caption on page 184*).

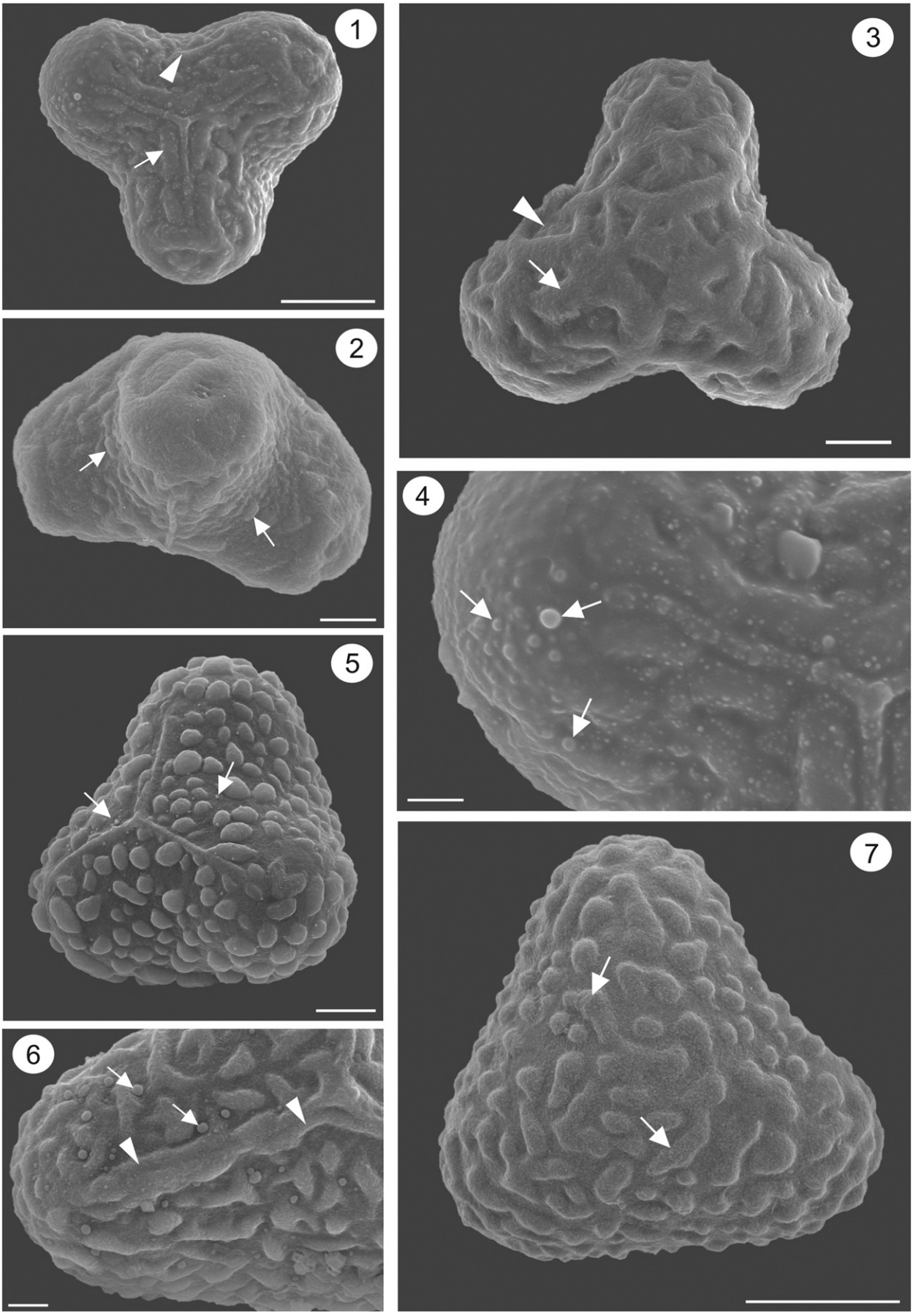


Plate III (*caption on page 184*).

Table 1
Morphological data of the spores of *Dennstaedtia* from Paranaense Phytogeographic Province.

Species	PS	ES	PD (μm)	DE (μm)		Exospore	Perispore	
				>	<	MO	MO	Distal Sculpture
D. cicutaria	Triangular	Convex-hemispheric	19–27	26–37	23–33	Light brown	Dark brown	Verrucate (micro ornate verrucae)
D. cornuta	Triangular	Plane-hemispheric	21–27	27–36	25–32	Light brown	Brown	Rugate
D. dissecta	Triangular	Plane-hemispheric	21–32	25–42	25–40	Light brown	Brown	Verrucate-ridged
D. globulifera	Triangular	Plane-hemispheric	17–27	27–39	21–34	Light brown	Brown	Reticulate
D. obtusifolia	Triangular	Plane-hemispheric	21–25	28–38	25–33	Light brown	Brown	Verrucate-ridged

PS: Shape in polar view; ES: Shape in equatorial view; PD: polar diameter; DE: Equatorial diameter; >: Major; <: Minor.

this regard, the presence of verrucae and rugae in phylogenetically unrelated groups would indicate that it does not have any evolutionary value. The third pattern is observed in *Dennstaedtia globulifera*, where the fusion of verrucae and ridges determines a reticule on the distal face of the spore. The relationship between the types of ornamentation observed and the geographical distribution of the studied species partially coincides with the description made by Tryon and Tryon (1982) and Tryon and Lugardon (1991). Along this line, a verrucate pattern for most of the American taxa is defined by these authors, which, in general terms, coincides with the pattern of the Paranaense species. Even though the reticulate pattern observed in *D. globulifera* and *D. cornuta* is less regular and limited to the distal face and angles of the spore, it is quite similar to the pattern found in the paleotropical species.

Although there are differences in the characteristics of the verrucae (form, distribution and surface), at ultrastructural level, the perispore in all the Paranaense species is alveolar, and it shows variations in the density of its structure. The verrucae are formed by the differences in the thickness of the wall. However, *Dennstaedtia cicutaria* is the only species with a two-layered perispore.

The before-mentioned observation does not match the conclusions of Giudice et al. (2006). They included the spores of *Dennstaedtia dissecta* in *D. cicutaria* due to a misunderstanding concerning the identification of the reference samples (Yañez et al., 2012). According to their observations, the perispore of *D. dissecta* consists of two layers: an inner layer with an alveolar structure forming the body of the verrucae, and an outer layer, which seems to be very thin and is apparently discontinuous. From our point of view, these two layers correspond, in fact, to variations in the density of the alveolar structure of a single layer. These variations are seen as gradual differences in contrast from the innermost portion to the perispore margin.

Even though the description of the perispore of *Dennstaedtia bipinnata* by Lugardon (1971; 1974) using TEM broadly matches the observations made for *D. dissecta* and *D. globulifera*, its ultrastructure is interpreted by the author as compact, consisting of substances that show a granulose and uniform aspect. The data giving in this work do not corroborate those of Lugardon.

The characteristics of the exospore found in all the studied species match the blechnoide type described by Lugardon (1971, 1974). This type of exospore typically has two layers: a thin inner one which is more evident in the apertural area; and an outer one consisting of two strata. The channels and cavities observed in the inner stratum of the Paranaense Dennstaedtiaceae are coincident with the "fissured stratum" of the outer exospore.

All the species share a common characteristic: they all show spheroid bodies scattered on the perispore surface, as well as an inner structure similar to that of the exospore. Lugardon (1974) described similar bodies ("globules") in the surface of *Dennstaedtia bipinnata*, which were also observed by Giudice et al. (2006) in the wall of *D. globulifera*. In later works, they were defined by Tryon and Lugardon (1991) as small spheroid bodies of sporopollenin, with a central structure similar to the exospore, wrapped in a perispore-like layer. The globules resemble structures found on the pollen grains of angiosperms known as Ubisch bodies (Morbelli, 1977; Lugardon, 1981). Besides, the spheroid bodies observed within the perispore of *D. cicutaria* and *D. dissecta* were more abundant in early stages of the spore development; for this reason they could be associated to young stages in wall formation.

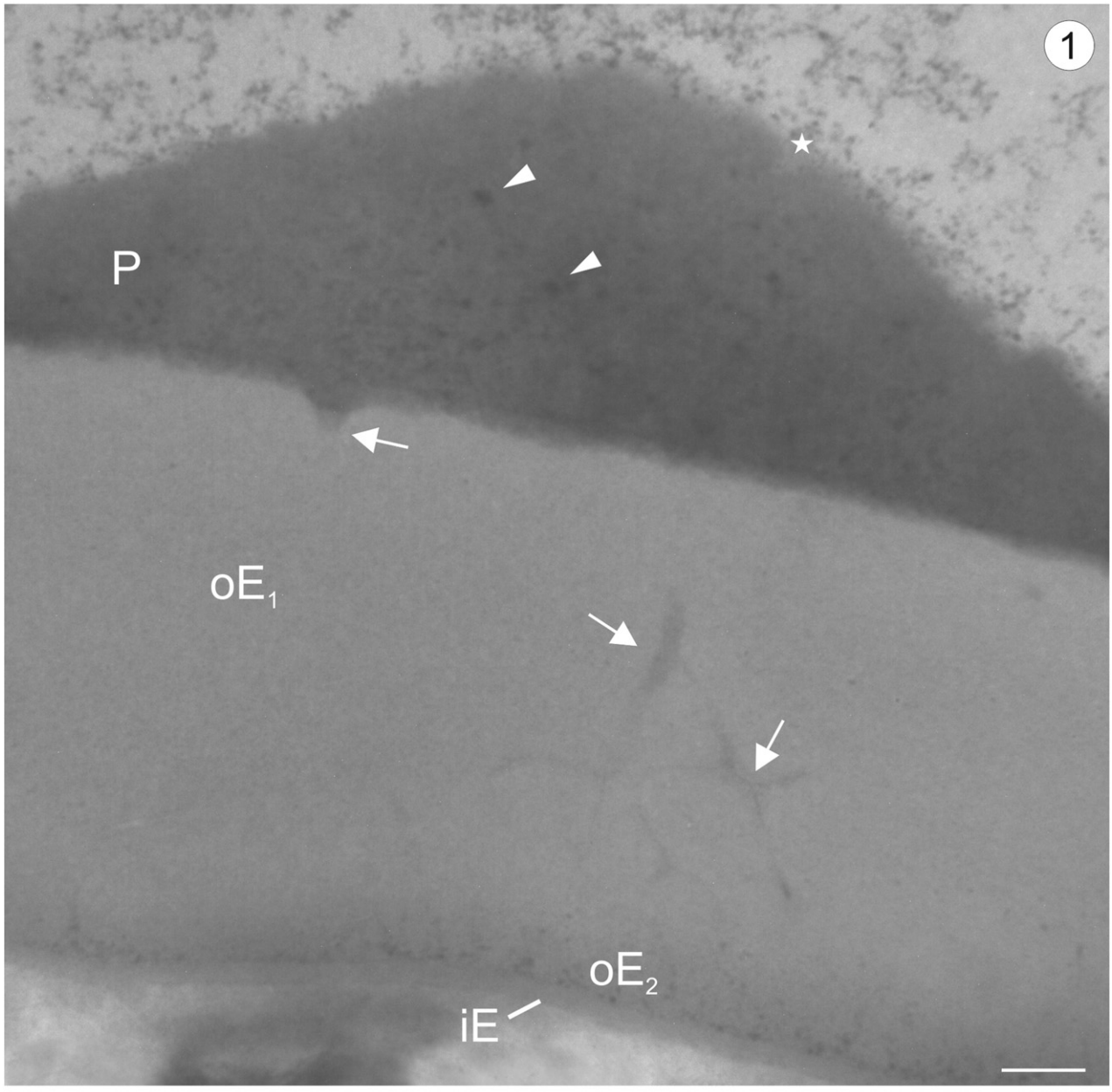
5. Conclusions

1) The ornamentation, degree of fusion and the distribution of ridges and verrucae on the perispore allow for a characterization of the

Plate IV. Figs. 1–3. Spores of *Dennstaedtia globulifera* with SEM and TEM. 1. The inner exospore (iE) is thin and homogeneous, with lower density to the electrons and makes contrast to the fissures and adjacent small canals which are filled with electrodense material, that constitute the inner exospore stratum of the exospore (oE2). The outer exospore stratum (oE1) is a homogenous stratum traversed by channels that fuse and reach the perispore inner layer (arrow). The perispore have variations in thickness and form verrucae (P). Its ultrastructure is alveolar with spaces filled with electrodense material (arrowheads) with flayed margins (star). Scale bar = 0,2 μm. 2. An aspect of a peace of corroded wall surface with SEM. The irregular surface of the outer exospore (oE1). P: Perispore. Scale bar = 1 μm. 3. Section through the spore angle with TEM. The exospore is thinner and has lower electrodensity than the perispore. The perispore has large spaces filled with electrodense material, that constitute part of the microalveolar structure (arrowheads). Scale bar = 0,5 μm.

Plate V. 1–3. Sporoderm section of *Dennstaedtia dissecta* with TEM. 1. Section through the apertural fold. The inner exospore layer (iE) is thin, homogeneous and evident at the en lesura base. The outer layer is thicker than the inner one and has a inner stratum (oE1) formed cavities filled of material of hight electrodensity and a outer stratum (oE2) with homogeneous structure with and irregular margin (circle), traversed by channels that reach the perispore inner layer (arrow) The perispore (P) has its thinner part at the lesura apex. Has a alveolar structure denser at the center and with flayed margins (star). Scale bar = 200 nm. 2. Section at the apertural fold and probably in an immature spore stage. Globules are evident (arrow) at the surface while other are embodied within the perispore (P). The wall margins have a lax alveolar (star) structure. oE = Outer exospore, iE = inner exospore. Scale bar = 200 nm. 3. The base of the lesurae. The outer exospore stratum (oE2) is homogeneous and has cavities (arrowhead) and channels filled with material highly electrodense (arrow). Those channels have a continuity with the inner fissurate stratum (oE1). The inner exospore (iE) is compact and scarcely contrasted. Scale bar = 200 nm. (See on page 10)

Plate VI. 1–3. Spores of *Dennstaedtia dissecta* with TEM and SEM. 1–2. Sections through the sporoderm. 1. The exospore (E) is homogenous, with irregular margin and less electrodense than the perispore (P). The perispore has variations in thickness and forms verrucae (asterisks). The perispore structure is alveolar and is laxer towards its outer margin, where it has a flayed aspect (arrow). Scale bar = 1 μm. 2. Probably early step in perispore maturation. There are globules (arrows) on the perispore surface. The perispore has a alveolar structure with spaces filled with electrodense material (arrowheads). E = Exospore. Scale bar = 0, 1 μm. 3. The perispore surface was abraded and the SEM exposes the outer exospore surface (E). P: Perispore. Scale bar = 2 μm. (See on page 11)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P
oE1
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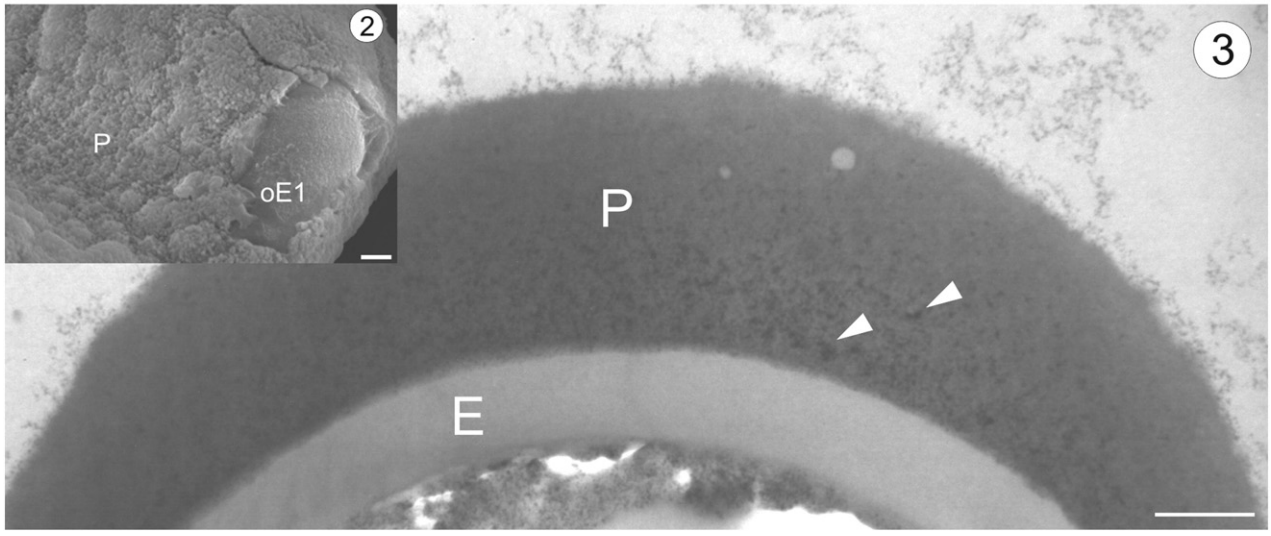
iE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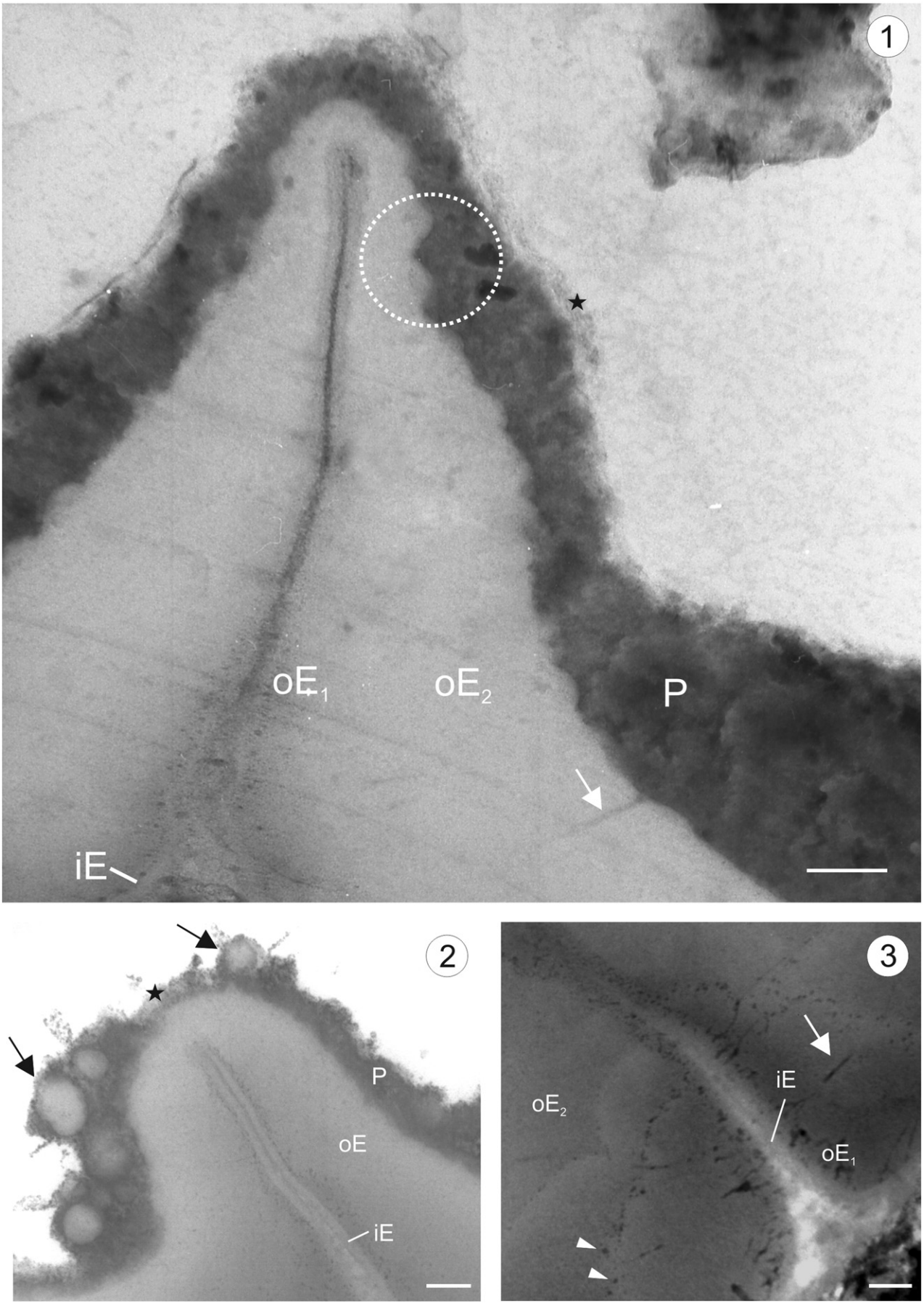

Plate V (*caption on page 188*).

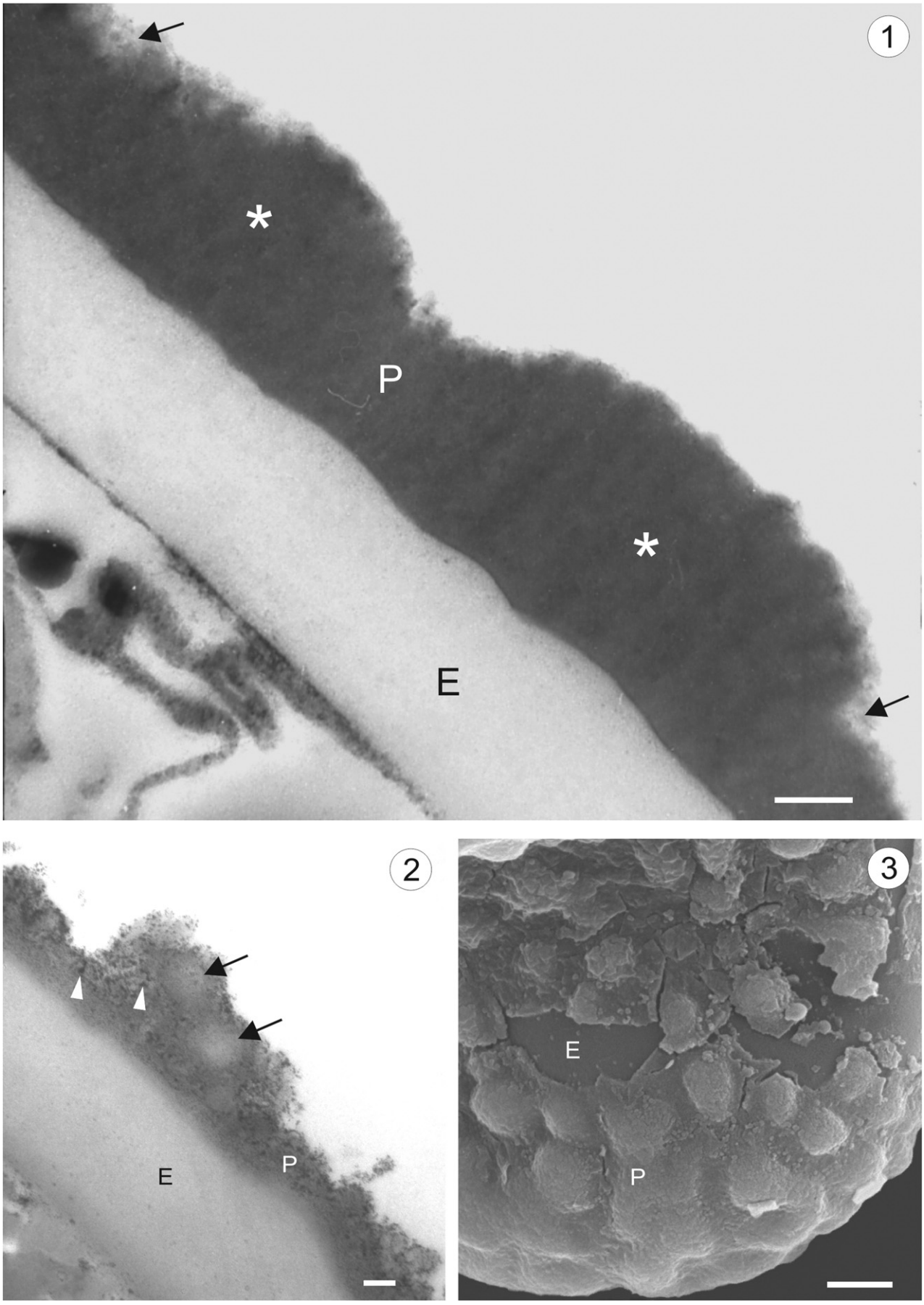

Plate VI (*caption on page 188*).

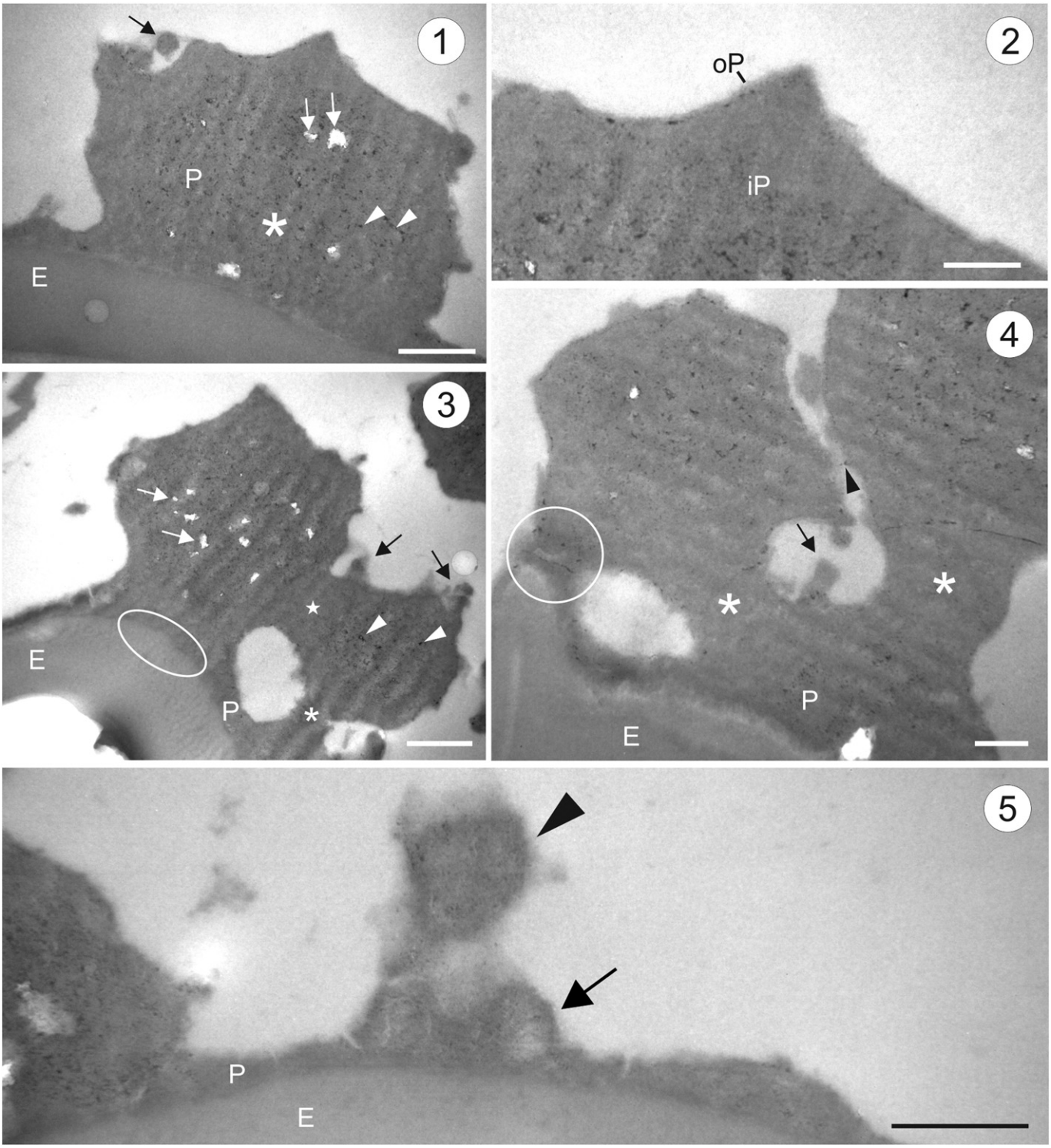

Plate VII. 1–5. Sporoderm section of *Dennstaedtia cicutaria* with TEM. 1. The exospore (E) is homogeneous less electrodense than the perispore. The perispore (P) forms verrucae (asterisk) and has a alveolar structure with spaces filled with electrodense material (arrowhead) and cavities (white arrow). Spherules are in contact with or embodied in the perispore (black arrow). Scale bar = 0, 8 μm. 2. Detail of figure 1. The outer perispore (oP) is compact, discontinuous and covers the inner perispore (iP). Scale bar = 0, 8 μm. 3. The exospore has irregular margin (circle). The perispore forms verrucae (asterisks), fused by narrow processes (star). The verrucae have projections (black arrows). Spaces filled with an electrodense material (arrowheads) and cavities (white arrow) are observed in the perispore. Scale bar = 1 μm. 4. Section through the apertural fold. The verrucae of the perispore partially cover the lesura (circle). The verrucae (asterisks), have projections (arrow) and are fused by narrow processes (arrowhead). Exospore (E), Perispore (P). Scale bar = 0,2 μm. 5. Exospore/perispore contact. Globules are evident on the perispore (arrowhead) and embodied within the perispore (arrow), with a core with structure similar to that of the exospore and covered of a layer similar to that of the perispore. Exospore (E), Perispore (P). Scale bar = 0,8 μm.

species or groups of species of *Dennstaedtia* in the phytogeographic Paranaense province. The differences are more evident on the distal face of the spores.

2) The spores constitute an important source of characters with a systematic value for the genus *Dennstaedtia*, and they are a useful tool for the identification of herbarium samples, since the differences

are easily observed by LM. In this sense, three different types of ornamentation can be found:

A. Verrucate with verrucae covered with rodlets in *Dennstaedtia cicutaria*.
B. Verrucate–rugate with verrucae and smooth ridges in *Dennstaedtia dissecta*, *D. obtusifolia* and *D. cornuta*.
C. Reticulate in *Dennstaedtia globulifera*.

3) The systematic and phylogenetic value of the spore ornamentation should be evaluated if a previous study of sporoderm ultrastructure is performed previously.
4) The ornamentation patterns observed in *Dennstaedtia* species in the Paranaense province are shared, not only with other American species of the genus but also with paleotropical species. The presence of verrucae, ridges and reticules are common elements in all the species of *Dennstaedtia*, regardless of their geographic distribution.

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